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A Tribute to Henry S. Fitch

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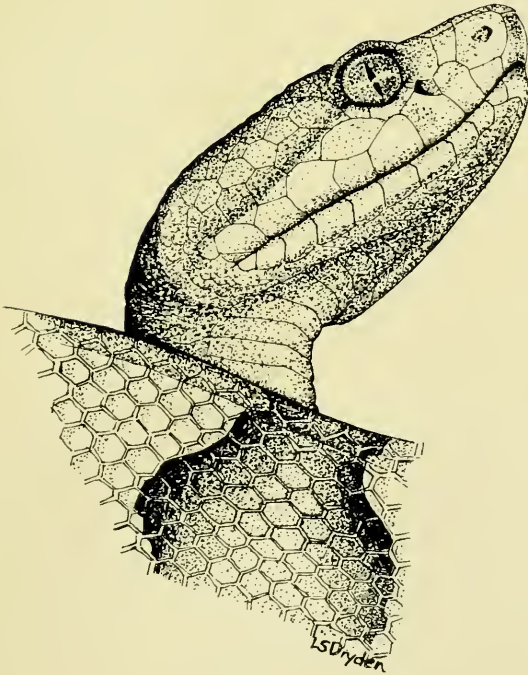
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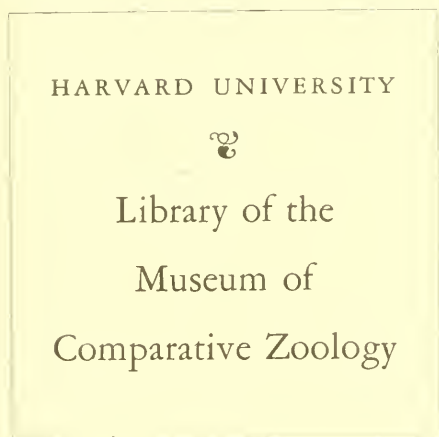


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Front cover: The head of an adult Osage Copperhead (*Agkistrodon contortrix phaeogaster*) from Douglas County, Kansas. Drawing © 1984 by Linda Dryden.

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Museum of Natural History

Special Publication No. 10

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Vertebrate Ecology and Systematics

A Tribute to Henry S. Fitch

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PREFACE

This volume is the result of a symposium entitled, "Perspectives in Fitchian Ecology," held on 9 August 1980 in conjunction with the annual meetings of the Society for the Study of Amphibians and Reptiles and the Herpetologists' League at Milwaukee, Wisconsin. The symposium was organized to honor Dr. Henry S. Fitch on the occasion of his retirement in June 1980 after 32 years with the Department of Systematics and Ecology at the University of Kansas.

Sixteen papers were presented in two sessions during the symposium and, aside from a few additions, the organizational format of this volume closely follows that of the symposium. Manuscripts were submitted and accepted in late 1980 and 1981, but authors were given an opportunity to update their contributions in early 1983. In organizing the symposium we were surprised by the breadth of research conducted by the participants. Because of Fitch's influence on his past and present students and colleagues, this volume is not restricted to herpetological contributions. Thus, the topical emphasis of this volume reflects Fitch's own research interests. The following is a breakdown by subject of the papers contained in this volume versus Fitch's published papers: ecology (this volume: 78%, Fitch: 73%); systematics and biogeography (17% vs. 19%); conservation (5% vs. 5%); and by taxonomic emphasis: squamates (this volume: 73%; Fitch: 62%); other amphibians and reptiles (14% vs. 7%); other vertebrates (13% vs. 23%).

We wish to thank Max A. Nickerson of the Milwaukee Public Museum and Al Williams of the University of Wisconsin—Milwaukee and their respective staffs for logistical support in arranging and conducting the symposium. A special note of thanks is extended to Virginia Fitch and other members of the Fitch family for assistance in the development of the symposium. The organizational advice and encouragement of William E. Duellman, Curator, Division of Herpe-

tology; Philip S. Humphrey, Director, Museum of Natural History; and Richard F. Johnston, Chairman, Department of Systematics and Ecology, is greatly appreciated.

Joseph T. Collins, Editor, Museum Publications, deserves special recognition for his helpful advice and continued patience in answering our many questions concerning the development and execution of the symposium and this volume. The cheerful and patient assistance of Rose Etta Kurtz was invaluable.

Finally, we are most grateful to the following persons for reviewing the manuscripts appearing in this volume: Robert D. Aldridge, Stevan J. Arnold, Reeve M. Bailey, Royce E. Ballinger, Thomas J. Berger, William S. Brown, Gordon M. Burghardt, Janalee P. Caldwell, Jonathan A. Campbell, David C. Cannatella, David K. Chiszar, Martha L. Crump, Arthur E. Dunham, Donald G. Dunlap, Henry S. Fitch, Darrell Frost, J. Whitfield Gibbons, Peter Gray, Harry W. Greene, Wendy Gorman, Harold Heatwole, James E. Huheey, John B. Iverson, Keith V. Kardong, Peter Klopfer, Carl Lieb, Harvey B. Lillywhite, John D. Lynch, Richard Mayden, Roy W. McDiarmid, Lawrence M. Page, William S. Parker, F. Harvey Pough, Rebecca A. Pyles, Steven M. Roble, Albert Schwartz, Richard Shine, Norman A. Slade, Linda Trueb, John Wiens, and Bernard Willard.

Without the help of all these individuals this tribute to an outstanding biologist would not have been possible.

Richard A. Seigel
Lawrence F. Hunt
James L. Knight
Luis Malaret
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Lawrence, Kansas
October 10, 1981

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Frontispiece: Holotype of *Anolis fitchi* (KU 142865, ♂, 88 mm snout-vent length). Drawn by Linda Trueb from color photographs taken in life.

Part I

Introduction



FIG. 1. Henry S. Fitch in the field. Photograph by David M. Hillis.

Henry S. Fitch in Perspective

WILLIAM E. DUELLMAN

Who is Henry Sheldon Fitch? This quiet, modest, unassuming man made his first entrance into the world of biologists by publishing on Oregon birds in the *Condor* in 1933. Yes, birds! Most of us think of Henry S. Fitch as a herpetologist. Yet, of his 150 published papers in the past 50 years, only about two-thirds of them deal with amphibians and reptiles. Twenty others have been on mammals, 12 on birds, and others on spiders, molluscs, and plants.

Most of us think of Henry S. Fitch as an ecologist, but 25 of his papers are on systematics and include his classic work on alligator lizards published in 1934 and his highly perceptive study of western garter snakes published in 1940 (doctoral dissertation at the University of California, Berkeley). His more recent systematic work has dealt with Middle American anoles—a field where most systematists have feared to tread.

Fitch's best known works are on the natural history of reptiles. From his earliest papers on reptiles, he has provided extensive field observations. In 1948, he entered a "naturalist's heaven"—the University of Kansas Natural History Reservation. There he began intensive studies on the biota of one square mile of deciduous hardwood forest—studies involving population densities, movements, food, growth rates, hibernation, and reproduction—all substantiated with massive quantities of data. Through his efforts this square mile is better known herpetologically than any other in the world.

His studies on the natural history of reptiles are classics. Outstanding examples are the thorough study of the five-lined skink (1954) and the exhaustive study of the copperhead (1960). More recently he has worked on the interactions of behavior and ecology, communities of anoles, and populations and conservation of iguanas.

In addition to these systematic and ecological works, Fitch has provided us with important syntheses—reproductive cycles in lizards and snakes (1970) and sexual size differences in reptiles (1981). All of his works are characterized by careful and detailed studies on the existence of populations in nature. Vast quantities of such data combined with extensive laboratory and lit-

erature research are reflected in his syntheses. These traits combined with dogged determination to learn all there is to know about his subjects of study, his continued productivity, and his willingness to share his ideas, knowledge, and enthusiasm with students have assured him of a permanent place in the herpetological hall of fame.

At the present time, many biologists commonly are narrow specialists. Henry Fitch doesn't fit into a modern pigeon hole. He is a naturalist in the broadest sense of the word. His breadth of knowledge is matched by very few of his contemporaries and scarcely imagined by most of his younger colleagues. An analogy can be drawn with the story of the hare and the tortoise, with Henry Fitch as the tortoise steadily plodding along his path of scientific endeavor, frequently being passed by various biological bandwagons, only to find them sometimes morassed or abandoned further down the road.

He has avoided biopolitics. He has not been a vigorous proponent of controversial theories. Instead, he has continued to be a fine naturalist. But, his published works are among those commonly cited in support of some theories or in the falsification of others.

Thus, for half a century Henry S. Fitch has been a major contributor to our knowledge of the natural history of diverse kinds of animals. During this time he has introduced innumerable students to intensive field studies, has thoughtfully guided the research of many graduate students, and has collaborated with a diversity of colleagues. A major factor in his remarkable and successful career has been a collaborator, assistant, caretaker and charming lady—Virginia R. Fitch.

Few scientists can reflect on such a long and productive career, and yet upon officially retiring maintain such enthusiasm for an active research program. Henry Fitch's careful work on natural history is well worth emulating. Our knowledge of animals in nature would be far greater if there were many more biologists in the world who followed in the footsteps of Henry S. Fitch.

The Published Contributions of Henry S. Fitch

VIRGINIA R. FITCH

- Beginning with his first published paper in 1933, the writings of Henry S. Fitch have encompassed a wide range of subjects and disciplines, from reptilian ecology to bird behavior, from the economic relationships of rodents to an intensive study of spiders, and include such areas as taxonomy, life history, behavior, and reproductive biology. To date, he has produced 150 papers, all of which appear in the following list. Fitch's published works include as their subjects mammals (19 papers), birds (12), vertebrates in general (5), spiders (3), vegetation and habitats (4), and mollusks (1), as well as five book reviews, but papers on amphibians and reptiles (100) predominate. His works are widely cited throughout scientific periodicals, and this list is presented both as a service to biologists and to document the impressive extent of the knowledge and breadth of interest of Henry S. Fitch.
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Part II
Reproductive Biology and Population Dynamics

Growth, Reproduction and Demography of the Racer, *Coluber constrictor mormon*, in Northern Utah

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INTRODUCTION

Considerable interest has developed recently in comparative life history and demographic studies because the data point up a number of evolutionary strategies taken by separate inter- and intraspecific populations. To date, the data have been effective mostly in illustrating the selection and adaptive basis for the life histories of lizards, birds, and mammals among the vertebrates (Stearns 1976; Hutchinson 1978). Rarely have data on snakes perfused the general literature even though a number of sound field studies of snake populations have been completed (Blanchard *et al.* 1979; Branson and Baker 1974; Brown 1973; Carpenter 1952; Clark 1970, 1974; Clark and Fleet 1976; Feaver 1977; Fitch 1949, 1960, 1963, 1965, 1975; Gregory 1977; Hall 1969; Parker and Brown 1974, 1980; Platt 1969; Prestt 1971; Spellerberg and Phelps 1977; Stewart 1968; Tinkle 1957, 1960; Viitanen 1967).

Coluber constrictor (Serpentes, Colubridae) is known to occur from Guatemala to southern Canada (Conant 1975; Etheridge 1952; Stebbins 1966). The species is polytypic, with 10 described subspecies (Wilson 1970). In the United States, eight of the nine recognized geographic races occur east of the Rocky Mountains (Auffenberg 1955; Fitch 1963; Wilson 1970). *C. c. mormon* occurs west of the Continental Divide. This subspecies has been recorded in most of the states in the western third of the U.S. (Auffenberg 1955; Stebbins 1966; Wilson 1978:218.1). An extensive range hiatus in the Rocky Mountains, lack of intergradation, and differences in morphology and ecology between the midwestern subspecies, *C. c. flaviventris*, and *C. c. mormon* may warrant elevation of the latter taxon to species rank (Fitch, Brown and Parker 1981). Aside from several brief reports on various aspects of the biology of *C. c. mormon* (see review of the literature in Fitch 1963), no comprehensive ecological study of this wide-ranging western form has been conducted. Fitch's (1963) study in Kansas of *C. c. flaviventris* is, to date, the most extensive ecological investigation of any population of *Coluber constrictor*.

The present study focuses on the biology of the Western yellow-bellied racer, *Coluber constrictor mormon* Baird and Girard, hereinafter called simply "racer." Our approach has been empirical and autecological and has concentrated on one large population of this snake at a single locality in northern Utah over a four-year period. This paper treats growth, maturity, reproduction, population structure, and demography of the racer. Widespread and abundant in North America, *C. constrictor* lends itself well to a study of its adaptive biology in several parts of its geographic range. Our attempt is to provide ecological comparisons of populations in Utah and Kansas. This study reveals different life history strategies at the intraspecific level.

METHODS

Snakes were captured in autumn 1969 through spring 1973 at a communal denning area in a desert shrub habitat located 4 km W of Grantsville, Tooele County, Utah (40°36'N, 112°32'W, elevation 1580 m), ca. 58 km WSW of Salt Lake City. This area is our primary study locality (area M) where all long-term mark and recapture field work was conducted. We recorded a total of 1694 captures of 1046 racers at this site.

Originally studied by Woodbury and his co-workers in the 1940's (Woodbury *et al.*, 1951), the "main den" (den M) was later sampled in the mid-1960's by Hirth and King (1968) and again in the early 1970's by us. We discovered other actively used dens near den M; these were considered part of a discrete group which we called "M complex." A separate series of newly-discovered dens located 0.8 km to the south was designated "S complex" (Parker and Brown 1973; Brown and Parker 1976a).

The technique we used to capture snakes was to intercept them with a screen wire fence erected around their hibernaculum. As the dens were single small rock piles located in fairly level terrain with sandy soils, it was possible to encircle each den completely. We sank steel reinforcing bars around a den, attached screening (ca. 95 cm high) to the stakes, and buried the base of the fence by

covering it with soil from a perimeter trench. Captures occurred almost daily in favorable weather as snakes attempted to enter a den in autumn and leave it in spring. The chronology of sampling *Coleuber* and other snakes at area M is summarized in Parker and Brown (1980). Our results pertain to the four-year period 1969–1972 by sampling dens each autumn and spring from autumn 1969 through spring 1973. Data presented for a given calendar year were derived from sampling in the autumn of that year (den M only) and the spring of the next (den M and other dens).

Individuals were processed in the laboratory and most were released within 24 h after capture. Each snake was permanently marked by clipping ventral scutes (Brown and Parker 1976b). Snout-vent length (SVL = distance from tip of snout to posterior edge of anal scute) and tail length to the nearest 0.5 cm (snakes ≥ 1 year old) or to the nearest mm (hatchlings and juveniles) and live body weight to the nearest 0.1 g (all snakes) were recorded for each individual at all captures. Reproductive condition of males was determined by obtaining cloacal smears and examining them microscopically for the presence of spermatozoa. Snakes in spring were released outside of their den fence, those in autumn were released inside. Snakes caught by hand on their summer range were released at the capture site.

Other racers were collected from two nearby localities in northern Utah. Most snakes from these areas were sacrificed for food and reproductive data. These localities are designated as area SLC, vicinity of Salt Lake City, Salt Lake County, Utah; and area RB, Red Butte Canyon, 5 km E of Salt Lake City, Salt Lake County, Utah. Both areas SLC and RB provided data on clutch size. Female racers were marked and released in area RB and provided data on body weight changes. Some other females killed for examination of reproductive tracts were from area M. These snakes included several casualties from our marked population and a few others taken > 2 km from the study dens and beyond the maximum dispersal limits of racers from area M.

In most years at area M hatching occurred around mid-August. Juveniles normally arrived at den M in early October at an average age of ca. 1.5 months. Winter dormancy lasted ca. 7 months (Oct.–Apr.) and the activity season ca. 5 months (May–Sept.) (Brown 1973; Parker and Brown 1980). As our sampling was in autumn

and spring, snakes placed in a designated year class differed from their actual age by about 7 months. No growth occurred during hibernation so we assigned an equivalent age to autumn and spring-captured snakes as follows: hatchling (age 0), juvenile (1.5 and 8.5 months), 1-year-old (13.5 and 20.5 months), 2-year-old (25.5 and 32.5 months), and so on. The simpler age designation in years corresponds to the number of full 5-month growing seasons which a snake had been through and facilitates analysis of age-specific aspects of the life history.

Racers ≥ 1 year old were sexed visually by the relatively thick (males) or thin (females) tail base. Juveniles lacked external sexual differences and those in 1972–1973 were sexed using a blunt probe to detect presence (males) or absence (females) of hemipenial sacs. In earlier sample periods juveniles were not sexed and numbers of male and female juveniles were apportioned assuming a 1:1 sex ratio. Some of these juveniles were sexed later by recapturing them as marked 1-year-olds after they had attained sufficient discernible sexual dimorphism as yearlings.

Assignment of males and females to specific age classes was based on size and growth of marked individuals. Sample means and 95% confidence intervals of length and weight were calculated for recaptured 1-year-olds marked initially as juveniles. Snakes in all sampling periods that compared closely to these values were assigned as 1-year-olds. Records for these initial juveniles and 1-year-olds that were later recaptured were then used to determine preliminary length and weight characteristics for 2- and 3-year-olds. Some individuals were thus followed from age 3 in 1969–1970 to age 6 in 1972–1973. By working in this step-wise procedure, many individuals were aged through 6 years and a few through 7 years. Lacking prior captures made some error possible in assigning ages of 4 and 5 years to snakes early in the study, but our method of comparing sizes to known-age statistical values was consistent and uniformly applied over all ages. We tended to be conservative in cases involving a size intermediate between two ages, e.g., if the snake was between the two- and three-year-old size, we designated it as a 2-year-old. Snakes too large for age determination, whether recaptured or not, were pooled as older adults (≥ 6 years old).

Yearly individual length and weight changes are based on successive spring or successive au-

tumn captures. Annual growth increments thus include one intervening period of hibernation. Weight losses during winter dormancy did not differ significantly from year to year so both the spring-to-spring and autumn-to-autumn intervals used for determining annual growth rates are considered equivalent. Proportional annual increases or decreases in SVL or weight were calculated as the amount increased or decreased during the year divided by the initial size at the beginning of the year. For example, if a 1-year-old male increased from 31.9 to 48.9 g (an absolute increase of 17.0 g/yr), the proportional increase would be $17.0 \div 31.9 = 0.533/\text{yr}$, or 53%.

Survival rates were measured over two major periods in the annual cycle of *Coluber* at area M: (1) the winter period of hibernation and (2) the full year. Like growth rate calculations, annual survival rates include one intervening winter period and were calculated from spring-to-spring or autumn-to-autumn capture records.

Population size estimates based on capture-recapture were calculated using the Jolly-Seber stochastic method following Caughley (1977) and Krebs (1978). Eight censuses at den M provided data for the Jolly-Seber analysis over three years (1970–1972). Snakes recaptured following their movement to a different den of M complex were included in the tabulations as were den M individuals that were experimentally displaced from that den in autumn 1971 (cf. Brown and Parker 1976a). Thus, bias due to these factors was eliminated. Population sizes were calculated separately for juveniles (both sexes combined) and for yearling and older (≥ 1 year inclusive) males and females.

Statistical methods in this paper follow Sokal and Rohlf (1969) and Woolf (1968). Mean values are followed by \pm one standard error of the mean (SE) with the extremes in parentheses.

RESULTS

Sexual Dimorphism.—Weights of 73 male and 72 female snakes ≥ 1 year old collected during the autumns of 1969–1972 were regressed on snout–vent lengths (Fig. 1). There was a highly significant ($\delta\delta r = 0.96$, $\varrho\varrho r = 0.97$; $P < 0.01$) correlation between body length and weight in both sexes; 93% ($\delta\delta$) and 95% ($\varrho\varrho$) of the variation in body weight is explained by linear regression on body length. A significant difference ($t = 3.6$,

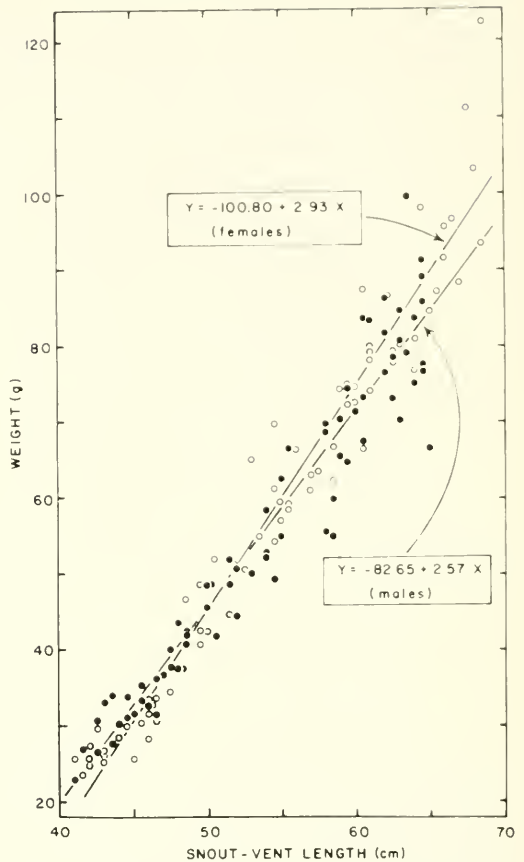


FIG. 1. Relationship between snout–vent length (X) and body weight (Y) in an autumn sample of 73 $\delta\delta$ (solid circles) and 72 $\varrho\varrho$ (open circles) *Coluber constrictor mormon* in northern Utah. Size records were chosen at random from September and October 1969–1972 samples at den M. Regression lines were fitted by least squares. At the time of year these data were obtained, females were nonreproductive.

$P < 0.01$) was obtained between the male and female regression coefficients, indicating statistically significant slope divergence between the two lines. This resulted from large females weighing more than large males.

Mean relative tail length (percentage of total length) was significantly ($t = 12.1$, $P < 0.01$) greater in males ($26.76 \pm 0.11\%$, range 23.9–28.9%, $N = 73$) than in females ($25.07 \pm 0.09\%$, range 23.1–27.0%, $N = 72$). Although statistically significant, this distinction could not be used in visual sex determination.

Size of Snakes of Known Age.—Snout–vent lengths and weights of 1236 *Coluber* of known

TABLE 1. Sizes of *Coluber constrictor mormon* of known age, 1969–1972. Ages: H = hatchling (not sexed), J = juvenile, 1–7 = years (see text for method of designating age). Except for hatchlings, all measurements were recorded in spring at emergence from hibernation. Mean \pm 1 SE, sample size and extremes in parentheses.

Age	Snout-vent length (cm)		Weight (g)	
	♂	♀	♂	♀
H	22.57 \pm 0.20 (26) (19.7–23.8)		5.98 \pm 0.17 (26) (4.1–7.7)	
J*	26.64 \pm 0.48 (11) (23.1–28.7)	27.17 \pm 0.40 (16) (24.3–29.7)	8.30 \pm 0.33 (11) (6.4–9.8)	8.78 \pm 0.39 (16) (6.4–12.2)
1	42.07 \pm 0.19 (141) (36.5–47.0)	43.01 \pm 0.24 (130) (35.5–48.0)	26.98 \pm 0.34 (141) (16.9–36.3)	28.36 \pm 0.44 (130) (16.1–39.9)
2	48.61 \pm 0.13 (149) (44.0–53.5)	52.41 \pm 0.29 (110) (43.5–59.0)	40.95 \pm 0.35 (149) (26.6–52.9)	51.59 \pm 0.73 (110) (35.0–69.3)
3	52.03 \pm 0.13 (116) (48.0–57.0)	57.49 \pm 0.18 (137) (47.5–63.5)	49.14 \pm 0.44 (116) (36.2–60.5)	66.25 \pm 0.59 (137) (43.4–79.2)
4	54.08 \pm 0.16 (77) (51.0–57.5)	59.95 \pm 0.25 (90) (53.0–65.0)	53.41 \pm 0.54 (77) (39.6–64.9)	71.38 \pm 0.95 (90) (49.8–96.2)
5	56.44 \pm 0.15 (67) (54.0–60.0)	62.03 \pm 0.25 (47) (55.5–66.0)	60.40 \pm 0.63 (67) (47.7–75.4)	79.47 \pm 1.13 (47) (65.1–93.1)
6	57.33 \pm 0.30 (21) (55.5–60.0)	63.25 \pm 0.62 (16) (56.5–66.5)	61.18 \pm 1.40 (21) (50.4–75.0)	83.95 \pm 2.47 (16) (68.9–103.8)
7	58.35 \pm 0.37 (7) (57.0–60.0)	—	64.31 \pm 2.22 (7) (58.4–75.0)	—

* Additional 82 not sexed gives a total sample of N = 109 juveniles (sexes pooled; cf. Figs. 2 and 3).

age up to 6 years in females and 7 years in males are shown in Table 1. A sample of 26 hatchling racers (age 0–1 day) was lab-reared in August 1972. Male and female juveniles that were sexed did not differ significantly in mean SVL ($t = 0.8$, $0.50 > P > 0.30$) or weight ($t = 0.9$, $0.50 > P > 0.30$). Sexes were pooled to obtain a larger sample by including 82 juveniles not sexed in the first three years of the study. By the spring following hatching (age ca. 8.5 months) the mean weight of 109 juveniles was 8.52 ± 0.14 (5.1–12.4) g. At an age of 1 year there was a significant difference between males and females in SVL ($t = 3.0$, $P < 0.01$) and weight ($t = 2.5$, $0.02 > P > 0.01$) (Table 1). Thereafter, a more rapid growth rate in females maintained a significant sexual disparity in size at all ages (cf. nonoverlapping 95% confidence limits in growth curves, Figs. 2 and 3). Asymptotic levels for length and weight were approached by the sixth year in both sexes.

Female Age at Maturity.—The mean snout-vent length of 18 gravid females of unknown age from area M was 63.3 ± 1.25 (54.5–74.5) cm. Mean SVL \pm 1 SD of 2-year-olds was 49.4–55.4 cm (Fig. 2), so most were probably immature. An estimate of the minimum size of sexual maturity (57 cm) was calculated by averaging SVL's

of the smallest five gravid females and of the largest five 2-year-olds. In all years, the following proportions of known-age females ≥ 56.5 cm in spring were considered mature: 2-year-olds, 9 of 110 (8%); 3-year-olds, 105 of 137 (77%); 4-year-olds, 81 of 90 (90%); 5-year-olds, 46 of 47 (98%); 6-year-olds, 16 of 16 (100%).

Male Age at Maturity.—Seminal fluid samples showed the presence of sperm in all of 21 males in autumn after the first full activity season at an age of ca. 13.5 months. Three yearlings having sperm in early October had been marked as juveniles a year earlier. In spring, all of 76 1-year-olds and all of 98 2-year-olds tested had sperm. Positive samples in yearlings were obtained as early as 22 March at emergence and 22 September at ingress. The smallest sexually mature male was 39 cm SVL and 17.8 g. None of the 195 one and 2-year-old males lacked sperm, and 250 of 261 older snakes (96%) had positive cloacal samples.

Weight Change during Hibernation.—Body weights of individual *Coluber* in spring following hibernation at den M were usually less than weights the previous autumn, indicating that most snakes had lost weight through the winter. A total of 333 autumn to spring records was obtained for snakes ≥ 1 year old. Of these, 315 (94.6%)

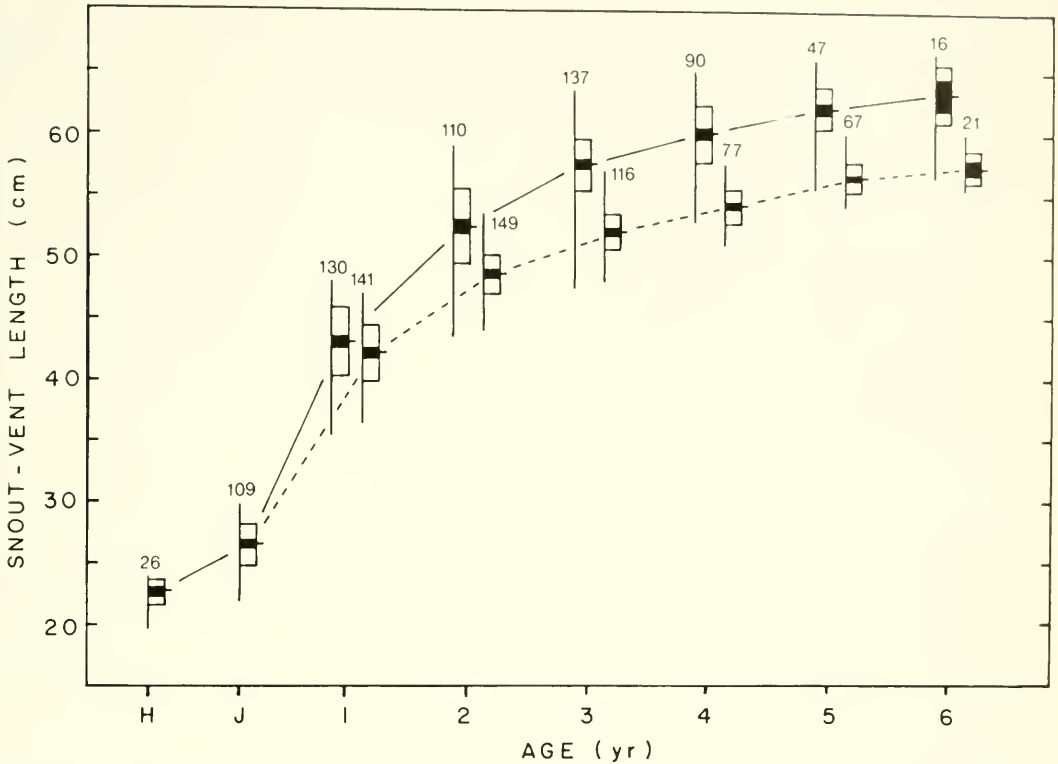


FIG. 2. Growth in snout-vent length of *Coluber constrictor mormon*, 1969-1972. Data for hatchlings (H) and juveniles (J) include both ♂♂ and ♀♀ (sexes combined). Except for hatchlings, all records pertain to spring only. Horizontal lines = sample mean; solid rectangles = 95% confidence limits for population mean; open rectangles = ± 1 standard deviation (SD); vertical line = range. Means of ♂♂ connected by dashed line, ♀♀ by solid line. Sample sizes indicated above each bar diagram.

involved a decrease in weight during the interval (Table 2). Proportions of weight loss records for 178 males (95.5%) and 155 females (93.5%) were similar, as were proportions for both sexes over four winters (1969-1970, 86.8%; 1970-1971, 92.5%; 1971-1972, 96.3%; 1972-1973, 97.2%). Females, averaging larger in size than males, lost significantly ($t = 3.5, P < 0.01$) more weight than did males (Table 2). Eleven of 13 juveniles lost an average of 0.67 ± 0.13 (0.3-1.6) g/snake. On a relative basis, juveniles lost 7.7% of their autumn body weights, not significantly more ($F = 1.44, P > 0.05$) than males (7.4%) and females (7.3%). Analysis of variance also showed that there were no significant between-years differences in weight loss in males (absolute $F = 1.15, P > 0.05$; relative $F = 0.30, P > 0.05$) and in females (absolute $F = 0.66, P > 0.05$; relative $F = 2.49, P > 0.05$).

Annual Age-specific Growth.—Absolute and

relative yearly rates of increase in snout-vent length and weight are summarized in Tables 3-6. As no recapture records were available to measure growth in the season of hatching directly, growth calculations were based on differences between means of hatchling (mid-August) and juvenile (October) sizes. Young racers increased 16.0% in SVL and 36.3% in weight during this 1.5-month interval.

Weight increase during the first year was rapid. Males increased an average of 225% and females 223% of initial juvenile weights (3.2-fold increases). One-year-old females nearly doubled their weight again in their second year (mean proportional increase 82%), achieving a growth rate 1.2 times greater than 1-year-old males. By the time females reached an age of 3 years and most became sexually mature, they were 1.3 times heavier than an average 3-year-old male and 11 times heavier than the average hatchling. The

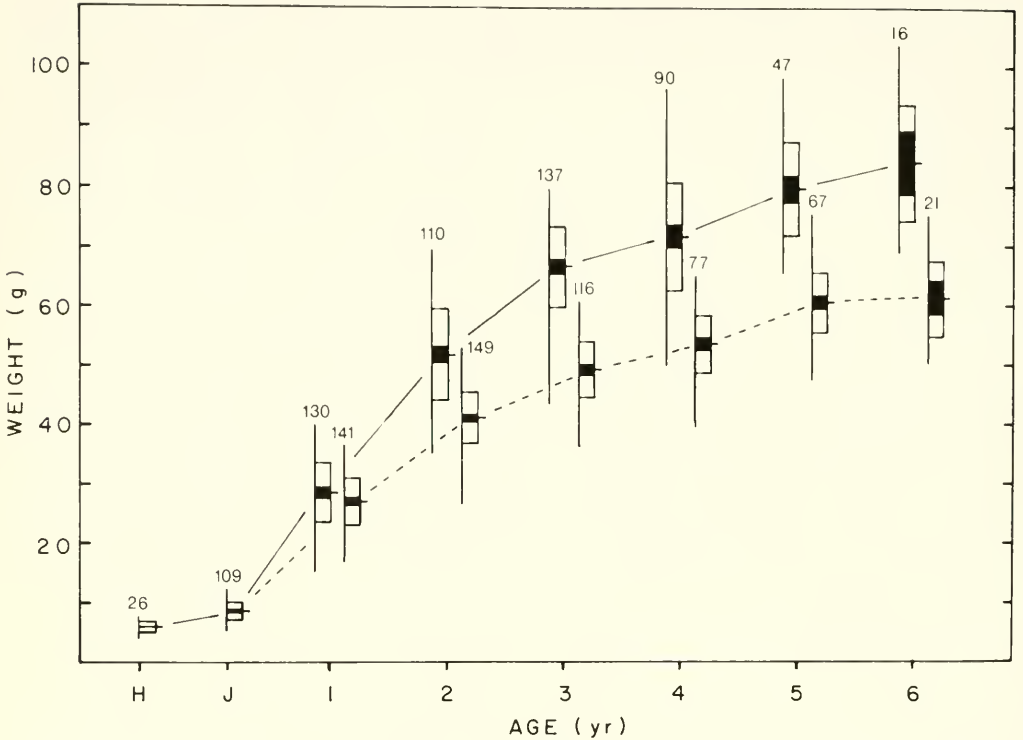


FIG. 3. Growth in weight of *Coluber constrictor mormon*, 1969–1972. Explanation and symbols as in Fig. 2.

first full growing season was clearly the period of greatest rate of increase; thereafter growth rates declined steadily with age. Both absolute and relative growth rates in males were less than corresponding rates in females at all ages.

Unequal growth rates between years are indicated (Tables 3–6). We compared all age-specific absolute rates of growth recorded in 1970 and 1971 against those in 1972. Five age intervals from 1–2 yr to 5–6 yr for each sex were tested. Significant ($P < 0.05$) between-years differences appeared in seven of 10 t -tests of SVL increases and in eight of 10 t -tests of weight increases. In particular, *Coluber* that were ≤ 5 years old grew significantly faster in 1970 and 1971 than in 1972.

Annual Variation in Weight Changes.—To include records of individuals of unknown age not analyzed above, proportions of all large snakes (males mostly > 6 years old, females > 4 years old) that increased in weight each year were compared to each year's rainfall (Fig. 4). A greater

proportion of snakes gained weight during 1971 (85% of 142 records) than in either 1970 (70% of 46 records) or 1972 (44% of 162 records). Proportions of total annual rainfall in the 5-month activity period (May–Sept.) each year were 40% (1970), 39% (1971), and 19% (1972).

Amounts of weight gained and lost are shown in Table 7. Individual weight gains were significantly greater in 1970–1971 than in 1972 in males ($t = 4.75$, $P < 0.001$) and females ($t = 3.40$, $P < 0.01$). Individual weight losses were not significantly greater in 1972 than in 1970–1971 in males ($t = 0.30$, $0.80 > P > 0.70$) and females ($t = 1.84$, $0.10 > P > 0.05$).

Female Reproductive Cycle.—Females contained enlarged prevulatory oocytes in late April, May, and early June (Brown, unpubl. data). At other times of the year ovaries were small and contained no enlarging oocytes. Available evidence indicates production of a single clutch of eggs/♀ per year in northern Utah.

Clutch Size.—Clutch size was determined from

TABLE 2. Winter weight losses in *Coluber constrictor mormon* ≥ 1 year old. Absolute loss is difference in body weight between last autumn capture and first spring capture at den M; relative loss is percentage of autumn weight. Mean ± 1 SE, sample size and extremes in parentheses.

Year	Absolute weight loss (g. snake)		Relative weight loss (%)	
	♂♂	♀♀	♂♂	♀♀
1969-1970	4.04 \pm 0.56 (15) (0.7-8.6)	5.11 \pm 0.75 (18) (1.6-12.5)	6.59 \pm 0.80 (15) (0.9-11.4)	9.17 \pm 0.74 (18) (3.2-14.3)
1970-1971	3.81 \pm 0.34 (39) (0.2-9.5)	6.09 \pm 0.72 (35) (0.1-20.7)	7.25 \pm 0.68 (39) (0.3-20.1)	7.16 \pm 0.63 (35) (0.2-16.9)
1971-1972	4.72 \pm 0.34 (56) (0.3-12.2)	5.25 \pm 0.33 (49) (0.9-10.4)	7.54 \pm 0.42 (56) (1.0-21.3)	6.61 \pm 0.38 (49) (1.7-14.2)
1972-1973	4.10 \pm 0.36 (60) (0.1-15.1)	5.11 \pm 0.57 (43) (0.3-15.6)	7.56 \pm 0.55 (60) (0.2-21.9)	7.53 \pm 0.61 (43) (0.5-18.6)
All snakes	4.23 \pm 0.20 (170) (0.1-15.1)	5.39 \pm 0.28 (145) (0.1-20.7)	7.40 \pm 0.29 (170) (0.2-21.9)	7.33 \pm 0.29 (145) (0.2-18.6)

a sample of 43 reproductive females (Fig. 5). At area M the mean number of eggs/♀ was 5.78 ± 0.24 (4-8), mode 5 (N = 18). For these females, a significant ($r = 0.53$, $0.05 > P > 0.01$) linear correlation existed between body size and clutch size: SVL explained 28% of the variation in clutch size.

Size of Eggs.—Measurements of 54 eggs in nine clutches were recorded after oviposition in the laboratory. Eggs averaged 37.78 ± 0.75 (29.2-54.3) mm in length, 18.00 ± 0.14 (15.9-20.0) mm in width, and 7.80 ± 0.17 (5.9-10.8) g. Data on egg size were not recorded in ten additional lab-deposited clutches. Eggs in three of these were weighed indirectly by dividing the female's ovipositional weight loss by her clutch size. Mean egg weights calculated in this manner were 7.6, 7.8, and 9.8 g (overall, 8.4 g/egg, N = 18).

Analysis of variance (model I) demonstrated a significant difference between clutch means of all three measurements of egg size (length $F = 20.6$, width $F = 16.8$, weight $F = 38.2$; $P < 0.01$). A model II analysis of the components of variance showed that relatively more of the total variation occurred among clutches (73-86%) than among eggs within clutches (14-27%). The smallest clutch (mean weight 6.2 g/egg) differed from the largest (mean weight 10.6 g/egg) by a mean difference of 4.4 g/egg. There was no significant correlation between female size (SVL) and the mean weight of eggs in her clutch ($r = 0.19$, $P > 0.05$; N = 9).

Incubation and Hatching.—Between 27 June and 1 July 1971 seven gravid females were collected in area RB. These females oviposited be-

tween 8-25 July after 9-28 days in an environmental chamber maintained at 29°C. Three gravid females from area M collected between 27 June-3 July oviposited in the laboratory between 12-15 July. Hatching in the 1971 clutches occurred between 19-27 August, after a mean incubation period of 42.6 (41-44) days at 29°C. Nine area M females had enlarged ovarian oocytes between 3-7 June 1972. Four collected between 18-26 June oviposited in the laboratory between 26 June and 9 July. Eggs in three 1972 clutches hatched between 8-23 August after 44-45 days of incubation at 29°C.

We followed three gravid females with implanted radio transmitters at area M in 1972 (Brown and Parker 1976a). Two of these females oviposited on 21 and 23 June. Eggs of one clutch were excavated 36 days later and were lab-incubated at 29°C an additional 12-13 days; hatching occurred on 11-12 August after 48 and 49 days incubation. At the second field site a hatchling was captured by fencing on 10 August, 50 days after oviposition. The third site was excavated on 6 August, 41 days after oviposition, and one freshly-hatched egg was recovered.

In 1971, timing of reproduction between areas RB and M (located 65 km apart) was similar. If most females at area M had oviposited between 5-15 July 1971 and between 20-30 June 1972, with a probable natural incubation period of 45-50 days, most hatching in the field around the communal dens occurred between 20-30 August 1971 and between 10-20 August 1972.

Hatching Success.—In 1971 and 1972, 20 females oviposited in the laboratory. A total of

TABLE 3. Age-specific growth in snout-vent length of 199 ♂♂ *Coluber constrictor mormon* during 3 years. Mean \pm 1 SE, sample size and extremes in parentheses.

Age interval	Absolute increase (cm/year)		
	1970 + 1971	1972	1970-1972
J-1	15.85 \pm 0.95 (2) (14.9-16.8)	13.14 \pm 1.33 (5) (10.8-18.1)	13.91 \pm 1.06 (7) (10.8-18.1)
1-2	7.27 \pm 0.35 (37) (1.5-11.0)	5.31 \pm 0.37 (16) (2.5-8.0)	6.68 \pm 0.29 (53) (1.5-11.0)
2-3	4.33 \pm 0.26 (43) (1.5-7.5)	2.03 \pm 0.19 (16) (0.5-3.0)	3.70 \pm 0.24 (59) (0.5-7.5)
3-4	2.69 \pm 0.25 (16) (0.0-6.5)	1.55 \pm 0.15 (19) (0.5-2.5)	2.07 \pm 0.24 (35) (0.0-6.5)
4-5	2.31 \pm 0.50 (8) (0.0-4.5)	1.31 \pm 0.18 (21) (0.0-3.0)	1.58 \pm 0.20 (29) (0.0-4.5)
5-6	1.50 \pm 0.48 (6) (0.0-3.5)	1.05 \pm 0.20 (10) (0.0-3.0)	1.22 \pm 0.26 (16) (0.0-3.5)

121 eggs were produced of which 105 (86.8%) were normal. Eggs that were improperly shelled and much smaller than usual were considered abnormal. Eight females that produced abnormal eggs had been maintained in captivity at 29°C for a mean of 17.5 (10-28) days prior to oviposition. Females that produced clutches of totally normal eggs were maintained for 11.0 (3-19) days prior to egg laying. Thus, the production of abnormal eggs may have been a function of the constant temperature and lengthy periods of captivity. The frequency of abnormal eggs produced by these females is probably not representative of most gravid females in nature.

Eggs laid by females from area M in 1972 were incubated at 29°C on soil from the locality where

the animals were collected. Eggs were left undisturbed in the same container in which the gravid female had been maintained prior to oviposition. Of 21 normal eggs produced by four females with completely normal clutches, 19 (90.5%) hatched. On 30 August 1971, we excavated a burrow system where a whipsnake (*Masticophis taeniatus*) had oviposited (Parker and Brown 1972). Fifteen *Coluber* eggs of a previous year were unearthed (one group of 10 eggs and one group of five). Of the 15 eggs, 14 (93.4%) had hatched successfully as indicated by egg slits made by the hatchlings. The combined sample (33 of 36 eggs hatched) indicates a hatching success of 92%.

Weight Changes in Reproductive Females.—By recapturing females whose reproductive state

TABLE 4. Age-specific growth in snout-vent length of 204 ♀♀ *Coluber constrictor mormon* during 3 years. Mean \pm 1 SE, sample size and extremes in parentheses.

Age interval	Absolute increase (cm/year)		
	1970 + 1971	1972	1970-1972
J-1	16.56 \pm 0.84 (3) (15.4-18.2)	14.90 \pm 0.74 (7) (13.0-17.7)	15.40 \pm 0.61 (10) (13.0-18.2)
1-2	10.27 \pm 0.33 (39) (6.5-15.5)	9.10 \pm 0.86 (10) (4.5-13.5)	10.30 \pm 0.32 (49) (4.5-15.5)
2-3	6.88 \pm 0.35 (38) (3.5-12.0)	4.45 \pm 0.47 (19) (1.0-10.0)	6.07 \pm 0.32 (57) (1.0-12.0)
3-4	3.62 \pm 0.56 (21) (0.5-10.5)	1.92 \pm 0.22 (26) (0.5-4.0)	2.68 \pm 0.30 (47) (0.5-10.5)
4-5	2.08 \pm 0.37 (13) (0.0-4.0)	2.77 \pm 0.43 (13) (1.0-5.5)	2.42 \pm 0.29 (26) (0.5-5.5)
5-6	2.17 \pm 0.29 (9) (1.0-3.5)	0.75 \pm 0.34 (6) (0.0-2.0)	1.60 \pm 0.28 (15) (0.0-3.5)

TABLE 3. Continued.

Proportional increase/year		
1970 + 1971	1972	1970-1972
.589 ± .029 (2) (.560-.618)	.502 ± .059 (5) (.404-.727)	.527 ± .045 (7) (.404-.727)
.178 ± .009 (37) (.032-.293)	.124 ± .010 (16) (.054-.187)	.162 ± .008 (53) (.032-.293)
.090 ± .006 (43) (.029-.160)	.041 ± .004 (16) (.010-.064)	.077 ± .005 (59) (.010-.160)
.053 ± .009 (16) (.000-.127)	.030 ± .003 (19) (.009-.057)	.040 ± .004 (29) (.000-.085)
.042 ± .009 (8) (.000-.085)	.024 ± .003 (21) (.000-.057)	.029 ± .004 (29) (.000-.085)
.027 ± .009 (6) (.000-.064)	.019 ± .005 (10) (.000-.053)	.022 ± .005 (16) (.000-.064)

was determined, changes in weight prior to oviposition were recorded. Ten females captured in spring at emergence and released between 26 April-20 May were later recaptured between 4-26 June (Table 8). These animals were gravid as determined by palpation of enlarged ovarian oocytes or by subsequent oviposition in the field or laboratory. Recaptures occurred 17-47 (mean 31) days after release during which time these females had increased by an average of 32.6% of their initial body weights. Absolute increases averaged 30.1 (14.6-48.8) g/snake during the pre-reproductive interval; the mean rate of weight gain was 0.97 ± 0.08 g/day.

After ovipositing in the laboratory between 1-14 July, parturient females were released in the field in July 1971 (3 ♀♀) and 1972 (2 ♀♀) (Table

9). One female oviposited in the laboratory both years. The four females were later recaptured in August and early September, 31-53 days after release. These spent females recovered an average of 53% (24.7-71.1%) of their parturient weights (Table 9). Mean postreproductive weight recovery was 0.92 (0.45-1.38) g/day.

For some area M females, additional weight records were obtained in a following year as they were again recaptured emerging from hibernation. One female (No. 4, Table 9), weighed 114.0 g on 5 Sept. 1971 after reproduction, 100.5 g in spring 1972, and 109.2 g in spring 1973. Data showing very similar weights in the spring following a known reproductive year as in the spring preceding that year are available for three females in Table 8.

TABLE 4. Continued.

Proportional increase/year		
1970 + 1971	1972	1970-1972
.644 ± .041 (3) (.579-.719)	.550 ± .015 (7) (.448-.728)	.579 ± .032 (10) (.448-.728)
.247 ± .008 (39) (.141-.356)	.202 ± .022 (10) (.095-.333)	.238 ± .008 (49) (.095-.356)
.135 ± .007 (38) (.048-.261)	.085 ± .010 (19) (.018-.208)	.119 ± .007 (57) (.018-.261)
.063 ± .010 (21) (.017-.193)	.033 ± .004 (26) (.008-.071)	.047 ± .005 (47) (.008-.193)
.035 ± .007 (13) (.008-.068)	.046 ± .007 (13) (.017-.091)	.041 ± .005 (26) (.008-.091)
.035 ± .005 (9) (.016-.056)	.012 ± .005 (6) (.000-.032)	.026 ± .005 (15) (.000-.056)

TABLE 5. Age-specific growth in weight of 179 ♂♂ *Coluber constrictor mormon* during 3 years. Mean \pm 1 SE, sample size and extremes in parentheses.

Age interval	Absolute increase (g/year)		
	1970 + 1971	1972	1970-1972
J-1	19.75 \pm 1.15 (2) (18.6-20.9)	14.44 \pm 1.29 (5) (12.0-18.9)	15.96 \pm 1.35 (7) (12.0-20.9)
1-2	16.30 \pm 0.72 (37) (3.2-23.3)	10.48 \pm 1.07 (16) (2.3-20.5)	14.54 \pm 0.70 (53) (2.3-23.3)
2-3	11.34 \pm 0.58 (43) (5.3-18.2)	4.60 \pm 0.97 (13) (0.2-12.1)	9.77 \pm 0.63 (56) (0.2-18.2)
3-4	8.09 \pm 0.85 (16) (1.7-17.1)	2.88 \pm 0.75 (12) (0.1-8.8)	5.86 \pm 0.76 (28) (0.1-17.1)
4-5	7.64 \pm 1.29 (8) (1.5-12.8)	3.36 \pm 0.82 (15) (0.6-11.0)	4.85 \pm 0.81 (23) (0.6-12.8)
5-6	5.89 \pm 1.07 (9) (1.1-10.9)	2.97 \pm 0.15 (3) (2.7-3.2)	5.16 \pm 0.88 (12) (1.1-10.9)

Frequency of Reproduction.—In 1971, five females \geq 57.0 cm SVL were captured in early summer between 15 June and 4 July. Of these, three were gravid. No enlarged oocytes were discerned by palpation in two others, but they may have been gravid on the basis of post-emergence weight increases of 23.4% (1.11 g/day) in 14 days, and 34.2% (0.64 g/day) in 39 days, increase values comparable to those for known gravid females (Table 8).

In 1972, 21 females \geq 57.0 cm SVL were hand-captured in early summer between 2 and 28 June (nine records of those with a spring emergence capture are in Table 8). Of these, 18 were either gravid or recently parturient (bearing postero-lateral skin folds) when collected. One of the two

apparently non-gravid females was a snake that had been followed by telemetry in August and early September 1971. Her apparent nonreproductive state in 1972 may have been influenced by the transmitter in late 1971, perhaps by preventing normal feeding and weight recovery. Considering the combined sample (telemetry snake excluded) of 25 females captured in early summer, 22 (88%) were believed to be reproductively active. This evidence indicates egg laying each year by a large proportion of mature females in the study area.

Relative Chuch Mass.—In 12 female *Coluber* that produced clutches of normal eggs in the laboratory, RCM (Vitt and Congdon 1978) was calculated as the proportionate weight loss imme-

TABLE 6. Age-specific growth in weight of 179 ♀♀ *Coluber constrictor mormon*. Mean \pm 1 SE, sample size and extremes in parentheses.

Age interval	Absolute increase (g/year)		
	1970 + 1971	1972	1970-1972
J-1	20.13 \pm 1.49 (3) (18.4-23.1)	17.30 \pm 1.09 (7) (14.1-21.2)	18.15 \pm 0.94 (10) (14.1-23.1)
1-2	26.05 \pm 0.93 (39) (15.8-38.0)	21.53 \pm 2.21 (10) (9.7-28.9)	25.12 \pm 0.89 (49) (9.7-38.0)
2-3	20.70 \pm 1.05 (38) (6.8-34.4)	11.16 \pm 1.50 (18) (3.1-28.9)	17.63 \pm 1.04 (56) (3.1-34.4)
3-4	16.53 \pm 2.49 (20) (1.0-42.3)	6.38 \pm 1.34 (13) (0.1-18.9)	12.53 \pm 1.80 (33) (0.1-42.3)
4-5	11.43 \pm 1.28 (13) (3.9-18.4)	5.48 \pm 1.55 (8) (0.2-15.1)	9.16 \pm 1.16 (21) (0.2-18.4)
5-6	9.41 \pm 1.65 (8) (4.5-18.1)	6.65 \pm 3.65 (2) (3.0-10.3)	8.86 \pm 1.46 (10) (3.0-18.1)

TABLE 5. Continued.

Proportional increase year		
1970 + 1971	1972	1970-1972
2.153 ± .195 (2) (1.958-2.348)	1.744 ± .177 (5) (1.316-2.363)	1.882 ± .147 (7) (1.316-2.363)
.647 ± .035 (37) (.137-1.081)	.384 ± .047 (16) (.076-.756)	.568 ± .033 (53) (.076-1.081)
.283 ± .016 (43) (.124-.579)	.110 ± .025 (13) (.004-.314)	.243 ± .017 (56) (.004-.579)
.171 ± .021 (16) (.003-.409)	.058 ± .014 (12) (.002-.157)	.123 ± .017 (28) (.002-.409)
.136 ± .022 (8) (.030-.223)	.062 ± .016 (15) (.010-.232)	.088 ± .015 (23) (.010-.232)
.099 ± .018 (9) (.019-.188)	.046 ± .004 (3) (.038-.053)	.086 ± .015 (12) (.019-.188)

diately following egg laying (weight lost at oviposition/body weight prior to oviposition). Mean gravid weight of the 12 females was 111.6 ± 4.47 (82.3-137.2) g; mean parturient weight was 62.7 ± 2.73 (43.1-77.0) g. Mean RCM was 43.8 ± 1.03% (37.9-49.2%). Females were weighed an average of 6 (1-13) days prior to oviposition during which time some weight loss would be expected through dehydration (although water was supplied *ad libitum*), so the measured relative weight loss due to oviposition was probably slightly higher than actual losses had weighing immediately preceded oviposition. However, there was no significant correlation between weighing interval and percentage weight loss ($r = 0.30, P > 0.05$).

Estimates of Population Size.—Total numbers of all individual racers captured at the various

dens between 1969 and 1972 (Table 10) constitute a direct census which was influenced by (1) the snakes' fidelity to the several communal hibernacula and (2) the effectiveness of our encircling fences in capturing them. We believe both possible sources of error were minimal, assuring a high reliability of our direct counts of individuals captured. Nonetheless, each year some unmarked snakes of all ages were caught (see "Age Structure"). Among all snakes one year old or older in 1971, 26-29% at dens M, 1, and 5 were captures of unmarked individuals (Table 11). In 1972 at dens M and S3, new captures comprised 22% and 33% of the samples, respectively.

Mark-recapture population estimates using the Jolly-Seber method resulted in population estimates for males and females ≥ 1 year old only slightly higher than the actual number of snakes

TABLE 6. Continued.

Proportional increase year		
1970 + 1971	1972	1970-1972
2.653 ± .384 (3) (.022-3.348)	2.055 ± .252 (7) (1.156-3.313)	2.235 ± .219 (10) (1.156-3.348)
1.000 ± .038 (39) (.399-1.510)	.675 ± .076 (10) (.281-1.061)	.934 ± .038 (49) (.281-1.510)
.442 ± .028 (38) (.159-.873)	.219 ± .037 (18) (.052-.754)	.370 ± .026 (56) (.052-.873)
.264 ± .047 (20) (.010-.789)	.098 ± .021 (13) (.001-.285)	.199 ± .032 (33) (.001-.789)
.160 ± .019 (13) (.049-.297)	.078 ± .022 (8) (.003-.219)	.129 ± .017 (21) (.003-.297)
.106 ± .027 (8) (.010-.247)	.081 ± .044 (2) (.037-.124)	.101 ± .022 (10) (.010-.247)

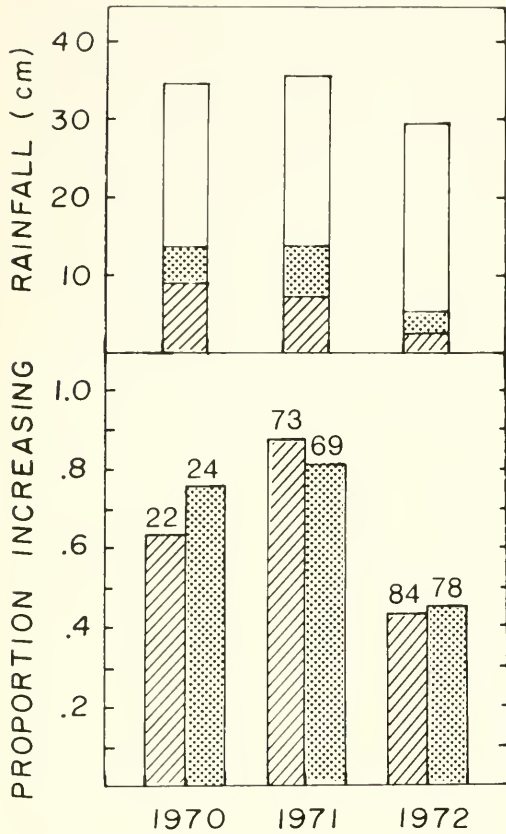


FIG. 4. Annual proportions of *Coluber constrictor mormon* that increased in weight in three successive years (1970–1972) compared to yearly rainfall. Upper histogram shows total annual rainfall (unshaded), May–Sept. total (stippled), and June–Aug. total (hatched) recorded at Grantsville, Utah. Weight change records (lower histogram) are for 179 ♂♂ ≥ 50.0 g (hatched bars) and 171 ♀♀ ≥ 60.0 g (stippled bars) initial body weight; sample sizes above each bar.

caught at den M in 1970 and 1971 (Table 12). The disparity was greater for juveniles, reflecting the greater difficulty of capturing them and their higher mortality rate. These factors lowered recapture proportions and tended to raise the estimated population of juveniles relatively more than the estimates for adults. The relatively low “difference factors” for older snakes indicated that the sampling technique effectively captured a high proportion of the adult population.

Population Density.—Using maximum dispersal distances recorded by Brown and Parker

(1976a) (1.6 km from M complex, 1.8 km from S complex) as radii of circular areas, and assuming uniform dispersal in all directions from each den complex, areas occupied by the *Coluber* populations were 804 ha at M complex and 1017 ha at S complex. In autumn 1971 and spring 1972, when sampling was most complete, 528 *Coluber* weighing 29,728 kg were recorded at M complex, and in spring 1972, 271 *Coluber* weighing 15,795 kg were recorded at den S-3 in S complex (Table 10). Population and biomass densities at M and S complexes in 1971 were 0.66 and 0.27 snakes/ha and 37 and 16 g/ha, respectively. Population census data were adjusted by calculated difference factors (Table 12) to estimate total populations. Adjusted population densities were 0.79 snakes/ha at M complex and 0.32 snakes/ha at S complex. Adjusted biomass densities were 39.8 g/ha at M complex and 16.7 g/ha at S complex (Table 13).

The two den complexes are located ca. 875 m apart. Thus, a 600-ha region of overlap, encompassing 60% of the S dispersal area and 75% of the M, could contain additive densities. The overlap densities were 0.78 snakes/ha and 39.6 g/ha. These are the most representative estimates of these parameters under the conditions of sampling and assumptions employed in the calculations.

Population Changes.—Population changes during our sampling are shown in Table 14. The racer population increased by 16.5% in 1970 (den M), and by 16.7% (den M) and 18.9% (dens 1 and 5) in 1971. The population increases noted in 1970 and 1971 were not sustained during 1972 when the populations declined by 22.2% (den M) and 20.3% (den S3).

Sex Ratio.—For each den and sampling period, proportions of total numbers of males (822) and females (725) ≥ 1 year old were 0.531 and 0.469, respectively. In all but two sampling periods, males outnumbered females (Table 10). Sex ratios were never significantly different from a 1:1 expectation as tested by chi-square for any den or sampling period.

Sex ratio at birth was determined by eversion of hemipenes after injection for 18 lab-reared hatchlings randomly preserved in 1971. There were 9 males and 9 females in this sample. A sample of 17 juveniles in autumn 1972 and spring 1973 was sexed. There were 10 males and 7 females in this sample ($\chi^2 = 0.24$, $0.70 > P >$

TABLE 7. Annual absolute weight changes of 350 *Coluber constrictor mormon* in three successive years. Data are for 179 ♂♂ ≥ 50.0 g and 171 ♀♀ ≥ 60.0 g that gained or lost weight during a yearly interval. Mean \pm 1 SE, sample size and extremes in parentheses.

Sex	Increase (g/yr)		
	1970	1971	1972
♂♂	4.00 \pm 0.77 (14) (0.1–9.0)	6.62 \pm 0.45 (64) (0.2–14.8)	2.98 \pm 0.44 (36) (0.3–9.3)
♀♀	13.53 \pm 2.23 (18) (1.0–31.5)	14.26 \pm 1.11 (56) (1.9–41.6)	8.41 \pm 1.20 (35) (0.1–32.6)
Sex	Decrease (g/yr)		
	1970	1971	1972
♂♂	6.44 \pm 1.12 (8) (2.9–10.9)	1.76 \pm 0.53 (9) (0.3–5.5)	4.28 \pm 0.56 (48) (0.1–19.7)
♀♀	5.73 \pm 1.17 (6) (1.6–9.4)	4.48 \pm 1.35 (13) (0.4–18.6)	7.59 \pm 0.88 (43) (0.4–25.3)

0.50). Of 22 snakes marked as hatchlings (not sexed) and later recaptured as 1-year-olds, there were 9 males and 13 females ($\chi^2 = 0.41$, $0.70 > P > 0.50$). These combined samples indicate that sex ratio at hatching did not differ significantly from 1:1.

Age Structure.—Ages of males and females at den M in each of four successive years and at other dens (dens 1 and 5 in M complex, den S3 in S complex) in two successive years are shown in Figs. 6 and 7. In samples following the initial sampling period at a den, proportions of marked snakes we recaptured were high, particularly if 1-year-olds are excluded from the tabulations. Proportions of marked snakes ≥ 2 years of age averaged 80% in dens M, 1, 5, and S3 between 1970–1972. The greatest proportion of “new” animals consisted of 1- and 2-year-old snakes. These ages accounted for 60.6–79.4% of all unmarked snakes during three years (Table 15).

Pooled composite ratios of annual age groups for all dens (Fig. 8) show that in all years there were many immatures and young adults. Juveniles through 5-year-olds comprised 61.9–75.7% of all ages. Older individuals (all snakes aged 6+ years) represented 24.3–38.1% of the population in different years.

Two distinct ages were evident among the younger classes. The first was the 1-year-old group in 1969 which remained distinct as a cohort of 2-, 3-, and 4-year-olds through 1972. The second was the juvenile age class in 1971 which showed up as a prominent cohort of 1-year-olds in 1972. These 1-year-old cohorts represented hatchlings

produced in 1968 and 1971, respectively. In 1969, yearlings accounted for 27.4% of the population; in 1972 they made up 20.3% of the population (Fig. 8).

The waves of age classes in the composite age distributions may correlate with yearly variation in climatic conditions and varying annual proportions of *Coluber* that increased in weight. A favorable year for growth (1971) apparently also was favorable for reproduction as reflected in the large 1-year-old cohort in 1972. Prior to our study, 1968 also appears to have been a favorable year as implied by the age structure showing a large proportion of 1-year-olds in 1969. Juveniles recruited into the population in 1972 made up 4.6% of the population as compared to 11.2% in 1971, 7.8% in 1970 and 7.9% in 1969. In contrast to 1970 and 1971, the poorest year for juvenile recruitment was 1972 when the proportion of juveniles was 4.6% (58% lower than in 1971).

Survivorship.—Overwintering survival rates averaged 93.3% per winter for males (range 80–98% per winter) and 93.4% per winter for females (range 89–98% per winter). Relatively little mortality (7% per winter) occurred during hibernation in the four years of this study (Table 16).

Annual age-specific survival rates of males (all ages ≥ 1 year) averaged .688 (1970), .810 (1971), and .620 (1972). Female annual survivorship (all ages ≥ 1 year) averaged .790 (1970), .782 (1971), and .553 (1972). Annual survival rates for juveniles were .273 (1970), .233 (1971), and .226 (1972). Growth rates and age compositions also suggest that 1972 was an unfavorable year for

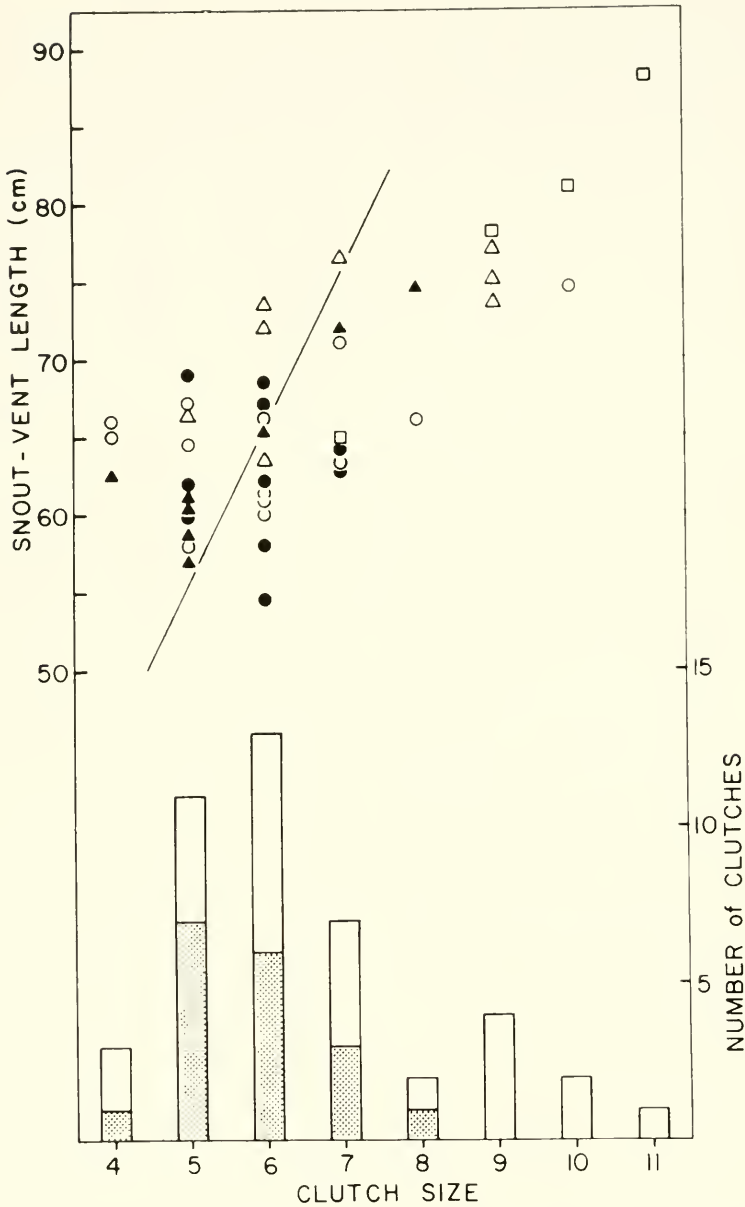


FIG. 5. Clutch sizes—♀ body size (SVL) relationship for *Coluber constrictor mormon* in 1971 and 1972. Circles represent laboratory oviposition records; triangles represent enlarged preovulatory oocytes. Solid symbols in scatter diagram (upper portion of figure) and corresponding shaded bars in histogram (lower portion of figure) are records from area M. Open circles and triangles (upper) and unshaded bars (lower) represent records from area RB, and squares area SLC. The regression line shows clutch size (Y) vs. snout-vent length (X) for area M females and is described by the equation $Y = -0.56 + 0.10X$.

TABLE 8. Prereproductive (late spring-early summer) weight increases in 10 gravid female *Coluber constrictor mormon* at area M, 1971 and 1972. O = ovarian oocytes, E = oviducal eggs. Last two snakes were recaptured prior to being tracked by telemetry.

Clutch size	Spring weight (g)	Summer weight (g)	Interval (days)	Weight increase		
				g	g day	%
6, O	97.4	123.5	38	26.1	0.68	26.8
5, O	69.4	90.1	25	20.7	0.83	29.8
7, O	123.8	149.9	26	26.1	1.00	21.1
8, O	128.6	169.0	29	40.4	1.39	31.4
4, O	76.4	94.9	17	18.5	1.09	24.2
5, O	68.7	83.3	24	14.6	0.61	21.3
5, E ^a	111.3	152.1	36	40.8	1.13	36.7
7, E ^b	89.0	119.0	47	30.0	0.64	33.7
6, E ^c	93.2	142.0	41	48.8	1.19	52.4
?, E ^d	72.5	107.5	29	35.0	1.21	48.3

^a Oviposited in laboratory 3 July 1972, 15 days after recapture.

^b Oviposited in laboratory 26 June 1972, 4 days after recapture.

^c Oviposited in field 24 June 1972, 16 days after release with transmitter (8 June).

^d Oviposited in field, date unknown; still gravid when last seen on 26 June 1972, 8 days after release with transmitter (18 June).

Coluber compared to 1970 and 1971. Survivorship data for these two years were pooled for comparison to 1972 data (Table 17).

Survivorship over all ages increased by 18% in males from 1970 to 1971 and remained about the same in females between these two favorable years. In 1972, survivorship in males declined 20% from the combined 1970-1971 rate (.779). Female survivorship (all ages ≥ 1 year) dropped 29% in 1972 from the combined 1970-1971 rate (.784). Age differences in survival rates between 1971 and 1972 indicate that a greater relative

decline in 1972 (44%) occurred among 1-year-olds (both sexes) and among snakes aged 6 years or older (26% decline in males, 39% in females; Fig. 9). Young to middle-aged individuals (ages 2-5) suffered a lower relative reduction in survival from 1971 to 1972 (4-28% in males, 20-28% in females). Overall, males fared better than females in 1972 (Fig. 9). In the favorable years 1970 and 1971, survivorship among all females of reproductive age (≥ 3 years old) averaged .791 per year. In 1972, survivorship among all reproductive-aged females was .558.

Our estimate of the survival rate of juveniles from the time they were captured at dens to an age of one year is 23%. We believe this value is based on sufficient data (22 1-year-olds recaptured of 94 juveniles released) to allow confidence in this estimate. Our life table (see below) utilizes an estimate of 17% survivorship during the first year (from egg to 1-year-old). This suggests that the 1.5-month interval between hatching (mid-August) and arriving at the dens upon attaining juvenile age status (late September to early October) involved a 79% survival rate, and a survivorship of 72% from egg to juvenile (Table 18).

Applying our estimates of survivorship to the estimated total production of female eggs (302) by 106 reproductive-sized females captured at three dens (M, 1, 5) in 1971 yields an expected 221 female juveniles. We actually caught 32 female juveniles at these dens in 1971, only 14% of the expected number. This could indicate one of three possibilities: (1) that our first-year survivorship estimate is too high, (2) that the estimate of female productivity is too high, or (3) that a fairly large proportion of the annual crop

TABLE 9. Postreproductive (late summer) weight increases in four parturient female *Coluber constrictor mormon*.

Snake no. (area, year)	Clutch size	Gravid weight (g)	Parturient weight (g)	Late summer weight (g)	Interval (days)	Weight increase		
						g	g day	%
1. (RB, 1971)	10	156.6	87.3	149.4	45	62.1	1.38	71.1
2. (RB, 1971)	8	127.2	73.3	124.2	45	50.9	1.13	69.4
3. (RB, 1971)	5	120.8	65.4	—	318	37.7*	—	57.6*
3. (RB, 1972)	4	103.1	57.2	71.3	31	14.1	0.45	24.7
4. (M, 1972)	6	125.5	77.0	114.0	53	37.0	0.70	48.1

* Increase that occurred in the 318-day interval between 1971 and 1972.

TABLE 10. Numbers, live-weight biomass, and sex ratios of *Coluber constrictor mormon* captured at five hibernacula in M complex (dens M, 1, 2, 3, 5) 1969–1972 and at one hibernaculum in S complex (den S3) in 1972. Number of snakes at den M is total different individuals for both autumn and spring sampling; for all other hibernacula totals are different individuals in spring only. Weights are for animals in spring unless only autumn capture was recorded. Males and females include all ages ≥ 1 year old, juveniles (J) include both sexes < 1 year old (see text).

Year	Den	♂♂			♀♀			JJ		All snakes	
		N captured	Proportion	Weight (kg)	N captured	Proportion	Weight (kg)	N captured	Weight (kg)	Total N captured	Total weight (kg)
1969	M	65	.508	3.667	63	.492	3.661	11	.091	139	7.419
1970	M	73	.507	3.709	71	.493	4.703	18	.138	162	8.550
1970	1	39	.534	2.055	34	.466	2.343	2	.016	75	4.414
1970	5	72	.518	3.727	67	.482	4.360	10	.081	149	8.168
1971	M	77	.484	4.318	82	.516	6.054	34	.281	193	10.653
1971	1	48	.533	2.767	42	.467	3.127	8	.067	98	5.961
1971	2	17	.654	0.760	9	.346	0.547	3	.025	29	1.332
1971	3	13	.448	0.697	16	.552	1.236	2	.014	31	1.947
1971	5	81	.526	4.439	73	.474	5.214	23	.182	177	9.835
1971	S3	137	.544	7.604	115	.456	8.011	19	.180	271	15.795
1972	M	75	.543	3.656	63	.457	3.852	10	.089	148	7.597
1972	S3	125	.581	6.170	90	.419	5.650	7	.067	222	11.887

of juveniles did not utilize the communal dens in their hatching year. We favor the third possibility. Young snakes are perhaps not able to travel the distances necessary to get back to the dens for a variety of behavioral reasons. Many first-time users of the dens were yearlings (Table 15). The 302 female eggs should have resulted in 39 1-year-olds the following year. Lacking den-fenced samples for dens 1 and 5 in spring 1973, however, we have no direct confirmation of the actual arrival of 1-year-olds to any den except den M in 1972 (14 yearlings taken). If we assume that the population had remained stable between 1971 and 1972, the 39 expected yearlings would have comprised 19.9% of all 196 females (the total number captured in 1971). This percentage compares closely to 17.7%, the actual mean proportion of 1-year-olds to all females (6.1–35.3%.

$N = 10$ den samples, all years). Thus, we feel that a 17% survivorship estimate from egg to yearling is accurate.

Life Table.—Table 19 presents a life table for area M females. This life table is based on the following data and assumptions:

- (1) Sex ratio at hatching was 1:1.
- (2) Mean unadjusted age-specific fecundity for all younger females (5.0–5.8 eggs/♀/yr, ages 2–6) was calculated from all body size (SVL) records in spring 1971 and an expected clutch size based on the appropriate regression. For all older females (ages ≥ 7), the mean unadjusted fecundity (6.0–7.0 eggs/♀/yr) was calculated by the same procedure in the body size range 66–75 cm.
- (3) Mean fecundity values were adjusted by as-

TABLE 11. Proportions of marked *Coluber constrictor mormon* among recapture samples at four dens in three successive years. Total number of snakes captured in parentheses.

Year	Den	≥ 1 -year-old		≥ 2 -year-old	
		♂♂	♀♀	♂♂	♀♀
1970	M	.520 (73)	.605 (71)	.603 (63)	.666 (63)
1971	M	.722 (77)	.743 (82)	.823 (68)	.789 (76)
1971	1, 5	.736 (129)	.713 (115)	.814 (113)	.832 (95)
1972	M	.773 (75)	.794 (63)	.887 (62)	.938 (49)
1972	S3	.648 (125)	.689 (90)	.788 (99)	.867 (68)

TABLE 12. Comparison of sampled and estimated population sizes of *Coluber constrictor mormon* at den M in 1970 and 1971. Difference factor is a proportion calculated by dividing the Jolly-Seber population estimate by the actual number of snakes caught.

Year	Age	Sex	Number caught	Jolly-Seber estimate	Difference factor
1970	JJ	♂ + ♀	18	49.8	2.77
	≥ 1 year	♂♂	73	79.6	1.09
	≥ 1 year	♀♀	71	80.0	1.13
	All snakes		162	209.4	1.29
1971	JJ	♂ + ♀	34	63.4	1.86
	≥ 1 year	♂♂	77	84.5	1.10
	≥ 1 year	♀♀	82	84.8	1.03
	All snakes		193	232.7	1.21

suming no reproduction at age 1, 8% at age 2, 77% at age 3, and 90% at age 4 and all subsequent ages; hatching success was assumed to be 92% at all ages.

- (4) Estimated survivorship from age 0 to 1 (17%) was based on the proportion of unmarked 1-year-old females (above).
- (5) Age-specific survival rates were based on all recapture records for the years 1970 and 1971 combined.

The life table (Table 19) calculated for *Coluber* indicates an increasing population ($R_0 = 1.187$). An approximate value of the mean generation time was calculated as $T_c = (\sum x l_x m_x) / R_0 = 6.89$ years. The highest proportion (15.8%) of the net reproductive rate was contributed by 3-year-old females. Relative contributions to R_0 from the other adjacent age classes were 15.0% by 4-year-olds, 13.5% by 5-year-olds, and 10.8% by 6-year-olds.

The life table for *Coluber* in Utah indicates a maximum longevity of some 15 years in the population studied. That a few racers survive to this age is not unreasonable. Two males originally marked with metal jaw tags in autumn 1964 by Hirth (1966) survived through 1970 and 1971, periods of 6 and 7 years after marking. We estimate these snakes were at least three years old when tagged (at a body size that would permit such tagging), so they reached minimum ages of 9 and 10 years. In autumn 1972 and spring 1973, 15 males were recaptured at den M that

TABLE 13. Population and biomass densities of *Coluber constrictor mormon* in 1971. Difference factors used to adjust population sizes and total weights were calculated from data in Table 12.

Den complex		Age/sex		Population density		
				Total number snakes captured	Difference factor	Estimated total population size
M	all	528	1.21	639	0.79	
S	all	271	1.21	328	0.32	
		Biomass density				
		Total live weight (kg)	Difference factor	Estimated total weight (kg)	Grams/ha	
M	JJ	0.569	1.86	1.058		
	♂♂	12.981	1.10	14.279		
	♀♀	16.178	1.03	16.663		
	all	29.728		32.000	39.8	
S	JJ	0.180	1.86	0.335		
	♂♂	7.604	1.10	8.364		
	♀♀	8.011	1.03	8.251		
	all	15.795		16.950	16.7	

had been among an original group of 37 at least 3 years old when initially marked in 1969–1970. These animals were all 6 years old or older when last handled.

At average growth rates calculated in this study both sexes of *Coluber* would reach maximum

TABLE 14. Annual population changes of *Coluber constrictor mormon* in three successive years as measured by total captures (all ages, both sexes) at four dens. Sampling periods: A = autumn, S = spring, number = year.

Year	Den	Sampling period	Number of snakes captured	Rate of increase/yr	
				Finite (λ)	Exponential (r)
1969	M	A69, S70	139	—	—
1970	M	A70, S71	162	1.165	0.153
1971	M	A71, S72	189 ^a	1.167	0.154
1971	1, 5	S71	217 ^b	—	—
1971	1, 5	S72	258 ^c	1.189	0.173
1972	M	A72, S73	147 ^d	0.778	-0.251
1972	S3	S72	271	—	—
1972	S3	S73	216	0.797	-0.227

^a 193 (total)—4 (den shifts).
^b 224 (total)—7 (den shifts).
^c 275 (total)—17 (den shifts or displacement returns).
^d 148 (total)—1 (den shift).

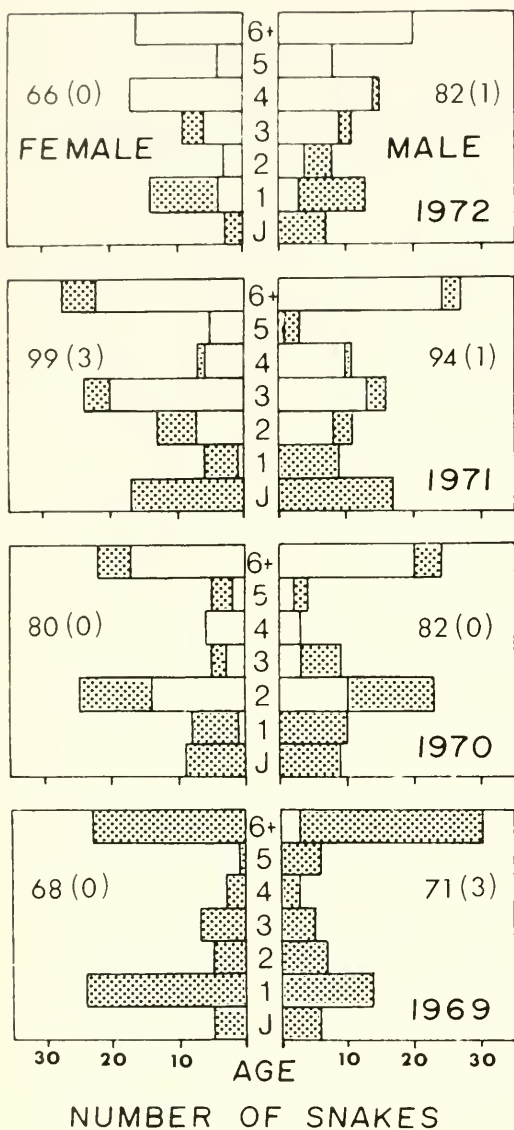


FIG. 6. Age and sex structure of *Coluber constrictor mormon* at den M in four successive years. For 1970–1972 stippling = unmarked individuals and snakes not using den in previous year. For 1969 no stippling = individuals marked between 1964–1966 (Hirth, 1966); for other years no stippling = marked individuals (present study). Number in parentheses following number of snakes indicates marked snakes which shifted to this den from another den and included among unmarked snakes. J = juvenile (sexed only in 1972–1973); other numbers = age in years.

sizes observed (ca. 75 cm SVL in females, 65 cm SVL in males) in about 10 years. Yearly variation in environmental favorability for growth and individual variation in response to these conditions naturally would affect this estimate, but our size data indicate that larger racers may have been 10 years old or older. A body size distribution of large (>65 cm SVL) females of unknown age in 1971 was tabulated. Size range, number of individuals, percentage of total females caught in 1971, and probable ages of these snakes were as follows:

65–66.5 cm, 17 (5.3%), 7–8 yr;
 67–68.5 cm, 15 (4.7%), 9–10 yr;
 69–70.5 cm, 15 (4.7%), 11–12 yr;
 71–72.5 cm, 13 (4.1%), 13–14 yr;
 73–75.0 cm, 4 (1.2%), ≥ 15 yr.

Two extremely robust individuals were recorded that far surpassed sizes even of snakes normally considered "large." One male measured 94.0 cm SVL and 153.6 g, and one female was 85.0 cm SVL and 194.2 g. These animals may have been unusually old individuals.

DISCUSSION

Prior Studies at Utah Dens.—During our study of *C. c. mormon* in Utah, we investigated also two other colubrids, the desert striped whipsnake (*Masticophis t. taeniatus*) and the Great Basin gopher snake (*Pituophis melanoleucus deserticola*) (Parker and Brown 1980), as well as the Great Basin rattlesnake (*Crotalus viridis lutosus*; Parker and Brown 1974). The den M *Coluber* population was sampled for seven years in a 10-year period, from 1963–1965 (corresponding to spring 1964–1966 den fenceings) by Hirth and King (1968), and from 1969–1972 (present study). Den M was not studied in the three-year period 1966–1968. Population growth, age structure, and overwintering survival rates may be compared with the earlier results of Hirth and King (1968) and Hirth (1966).

Increases apparently occurred in the *Coluber* population in 1964 (49 to 63 snakes) and 1965 (63 to 67 snakes) (Hirth and King 1968). In the three intervening years between studies, the population grew from 67 to 139 individuals, an average rate of increase of 26.7% per year ($r = 0.182/\text{yr}$). Two favorable years of high individual growth, high survival rates, and high juvenile

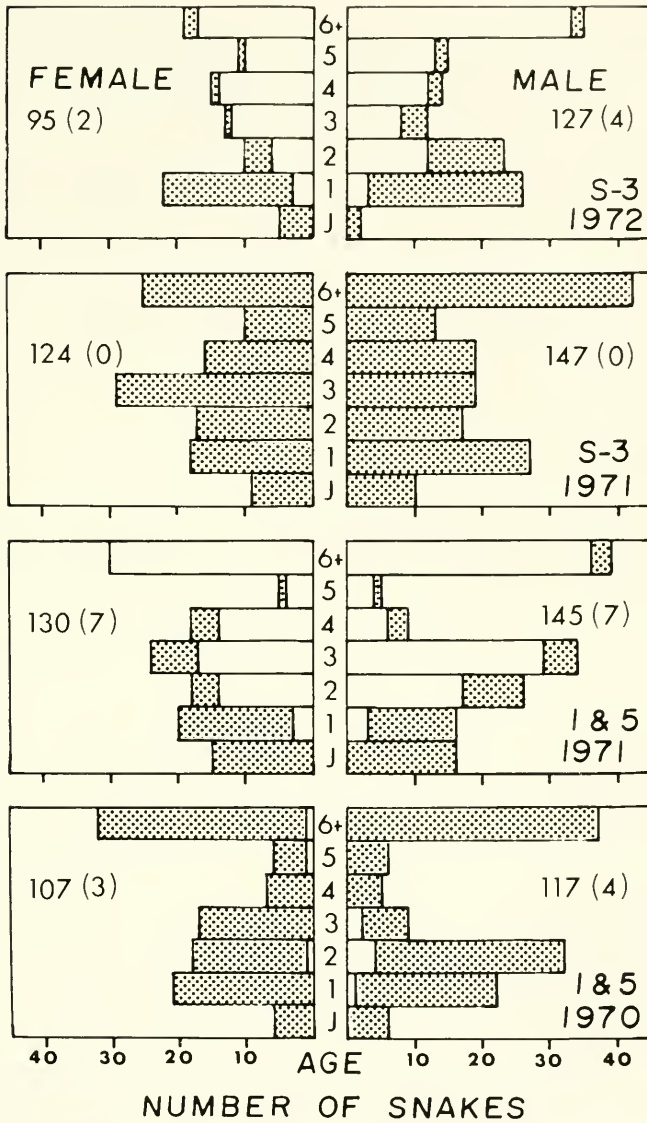


FIG. 7. Age and sex structure of *Coluber constrictor mormon* at three dens in two successive years. Lower two histograms show M complex dens 1 and 5 in 1970 and 1971 (spring 1971 and 1972 samples); upper two histograms show S complex den S3 in 1971 and 1972 (spring 1972 and 1973 samples). Symbols as in Fig. 6.

recruitment (1970 and 1971) resulted in continued expansion of the population. An unfavorable year (1972) reversed these trends because of the adverse effects of a summer drought.

Age structure in the *Coluber* population also may be compared with results of Hirth and King (1968). Their designation "hatchling" is equivalent to our juvenile age class, and their "juve-

nile" group is equivalent to our 1-year-old snakes based on average body weights calculated from their data (25.5–34.2 g/snake). Their proportions of "juveniles" were .245 (1963), .222 (1964), and .493 (1965). These values compare to our proportions of .274 (1969), .158 (1970), .130 (1971), and .203 (1972) for 1-year-olds. Evidently, 1964 seems to have been a favorable year for *Coluber*

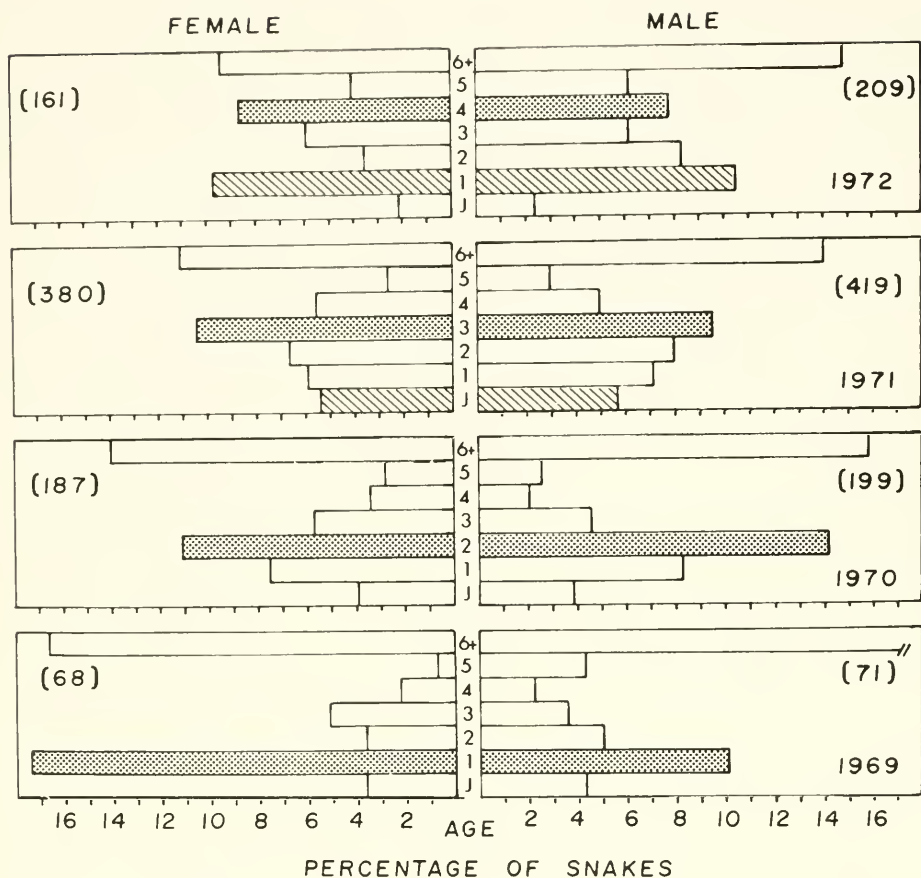


FIG. 8. Proportional age and sex structure of *Coluber constrictor mormon* at all hibernacula in four successive years (1969–1972). Number of individuals in parentheses. Age-specific proportions were calculated on the basis of the total number of snakes (both sexes) for each year. Stippling = 1-year-old cohort in 1969 continuing as prominent older age groups in later years; hatching = juveniles in 1971 and 1-year-olds in 1972. Annual total number of individuals reflects a varying number of dens sampled each year, not population changes.

reproduction if nearly half of the population in 1965 consisted of 1-year-olds as the data of Hirth and King (1968) imply. This is corroborated by rainfall data which show that 1964 had the high-

est precipitation in the 13-year period 1960–1972 at the study area (Brown and Parker 1982).

Overwintering survivorship in 1964–1965 was estimated to be 54% among 13 fall-released *Col-*

TABLE 15. Proportions of new (unmarked) *Coluber constrictor mormon* of each age at four dens in three successive years. Data are for subsequent sampling periods following initial marking (sexes combined). Marked individuals (N = 35) that shifted from one den to another (thus "new" to that den) were excluded.

Year	Den	No. unmarked snakes	Age (years)					
			1	2	3	4	5	6+
1970	M	63	.270	.381	.127	—	.079	.143
1971	M, 1, 5	109	.404	.202	.174	.083	.037	.101
1972	M, S3	102	.608	.186	.098	.039	.029	.039

TABLE 16. Overwintering survivorship of *Coluber constrictor mormon* ≥ 1 year old estimated by recapture proportions at den M.

Year	♂♂			♀♀		
	N snakes released in autumn	N surviving to following spring or later	Survival rate	N snakes released in autumn	N surviving to following spring or later	Survival rate
1969-1970	25	20	.800	29	27	.931
1970-1971	52	49	.942	47	45	.957
1971-1972	67	66	.985	74	66	.892
1972-1973	66	61	.924	47	46	.979
Totals	210	196	.933	197	184	.934

uber ≥ 1 year old (Hirth 1966). In contrast, our data indicate that winter survival was 93% in racers. Winter survivorship in adult *Masticophis* was reported to be 65%, and among juvenile and adult *Crotalus* 66% (Hirth 1966). Our results for these species are 95% winter survival in adult *Masticophis* (Parker and Brown 1980) and 96% in *Crotalus* (Parker and Brown 1974). Had the sampling effort in Hirth's study continued into the next year, snakes not caught at spring emergence may well have been captured later. We made a particular effort to ensure high catchability of each den fence and searched the fenced dens continuously in favorable weather. Despite these precautions, some fall-released snakes were not recaptured until the next fall or spring when they were credited as having survived the previous winter.

For similar reasons, little can be concluded about the rates of increase of *Coluber* between 1964 and 1966 (Hirth and King 1968). There has been, however, a definite general trend of increase in the racer population over a 30-year period at area M (Parker and Brown 1973). Factors involved in the population changes in this snake community, and the probable destruction of the communal dens resulting from burial by sand after an extensive range fire in 1974, are discussed in Brown and Parker (1982).

Life History Strategies.—Several workers have generated new results from a demographic-evolutionary perspective of snakes (e.g., Vial *et al.* 1977, using data of Fitch 1960) or have summarized the literature from this perspective (Turner 1977; Feaver 1977). We will attempt in this section, first, to focus on the reviews of Tur-

TABLE 17. Annual survivorship of *Coluber constrictor mormon* estimated by recapture proportions at three dens (M, 1, 5) in 1970 and 1971 (years combined) and at two dens (M, S3) in 1972.

Age	1970 + 1971			1972		
	N released	N surviving to next age	Survival rate	N released	N surviving to next age	Survival rate
♂♂						
1	49	38	.776	36	15	.417
2	62	49	.790	27	16	.593
3	23	18	.783	35	25	.714
4	11	8	.727	29	21	.724
5	16	13	.813	15	10	.666
6+	92	71	.772	66	42	.636
♀♀						
1	53	39	.736	23	9	.391
2	54	44	.815	29	19	.655
3	30	23	.767	54	31	.574
4	16	14	.875	21	14	.666
5	13	10	.769	15	9	.600
6+	75	59	.787	48	23	.479
JJ						
	41	10	.244	53	12	.226

ner (1977) and Feaver (1977) as they bear on other species of snakes for comparison with *Coluber constrictor mormon*, and second, we will compare our data with those of Fitch (1963) on the midwestern subspecies, *C. c. flaviventris*.

Survivorship in snakes is a parameter whose measurement is receiving increasing attention by field ecologists. Our data on annual survivorship of four species over three years (both sexes ≥ 1 year old, number of individuals released in parentheses) are as follows: *Masticophis* .862 (109), *Crotalus* .820 (44), *Pituophis* .750 (104), and *Coluber* .695 (892). Survivorship of *Coluber* in 1970 and 1971 was .781 (494). The other colubrid species (*Masticophis* and *Pituophis*) did not seem to be as subject to between-year variation in survivorship as did *Coluber*. Whatever the factors may be in causing such interspecific differences in survival rates (discussed further in Brown and Parker 1982), all of these snakes had similar survival rates of around 80% per year in the more favorable years.

Turner (1977) reviewed annual survivorship data of eleven other species of colubrids. These range from 0.30 to 0.75, with a mean survivor-

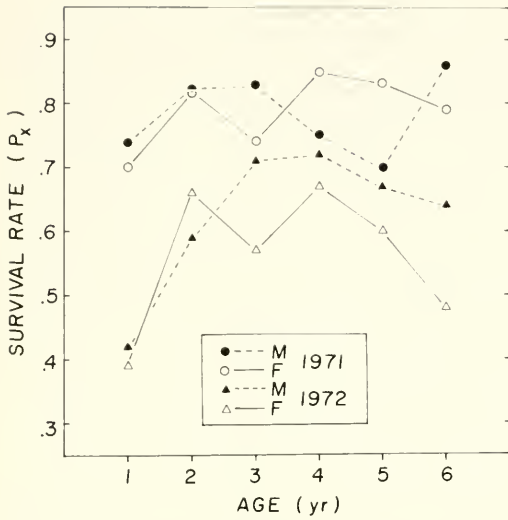


FIG. 9. Annual age-specific survivorship of *Coluber constrictor mormon*. Circles = 1971, triangles = 1972; solid symbols and dashed line = ♂♂, open symbols and solid line = ♀♀.

ship of 0.50/yr. Feaver (1977) measured survivorship by mark-recapture proportions of *Nerodia sipedon* over four years in Michigan and found the mean annual survival to be 0.35 in individuals ≥ 1 year old. Apparently, the survival rates we measured for the three species in Utah are among the highest known for colubrid snakes, and are more similar to the values reported for four species of viperids (0.70–0.82; Turner 1977) and for one colubrid, *Diadophis punctatus* (0.75; Fitch 1975).

One of the most difficult values to obtain in this study was an accurate estimate of survivorship in the first year of life. We have given our

bases for arriving at an estimate of a 17% survival rate from egg to yearling. Fitch (1963) estimated that survival through the egg stage was 50% in *C. c. flaviventris*, followed by a 31.3% survival from hatchling to yearling; these combined estimates suggest a first-year survival rate of 15.6%, not greatly different from our estimate in Utah. Parker and Brown (1980) estimated first-year survival rates in *Masticophis taeniatus* and *Pituophis melanoleucus* to be 8.3% and 20.0%, respectively. Feaver (1977) reported juvenile survivorship rates of 19.3% in male and 23.5% in female *Nerodia sipedon*. It appears that juvenile and first-year mortality is considerably higher than adult mortality in these four species. This is not particularly surprising in view of the considerable number of potential predators of small-sized snakes in the habitats of some of these species (cf. Fitch 1963; Parker and Brown 1980). The resulting survivorship curves of the three Utah colubrids are type III curves (Deevey 1947; cf. Fig. 11 in Brown and Parker 1982).

Of the average annual mortality in *C. c. mormon* (around 21% per year in mature females), one third occurred during hibernation (7% per year). The remaining 14% per year mortality in females occurred during the summer. The summer activity season may be divided into prereproductive and postreproductive periods. The prereproductive interval is approximately two months long, from emergence (early to mid-May) to egg laying (late June to mid-July). The postreproductive period lasts approximately three months from the end of oviposition until ingress into hibernation (mid to late September). We have no data that measure the relative degree of summer mortality and how it is partitioned during the activity season. Additional risks likely

TABLE 18. Estimates of the components of survivorship during the first year of life of *Coluber constrictor mormon*.

Life history interval	Approximate duration of interval	Survivorship during interval
Egg to hatchling	45 days (late June–mid Aug., same year)	0.92 (.0204/day)
Hatchling to juvenile	45 days (mid Aug.–early Oct., same year)	0.79 (.0175/day)
Juvenile to yearling	345 days (Oct.–mid Sept., successive years)	0.23 (.0006/day)
Egg to yearling	450 days (late June–early Oct., successive years)	0.17 (.0004/day)

TABLE 19. Schedule of age-specific survivorship and fecundity of female *Coluber constrictor mormon*. x = age (years); P_x = age-specific survival rate; l_x = survivorship to age x ; m_x = number of female eggs produced each year by a female of age x ; R_0 = net reproductive rate. See text for assumptions and for adjustment factors of m_x schedule.

x	P_x	l_x	Unad-justed m_x	Adjusted m_x	$l_x m_x$	
						0
1	.736	.170	0	0	0	
2	.815	.125	2.50	0.18	.023	
3	.767	.102	2.60	1.84	.188	
4	.875	.078	2.75	2.28	.178	
5	.769	.068	2.85	2.36	.160	
6	.787	.053	2.90	2.41	.128	
7	.787	.041	3.00	2.49	.102	
8	.787	.033	3.10	2.57	.085	
9	.787	.026	3.20	2.66	.069	
10	.787	.020	3.30	2.74	.055	
11	.787	.016	3.40	2.82	.045	
12	.787	.013	3.50	2.91	.038	
13	.787	.010	3.50	2.91	.029	
14	.787	.008	3.50	2.91	.023	
15	.787	.006	3.50	2.91	.017	
					$R_0 =$	1.187

TABLE 20. Age-specific body size and fecundity in two populations of *Coluber constrictor*. Data are for *C. c. flaviventris* in Kansas (Fitch 1963) and *C. c. mormon* in Utah (present study). H = hatchling, J = juvenile, numeral = years.

Age	Mean weight (g)				Mean clutch size	
	♂♂		♀♀		Kansas	Utah
	Kansas	Utah	Kansas	Utah		
H	4.2	6.0	4.2	6.0	—	—
J	12.3	8.3	12.3	8.8	—	—
1	52.6	27.0	51.6	28.4	—	—
2	68.2	41.0	83.5	51.6	9.2	5.0
3	102.1	49.1	149.4	66.3	9.9	5.2
4	139.0	53.4	212.3	71.4	10.8	5.5
5	152.4	60.4	209.6	79.5	13.0	5.7
6	175.9	61.2	245.9	84.0	15.7	5.9

accrue to females during their increased movements in search of oviposition sites (Brown and Parker 1976a; Parker and Brown 1972, 1980) so it seems reasonable to suppose that a higher mortality may occur during the shorter prereproductive phase than during the longer postreproductive phase. In both a "good" and a "bad" year (1971 and 1972, respectively), three-year-old females had lower survival rates than either of the adjacent age classes. As most females matured and presumably began reproduction for the first time at age 3, our data on higher mortality in 3-year-old females support this argument.

To our knowledge, the only other attempt to measure the components of mortality in a snake population is that of Feaver (1977). Adult female *N. sipedon* suffered their heaviest losses (50% of the total annual mortality) in summer, adult males in spring (47% of the total). In each sex, mortality was higher in the season of most active reproductive behavior, i.e., spring mating activity in males, summer gestation and parturition in females (Feaver 1977). Of the total annual mortality in *N. sipedon*, 32% occurred over the winter. This value is almost identical to our data (33% of the annual mortality was overwintering

mortality in *C. c. mormon*). Feaver (1977) also reported a higher survivorship among *N. sipedon* males (38%) than among females (30%) which is also the case for *C. c. mormon* (males 71%, females 68% over all three years of our study).

In Utah, the life history and demography of *C. c. mormon* may be summarized as follows: maturity in one year (males) and three years (females), larger size and more rapid growth in females than males, slight increase in fecundity with female size and age, large size of eggs relative to female size, iteroparity, low juvenile survivorship, and high adult survivorship. To develop insight into the possible adaptive aspects of the life history strategy of the Utah subspecies, it is helpful to compare it to the Kansas population of *C. c. flaviventris* studied over a number of years by Fitch (1963).

Kansas racers (*C. c. flaviventris*) are larger than Utah racers (*C. c. mormon*) at all ages except at hatching (Table 20); therefore, racers in Kansas have a more rapid growth rate. Sexual maturity is reached in one year (males) and three years (females) in both populations. Racers in Kansas have an age-specific fecundity about twice as high as in Utah (Table 20), but Utah racers produce larger eggs and hatchlings and have a higher relative clutch mass at all ages (Fig. 10). A considerable difference appears to exist in the age distribution between the two populations, with Kansas racers constituting a younger-structured population than Utah racers (Fig. 11). The net fecundity distributions (age-specific contribution to the female replacement rate) of the two populations are similar, but Kansas females make a

TABLE 21. Comparison of the major life history traits in two populations of *Coleuber constrictor*. Where possible a measured value is given for each trait. Data from Fitch (1963) for Kansas (*C. c. flaviventris*) and present study for Utah (*C. c. mormon*).

Life history parameter	Kansas	Utah
Population density*	higher (5.0/ha)	lower (0.8/ha)
Body size**	larger (♂♂ 123 g ♀♀ 155 g)	smaller (♂♂ 56 g ♀♀ 69 g)
Growth rate	faster	slower
Reproduction		
Sexual maturity	1 year (♂♂) 3 years (♀♀)	1 year (♂♂) 3 years (♀♀)
Clutch size	larger (11.7 eggs)	smaller (5.8 eggs)
Egg size	smaller (5.7 g)	larger (7.8 g)
Hatchling size	smaller (4.2 g)	larger (6.0 g)
Relative clutch mass†	lower (.40)	higher (.62)
Demography		
Age distribution	younger (72% 1–3 yr 28% 4+ yr)	older (52% 1–3 yr 48% 4+ yr)
Relative contribution to R_0 by female of age x	higher over ages 2–6; peak at age 3 (19.3%)	lower over ages 2–6; peak at age 3 (15.8%)
Juvenile survivorship	higher (31%/yr)	lower (23%/yr)
Adult female survivorship	lower (62%/yr)	higher (79%/yr)
Generation time	shorter (5.1 yr)	longer (6.9 yr)

* Value for Kansas from Turner (1977).

** Mean body weight, random samples ≥ 1 year old *C. c. flaviventris* (N = 50 each sex; Fitch 1963) and *C. c. mormon* (136 ♂♂, 114 ♀♀, den S3, spring 1972).

† Mean clutch weight/mean body weight of non-gravid ♀♀; mean RCM value for 5 ages (2–6+ years).

somewhat higher relative contribution to R_0 between ages 2–6 years (Fig. 12). The distributions indicate that 3-year-old females contribute the most to R_0 in each population. Utah racers have higher adult survival rates than do Kansas racers. Life tables developed for each population show that Utah racers have a somewhat longer estimated generation time, suggesting a less frequent turnover of the population. An overall summary of the major life history comparisons is presented in Table 21.

It is apparent that there are several prominent reproductive and demographic differences between racers in Kansas and Utah superimposed on a basic plan of biological similarities. Both subspecies of *C. constrictor* exhibit an identical growth pattern in which females mature later and grow larger than males. Feaver (1977) placed *C. constrictor*, *Rhabdophis tigrinus*, *Thamnophis butleri*, and *Nerodia sipedon* in this group as contrasted with *Crotalus viridis*, *Agkistrodon contortrix*, and *Elaphe quadrivirgata* in which males grow to the larger size. There are several impor-

tant reproductive and behavioral differences between the two groups of snakes (cf. Shine 1978); generally the last group of species tends to show late maturity, high adult survivorship, small clutches, and large young as contrasted to the first species group which shows the opposite trends. Viewed at this level, one could apply a "K-selected" label to the second group and an "r-selected" label to the first. Whereas such a comparison may help to visualize the broad strategies, it is less capable of showing differences in an intraspecific comparison. *C. c. flaviventris* and *C. c. mormon* each seems to possess some "K" and some "r" attributes (cf. Pianka 1970; Stearns 1976).

Our data on survivorship of *C. c. mormon* show that there were considerable between-years effects on survival in adult females and lesser effects in adult males when a dry year (1972) followed wetter, more favorable years (1970 and 1971). Juvenile survivorship, on the other hand, was not as strongly reduced in 1972 from 1970–1971 levels. Under this regime (with adult mor-

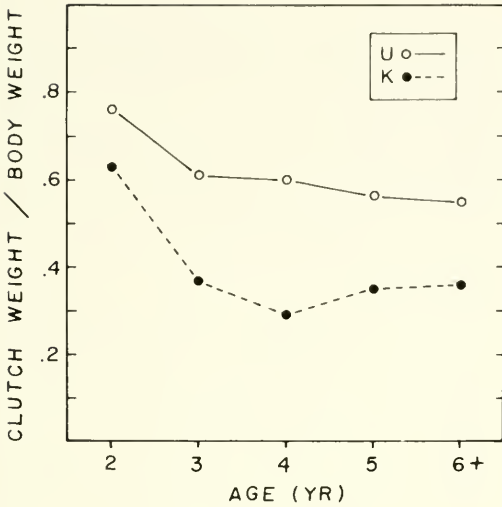


FIG. 10. Mean age-specific relative clutch mass in two populations of *Coluber constrictor* calculated as the clutch weight as a proportion of the mean non-gravid ♀ body weight. Mean clutch weight was calculated from clutch size and mean weight of eggs for *C. c. flaviventris* in Kansas (K; Fitch 1963) and *C. c. mormon* in Utah (U; present study).

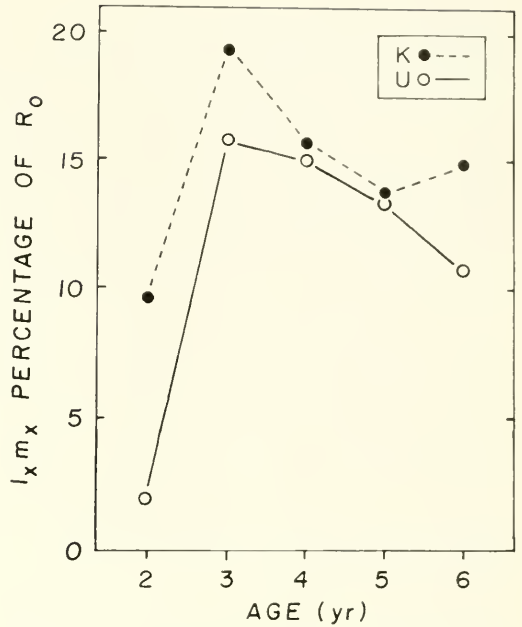


FIG. 12. Net fecundity distributions in two populations of *Coluber constrictor*. Data plotted are $I_x m_x$ values as a percentage of R_0 contributed by females of each age. Data are based on a life table for *C. c. flaviventris* in Kansas (K) developed by F. B. Turner (unpublished) from data of Fitch (1963) and on a life table for *C. c. mormon* in Utah (U; present study).

tality variable), a stable environment should favor such traits as fewer young, longer life span, smaller reproductive effort, and slower development (Stearns 1976). It is not clear from the data available whether *C. c. flaviventris* has a more variable adult or juvenile survivorship and which environment, Kansas or Utah, is the more "stable." The Kansas habitat appears to be trophically more diverse. Insects (grasshoppers, crickets) are eaten by *C. c. mormon* almost exclusively, whereas *C. c. flaviventris* takes a mod-

erate proportion of small mammals, snakes, and lizards in addition to insects (Fitch 1963). No readily identifiable parameters of environmental predictability, resource limitation, or predation levels affecting racers at either locality are known. As Wilbur, Tinkle, and Collins (1974) have pointed out, until the precise role of these factors can be identified, the selective basis for the differences between the two taxa cannot be explained by a simplistic dichotomous key of life history traits.

SUMMARY

An intensive mark-recapture study of the Western yellow-bellied racer, *Coluber constrictor mormon*, was conducted over a 4-year period at two complexes of communal hibernacula in northern Utah. The objectives of the study were: (1) to gather detailed data on growth rates, sexual maturity, clutch size, population structure, and age-specific survivorship; and (2) to compare

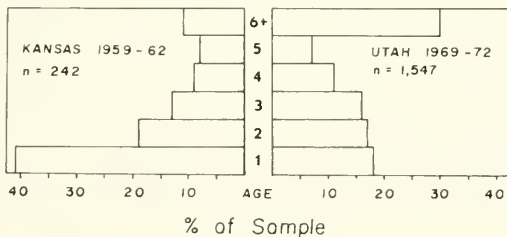


FIG. 11. Age distributions in two populations of *Coluber constrictor*. Data are based on the proportion of snakes (both sexes combined, juveniles excluded) in six ages pooled over 4 years in Kansas (*C. c. flaviventris*; Fitch 1963) and Utah (*C. c. mormon*, present study).

these data with those of a population of *C. c. flaviventris* in Kansas studied by Fitch (1963).

Racers were captured at their dens with encircling screen fences each autumn and spring between 1969–1973. Snakes were measured, weighed, sexed, and permanently marked by scale clipping. The age of each individual was determined by comparing its size to confidence intervals for length and weight of recaptured known-age snakes. A total of 1046 racers was captured 1694 times.

Males became sexually mature at an age of ≤ 13.5 months. In females, 8% of 2-year-olds, 77% of 3-year-olds, and 90% of 4-year-olds were considered mature. Mean weight of hatchlings was 6.0 g. and juveniles 8.5 g. At an age of 1 year, females ($\bar{x} = 28.4$ g) weighed significantly more than males ($\bar{x} = 27.0$ g) and females continued to be significantly larger in both snout-vent length and weight at all ages.

Body weight declined in 95% of the snakes over the winter; losses averaged 7.4% of initial autumn weight in both sexes. In 1971, a year of relatively high rainfall, 85% of racers gained weight over the summer, whereas in 1972, a dry year, only 44% gained weight. Age-specific growth rates were significantly higher in 1970 and 1971 than in 1972.

Females produced a single clutch per year averaging 5.8 eggs. Eggs averaged 38×18 mm and 7.8 g. Mean clutch weight/female body weight ratio was 44%. Oviposition occurred in late June through early July; hatching occurred in mid to late August after an incubation period of 45–50 days. Hatching success was 92%. Sex ratio at hatching did not differ significantly from 1:1. Weight increases in prereproductive females in early summer averaged ca. 1 g/day as did post-reproductive weight recovery in late summer. Among randomly-collected females in early summer, 88% were gravid or parturient.

In 1971, sampling at six dens yielded 528 racers. The largest number recorded at a single den in one season (spring 1972) was 271 snakes. Using maximum dispersal distances and assuming a uniform radial movement pattern from the dens, population density was 0.8 snakes/ha and biomass density was 40 g/ha. The population at den M increased from 139 to 189 individuals (18%/yr) over two successive favorable years (1970, 1971) and declined to 147 individuals (21% decrease) in an unfavorable year (1972).

In all samples of snakes ≥ 1 year old, males comprised 53% and females 47% of the population. Age structure favored younger (≤ 5 years) animals which comprised 62–76% of the population in different years. Large proportions of 1-year-olds in 1969 (27.4%) and juveniles in 1971 (11.1%) indicated that 1968 and 1971 were years of high productivity. In contrast, 1972 was a poor year for recruitment of juveniles (4.6% of the population).

Overwintering survival rates averaged 93% in both sexes. Annual survivorship in juveniles was 23%. First year survival (egg to age 1) was estimated to be 17%. Adult survivorship in favorable years was 78% in males and 79% in females. In an unfavorable year adult survivorship was 62% in males and 56% in females. Two other species of sympatric colubrid snakes in Utah had annual survival rates of around 80% per year. In contrast, literature reports for 11 species of colubrids indicate an average survivorship of ca. 50% per year. The 21% annual mortality in *C. c. mormon* may be partitioned into overwintering (7%), prereproductive, and postreproductive mortality. We suggest that prereproductive mortality is higher in females from exposure to additional risks associated with egg laying.

A life table for *C. c. mormon* calculated using the combined female survival rate in 1970 and 1971 showed a net reproductive rate (R_0) of 1.187, a value indicating an increasing population. Three-year-old females contributed the highest proportion (15.8%) to R_0 .

Compared to the life history of *C. c. flaviventris* in Kansas, *C. c. mormon* in Utah is distinct in the following ways: (1) lower growth rates and smaller adult size; (2) lower age-specific fecundity; (3) larger eggs and hatchlings; (4) higher clutch weight/female body weight ratio; (5) lower juvenile survivorship and higher adult survivorship; and (6) older age distribution and longer generation time. These life history traits appear to fit some "r" and some "K" strategies in each population. Without more detailed work on resource levels, environmental stability, and predation, we caution against simplistic interpretations in contrasting the two populations.

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Growth of Bullsnares (*Pituophis melanoleucus sayi*) on a Sand Prairie in South Central Kansas

DWIGHT R. PLATT

INTRODUCTION

Growth rates of snakes in natural populations have been studied for fifty years. Blanchard and Finster (1933) presented limited data on growth rates of recaptured garter snakes and water snakes. Klauber (1937) derived a growth curve for the southern pacific rattlesnake (*Crotalus viridis helleri* = *C. v. oreganus*) by analyzing a collection of preserved specimens and pointed out that the growth of captive snakes may be distorted. Seibert and Hagen (1947) presented growth data for the plains garter snake (*Thamnophis radix*) and smooth green snake (*Ophedrys vernalis*) from a mark-recapture study of populations in Illinois.

Henry S. Fitch (1949) was a pioneer in the study of free-living snake populations with his field work in central California. His analysis of growth in the northern pacific rattlesnake (*Crotalus viridis oreganus*) has been widely cited. He and his students have provided many reports on growth rates of snakes in natural populations (Clark 1970, 1974; Clark and Fleet 1976; Fitch 1960, 1963a, 1963b, 1965, 1975; Fitch and Fleet 1970; Platt 1969). Other notable studies on growth rates in free-living populations of colubrid snakes include those by Brown and Parker (1984), Carpenter (1952), Feaver (1977), Fukada (1959, 1960, 1972, 1978), Heyrend and Call (1951), Imler (1945) and Parker and Brown (1980). Growth has previously been studied in the bullsnake (*Pituophis melanoleucus sayi*) in Nebraska by Imler (1945), in the pacific gopher snake (*P. m. catenifer*) in California by Fitch (1949) and in the great basin gopher snake (*P. m. deserticola*) by Parker and Brown (1980). Growth of several species of elapid and viperid snakes has been studied, including studies by Gibbons (1972), Heyrend and Call (1951), Klauber (1956), Prestt (1971), Shine (1978, 1980), Volsoe (1944) and Wharton (1966). Most of these investigations have indicated a high degree of individual variability in growth rates.

Two methods have been used to study growth of snakes in natural populations: 1) summarizing

growth records from marked, released and recaptured individuals; and 2) determining size at different ages, usually up to one year old, by an analysis of size frequencies in population samples.

My study of growth rates in snakes was part of a larger study of the ecology and population dynamics of sympatric species of snakes on the Sand Prairie Natural History Reservation in western Harvey County in south central Kansas. The objectives of the present study were: 1) to investigate the range and patterns of variability in growth rates and the effects of prey availability and of age and sex on growth; 2) to compare the growth rates and strategies of five species of snakes living in the same general environment; 3) to compare the two methods (above) of determining growth rates.

This paper reports results based on 709 captures of 471 bullsnares (*Pituophis melanoleucus sayi*) and on nine young which were hatched in the laboratory. Subsequent papers will describe other species studied and comparative aspects of the study.

METHODS

This study used standard mark-recapture techniques with snakes trapped alive in drift fence traps (Fitch 1951, 1960; Platt 1969). Thirty to fifty trapping stations were used on a study area of 80 acres (32.4 hectares) in 1966, 1967 and early 1968. From late 1968 through 1974, traps at 100 to 120 stations were in operation on the study area and at up to 20 stations on adjacent pastures. A trapping station consisted of a low metal drift fence with a funnel trap fitted under each end. These traps set without bait intercepted movement of the animals.

Most measurements were made in the laboratory. Snout-vent length (SVL) and tail length were measured to the nearest one millimeter with the snake stretched along a metal tape until it relaxed. Weights to the nearest 0.1 gram were measured on a triple beam balance. The snakes

were released within three to four days at the site of capture.

Marking was accomplished by clipping or branding subcaudals or ventrals so that each snake was individually recognizable. Individual variations in color pattern and scutellation were also recorded so that almost all recaptured snakes were individually identified with certainty. Sexing was accomplished by probing through the vent for the hemipenial sacs and was checked later by body proportions. Food records were obtained by palpating fecal matter from the intestine and forcing stomach contents back up the gullet into the mouth for identification and then repalping into the stomach.

Previous studies of growth have used snout-vent lengths, total lengths and/or weights as a measure of size. I used snout-vent length (SVL) because it is one of the least variable measures of size. Weight is more affected by the stage of the feeding cycle or the reproductive cycle while total length is affected by partial loss or differential growth of the tail. Only measurements of live snakes were used in the analysis.

Growth rates from recapture records were calculated by averaging growth increments during the period between captures for samples of recaptured snakes. Recapture records were used to calculate growth rates only if three weeks or more had elapsed since the previous capture. Although bullsnake eggs probably hatch on the study area in August, young snakes were not caught in traps until September. First-year snakes were defined in this study as those caught between September of their hatching year and the end of the next August. Records of recaptured first-year and older bullsnakes were readily distinguished by plotting the SVLs of snakes with respect to capture date.

Growth rates were also calculated from the changes in mean SVL of population samples of identified age. Frequency distributions were calculated for the lengths of all bullsnakes caught in each two-week interval throughout the trapping season in each year. First-year snakes were readily identified in these frequency distributions and they did not overlap samples of older snakes in size until they had completed their first full year of growth. Mean snout-vent lengths were calculated for these first-year snakes captured in each month and growth rates were calculated from the means of these monthly samples.

Snakes were trapped from late April or early

May to the end of October or early November over a nine year period, 1966–1974. Growth was not continuous throughout the year. On my study area it was usually most rapid in early summer but occurred throughout the period of activity and trapping; probably little or no growth occurred during dormancy. Therefore the mean growth rates in this study were calculated using the 184 days from the first of May to the end of October as the growth season.

Absolute growth rates were calculated as growth increment in SVL per month (30 days) excluding the period from 1 November to 30 April. Relative growth rates were calculated as the growth increment per month per 100 mm median SVL. The median SVL was defined as the midpoint between the lengths at two successive captures or between the mean lengths of two successive population samples. Some studies (Carpenter 1952; Fukada 1959, 1960, 1978) have used the initial length at first capture to calculate relative growth rates. The median length is more similar to the length of the snake during the growing period. Relative growth rates calculated from median lengths are less affected by the duration of the period between captures.

Mean values in this paper are usually accompanied by one standard error. Homogeneity of variances was tested by an *F* test. Differences in the central tendency of different samples were tested by Student's *t* test for samples having similar variances and by the Mann-Whitney *U* test when the variances were heterogeneous (Cox 1980). Regression equations of weight on length were calculated by Bartlett's method (Simpson *et al.* 1960).

Rodent populations, principal prey of bullsnakes, were sampled by the same drift fence traps used to capture snakes and by 100 baited small mammal live traps (constructed like traps described by Fitch 1950) set in a grid 150 meters on a side. Drift fence traps were operated continuously from May through October while baited live traps were operated for a few nights per month through the summer (May–August). Rodents caught in drift fence traps were recorded as number caught per 100 trap station days (TSD) while those caught in baited traps were recorded as number caught per 100 trap nights (TN).

STUDY AREA

The Sand Prairie Natural History Reservation is 80 acres (32.4 hectares) of prairie on sand dunes

TABLE 1. Rodents trapped on the Sand Prairie Natural History Reservation in Kansas.

Year	Drift fence traps			Baited traps		
	No. of trap station days (TSD)	No. rodents 100 TSD		No. of trap nights (TN)	No. rodents 100 TN	
		Medium sized species	Small sized species		Medium sized species	Small sized species
1967	7317	0.2	6.4	2369	1.3	5.2
1968	9989	3.2	9.8	1161	3.4	7.2
1969	19,775	0.3	1.1	1430	2.0	1.8
1970	17,076	0.2	1.9	1088	1.3	4.6
1971	19,962	0.1	0.4	1061	1.5	0.6
1972	15,272	0.3	4.5	1518	1.8	7.7
1973	17,014	0.1	0.8	2134	0.6	1.0
1974	17,908	0.2	1.1	1747	2.2	1.4

managed as a natural area. Prior to its acquisition by Bethel College in 1965, it was used as a pasture but was never cultivated. All snakes used in my analyses were captured on this study area or on immediately adjacent pastures.

The Sand Prairie Reservation is in a band of wind-blown sand deposits, the Hutchinson Dune Tract of the Great Bend Lowland physiographic division (Frye and Leonard 1952; Schoewe 1949). The upland grass communities on the reservation are dominated by little bluestem (*Andropogon scoparius*). Forbs and other genera of grasses (*Triplasis*, *Aristida* and *Panicum*) also occur. The unflooded lowlands have dense tall grass communities dominated by switchgrass (*Panicum virgatum*), sand bluestem (*Andropogon hallii*), indiagrass (*Sorghastrum avenaceum*), eastern gammagrass (*Tripsacum dactyloides*) and prairie cordgrass (*Spartina pectinata*). Thickets of chickasaw plum (*Prunus angustifolia*) are common on the uplands and buttonbush (*Cephalanthus occidentalis*) and black willow (*Salix nigra*) in the lowlands. The area is poorly drained and its low depressions between sand dunes are relatively wet, having ponds, shallow marshes or dry ground depending upon the amount of recent rainfall. A more complete description of the study area can be found in Platt (1973, 1975).

RESULTS

Prey Populations.—Prey of bullsnakes on the study area were predominantly rodents. Trapping success (Table 1) provides a rough measure of the size and activity of rodent populations. Medium-sized rodents, prairie voles (*Microtus*

TABLE 2. Proportions of bullsnakes (*Pituophis melanoleucus*) containing recoverable food items in the stomach or residues in the intestines. Chi square tests were run on the differences in proportions of snakes containing food in successive years. N = number of snakes examined.

Year	Summer (May–Aug.)			Autumn (Sept.–Oct.)		
	N	Percentage containing food	χ^2	N	Percentage containing food	χ^2
1966				22	95%	
1967	46	61%		29	76%	4.14*
1968	43	72%	2.43	29	93%	4.71*
1969	31	52%	7.54**	72	56%	156.68**
1970	55	58%	0.66	59	29%	17.61**
1971	65	26%	27.94**	27	22%	1.58
1972	15	33%	1.72	25	72%	30.01**
1973	42	52%	6.85**	50	48%	14.28**
1974	44	68%	4.46*			

* Significant at the 0.05 level.

** Significant at the 0.01 level.

ochrogaster) and cotton rats (*Sigmodon hispidus*), were caught most readily in baited traps. Trapping success for these species was highest in 1968, the only year of the study in which significant numbers of cotton rats were caught. After 1968 trapping success for *Microtus* and *Sigmodon* declined, reaching a low point in 1973 and recovering somewhat in 1974. Small rodents were predominantly western harvest mice (*Reithrodontomys megalotis*). There were significant numbers of woods mice (*Peromyscus leucopus*) and a few plains pocket mice (*Perognathus flavescens*). Success in trapping small rodents was high through 1968 and again in 1970 and 1972, but was lowest in 1971. Other prey such as small cottontail rabbits (*Sylvilagus floridanus*) and birds or bird eggs were also occasionally taken by bullsnakes but did not constitute an appreciable part of the diet.

The percentage of captured bullsnakes that had recoverable food items in the stomach or scats in the intestine is a measure of feeding success (Table 2). The data on both trapping success and feeding success (Tables 1 and 2) indicate that food was readily available from 1966 through 1968, with highest availability in 1968. The period of greatest food scarcity was from autumn 1970 through 1971. Data from rodent trapping suggest low rodent populations in 1973, but the feeding rate of bullsnakes was twice as high in summer 1973 as in 1971.

Growth Rates of Bullsnakes.—No significant

TABLE 3. Absolute and relative growth rates of bullsnakes (*Pituophis melanoleucus*) in Kansas (1966–1974) determined from recapture records. N = number of useable recapture records. Mean followed by ± 1 standard error.

Age	N	Mean absolute growth rate (mm/30 days)	Mean relative growth rate (%)
First year	100	56.5 \pm 2.9	9.4 \pm 0.5
0–3 mo.	26	34.2 \pm 3.5	7.3 \pm 0.7
8–12 mo.	74	64.4 \pm 3.3	10.2 \pm 0.5
>One year	64	17.9 \pm 2.0	1.9 \pm 0.2

differences between the sexes were discovered in the size of large snakes or in growth rates. Large males (>800 mm SVL) averaged 991 \pm 13.3 mm SVL (N = 105) and large females averaged 1014 \pm 13.4 mm (N = 91). Neither the variances nor the means of these samples were significantly different ($F = 1.14$, $P > .10$; $t = 1.23$, $P > .10$). Among large snakes from each of the nine years, four annual samples of males had higher mean lengths and five annual samples of females had higher means. In 1974, females (\bar{x} SVL = 1036 \pm 30.8 mm, N = 14) were significantly longer ($t = 3.565$, $P < .005$) than males (\bar{x} SVL = 886 \pm 25.0 mm, N = 10) but no other between-sex size differences were statistically significant.

Parker and Brown (1980) reported that the largest female gopher snakes (*P. m. desertiicola*) were 108 and 114 cm SVL, but males commonly exceeded 120 cm SVL. In *P. m. sayi* in Nebraska, Imler (1945) reported that males averaged slightly longer than females but a female was the largest specimen measured. In my study in Kansas, the largest specimens had a slight preponderance of males. Of 17 snakes 1200 mm or more SVL, nine were males (1200–1420 mm SVL) and eight were females (1210–1300 mm SVL).

The mean absolute growth rate calculated from recapture records for first-year males was 55.4 \pm 4.3 mm/month (N = 49) and for first-year females was 57.6 \pm 4.0 mm/month (N = 57). Neither the variances nor the means were significantly different ($F = 1.08$, $P > .05$; $t = 0.38$, $P > .50$). Males > 1-year had a mean growth rate of 16.0 \pm 2.2 mm/month (N = 30) and females > 1-year had a mean growth rate of 19.7 \pm 3.2 mm/month (N = 34). The variance was significantly higher in the female sample ($F = 2.20$, $P < .05$)

TABLE 4. Absolute and relative growth rates of bullsnakes (*Pituophis melanoleucus*) older than one year in Kansas determined from recapture records. The probable ages are based on size (see text). N = number of useable recapture records. Means followed by ± 1 standard error.

Probable age	N	Mean absolute growth rate (mm/30 days)	Mean relative growth rate (%)
Second year	34	26.9 \pm 3.16	3.1 \pm 0.39
Third year	12	12.2 \pm 2.66	1.2 \pm 0.26
>Three years	15	6.0 \pm 1.03	0.5 \pm 0.08

but the median lengths were not significantly different ($U = 0.81$, $P > .05$). There was no significant difference in average growth rate between the two sexes so samples of the two sexes were pooled.

Growth rates were calculated from the pooled sample of recapture records (Table 3). The mean absolute growth rate for the first (post-hatching) autumn season (0–3 months of age) was only 53% and the relative growth rate only 72% of those during the succeeding summer (8–12 months of age). The mean growth rates also indicated an abrupt decrease in both absolute and relative growth after the first year. Growth rates calculated from the recapture records of snakes > 1 year at initial capture were only 32% as great for absolute growth and 20% as great for relative growth as those for first-year snakes (Table 3). The abruptness of this change is somewhat accentuated by pooling the rates for all older snakes.

It was not possible to separate age groups older than one year with any certainty on the graphs of recapture records. However, size and growth rates (calculated for arbitrary size groupings) were used in assigning snakes to an older "probable" age. Large bullsnakes recaptured within an August to August year were assigned to one of three groups: 700–800 mm, 850–950 mm, and > 1000 mm SVL during the previous August. The first group was most probably in its second year of growth, the second in its third year, and the third older than three years. The growth rates calculated for these "probable" age groups from recapture records are in Table 4.

Mean snout–vent lengths were calculated for each monthly sample of first-year snakes in each year whenever sample size was greater than four (Table 5). Absolute and relative growth rates cal-

TABLE 5. Snout-vent lengths of bullsnakes (*Pituophis melanoleucus*) in successive months during their first year in Kansas. Young snakes were first caught in September and were dormant between October and May. Means were calculated only for sample sizes >4. Mean is followed by ±1 standard error. Sample size is listed under the mean. The range of lengths is listed in parentheses. The year 1971-1972 was omitted because few first-year snakes were caught.

Year	Snout-vent lengths					
	Sept.	Oct.	May	June	July	Aug.
1966-1967	441 ± 13.0 10 (386-495)	453 ± 12.4 11 (365-506)	— 1 (638)	652 ± 10.8 18 (593-740)	747 ± 24.0 17 (607-860)	805 ± 17.6 10 (714-885)
1967-1968	429 ± 9.5 9 (404-465)	464 ± 11.5 16 (406-566)	— 2 (503-529)	621 ± 16.8 15 (520-682)	— 3 (725-793)	— 3 (832-895)
1968-1969	— 1 (441)	488 ± 5.9 16 (375-560)	— 0	608 ± 16.0 7 (522-655)	— 3 (702-801)	842 ± 26.0 6 (808-911)
1969-1970	447 ± 4.4 44 (387-492)	470 ± 6.7 23 (425-545)	546 ± 8.5 8 (515-555)	650 ± 9.0 9 (612-710)	734 ± 10.8 11 (672-800)	— 4 (720-855)
1970-1971	439 ± 6.0 33 (363-508)	460 ± 6.6 18 (422-532)	528 ± 8.2 12 (474-565)	587 ± 7.9 15 (543-635)	— 3 (620-680)	714 ± 18.6 9 (660-822)
1972-1973	448 ± 12.5 11 (399-523)	447 ± 14.7 8 (414-542)	555 ± 15.5 10 (496-622)	650 ± 20.2 8 (547-719)	725 ± 14.4 6 (657-752)	— 1 (772)
1973-1974	445 ± 6.0 20 (392-495)	456 ± 7.0 29 (375-511)	515 ± 18.9 10 (397-587)	673 ± 23.9 5 (598-737)	749 ± 12.9 13 (662-816)	— 2 (777-814)
Total sample	443 ± 2.8 128	464 ± 3.3 121	537 ± 8.2 43	630 ± 6.1 77	736 ± 14.3 49	788 ± 11.9 35

culated from the mean SVL and mean capture dates of the monthly samples are presented in Table 6.

The composite sample from all years showed an absolute growth rate in the first autumn that was only 19% of the growth rate the succeeding summer (Table 6), an even greater difference than that shown by growth rates calculated from recapture records. To further analyze growth, the juvenile snakes caught each autumn were grouped into two-week samples. Samples with five or more individuals were divided into thirds according to SVL. The mean SVL of the upper and lower thirds, the maximum and minimum SVL and the proportion of snakes with food in the stomach or scats in the intestines were calculated for each sample (Table 7). In many years there were some individuals that grew slowly and remained between 360 and 460 mm SVL in October. These slowly growing snakes were one factor in the low

growth rates calculated for juvenile snakes in the first autumn.

Mean growth rates were calculated for each year from recapture records of first-year and older snakes (Table 8). The mean growth rate for first-year snakes in 1971 was significantly lower than that for each of the other years (comparison of 1971 to 1967, $t = 3.67, P < .005$; 1971 to 1968, $t = 6.16, P < .005$; 1971 to 1970, $t = 3.39, P < .01$; 1971 to 1973, $t = 3.56, P < .005$; 1971 to 1974, $t = 6.70, P < .005$). Other differences in mean growth rates of first-year snakes in Table 8 were not statistically significant with the exception that the growth rate for 1974 was significantly higher than that for 1967 ($t = 2.16, P < .05$). The differences in mean growth rates of older snakes were not significant because of the small sample sizes, but the between-year differences were similar to those of first-year snakes. The growth rates calculated from recapture rec-

TABLE 6. Absolute and relative growth rates of bullsnakes (*Pituophis melanoleucus*) during their first year in Kansas, determined from the data in Table 5. Values in parentheses are based on mean snout-vent lengths of small samples (<5).

Year	Absolute growth rates (mm/month)				Relative growth rates (mm/month/100 mm SVL)			
	Autumn Sp–Oc	Oc–May	Summer May–Au	1st yr. Sp–Au	Autumn Sp–Oc	Oc–May	Summer May–Au	1st yr. Sp–Au
1966–1967	18.0	—	72.8 ^a	72.8	4.0	—	10.0 ^a	11.7
1967–1968	42.0	—	(103.3)	(81.1)	9.4	—	(15.1)	(12.7)
1968–1969	—	—	121.0 ^a	88.3 ^b	—	—	16.7 ^a	13.3 ^b
1969–1970	30.0	60.0	97.2 ^c	72.4 ^c	6.6	11.8	15.2 ^c	12.3 ^c
1970–1971	26.2	49.8	65.6	55.0	5.8	10.1	10.6	9.5
1972–1973	0	90.0	86.4 ^c	71.0 ^c	0	18.0	13.5 ^c	12.1 ^c
1973–1974	14.3	63.2	113.2 ^c	80.7 ^c	3.2	13.0	17.9 ^c	13.5 ^c
Total sample	25.2	62.6	86.6	70.4	5.6	12.5	13.1	11.4

^a Because of inadequate samples in May, growth rates were calculated for the period June–August.

^b Because of inadequate samples in September, growth rates were calculated for the period October–August.

^c Because of inadequate samples in August, growth rates were calculated for the period May–July or September–July.

ords (Table 8) were much lower than those estimated from the mean SVL of samples of first-year snakes (Table 6) but they varied in parallel fashion; the lowest growth rates by both methods of estimation occurred in 1971 and the highest in 1968, 1969, and 1974.

Growth in weight is proportional to growth in length but more variable. Klauber (1956) found that the regression line of weight on length for rattlesnakes was of the form $W = CL^P$, where W is weight, L is length and C and P are constants characteristic for each population. Regression lines of this form were fitted to the data on weight in grams and SVL in meters of bullsnakes. The constants C and P for different samples of snakes and the projected weight at .8 meter SVL (approximate SVL at one year of age) are presented in Table 9. From these regression equations a normal weight can be calculated for any SVL.

DISCUSSION

Growth rates calculated from recaptures of first-year snakes (mean absolute growth rate was 56.5 mm/month; see Table 3) were consistently lower than growth rates calculated from changes in the mean length of monthly samples (mean absolute growth rate was 70.4 mm/month; see Table 6). The recapture records from the autumn of the hatching year may include a disproportionate number of small snakes. With the autumn records eliminated, the mean growth rate of recaptured first year snakes was 64.4 mm/month, still

somewhat lower than that calculated from mean lengths of monthly samples. This discrepancy may be partially due to a temporary decrease in growth after the capture experience. Fitch (1949, 1975) and Clark (1970) mentioned that recovery of normal growth after capture may take more than a month in rattlesnakes (*Crotalus viridis*), ringneck snakes (*Diadophis punctatus*) and worm snakes (*Carphophis vermis*). On the other hand, Fukada (1959) and Carpenter (1952) found no effect of capture on further growth of *Natrix tigrina* and garter snakes (*Thamnophis*). My results indicated that capture did cause a short-term decrease in growth in many first-year bullsnakes, primarily limited to the first month after capture and to the smaller snakes (Table 10). Decreased growth following capture would probably have a lesser effect on the growth rates of snakes > 1-year because most of the captures occurred over longer intervals. The decreased growth following capture was not due to deprivation of food by interruption of feeding since the weights of recaptured male bullsnakes were not below normal (Table 11). Females were not tested because their weights were more variable in an annual cycle.

Another cause of discrepancy in growth rates calculated by the two methods was differential mortality of less successful and more slowly growing snakes. Growth rates calculated from recaptures are based on a sample of all snakes in the population during the time interval, possibly biased in favor of those unsuccessful in feeding

TABLE 7. Snout-vent lengths and success of feeding for juvenile bullsnakes caught in half-month intervals in their first post-hatching autumn (September and October) in Kansas. From samples arranged in order of decreasing SVLs, mean and extreme SVLs are listed for the approximate upper and lower one-thirds of samples >4. Sample sizes for A and B are listed in C. The year 1971 was omitted because few juveniles were caught.

Year	Mean SVL				Extreme SVL			
	Half-month intervals				Half-month intervals			
	S 1-15	S 16-30	O 1-15	O 16-30	S 1-15	S 16-30	O 1-15	O 16-30
A. Lower 1/3 of sample								
1966	—	392	394	—	394	386	365	435
1967	—	402	409	432	—	389	406	414
1968	—	—	440	458	—	—	375	458
1969	415	412	436	458	387	392	425	442
1970	405	415	440	—	385	363	401	422
1972	—	404	417	—	—	399	414	—
1973	—	414	396	448	—	392	375	408
B. Upper 1/3 of sample								
1966	—	495	499	—	472	495	506	500
1967	—	450	504	530	—	466	512	566
1968	—	—	515	515	—	—	526	519
1969	475	482	496	515	491	496	545	523
1970	454	485	490	—	472	508	532	452
1972	—	490	451	—	—	523	461	—
1973	—	471	479	501	—	495	510	511
C. Percent with food in digestive tract								
Year	Half-month intervals							
	S 1-15		S 16-30		O 1-15		O 16-30	
	N	%	N	%	N	%	N	%
1966	3	100%	7	86%	7	100%	4	75%
1967	0	—	8	75%	7	57%	9	89%
1968	0	—	0	—	12	92%	6	100%
1969	17	82%	27	26%	17	76%	6	33%
1970	14	14%	19	22%	14	43%	4	25%
1972	0	—	11	73%	5	60%	0	—
1973	0	—	19	26%	15	47%	14	79%

if they were more active in searching for food. Growth rates calculated from the mean lengths of snakes at identified ages are based on those snakes that survive over the growth interval. The absolute growth rate of first-year bullsnakes (70.4 mm/month) estimated from the mean lengths of snakes in September when first caught and in the following August was a good estimate of the growth of those first-year snakes that survive to one year of age. The absolute growth rate (56.5 mm/month) calculated from recapture records of first-year snakes is an estimate of growth in both survivors and non-survivors somewhat biased by decreased growth following capture. Differential mortality can also distort growth rates calculated from mean lengths in successive monthly samples and probably accentuated the differences in growth rates in the autumn and the

following summer as estimated by both methods. Growth rates calculated by the two methods should be comparable for populations where growth is little affected by capture and there is little differential mortality based on size. Therefore growth rates calculated from recapture records were probably good measures of growth for older bullsnakes but less reliable for first-year snakes.

Individual variability in growth of bullsnakes is high. The extreme SVLs in monthly samples of first-year snakes (Table 5) showed that individual snakes grew much slower and much faster than the mean growth rate. Although there was probably high mortality among the slow-growing snakes in the first year, some one year old snakes were <750 mm SVL while others were >850 mm SVL.

TABLE 8. Absolute growth rates of bullsnakes (*Pituophis melanoleucus*) trapped more than once during a year in Kansas. N = number of useable recapture records. 1969 and 1972 were omitted because of the small number of recaptures. Means followed by ± 1 standard error.

Year	Age: first year summer only		Age: > one year	
	N	Mean	N	Mean
1967	14	61.3 \pm 6.5	0	—
1968	12	81.0 \pm 7.3	6	31.8 \pm 11.3
1970	10	66.2 \pm 10.2	5	22.0 \pm 11.4
1971	16	35.1 \pm 3.7	6	11.5 \pm 4.4
1973	6	67.9 \pm 11.7	0	—
1974	19	77.2 \pm 5.0	6	15.6 \pm 5.8

Nine young bullsnakes hatched in the laboratory on 19 August had a mean SVL at hatching of 363 \pm 1.6 mm (415 mm total length) and a mean weight of 18.3 \pm 0.39 gm. This is larger than the 334.4 mm SVL reported for hatchlings of the gopher snake (*P. m. deserticola*) (Parker and Brown 1980) and the 15 in. (381 mm) total length reported by Imler (1945) for *P. m. sayi* in Nebraska. No information was obtained about the variability in size of hatchlings on my study area.

Hatching dates on the study area are not known but young snakes were first captured in traps in September. Young snakes averaged 443 mm SVL in September (Table 5). Assuming that hatching occurred in mid-August, the growth rate for the first month would have been ca. 70 mm. On the basis of days in the period 1 May to 31 October, the growth rate calculated from the mean lengths

of the October and May samples of first-year snakes was 62.6 mm/month (Table 6). These growth rates are more than twice as high as the growth rates calculated for autumn both from recapture records (Table 3) and from mean lengths of samples (Table 6).

Growth is probably rapid in the first month after hatching but the estimate of the growth rate would be lower if the above estimated mean hatchling size was low and/or if hatching occurred earlier. The higher growth rate from October to May could be the result of growth occurring during the dormant period. Snakes captured in their first autumn and subsequently caught the next summer grew 68.6 \pm 4.28 mm/month (N = 31). This is significantly higher ($t = 2.62$, $P < .01$) than the mean growth rate of 55.6 mm/month (N = 100) for all recaptured first-year snakes, but it is not significantly higher than the growth rate of 64.4 mm/month (N = 74) of first-year snakes during the summer. Although some growth may have occurred between the first of November and the first of May, evidence of any significant growth during this period is lacking. The higher growth rates calculated from the mean lengths of first-year snakes in October and May were probably caused by high mortality of the smaller poorly nourished snakes during the winter. In three of the four years with adequate samples in both October and May, the difference between the minimum SVLs in October and May was greater than the difference between the maximums (Table 5).

Imler (1945) estimated that juvenile bullsnakes grew approximately four inches (100 mm) in September and October following hatching.

TABLE 9. Regression of weight in grams on SVL in meters of yearly samples of bullsnakes (*Pituophis melanoleucus*) in Kansas. The regression equation is of the form $W = CLP$.

Year	Male				Female			
	N	Regression constants		Normal weight gm/0.8 m	N	Regression constants		Normal weight gm/0.8 m
	C	P			C	P		
1967	38	247.7	2.7	135.6	38	274.5	2.8	147.0
1968	29	284.0	2.8	152.1	53	272.9	2.6	152.3
1969	56	275.7	3.1	138.0	49	271.4	3.1	135.9
1970	76	268.9	2.8	144.0	53	267.9	2.9	140.3
1971	63	240.4	2.7	131.6	24	230.7	2.6	129.2
1972	20	270.4	2.9	141.6	18	247.8	2.8	132.7
1973	48	261.3	2.8	140.0	44	290.5	3.0	148.8
1974	36	269.9	2.7	147.8	35	286.9	3.0	146.9
All years	384	265.6	2.8	142.2	325	274.1	2.9	143.5

TABLE 10. Absolute growth rates (GR) of recaptured bullsnakes (*Pituophis melanoleucus*) in Kansas after different lengths of intervals between captures. N = useable recapture records. Means followed by ± 1 standard error.

SVL at initial capture, mm	Interval between captures					
	< 30 days		30 to 60 days		> 60 days	
	N	Mean GR (mm month)	N	Mean GR (mm month)	N	Mean GR (mm month)
<500	23	22.8 \pm 5.6	16	53.0 \pm 7.4	33	65.6 \pm 4.0
500-599	11	28.6 \pm 11.1	6	51.0 \pm 8.1	10	52.7 \pm 8.6
600-699	8	44.3 \pm 10.7	14	53.2 \pm 7.3	12	48.4 \pm 5.7
700-799	14	27.0 \pm 7.2	6	63.4 \pm 17.2	12	39.9 \pm 5.7

Parker and Brown (1980) reported no growth in juvenile gopher snakes (*P. m. deserticola*) in the first autumn. My results indicated that growth of juvenile snakes in autumn was variable. Some grew rapidly becoming 500-550 mm SVL in October, or even in September in good years. Others grew more slowly and were 440 mm or less SVL in early October (Table 7). Growth of all juveniles slowed in October and they added extra weight in good years. In 1968, the 16 juveniles caught in October averaged 41 gm, 20 per cent higher than normal weight (weight calculated from regression equation of weight on length).

The low growth rates in autumn compared to summer for first-year bullsnakes (Tables 3 and 6) were partially due to high mortality of slow-growing snakes in late autumn and winter and partially due to an acceleration of growth in the summer. The most rapid growth of first-year bullsnakes was in June and July; growth declined toward late summer (Table 5).

Imler (1945) reported growth of 14 in. (356 mm) during the first year for bullsnakes in Nebraska, from an average length of 15 in. (381 mm) in September soon after hatching, to an average length of 29.5 in. (749 mm) at one year of age. These are probably total lengths. Parker and Brown (1980) indicated growth of ca. 280 mm for the first 13 months in gopher snakes (*P. m. deserticola*) in northern Utah. First-year bullsnakes on the Sand Prairie Reservation in Kansas had somewhat higher growth rates (422 mm/year) than these other two populations of the species. The absolute growth rate declined to approximately 40% of the first year rate in the second year, to 20% in the third year and to 10% or less after the third year (Table 4). The growth rate probably continued to decline in older snakes: individuals more than 1100 mm SVL grew 5.2

mm/month (N = 9) and those more than 1200 mm SVL grew 0.7 mm/month (N = 3). Relative growth rates declined even more rapidly. The age at sexual maturity was not determined in this study.

Growth rates showed a pattern of annual variability which was related to prey availability. The highest rates occurred in the summers of 1968, 1969, and 1974. The lowest rates occurred in the summer of 1971 (Tables 6 and 8). In both 1968 and 1969 all one-year old bullsnakes in samples collected in August were >800 mm SVL. In August 1971, some one-year old snakes had grown comparably to >800 mm SVL but others were <700 mm SVL (Table 5). These periods of high and low growth rates corresponded with the periods of highest and lowest prey availability and feeding activity (Tables 1 and 2).

The decrease in growth rates in 1971 was statistically significant. Scarcity of prey in that year, when populations of both small and medium-sized rodents were low, adversely affected growth of bullsnakes. Periods of exceptional prey abundance had a less evident effect on growth of bullsnakes. Growth rates in 1968 were not appreci-

TABLE 11. Comparisons of mean weights of male bullsnakes (*Pituophis melanoleucus*) recaptured within one growing season in Kansas to normal weights calculated from the regression equation of weight on SVL in samples with different intervals between captures. N = number of useable recapture records.

Interval between captures	N	Mean SVL (mm)	Mean weight (gm)	Normal weight (gm)
<21 days	19	634	79.4	74.2
21-30 days	13	649	81.5	79.1
31-60 days	16	730	114.2	110.0
>60 days	9	835	168.0	160.3

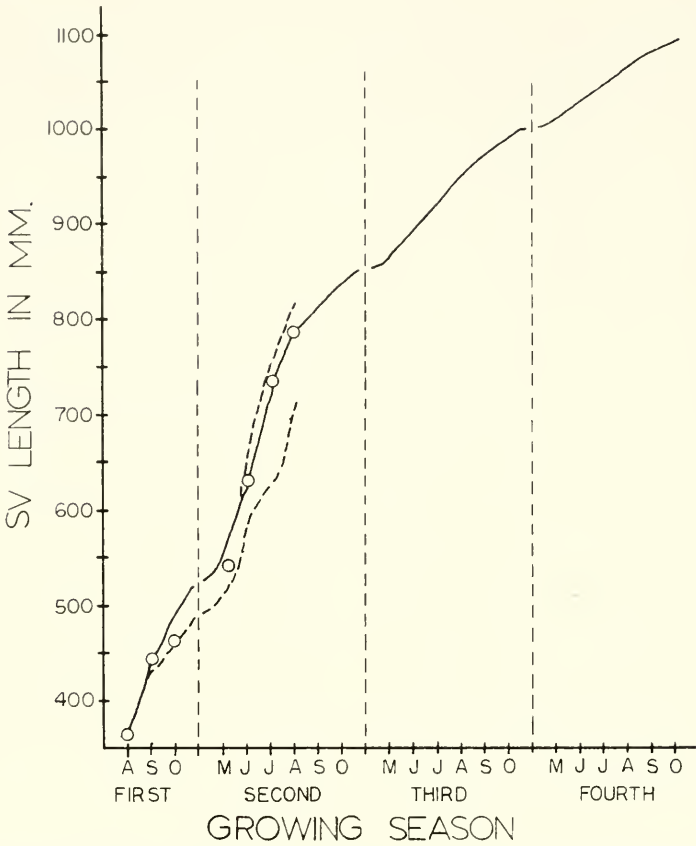


FIG. 1. Growth curve for bullsnakes (*Pituophis melanoleucus sayi*) in south central Kansas. Tick marks on the abscissa indicate the mid-point of each month. Vertical dashed lines represent the dormant period of six months. The solid growth line estimates the average growth of bullsnakes at different ages in nine years (1966–1974). Hollow circles represent mean lengths of snakes in monthly samples of first-year snakes (see text for age designations). Dashed lines represent mean growth rates in a poor year (1970–1971) and good years (1968–1969).

ably higher than in 1969 and 1974 when rodent trapping was much less successful. Growth would not be expected to increase in proportion to the increase in prey populations if the snakes were already satiated. Also, at high feeding levels, a large proportion of the increased food intake probably goes into fat reserves rather than into increased growth in length. In 1968, weights of bullsnakes for any given length were higher than in any other year (Table 9). In 1969, although growth rates were relatively high (Table 6), feeding activity was much lower (Table 2) and weights were relatively low (Table 9). Young bullsnakes that accumulated extra fat reserves in the autumn

of 1968 were able to maintain high growth rates in 1969 when rodent populations were probably only moderately high. The year 1974 had higher feeding activity (Table 2) and relatively high growth rates and weights (Tables 6, 8 and 9).

Growth rates of juveniles in the autumn were variable. Low production, low survival and/or low growth of juveniles occurred in the autumn in 1970, 1971, and 1972. Feeding rates were also generally low (Table 7).

A growth curve for bullsnakes for the years studied is presented in Fig. 1. The first year's growth was determined from the mean lengths of monthly samples while the growth curve be-

yond the first year was estimated from the growth rates of recaptured snakes. The lower dashed line represents the average growth in 1970–1971, a poor growth year, and the upper dashed line represents growth determined from the combined samples for 1967–1968 and 1968–1969, good years. The data were inadequate to estimate the monthly variation in growth for snakes older than one year so the growth rate is applied uniformly through the active season. This growth curve indicates that bullsnakes were approximately 790 mm SVL at one year of age in August, 950 mm SVL at two years and 1030 mm SVL at three years. These estimates may be slightly low for the second and third years, since growth was probably more rapid before August than after August. If older snakes grew at the rate of 35–40 mm per year (Table 4), a bullsnake 1100 mm SVL would be five years old and one 1200 mm SVL would be seven to eight years old. This is similar to the estimate by Imler (1945) that bullsnakes in Nebraska reach a total length of 49 inches (1245 mm; ca. 1100 mm SVL) in five to six years. Parker and Brown (1980) found that gopher snakes (*P. m. deserticola*) in Utah required 18–20 years to reach 1200 mm SVL. Fitch (1949) estimated that *P. m. catenifer* in central California reached a SVL of more than 800 mm at two years of age. Growth of bullsnakes in central Kansas was comparable to that of bullsnakes in Nebraska but more rapid than populations of the same species in Utah and California.

Different studies of growth rates in snakes cannot be precisely compared because of differences in methods used. But comparisons can be made on the basis of the general magnitude of growth in the first year of life. Information for some colubrid species on growth during the first year are presented in Table 12. The species are arranged in order of increasing hatchling size.

Growth rate of snakes in their first year is positively related to both size of hatchlings and to normal adult size (Table 12). Hatchling size was either listed in the reports cited or was determined from the growth curves reported and was rounded to the nearest five mm. Normal adult size was usually determined from length distributions as the mode of the snakes forming the largest size group in a population sample. The SVL was rounded to the closest 10 mm in small snakes, closest 50 mm in moderate-sized snakes and closest 100 mm in large snakes. If a fre-

quency distribution was not included in a growth study, normal adult size was taken from the growth curve or from the author's statements about adult size.

Other biological parameters modify the relation between first-year growth rate and size:

- a) Geographic variation in growth rate probably was mediated through environmental limitation. The studies of growth of *Thamnophis* and *Nerodia* in Michigan with a short growing season reported lower first-year growth than studies of related forms in Kansas. The growth rates of *Coluber constrictor mormon* and *Pituophis melanoleucus deserticola* in Utah, where ecosystem primary production is lower, were much lower than those of related subspecies in Kansas.
- b) Taxonomic differences in growth are evident. Species of the genus *Thamnophis* have high growth rates in proportion to hatchling and adult size while the species of *Elaphe* and *Lampropeltis* studied appear to have low relative growth rates.
- c) There is a relationship between first-year growth rate and age at sexual maturity. Females of most of the species of moderate-sized snakes studied become sexually mature at one year of age. First-year growth amounts to at least half of the growth from hatchling to adult size. Females of large snakes, such as *Elaphe*, *Pituophis*, *Coluber* and *Masticophis*, usually take more than one year to mature and growth rates are not as high relative to size. Females of moderate-sized species with low growth rates, *Lampropeltis triangulum* in Kansas and *Nerodia sipedon* in Michigan, take two to three years to mature. *Coluber constrictor mormon* in Utah with lower growth rates is both smaller as an adult and takes longer to mature than the faster growing subspecies from Kansas. The smallest species of *Elaphe* studied, *E. quadrivirgata*, matures in one year but the larger species, *E. climacophora* and *E. obsoleta*, mature in three years and have relatively slower growth rates.

First-year growth in viperid snakes ranged from 70–370 mm (10–45 mm/month) (Fitch 1949, 1960; Gibbons 1972; Klauber 1956; Prestt 1971; Volsoe 1944; Wharton 1966). Growth rates in elapid snakes in Australia up to 12 months of age ranged from 70 to 410 mm in a growth season

TABLE 12. Growth increments (mm SVL) for colubrid snakes during the first year. Sex symbols are used to designate growth increments when authors reported different growth rates for males and females. An X designates growth rates of a pooled sample of the two sexes. The two numbers following each symbol are SVL of hatchling

Species	Millimeters growth in first year			
	50-100	100-150	150-200	200-250
<i>Virginia striatula</i>	♀ 110-230 (8; 1)			
<i>Carphophis vermis</i>	♂ 110-230 (7; 2) ♀ 115-260			
<i>Diadophis p. arnyi</i>	♂ 110-260 (5; 2) ♀ 115-290			
<i>Heterodon nasicus</i>	♂ 150-400 (6; 1)		♀ 150-450	
<i>Natrix tigrina*</i>				
<i>Thamnophis s. parietalis</i>	♂ 170-550 (6; 1)			
<i>Nerodia sipedon</i>	♂ 190-550 (5; 2)		♀ 190-750	
<i>Heterodon platyrhinos</i>	♂ 195-500 (6; 1)			
<i>Thamnophis sauritus</i>	♂ 200-450 (5; 1)		♀ 200-550	
<i>Thamnophis s. sirtalis</i>	♂ 200-450 (5; 1)		♀ 200-550	
<i>Lampropeltis triangulum</i>	X 210-600 (6; 2-3)			
<i>Thamnophis proximus</i>				
<i>Coluber c. flaviventris</i>				
<i>Coluber c. mormon</i>			♂ 225-550 (5; 3) ♀ 225-600	
<i>Elaphe quadrivirgata*</i>	♀ 230-700			
<i>Masticophis taeniatus</i>				
<i>Elaphe climacophora*</i>	X 320-1600 (6; 3)			
<i>Elaphe obsoleta</i>	X 330-1200 (5; 3)			
<i>Pituophis m. deserticola</i>				
<i>Pituophis m. sayi*</i>				
<i>Pituophis m. sayi</i>				

* Values calculated by correction from data on total lengths.

TABLE 12. Continued.

and normal adult SVL (see text). Listed in parentheses are the number of active or growing months in the year and the age in years of females at sexual maturity. The geographic location of the population studied is listed.

		Millimeters growth in first year		
250-300	300-350	350-400	400-450	Authority
				Texas— Clark & Fleet 1976
				Kansas— Clark 1970
				Kansas— Fitch 1975
				Kansas— Platt 1969
♂ 165-500 (6; 1)	♀ 175-600			Japan— Fukada 1959
♀ 170-650				Kansas— Fitch 1965
				Michigan— Feaver 1977
♂ 195-600				Kansas— Platt 1969
				Michigan— Carpenter 1952
				Michigan— Carpenter 1952
				Kansas— Fitch & Fleet 1970
♀ 215-550 (10; 1)				Texas— Clark 1974
		♂ 215-800 (6; 2) ♀ 215-900		Kansas— Fitch 1963b
				Utah— Brown & Parker 1984
♂ 240-850 (6; 1)				Japan— Fukada 1960
	♂ 285-1000 (5; 3) ♀ 285-1000			Utah— Parker & Brown 1980
				Japan— Fukada 1978
				Kansas— Fitch 1963a
♂ 335-1100 (5; 3-4) ♀ 335-950				Utah— Parker & Brown 1980
	X 335-1100 (6)			Nebraska— Imler 1945
			X 360-1100 (6)	Kansas— Platt (this study)

of eight months (Shine 1978, 1980). It appears that bullsnakes on the Sand Prairie Reservation in Kansas have one of the highest first-year growth rates that has been reported for snakes in free-living populations.

SUMMARY

The growth of bullsnakes (*Pituophis melanoleucus sayi*) was studied by mark-recapture techniques on the Sand Prairie Natural History Reservation in south central Kansas. During the nine years of the study, 1966 through 1974, 709 captures of 471 bullsnakes were made. Growth rates were calculated from the records of recaptured snakes and from the mean snout-vent lengths of first-year bullsnakes in monthly samples. No significant sexual differences in size or growth rates of bullsnakes were found.

Bullsnares grew rapidly for the first year of life (absolute growth rate of 70.4 mm/month) and reached 790 mm SVL at one year of age. Growth rates declined to 40% of the first-year rate in the second year, to 20% in the third year and to 10% and less in older snakes.

Growth rates were significantly lower in 1971 when prey populations and feeding rates of bullsnares were low. Prey populations and feeding rates were very high in 1968 and growth rates were highest then.

Growth rates calculated from recapture records were consistently lower than growth rates calculated from the change in length of samples of first-year snakes. This discrepancy was due to a temporary decrease in growth after capture and to changes in the monthly samples caused by differential mortality of smaller snakes.

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Communal Denning in Snakes

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INTRODUCTION

The temperate zone, especially at higher latitudes, is characterized by a pronounced seasonality. Relatively few species of reptiles occur in such environments and those that do must be adapted to contend with this climatic variability. The most critical season for reptiles in the temperate zone is winter, when conditions may become much too cold for continued activity. In areas where winters are long and cold, reptiles must find shelter from the prevailing conditions and hibernate. Recent research has revealed that many species have important physiological adaptations which enhance their chances for survival over winter, mainly by depressing metabolic rate in hibernation below that predicted on a simple Q_{10} basis (Moberly 1963; Mayhew 1965; Aleksjuk 1976; Gatten 1978; Patterson and Davies 1978; Johansen and Lykkeboe 1979). This depression is interpreted as an important mechanism for conserving energy at a time when losses cannot be replaced (Gregory 1982). In addition to these physiological adaptations, however, the need to hibernate has had other important ecological and evolutionary effects on reptiles. In this paper, I discuss ecological aspects of one particular phenomenon in reptilian overwintering: communal denning of snakes.

Communal denning occurs mainly in snakes among reptiles, although it has been described for some lizards and turtles (Woodbury and Hardy 1949; Weintraub 1968; Ataev 1974; Vitt 1974). Communal hibernation has been reported for a few snakes in the southern hemisphere (e.g., *Aparallactus capensis* in southern Africa, FitzSimons 1962, p. 30; *Demansia reticulata* and *Pseudechis porphyriacus* in Australia, Kinghorn 1964; see also Shine 1979), but this behavior is most pronounced in the northern hemisphere, especially at higher latitudes. However, not all northern snakes hibernate communally.

In communal denning, large numbers of otherwise solitary animals aggregate at localized sites to pass the winter. Both single and mixed species aggregations occur (Gregory 1982). This type of behavior is often conspicuous. Snakes which ordinarily are not locally abundant suddenly be-

come extremely abundant in both fall and spring, the beginning and end of hibernation, respectively. This conspicuousness sometimes works to the disadvantage of snakes by advertising their presence to predators, including man. Rattlesnakes in particular have suffered major declines due to raids on denning populations (Klauber 1972; Galligan and Dunson 1974) and it is likely that preservation of some species depends in part on protection of communal dens (e.g., *Crotalus horridus*, Brown *et al.* 1982). On the other hand, the conspicuousness and abundance of snakes at some dens have provided us with an opportunity to learn much about the structure and dynamics of snake populations that we might not otherwise have learned (Brown 1973; Gregory 1977a; Parker and Brown 1980).

The den plays a central role in the annual cycle of some species of snakes. More than half the year is spent at the den in some cases, and mating often occurs in the vicinity of the den in spring or fall. The den may even function as a base of operations for part of the population during the summer months. In this paper, I want to emphasize this central role played by the den in communally hibernating species by describing the major ecological and behavioral features of communal denning, using studies of garter snakes (*Thamnophis*) in Canada as main examples. I hope to provide at least a partial answer to the question: "Why do snakes den communally?"

MAJOR FEATURES OF COMMUNAL DENNING

Although considerable variation exists from one case to another, several important features emerge from an examination of studies of communal dens. These are: type of site used for hibernation, spatial relationship of den to summer habitat, size and structure of denning populations, and fall and spring activity of snakes at denning sites.

1. Type of site.—Communal dens are usually relatively permanent structures with cavities or passageways which allow the snakes access below the frostline to pass the winter. For example, in southern British Columbia, the western rattlesnake (*Crotalus viridis*) usually hibernates com-

TABLE 1. Dispersal distances of snakes between hibernacula and summer ranges (modified from Gregory 1982).

Species	Mean dispersal distance	Range	Reference
<i>Storeria dekayi</i>		4–402 m	Noble and Clausen 1936
<i>Storeria occipitomaculata</i>	males: 378 m females: 246 m	46–838 m 30–716 m	Lang 1971
<i>Thamnophis sirtalis</i>	males: 347 m females: 532 m 10.7 km		Fitch 1965
<i>Coluber constrictor</i>		4.3–17.7 km up to 1000 m 713 m 8–1632 m	Gregory 1977a Hirth <i>et al.</i> 1969 Brown 1973; Brown and Parker 1976 Fitch 1963b
<i>Elaphe obsoleta</i>	males: 384–403 m females: 362 m		Fitch 1963a
<i>Masticophis taeniatus</i>		up to 1.3 km up to 3.6 km	Hirth 1966b Hirth <i>et al.</i> 1969
	males: 992 m females: 1455 m	368–1692 m 832–2750 m	Parker and Brown 1980
<i>Pituophis melanoleucus</i>	males: 510 m females: 508 m	120–862 m 176–875 m	Parker and Brown 1980
<i>Vipera berus</i>		600–1500 m up to 1190 m	Prestt 1971 Viitanen 1967
<i>Agkistrodon contortrix</i>	males: 656 m females: 406 m	366–1183 m 232–631 m	Fitch 1960
<i>Crotalus atrox</i>	1.4 km	0.7–3.5 km	Landreth 1973
<i>Crotalus viridis</i>		up to 2.01 km up to 1200 m 482 m 75–1040 m >610 m	Woodbury <i>et al.</i> 1951 Hirth <i>et al.</i> 1969 Parker and Brown 1974 Preston 1964
	males, non-gravid females, juveniles: gravid females: 50 m	650 m 210–1600 m 3–379 m	Macartney (pers. comm.)
<i>Crotalus horridus</i>	males: 1400 m females: 280 m	? (1 only) 191–425 m	Brown <i>et al.</i> 1982
<i>Sistrurus catenatus</i>		<200 m	Reinert and Kodrich 1982

munally in cavities in rock outcrops, sometimes associated with talus slopes (personal observation); similar observations have been made for rattlesnakes elsewhere (Klauber 1972). At one site in the Chilcotin-Cariboo area of British Columbia, the garter snakes *Thamnophis elegans* and *T. sirtalis* use a large cavity-riddled rocky mound which rises up from the surrounding grassland (Gregory, unpublished). Manitoba *T. sirtalis* hibernate in large sinkholes which are the result of slumps in the bedrock into subterranean cavities (Gregory 1977a). Some snakes, however,

den communally in impermanent structures such as prairie dog burrows (Klauber, 1972) or abandoned ant mounds (Carpenter 1953; Lang 1971), but these dens usually have a lifetime of several years before they are no longer usable. Communal den sites are usually traditional in that they are occupied by snakes every year. They also frequently face south; thus, annual exposure to solar radiation is maximized.

For other descriptions of communal hibernating sites of snakes, see reviews in Klauber (1972) and Parker and Brown (1973).

2. Relationship of den to summer habitat.—Snakes which hibernate singly or in very small groups may use sites within the summer range (Fitch and Glading 1947; Naulleau 1966). Communal dens of snakes, however, are frequently separated by fairly long distances from the summer range, necessitating an annual migration back and forth between the two. Distance travelled ranges from a few hundred m to several km (Table 1); perhaps length of migration is inversely related to the availability of sites suitable for housing snakes in winter, but this idea has not been tested. In *Coluber constrictor*, mean dispersal distance may be correlated with population density; presumably, in years with high numbers, individuals which disperse farther escape intraspecific competition for resources (Brown and Parker 1976).

Some snakes which move between discrete denning and summer areas show a highly directional form of dispersal (Gregory and Stewart 1975), while others do not (Parker 1976). Individual snakes often return to the same den or denning area year after year; measures of den fidelity of snakes in successive years are often in the 90–100% range (Fitch 1960; Viitanen 1967; Lang 1971; Brown and Parker 1976; Gregory 1977a, 1982; Parker and Brown 1980). Other authors have concluded that den fidelity is low (Noble and Clausen 1936); however, the definition of what constitutes a den or denning area varies from study to study so that results are not necessarily comparable. In addition, distance between neighboring dens may affect fidelity but is not always reported; Lang (1971) found lower fidelity and greater annual interchange between dens that were closer together. Nevertheless, a remarkable ability to home is shown by some species: Homing to specific den complexes less than 1000 m apart is almost 100% in *Coluber constrictor* in Utah (Brown 1973; Brown and Parker 1976) and homing *Thamnophis sirtalis* in Manitoba must apparently pass close by other dens en route to their own dens each fall (Gregory and Stewart 1975). Other similar examples are given by Viitanen (1967) and Lang (1971).

The exact mechanisms used in homing are not known, but there is presumably selective value in returning to a den in which overwintering has been successful previously, even where other hibernating sites are abundant. This is important since high rates of mortality during hibernation

have been reported for many snakes, especially the young (Bailey 1948; Carpenter 1953; Hirth 1966a; Viitanen 1967; Lang 1969, 1971; Gregory 1977a, 1982; Parker and Brown 1980). Parker and Brown (1974, 1980) suggest that high mortality figures in such studies may be an artifact of handling and marking snakes, but the evidence in support of this contention is minimal.

In cases where individuals generally return to the same den in successive years and where mating usually occurs at the den site (see below), communal denning produces a large departure from panmixia. Over large areas, isolation of different denning sites might ultimately be an important contributing factor to differentiation within species (Gannon 1978). At the local level, however, populations at particular dens are probably never completely isolated demes. Den fidelity is rarely 100% so that some interchange occurs between dens. In addition, even in species which normally mate at the den, occasional mating occurs away from the den when individuals from different hibernacula may come into contact (Gregory 1977a). Inter-den mating has been observed in some cases (Brown 1973; Brown and Parker 1976). Finally, there is no particular reason to believe that young snakes hibernating at a communal den for the first time necessarily use the same den as their parents, except when the young are born at the den.

3. Size and structure of denning populations.—Sizes of overwintering aggregations of snakes have been reviewed by Klauber (1972), Parker and Brown (1973), and Gregory (1982). Most aggregations probably consist of much fewer than 100 individuals of all species combined. Some denning populations, however, may include a few to several hundred individuals of a given species (Criddle 1937; Viitanen 1967; Lang 1969; Klauber 1972; Parker 1976). The largest denning populations known are those of *Thamnophis sirtalis* in Manitoba, where numbers at one den fluctuated between about 4000 and 8000 in a four-year period (Gregory 1977a).

Sampling the different size/age groups in a snake population in proportion to their relative abundance is difficult because young snakes are smaller and often more secretive than adults. Nevertheless, it seems clear that young-of-year and/or juveniles are frequently absent (Viitanen 1967; Gregory 1977a; Sexton and Hunt 1980) or greatly underrepresented (Hirth *et al.* 1969;

Klauber 1972; Parker and Brown 1973, 1980; Parker 1976; Brown and Parker 1976) at communal hibernacula. Prestt (1971), however, in contrast to Viitanen's (1967) observations of the same species (*Vipera berus*), found young hibernating with the adults. In some small species, the young also apparently hibernate with the adults (Noble and Clausen 1936; Lang 1971).

Why young snakes often do not use the same dens as the adults is puzzling. Perhaps whether or not they do depends to some extent on the distance between the den and the summer habitat. If the young are born in the summer range a long way from the den, it may simply be too expensive energetically to make the journey if they can find suitable hibernacula closer by. This seems quite likely as smaller snakes can use sites which are inaccessible to the adults because of their size. This is probably the case for *Thamnophis sirtalis* in Manitoba, where the adults, but no young-of-year, hibernate in limestone sinks several kilometres from the summer habitat (Gregory and Stewart 1975; Gregory 1977a). Young of this species are known to hibernate communally with two species of small snakes in ant mounds in nearby Minnesota (Lang 1971); this is presumably what occurs in the Manitoba summer habitat, where ant mounds are abundant. Young born or hatched closer to the den, on the other hand, may be more likely to hibernate with the adults (but see Viitanen 1967). Gravid females of many snake species show a tendency to aggregate in areas of localized shelter (Gregory 1975a); in some cases, this may occur at or near the den site (Viitanen 1967; Prestt 1971; Gregory, unpubl. obs.; see section on "Communal Denning and Mating Behavior in *Thamnophis*"). Other examples of gravid females occasionally being found at dens are given by Preston (1964) and Galligan and Dunson (1979).

Parker and Brown (1980) argue that young snakes hibernate elsewhere as a defense against intra- and interspecific predation by adults (in this case, *Masticophis taeniatus* and *Coluber constrictor*). The hypothesis that there is some disadvantage to young snakes in hibernating with the adults is supported by the observation that most young *Masticophis* using communal dens do not survive to age one and most one-year-olds at dens are not known to have used the dens the previous year (Parker and Brown 1980).

However, young *Thamnophis sirtalis* hibernate with adults at a communal hibernaculum in British Columbia despite occasional predation on them by adult *T. elegans* at the same den (Gregory, unpubl. obs.). Quantitative assessment of these ideas awaits further study, but it is clear that there is an important ontogenetic change in hibernation behavior in many species of snakes.

4. Fall and spring activity at dens.—Previous studies have revealed a great deal of variation in patterns and timing of entry into and emergence from hibernation of snakes at communal dens, including differences between species, sexes, and age/size groups at the same den (Viitanen 1967; Lang 1971; Prestt 1971; Brown 1973; Landreth 1973; Gregory 1974, 1977a, 1982; Brown and Parker 1976; Parker and Brown 1980). In most cases, fall and spring activity periods at dens span several days or weeks, but individual animals may be active above ground only briefly (e.g., Lang 1971). In other cases, however, individual snakes may remain active in the vicinity of the den for a large part of the fall and/or spring period (e.g., Viitanen 1967; Prestt 1971; Gregory 1974; Parker and Brown 1980), usually without feeding. The advantages of remaining active above ground at the den, rather than seeking cooler conditions below ground, are not clear, since such activity is energetically very expensive (Parker and Brown 1980). The significance of activity at dens is obvious in cases where snakes mate at the den site or nearby (Viitanen 1967; Prestt 1971; Gregory 1974, 1977a; Bennion and Parker 1976; Parker and Brown 1980). Some species, however, apparently mate away from the den (Brown 1973; Brown and Parker 1976; Parker and Brown 1980). Fall mating occurs in some snakes (Trapido 1940; Rahn 1942; Saint Girons 1957; Gregory 1977a), but in most cases is only an occasional phenomenon and less intense than in spring, which is the major breeding season for most temperate zone snakes. Prolonged activity at dens in fall is therefore generally not explained by mating behavior.

Perhaps spring and fall activity is related in other ways to the reproductive cycle. For example, male *Vipera berus* bask at dens in fall to promote spermatogenesis, which will be completed during basking the following spring (Volsoc 1944). *Vipera* species, however, are different from all other temperate zone snakes, in which spermatogenesis is completed well before hiber-

nation (Aldridge 1979a). Thus, it is not obvious why individual male *Masticophis taeniatus*, which breed in spring, remain active at the den for up to 37 days before entering hibernation (Parker and Brown 1980). Females of some species of snakes undergo part of secondary vitellogenesis in fall (Aldridge 1979b), but presence or absence of this pattern has not been correlated with fall activity or lack of it. In females of all temperate zone species, all or part of secondary vitellogenesis occurs in spring (Aldridge 1979b). If basking is important to this process, snakes in some cases may trade off the lack of food at the den site for the advantage of readily available shelter at times when cold weather could arise suddenly. We do not yet know enough about details of reproductive cycles (and factors affecting them) or fall and spring activity periods of most snakes to be able to correlate these features.

WHY DO SNAKES DEN COMMUNALLY?

Certain disadvantages appear to be inherent in the habit of communal hibernation. First, animals at dens in spring and fall may be very conspicuous because of their abundance, and may therefore attract predators. For example, crows take a fairly heavy toll of *Thamnophis sirtalis* at dens in Manitoba in early spring when the ground vegetation cover is sparse (Gregory 1977a). Individuals hibernating singly at isolated locations would be much less conspicuous. [Professional collectors for biological supply companies make even greater inroads in populations at these dens (Gregory 1977b). The problem of collection and/or slaughter by humans at dens is also great for rattlesnakes, since these animals are often actively persecuted (Klauber 1972; Galligan and Dunson 1979). However, human collection is a relatively recent phenomenon and cannot be considered a long-term selective force.] Another possible disadvantage of communal denning is related to the fact that the den and summer habitat may be quite far apart. In such cases, snakes have to migrate, often through unfavorable habitat, expending energy and possibly exposing themselves to a higher risk of predation.

The question therefore arises as to why snakes den communally. Very small aggregations of snakes (see examples in Parker and Brown 1973) may simply be fortuitous and irregular in oc-

currence, but large aggregations probably have a different basis. There are at least three possible reasons, not mutually exclusive, for communal denning: 1. low availability of suitable hibernating sites; 2. aggregation of snakes in hibernation to minimize losses of endogenously produced heat; 3. enhancement of mating success in the breeding season. A fourth possible advantage of communal denning is that it may lead to more efficient utilization of resources around the den; the area occupied by a dispersed population may change according to annual changes in snake population density and/or resource abundance (the "refuging" hypothesis, Parker and Brown 1980). However, it is not clear to me that communal denning is necessary for this system to operate and even if so, it is more likely to be a consequence of communal hibernation rather than a reason for its occurrence in the first place.

Shortage of suitable hibernacula is undoubtedly the main cause of communal overwintering in many cases. This argument has been used to explain winter aggregations of some lizards (Weintraub 1968; Vitt 1974) and the rattlesnakes *Crotalus viridis* (Gannon 1978) and *C. horridus* (Brazaitis 1980) and the occurrence of more than one species in large communal dens (e.g., Carpenter 1953; Hirth *et al.* 1969; Lang 1969). Smaller species of snakes may be less influenced by this factor than larger snakes since they are presumably capable of using cavities unavailable to the latter because of size. The problem of limited availability of hibernacula is expected to be particularly serious in cold climates, where hibernation at considerable depth is critical for survival. This correlates well with the observation that communal denning is an especially well developed phenomenon at higher latitudes. Gannon (1978) feels that availability of hibernacula is an important factor limiting the distribution of *Crotalus viridis* in southern Saskatchewan and Alberta. On the other hand, several authors have noted that there may be apparently usable hibernacula which go unused in any winter, even at high latitudes (Viitanen 1967; Lang 1971; Klauber 1972; Gregory 1977a). Lang (1971) concluded that availability of ant mound hibernacula was therefore not a limiting factor on numbers of three species of small snakes in Minnesota. This could be true, however, even if all hibernacula were used since there might still be space for more animals within individual hibernacula

(Parker and Brown 1973). In addition, what appears to be a suitable den to the observer may not be seen as such by snakes: we need to know more about what qualities make a good hibernating site and to assess these qualities at potential sites before we can reach a conclusion regarding availability of hibernacula.

The argument that snakes hibernate communally so that they can aggregate below ground and reduce heat loss is difficult to support. It was put forward by White and Lasiewski (1971), with particular reference to rattlesnakes. In favor of this idea is the observation that rattlesnake dens blasted open in winter sometimes reveal large masses of animals (Klauber 1972); however, such behavior could be due to disturbance. Aleksiuik (1977) has also shown that *Thamnophis sirtalis* tend to huddle under cold conditions, but there is no evidence that this actually happens in the den during hibernation. Snakes hibernating in communal dens are frequently not in contact with one another, although small groups may be formed (Noble and Clausen 1936; Carpenter 1953; Lang 1971; Brown *et al.* 1974), and isolated individuals do not differ in body temperature from grouped individuals (Brown *et al.* 1974). Use of energy reserves during hibernation *per se* is probably very low in most cases (Parker and Brown 1980), consistent with the observation that hibernation usually takes place at a low temperature (e.g., Brown *et al.* 1974; Sexton and Hunt 1980; Brown 1982; Gregory 1982), not a high one; use of energy reserves may be very high during activity at dens in fall and spring, but this is not taken into account in most studies, yielding considerable overestimates of the energetic cost of hibernation (Bartlett 1976; Parker and Brown 1980). Finally, an important physiological adaptation of many hibernating reptiles seems to be that metabolism is significantly depressed at low temperatures (e.g., Aleksiuik 1976; Johansen and Lykkeboe 1979; Gregory 1982). If this is interpreted as an energy-saving device during hibernation, then it is not surprising that snakes hibernate at fairly low temperatures, contrary to the predictions of White and Lasiewski (1971).

Snakes hibernating with conspecifics at communal dens presumably have greater chances of finding mates in the mating season than they would have if they hibernated singly. This idea is difficult to test in the field, but it is obvious that mating opportunities at communal sites should be frequent simply because of the large

numbers of snakes involved, especially for species which mate at or near the den in fall or spring. Even in species which do not mate right at the den site, communal hibernation may still enhance mating chances since individuals dispersing from a small area should come into contact more often than when widely scattered (Parker and Brown 1980). As in the case of the "refuging" hypothesis above, it may be argued that high probability of reproductive success is not a primary reason for the occurrence of communal denning, but simply a secondary advantage of it. This problem is somewhat circular, however, since it is also possible that the prior evolution of early spring mating has resulted in selection for individuals that seek hibernacula used by conspecifics, or that the two have evolved jointly. We need studies which aim to unravel this question.

In some cases, the advantages of communal denning in terms of mating extend beyond mere numbers. Once the mass overwintering habit is established, an opportunity is presented for mating behaviors to evolve which take advantage of this situation. An example is provided by the garter snake, *Thamnophis sirtalis*. In this species, the different mating strategies of the two sexes seem to be reflected in significant differences in the dynamics of their behavior at the den during the breeding season. This example is examined in detail in the next section. Although the data analysis is largely *a posteriori*, its main function is to suggest testable hypotheses for further study and points for comparison with other communally denning species which show different behaviors.

COMMUNAL DENNING AND MATING BEHAVIOR IN *THAMNOPHIS*

The common garter snake, *Thamnophis sirtalis*, is the most widespread species of snake in North America. While this species does not den communally throughout its range, such behavior is well developed in the northern parts of its range. The study area in question here is in the Interlake region of Manitoba, near the northern limit of distribution of *T. sirtalis*. This region has a continental climate, with long cold winters and variable summers (Gregory 1977a). Only four species of snakes occur in the study area, and *T. sirtalis* is by far the most abundant of these.

Communal dens of *T. sirtalis* in the Interlake

are mainly limestone sinks, formed by the collapse of the ground surface into subterranean caves. The major den examined in this study (Den 1) is a large, bowl-like depression about 20 m long \times 12 m wide \times 3 m deep; the bottom of the bowl is riddled with cavities leading underground. These dens occur on ridges between large marsh belts. Dens are abundant in such areas and are frequently less than 1 km apart. Populations using dens may be very large. Den 1 is estimated to have housed as many as 8000 snakes during one winter, but population size fluctuates drastically from one year to another, apparently in response to variations in weather (Gregory 1977a). Den populations are exclusively adult (Fig. 1); it is not known where the young hibernate in this area. The summer habitat of these snakes is in the marshes between the ridges. Individuals may move as much as 18 km between den and summer range; migrations are unidirectional, with all animals moving south in summer despite the fact that suitable marshes are also found in other directions (Gregory and Stewart 1975). Despite these long migrations and the relative closeness of dens to one another, homing success of individual snakes to the same den in successive years is about 96% (Gregory 1977a).

The den is a central feature in the annual cycle of Interlake *T. sirtalis*. The hibernation period may be as long as six months; in addition, the fall and spring activity periods in the vicinity of the den may occupy up to 1½ months each (Gregory 1977a). In extreme cases, therefore, individual snakes may spend only three months away from the den during the year, and this is the only time in which feeding takes place (Gregory and Stewart 1975). Although occasional fall mating occurs, virtually all mating occurs at the den in spring after emergence (Gregory 1974, 1977a).

Mating activity of males is apparently stimulated by the change from the cool conditions experienced in hibernation to the warmer conditions above ground in spring (Aleksiuk and Gregory 1974; Hawley and Aleksiuk 1975; Crews and Gartska 1982; Gartska *et al.* 1982). Male courtship activity is directly related to temperature (Hawley and Aleksiuk 1975), but declines as the mating season progresses (Aleksiuk and Gregory 1974; Camazine *et al.* 1980). The temperature change associated with emergence from hibernation also stimulates sexual receptivity of females, but does not affect their attractivity to males (Licht and Bona-Gallo 1982). However,

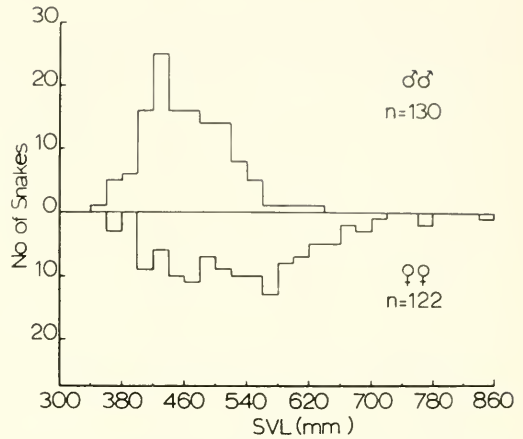


FIG. 1. Size frequency distribution of *T. sirtalis* at Den 1 in fall 1972. Animals are grouped into intervals of 20 mm snout-vent length (SVL). n = sample size. Data from Gregory (1977a).

Gartska *et al.* (1982) indicate that females, which probably have an active role in mating, are more likely to mate when still cold from emergence; females which have warmed up may not be sexually receptive. In both sexes, sexual behavior is independent of gonadal activity (Crews and Gartska 1982; Gartska *et al.* 1982).

The environmental problem faced by these snakes is that of a very short, and sometimes cold, active season. Time to reproduce and perform other essential functions is therefore at a premium. Under such conditions, we should expect the evolution of a mating system which maximizes the efficiency and success of mating for both sexes early in the season following hibernation. The two sexes have, in effect, different reproductive strategies: Males should mate as often as possible since this is their only means of increasing fitness; females, on the other hand, need mate only once per season (but see Gibson and Falls 1975 for evidence of multiple insemination of females, and discussion below) and should spend a minimum of time involved in mating activities *per se*, devoting instead more time to other activities critical to successful reproduction. Differences in behavioral dynamics of the two sexes of Interlake *T. sirtalis* during the mating season appear to reflect these differences in mating strategies.

The relationships described above are difficult to test directly for lack of an appropriate control situation. A reasonable substitute for a true con-

TABLE 2. Numbers of individuals of each sex of *T. sirtalis* caught at Den 1 in fall and spring of four overwintering seasons (data from Gregory 1977a).

		Males	Females
1969–1970	Fall	640	341
	Spring	869	56
1970–1971	Fall	90	80
	Spring	890	75
1971–1972	Fall	221	198
	Spring	846	70
1972–1973	Fall	130	122
	Spring	323	24

H_0 (no difference in proportion of females in fall and spring of same overwintering season) rejected with $P < .005$ in each case (χ^2 contingency table).

trol, however, should be the behavior of the two sexes at dens in fall, when virtually no mating occurs. If the spring behavior is not specifically related to mating, we should expect the autumn behavior to be similar to it (or the reverse of it, chronologically). The first part of my analysis therefore is a comparison of spring and fall activity patterns of these snakes.

I studied the population ecology of Interlake *T. sirtalis* from fall 1969 to spring 1973, a total of four overwintering seasons. The research was concentrated at Den 1 described above, but occasional samples taken at other dens confirmed that the results presented here are typical of denning populations in the study area. Samples of snakes were collected by hand at Den 1 on most days in each fall and spring in the period indicated above. Snakes were individually marked by clipping unique combinations of subcaudal scutes, measured (snout-vent length, SVL), and released, almost always on the day of capture. In each overwintering season, the ratio of number of individual males captured to the number of individual females captured was significantly different in fall and spring when compared by χ^2 contingency analysis (Table 2). Comparison of the four contingency table analyses by heterogeneity- χ^2 (Zar 1974) indicated that the data for all seasons except 1969–1970 could be pooled. In each case, the fall sex ratio was close to 1:1 (only fall 1969 was significantly different from 1:1, Gregory 1977a), whereas the spring sex ratio was extremely biased towards males. This bias in the spring samples was presumably a result of the sampling method and would probably not

have been observed if some other technique, such as fencing the den and capturing snakes leaving it, had been used. It seems very unlikely that it is due to any difference in winter mortality of males and females. The existence of this bias, however, is an important first piece of evidence that activity patterns of the snakes are different between fall and spring.

An analysis of daily samples sheds more light on these two activity periods. In fall, the proportion of females remained high throughout most of the sampling period and was usually not significantly different from 0.5 (Fig. 2). In the data in Fig. 2, from fall 1971, the proportion of females in samples seems to decrease gradually towards the end of the sampling period, suggesting that perhaps females begin arriving at the dens and entering hibernation before males; however, data from other autumns do not confirm this trend, but simply support the occurrence of high proportions of females in daily samples. In contrast to autumn samples, the proportions of females in daily samples in spring were always low, frequently not statistically different from zero (Fig. 2). In fall, individuals of both sexes were recaptured at similar, low rates (Fig. 3). The maximum number of captures of an individual during a given autumn was four for each sex, but maximum intervals between first and last captures were 43 days for males and 25 days for females. In spring, on the other hand, males were recaptured frequently, while females were rarely recaptured in the same spring (Fig. 3). Individual males were caught up to nine times in a given spring and the longest capture history was 36 days (Gregory 1974). No females were ever recaptured more than once in the same spring and the longest interval between first capture and recapture was four days (Gregory 1974). This difference between the sexes was particularly marked in spring 1971 (Fig. 4).

These observations are the result of different patterns of emergence from hibernation and dispersal from the den of males and females in spring. The proximate factors responsible for these differences are not known, but males begin emerging in large numbers a few days before females and build up in numbers to a maximum in about mid-May, coinciding with the peak in mating activity, then decline in numbers (Gregory 1974; Fig. 5). Female numbers presumably follow a similar curve since the proportion of females in

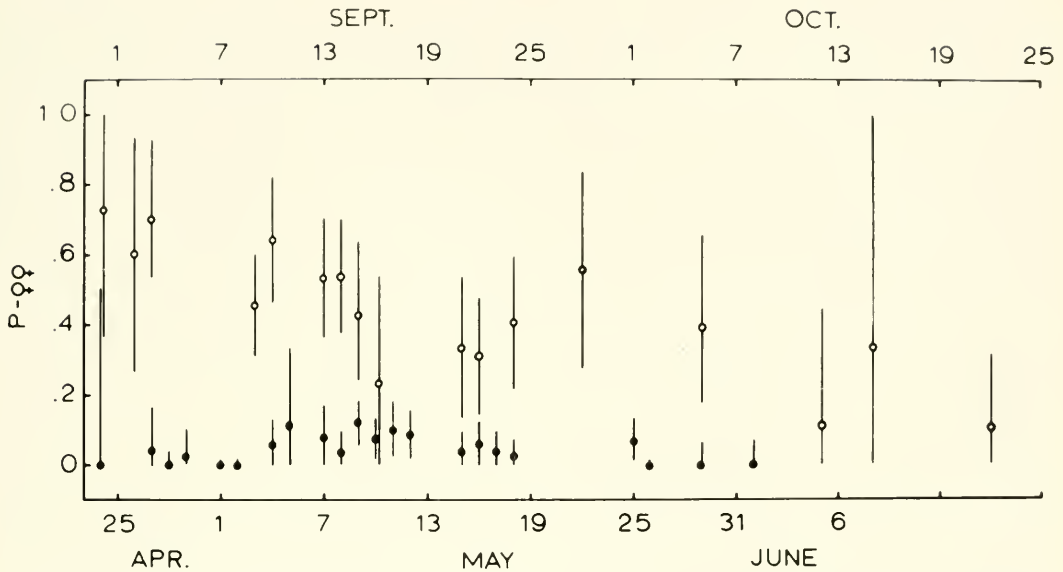


FIG. 2. Proportion of females (P-♀♀) in daily samples of *T. sirtalis* at Den 1 for fall 1971 (open circles) and spring 1972 (closed circles). Vertical lines are 95% confidence limits calculated on basis of binomial distribution. Daily sample sizes range from 3–55 for fall 1971 and 2–125 for spring 1972.

daily samples does not vary greatly over the spring period (Fig. 2). In contrast to males, however, females apparently emerge throughout the spring period and spend little time at the den, dispersing very soon after emergence; road counts of dispersing snakes indicate mostly females leaving early in the spring and increasing proportions of males leaving as the season progresses (Fig. 6). Females also emerge later in the day than do males, but they emerge progressively earlier as the season continues (Gartska *et al.* 1982).

Except for the early part of spring when weather is sometimes cool, females are courted as soon as they emerge, or even while emerging (Aleksiuk and Gregory 1974). Typically, many males simultaneously court a single female, creating a writhing mating "ball" (Aleksiuk and Gregory 1974). Not surprisingly, the head-to-head orientation of male and female shown by many colubrid snakes is not required for successful courtship in this species (Gillingham and Dickson 1980). Courtship and mating take several minutes, but it is not usually possible to see which male manages to copulate with the female. This contrasts with the observations of others (e.g., Devine 1977), in which unsuccessful males leave before the successful male has finished copulat-

ing. However, the numbers involved in mating activity in the Interlake are much larger than those reported elsewhere, obscuring actual copulation. Mating almost always occurs on the ground, but males may follow females into low bushes and mate there (Gregory 1975b). Following copulation, the mating group breaks up rapidly; the males seem to have no further interest in the female, which becomes unattractive for a day or more and even intolerant of further courtship (Crews and Gartska 1982; Gartska *et al.* 1982), but turn to other emerging females instead.

Devine (1977) and Ross and Crews (1977) have shown that male garter snakes can distinguish between mature, non-mated and recently mated females and only court the former. The cues used are apparently pheromonal. The female attractiveness pheromone is a non-volatile lipid, related to vitellogenin, the precursor of yolk which is manufactured in the liver and circulates in the blood (Gartska and Crews 1981; Crews and Gartska 1982; Gartska *et al.* 1982). This pheromone is presumably brought to the skin via a dermal vascular bed and is forced to the body surface through the thin skin between the dorsal and lateral scales. It is a contact pheromone. de-

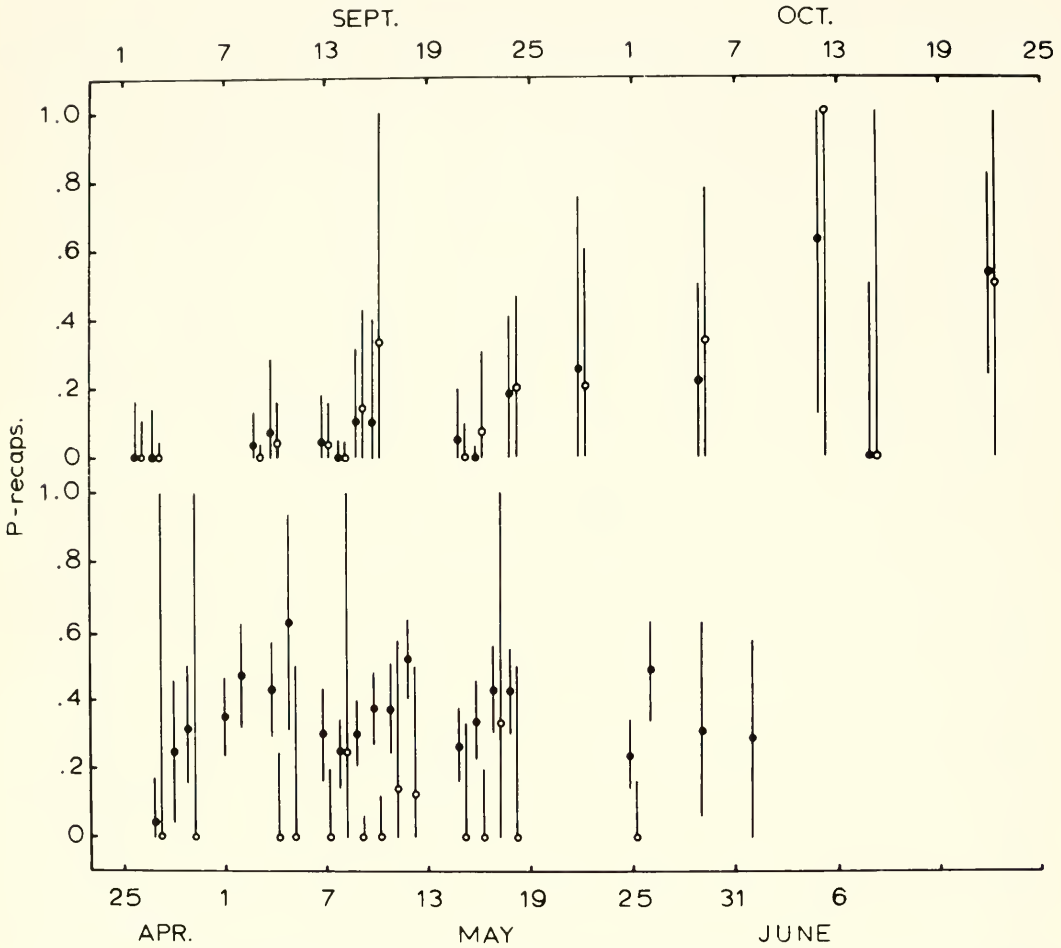


FIG. 3. Proportion of recaptures from same season (P-recaps) in daily samples of *T. sirtalis* at Den 1 for fall 1971 (upper level) and spring 1972 (lower level). Open circles represent females and closed circles males. Vertical lines are 95% confidence limits calculated on basis of binomial distribution. Daily sample sizes range from 3–30 (males) and 1–25 (females) for fall 1971, 2–110 (males) and 1–15 (females, plus some days with no captures) for spring 1972.

ected by the male via the vomeronasal system, and may or may not be the same as the trailing pheromone, which allows species-specific trailing of females by males and has its most pronounced effect during the spring mating period (Ford 1978, 1981, 1982; Ford and Low 1982). In any case, males are not sensitive to the female attractiveness pheromone early in the season when mating opportunities are very low; however, as the season progresses, females become slightly more abundant relative to males, and males become sensitive to the pheromone and

more discriminating about potential mates (Gartska *et al.* 1982).

Mated females are unattractive to males because of a male-inhibiting pheromone. Following copulation, a plug forms in the cloaca of the female (Devine 1975); this copulatory plug is apparently manufactured in the renal sex segment of the male (Crews and Gartska 1982). The male-inhibiting pheromone is probably made by the male at the same time as the plug (Ross and Crews 1977; Crews and Gartska 1982), although Devine (1977) suggests that the female produces

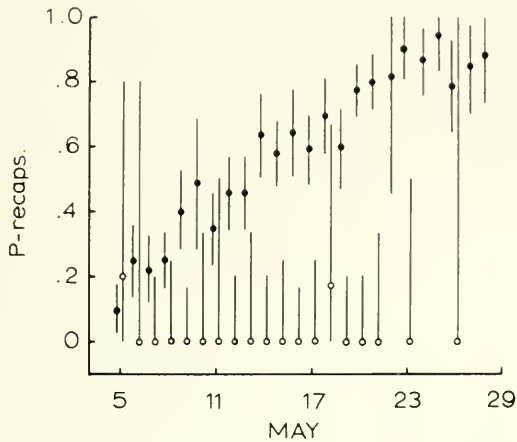


FIG. 4. Proportion of recaptures from same season in daily samples of *T. sirtalis* at Den 1 for spring 1971. Symbols as in Fig. 3. Daily sample sizes range from 11–123 for males and 1–6 (plus some days with no captures) for females.

the pheromone. In any case, females with plugs are unattractive to males. The plug is generally interpreted as a temporary mechanism for preventing insemination by rival males and therefore sperm competition, but not for ensuring sole paternity (Devine 1975; Gibson and Falls 1975). Since the plug is expelled by the female a few days after mating (Devine 1975), mated females may be only briefly unavailable or unattractive sexually.

An interesting question therefore is whether or not females mate more than once in a given spring, especially since Gibson and Falls (1975) provide indirect evidence of multiple insemination in *T. sirtalis* from Ontario. These authors argue that because ovulation and fertilization in *T. sirtalis* occur a few weeks after copulation (e.g., Gregory 1977a), all reproductive females represent mating opportunities for males and multiple insemination in a given mating season should be expected. For females, submitting to remating may simply be less risky (e.g., in terms of exposure to predators) than continually avoiding suitors (Gibson and Falls 1975). Multiple insemination is therefore most likely to occur in situations where females do not disperse rapidly from the denning area (e.g., Devine 1977). In the Interlake, however, females disperse almost immediately after emerging and mating, when they possess copulatory plugs and are presumably un-

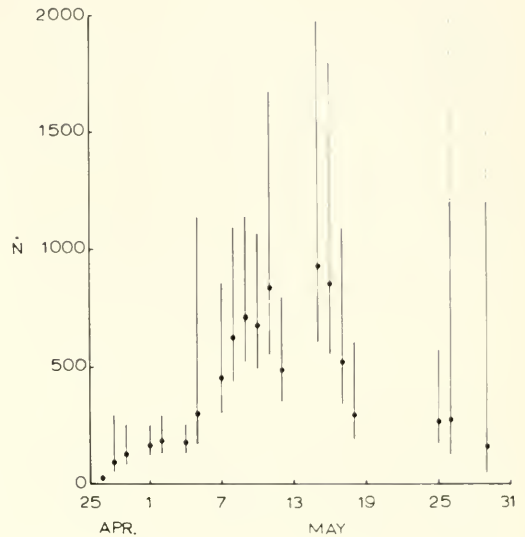


FIG. 5. Estimated above ground daily population sizes (N) of male *T. sirtalis* at Den 1 for spring 1972. Estimates from Jolly-Seber mark-recapture analysis (Jolly 1965). Vertical lines are 95% confidence limits (for method of calculation see Gregory 1974, 1977a). Data from Gregory (1974); note incorrect date of two data points in Fig. 3 of Gregory (1974).

attractive sexually. Multiple matings of females in spring are unlikely in this case. This does not preclude the possibility of multiple insemination from retention of sperm from a copulation the previous fall or earlier (Gibson and Falls 1975) or from a subsequent mating during dispersal, but these are probably rare events. Another possibility is simultaneous mating of a female by two males (polyandry, Gartska *et al.* 1982), but this is likely also rare.

What are the advantages to individuals of both sexes of the system of emergence and mating shown by the Interlake snakes? The emergence of males before females is a widespread phenomenon in snakes (Duguay 1963; Viitanen 1967; Lang 1971; Prestt 1971; Parker and Brown 1980; Gregory 1982), but other species do not show the same details of spring behavior as described here. The pattern of emergence of Interlake *T. sirtalis* appears to fit the model of Wiklund and Fagerström (1971), which is an attempt to account for the existence of protandry in butterflies. Wiklund and Fagerström conclude that protandry is a reproductive strategy of males which are capable of multiple mating, and is a result of

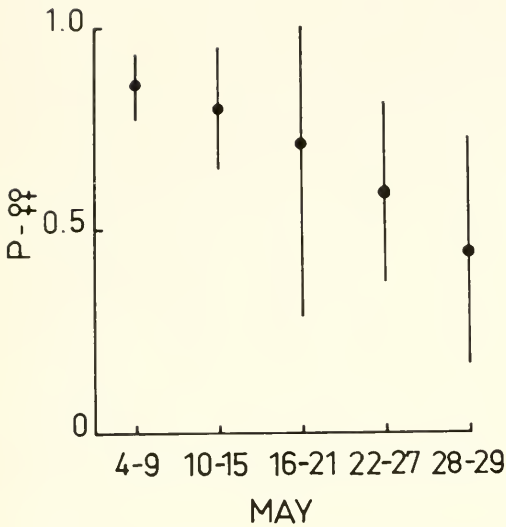


FIG. 6. Proportion of female (P-♀♀) *T. sirtalis* on roads in vicinity of Interlake dens in spring (1971 and 1972 combined). Data are grouped into 6-day intervals; vertical lines are 95% confidence limits calculated on basis of binomial distribution. Sample sizes range from 7–93. Data modified from Gregory (1974).

competition for mates (see also Gibson and Falls 1975). As long as the competitive ability of all males is equal, so that the number of receptive females encountered and mated by a male is a direct function of the proportion of such females in the population, males that emerge before females should mate with more females, on average, than should late emerging males. Competitive ability and relative mating success of individual male *T. sirtalis* in the Interlake have not been measured, but empirical observation of mating behavior in the field does not suggest any obvious variation in competitive ability. Perhaps mating success is reflected in the length of time individual males stay at the den in spring (i.e., males which mate several females early in the season might disperse earlier). Other species of snakes have different mating systems (e.g., *Masticophis taeniatus*, Bennion and Parker 1976; Parker and Brown 1980; *Vipera berus*, Viitanen 1967; Prestt 1971), but earlier emergence of males than females is still probably best explained in terms of competition (male-male aggression in these cases) among males for emerging females (Crews 1975; Parker and Brown 1980). Male *Vipera berus* also complete spermatogenesis by

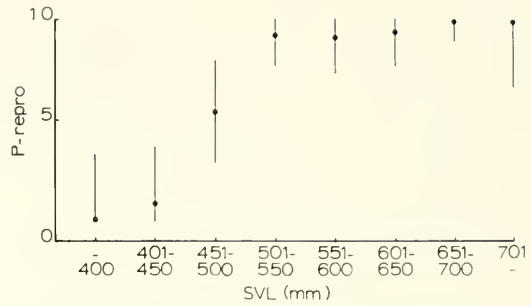


FIG. 7. Proportion of potentially reproductive (P-repro.) female *T. sirtalis* from Interlake dens (spring and fall 1972 and spring 1973 combined) in different snout-vent length (SVL) groups. Vertical lines are 95% confidence limits calculated on basis of binomial distribution. Samples sizes range from 3–35. Data from Gregory (1977a).

basking in spring (Volsoe 1944; Nilson 1980), thus acquiring additional benefits by emerging early. On the other hand, males of species which do not mate in spring should not be expected to emerge before females; this appears to be the case for *Crotalus viridis*, which mates in late summer in British Columbia (Macartney, pers. comm.).

Benefits accruing to females from this system are less obvious. One significant advantage is that reproductive females are almost certain to mate, although the extent, if any, to which females are able to exercise any choice of mate is unknown. The majority of females at dens are capable of reproduction (Fig. 7; compare with Fig. 1), but a significant number are not. However, probability of being reproductive is correlated with body size (Fig. 7; Gregory 1977a) and larger females are courted with much greater frequency than are smaller females (Hawley and Aleksuik 1976). Males therefore waste little energy on non-reproductive females. Copulatory plugs, indicating recent mating, are seen much more frequently in females over 500 mm SVL than in smaller females, an observation consistent with the data in Fig. 7. Hawley and Aleksuik (1976) also provide evidence from laboratory experiments that the probability of mating for females is correlated with body size. Almost all reproductive females leaving dens are mated whereas none of the non-reproductive females are (Table 3; Gregory 1977a).

[The female attractiveness pheromone may provide the basis for selection of large mates by

males (Crews and Gartska 1982; Gartska *et al.* 1982). Since the pheromone is related to vitellogenin and larger females produce more yolk because they have bigger broods (Gregory 1977a), larger females may be more attractive because they produce more pheromone (Crews and Gartska 1982; Gartska *et al.* 1982). Males might even choose mates on the basis of a previous year's reproductive output (Crews and Gartska 1982) since lipid may be stored in the skin of females (Gartska and Crews 1981; Crews and Gartska 1982; Gartska *et al.* 1982). In any case, males can select the potentially most fecund mate.]

A second advantage to females of this pattern of activity is that they are mated almost immediately upon emergence, reducing their time of exposure to predators (Crews and Gartska 1981) and allowing them to disperse quickly to the summer habitat and begin feeding. They thus spend a minimum of time active without feeding. This is important because summers are very short in this area and gravid females do not feed in advanced stages of gestation (Gregory and Stewart 1975). Late spring and early summer may therefore be an important time of year for reproducing females to balance their energy budgets. Males are not under such energetic constraints as reproductive females and may obtain additional benefits from being near shelter at the den if cold weather strikes in spring. Females apparently trade off this advantage for the others mentioned above. It is presumably also advantageous for non-reproductive (usually smaller) females to leave the den soon after emergence since they would then extend their feeding season and might reach a larger size by the end of summer; larger females tend to produce bigger broods (Gregory 1977a).

The observations and conclusions reported here are probably not unique to communal dens of garter snakes in the Interlake. Partly to answer this question, in 1979 I began monitoring activity patterns of *T. sirtalis* and *T. elegans* at a communal den in the Chilcotin-Cariboo region of British Columbia, also an area with long, cold winters. Data for only the first year and a half of the study are presented here, but some trends are apparent. Unlike the Interlake dens, this den is occupied in the summer by gravid females (Figs. 8 and 9); they apparently give birth there and the young remain at the den for their first winter. Few adult snakes are seen at the den in fall; per-

TABLE 3. Distribution of mated and non-mated female *T. sirtalis* in reproductive and non-reproductive categories. Samples from summer habitat and from roads in vicinity of dens in April and May 1972; reproductive and mating status determined by dissection (data from Gregory 1977a).

	Mated	Non-mated
Potentially reproductive	20	4
Non-reproductive	0	7

H_0 (no difference in proportion of mated females in reproductive and non-reproductive categories) rejected with $P < .001$ (χ^2 contingency table).

haps the fall activity period is very brief in this case. In other respects, however, activity at this den seems basically similar to that described for *T. sirtalis* in the Interlake. Spring collections from this den are again heavily biased in favor of males in both species (Figs. 8 and 9). Apparently, *T. sirtalis* leaves the den earlier in spring than *T. elegans*; it probably also emerges earlier. In *T. elegans*, as in Interlake *T. sirtalis*, the females that are caught in spring are usually not seen again at the den in the same season, whereas males are recaptured frequently over the spring period. Mating of both species occurs at the den in spring, although mating balls are seen much less frequently than in the Interlake. More often, evidence of spring mating is obtained from occasional females found with copulatory plugs in their cloacas.

The spring activity pattern of Interlake *T. sirtalis* is therefore probably typical of communally denning garter snakes. If so, it may be an important part of the suite of adaptations allowing garter snakes to be so successful in the rigorous environments which limit the northern distribution of most other North American reptiles.

QUESTIONS

Although various aspects of communal denning in snakes have been studied in some detail, there remain many gaps in our knowledge of this phenomenon. Many of the questions which need to be answered are interrelated and include the following: What are the important physical features of suitable hibernating sites? How do dispersion and abundance of suitable hibernating sites in a given area affect the distance snakes migrate between hibernacula and summer range?

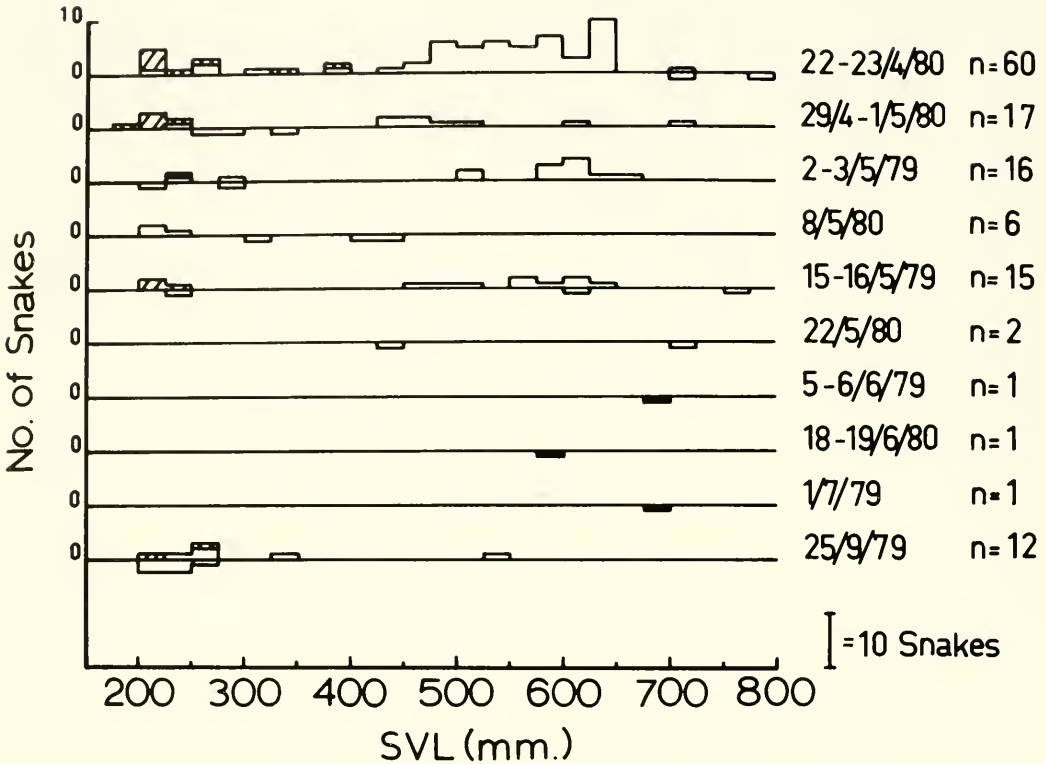


FIG. 8. Size frequency distribution of *T. sirtalis* at den in Chilcotin-Cariboo region for various times of year (1979 and 1980 combined). Animals are grouped into intervals of 25 mm snout-vent length (SVL). Dates given are day/month/year; n = sample size. Data above each line represent males (open areas) and unsexed juveniles (hatched areas); data below line represent females (dark areas represent obviously gravid females).

Why do some snakes disperse in a particular direction, especially if suitable habitat is also available in other directions? Why are young snakes often poorly represented at communal dens and where do they hibernate? Where, in relation to the den, are young snakes born or hatched, and does this influence the likelihood of them using the same den as the adults? How do individual snakes find their way back to the same den over long distances year after year, especially where several dens are present in the same general area? Are new dens occasionally colonized (or old ones recolonized following a disturbance) and if so, how and at what rate? What is the extent of genetic isolation among populations at dens in a given area and how is new genetic material introduced to a den? Why are snakes sometimes active at dens for long periods of time in fall and/or spring without feeding or mating? Several of these questions are discussed by Parker and

Brown (1980), who also suggest possible approaches to some of them.

Underlying all of this is the question of why snakes den communally. Complex, apparently co-ordinated patterns of emergence and mating, such as that shown by Interlake *Thamnophis sirtalis*, can probably function only in a communal denning situation. An important hypothesis therefore is that snakes which hibernate communally have a reproductive advantage over those which hibernate as isolated individuals. This hypothesis should be testable. The ideal way to make such a test would be to make direct comparisons of communal and non-communal hibernators within the same population, but I know of no examples in which both types occur. Comparison of the same species in widely separated parts of its range is somewhat risky because the environmental pressures may differ markedly in the two locations. A more useful

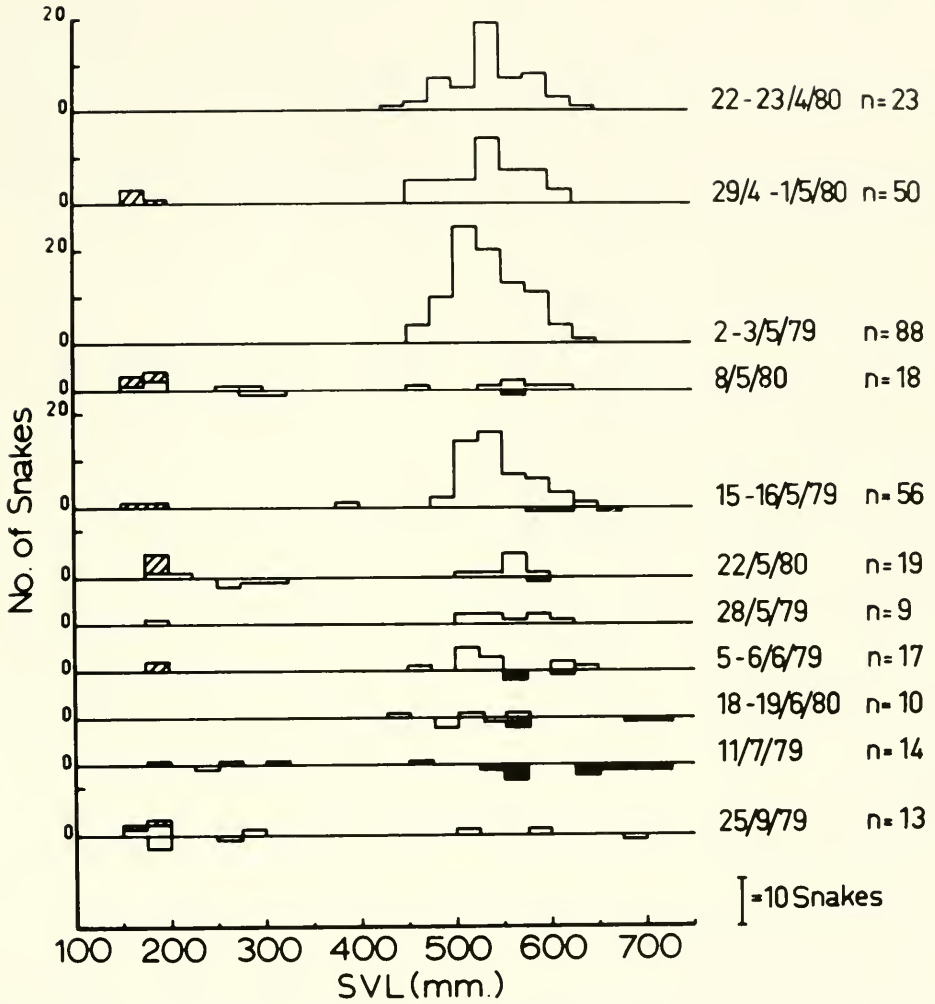


FIG. 9. Size frequency distribution of *T. elegans* at den in Chilcotin-Cariboo region for various times of year (1979 and 1980 combined). Symbols as in Fig. 8.

approach might be to compare the ecology of communally and non-communally hibernating species within the same region; if the species involved are similar in abundance, size, temperature tolerance, etc., it might at least be possible to eliminate the alternative hypothesis that communal hibernation results from a shortage of overwintering sites. However, different species may use different strategies to solve the same environmental problem (Wilbur *et al.* 1974; Stearns 1976) and different species may hibernate communally for different reasons. In fact, the hypotheses put forward in this paper to account for communal denning are not mutually

exclusive and may be difficult to separate by observation. The most fruitful approach to this problem therefore is probably through carefully planned manipulative experiments on specific cases. I am now designing such studies.

SUMMARY

In northern regions, where winter may be several months long, many snake species hibernate communally in large aggregations of up to a few thousand individuals in extreme cases. Communal hibernacula are usually permanent structures, often used annually by the same individ-

uals, and are sometimes a considerable distance from the summer habitat. Denning populations frequently consist mainly of adults and the snakes may be active at dens for some time each spring and fall. Communal hibernation probably reflects low availability of overwintering sites in many cases. Another advantage, however, may be that individuals hibernating with conspecifics have enhanced chances of successfully mating early in the active season, an important adaptation where summers are short. Analysis of activity of garter snakes (*Thamnophis sirtalis*) in spring at dens in Manitoba indicates that the two sexes have different behavior patterns consistent with their different reproductive strategies (i.e., males mate more than once per season, females probably once only). Males emerge in fairly large numbers early in spring, whereas females emerge in smaller numbers throughout the spring. Most reproductive females mate immediately upon emergence and then disperse to the summer habitat, thereby presumably maximizing the length of their summer activity period. Males, in contrast, remain at the den for longer periods in spring and continue mating. Thus, emergence patterns are co-ordinated in such a way that mating opportunities are maximized for all individuals in the population. Such a system can operate only in the context of communal denning. In fall, when mating is rare, the two sexes do not behave differently from one another. Preliminary data from a garter snake (*T. sirtalis* and *T. elegans*) den in British Columbia suggest similar behaviors. Other communally denning snakes do not necessarily show these kinds of behavior patterns, but this does not negate the presumed advantages of such behaviors. It should be possible to design experiments which test hypotheses arising from the garter snake model.

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Parameters of Two Populations of Diamondback Terrapins (*Malaclemys terrapin*) on the Atlantic Coast of Florida

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INTRODUCTION

The diamondback terrapin, *Malaclemys terrapin* has several attributes which would seem to make it an interesting subject for ecological study. These include a unique habitat for chelonians (brackish water), an extremely wide linear range (Massachusetts–Texas), and the distinction of being the “most celebrated of American turtles,” a reflection of the popularity of this turtle as a gourmet food item in the early 20th century (Conant 1975). Despite these features, our knowledge of the life history of this species remains surprisingly limited. Studies of terrapins in the wild have dealt mainly with reproduction (Finneran 1948; Reid 1955; Burger and Montevecchi 1975; Montevecchi and Burger 1975; Burger 1976a, 1976b, 1977; Auger and Giovannone 1979; Seigel 1980b, 1980c), epizootic fouling (Jackson and Ross 1971; Ross and Jackson 1972; Jackson *et al.* 1973), mortality (Seigel 1978, 1980a) and hibernation (Lawler and Muisick 1972; Yearicks *et al.* 1981). Data on the population biology of *Malaclemys* are few, especially under natural conditions. Cagle (1952) reported growth rates and age at maturity for Louisiana intergrades (*M. t. pileata* × *littoralis*), and Hurd *et al.* (1979) described the size structure and population size of *M. t. terrapin* from Delaware. Most data on population biology are based on captives (Hildebrand 1929, 1932; Allen and Littleford 1955), and must be viewed with caution due to the unnatural conditions under which the turtles were maintained (Carr 1952; Burnley 1969).

From 1977 to 1979 I studied the life history and ecology of the Florida east coast terrapin, *M. t. tequesta*, at the Merritt Island National Wildlife Refuge, Brevard County, Florida. This paper presents data on the growth rates, population structure, and age at maturity for two populations of *Malaclemys* under natural conditions.

MATERIALS AND METHODS

The Merritt Island refuge consists of three large, brackish water lagoons, each surrounded by a

series of canals and ditches which are permanently filled with water. A more detailed description of the area is presented elsewhere (Seigel 1979). For the purposes of this study, terrapins were collected primarily from the northern ends of two lagoons, known locally as the Indian and Banana rivers (Fig. 1). Indian River turtles were collected by deploying small mesh (maximum diameter = 6 cm) gill nets along a narrow canal bordering a dike road. Two nets were set perpendicular to the shoreline to block off a 100 m section of the canal. Turtles moving up and down the canal became entangled in the nets and were removed within two hours of capture. Turtles from the Banana River were collected by walking surveys around a small man-made spoil island. Turtles were captured by hand while they basked along the shoreline, or while they swam and fed in the clear waters surrounding the island.

The following straight-line measurements were recorded to the nearest 0.1 cm using vernier calipers; carapace (CL) and plastron (PL) length, length of the right abdominal scute, and medial length of visible abdominal annuli. Wet body weight was recorded to the nearest 10 g with a spring balance. All turtles were given an individual mark (Ernst *et al.* 1974) and released at point of capture.

Plastral annuli have been used to estimate the growth rate and age of several species of turtles, using a variety of techniques (see Graham 1979 for review). In my study, age was estimated using the method of Sexton (1959). Growth was estimated using Sergeev's (1937) formula of $L_1/L_2 = C_1/C_2$, where C_1 represents the annuli length, C_2 the abdominal scute length, L_1 the plastron length when the annuli was formed, and L_2 the current plastron length. Since large, female *Malaclemys* > 16 cm PL often lacked one or more annuli, they were excluded from this analysis.

Statistical tests follow Ott (1977). Means are followed by \pm one standard deviation.

RESULTS AND DISCUSSION

Growth and Sexual Maturity.—One hundred thirteen *Malaclemys* were examined from the

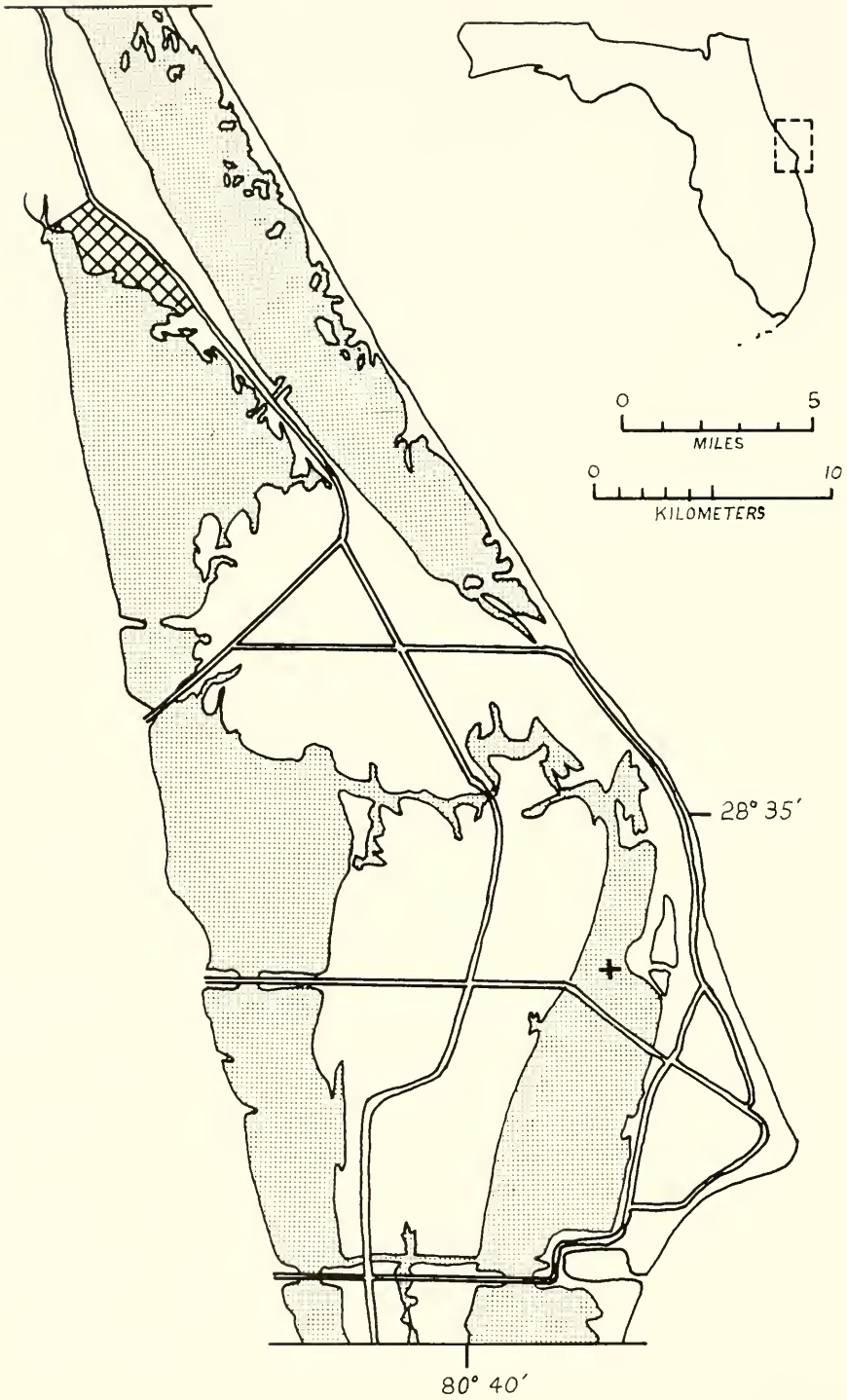


FIG. 1. Merritt Island National Wildlife Refuge. Shaded areas represent lagoonal waters. Indian River study site is shown by cross-hatching. Banana River study site by cross.

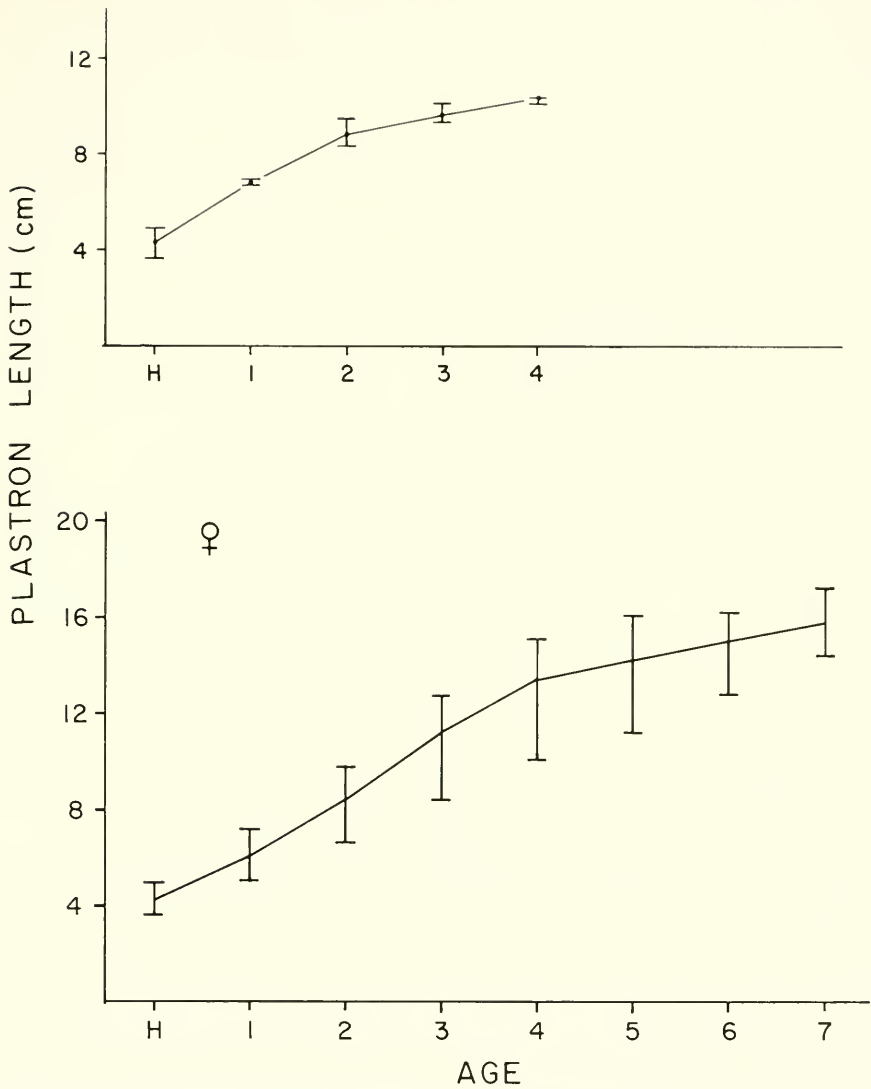


FIG. 2. Relationship between age and plastron length in 53 female and 13 male *Malaclemys* from the Indian River. Vertical bars represent sample range.

Indian River and 44 from the Banana River. Fifty-three of the Indian River turtles bore distinct growth annuli, but heavy shell damage from barnacles (Seigel 1983) obliterated most annuli on terrapins from the Banana River. Ontogenetic change in the relative size of the abdominal scute, such as that noted by Moll and Legler (1971) for tropical *Pseudemys scripta*, was minor in this study (<2%), so no correction factor was needed.

Fig. 2 shows the relationship between age and plastron size. The wide variability in size within

a particular age class observed in *Malaclemys* frequently occurs in other turtles (Gibbons 1968; Ernst 1971, 1975, 1977; Plummer 1977b). Growth of the sexes is relatively constant and similar for the first two years of life, but begins to diverge after age three, when male growth rates decline, but females continue to grow at a steady rate. The curve for both sexes shows a marked decline in growth as sexual maturity is reached (see below). Fig. 3 shows the relationship between percent growth/year and plastron size. Most

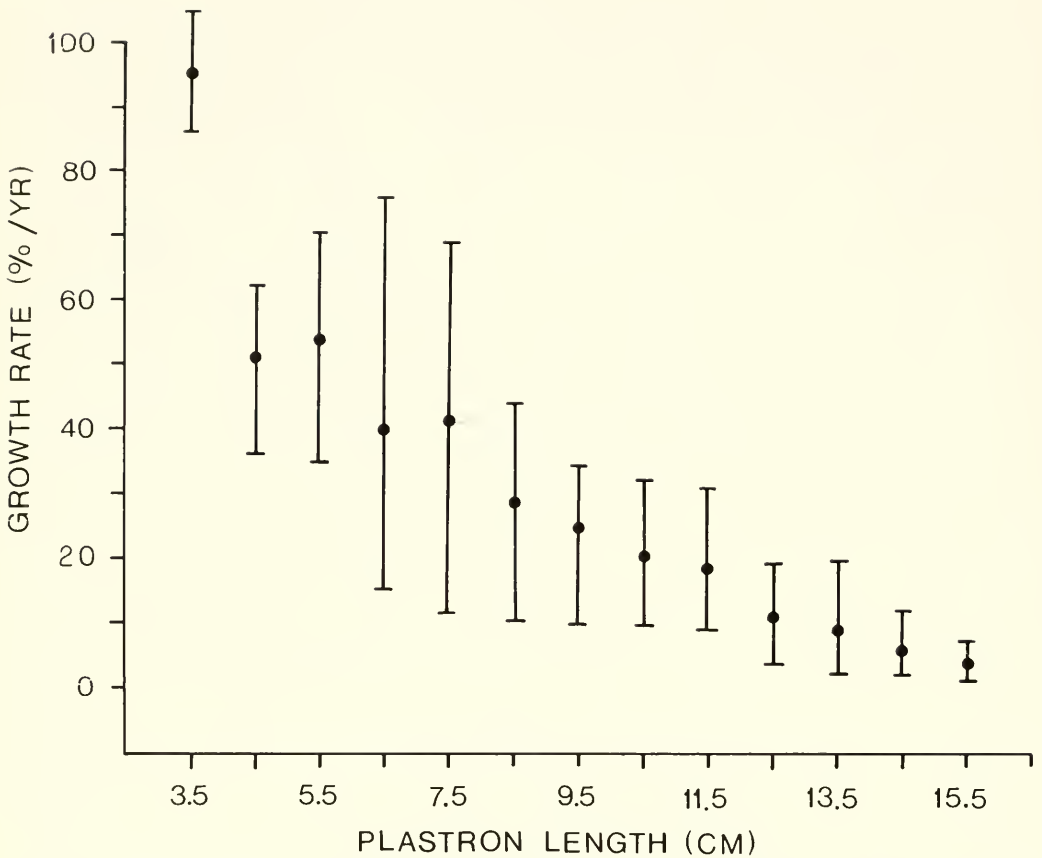


FIG. 3. Relationship between growth rate (%/year) and plastron length for Indian River *Malaclemys*. Vertical bars represent sample range.

rapid growth occurs at PL 3–3.9 cm, followed by a sharp decrease, and then a more gradual decline in growth to <5%/year in mature individuals. This pattern is similar to that of most other freshwater turtles, especially the genera *Chrysemys* and *Pseudemys* (see Bury 1979 for review). Limited data from turtles recaptured after six months or more support the above growth estimates. Two mature females of 13.8 and 14.6 cm PL grew at annual rates of 5.4% and 2.9% respectively. Six mature females of >15.0 cm PL grew at a mean annual rate of 2.2% (range = 0–7.1%). Based on these values, the largest female in the Indian River population (PL = 17.7 cm) would be approximately 15 years old. Longevity in this population is estimated to be about 20 years.

Fig. 4 compares the PL/age relationships of *Malaclemys* from different parts of the range. Florida *Malaclemys* grow at a slightly faster rate

than terrapins from North Carolina or Louisiana (Cagle 1952). Although Florida *Malaclemys* are larger at hatching than turtles from the other populations (Seigel 1980c), this difference in initial size is insufficient to account for the differences in Fig. 4. Gibbons (1967) showed that even local populations of *Chrysemys picta* varied widely in growth rates because of differences in local feeding habits and food quality. Most data suggest that the feeding habits of *Malaclemys* are relatively similar throughout its range (Cagle 1952; Wood 1976; Hurd *et al.* 1979; R. Seigel, pers. obs.; but see Cochran 1976), with no comparable dramatic differences such as Gibbons (1967) noted. It therefore seems unlikely that the differences in growth rates seen in Fig. 4 are due to differences in local feeding habits. However, the North Carolina turtles were captives, and were fed fish as supplements to their normal food

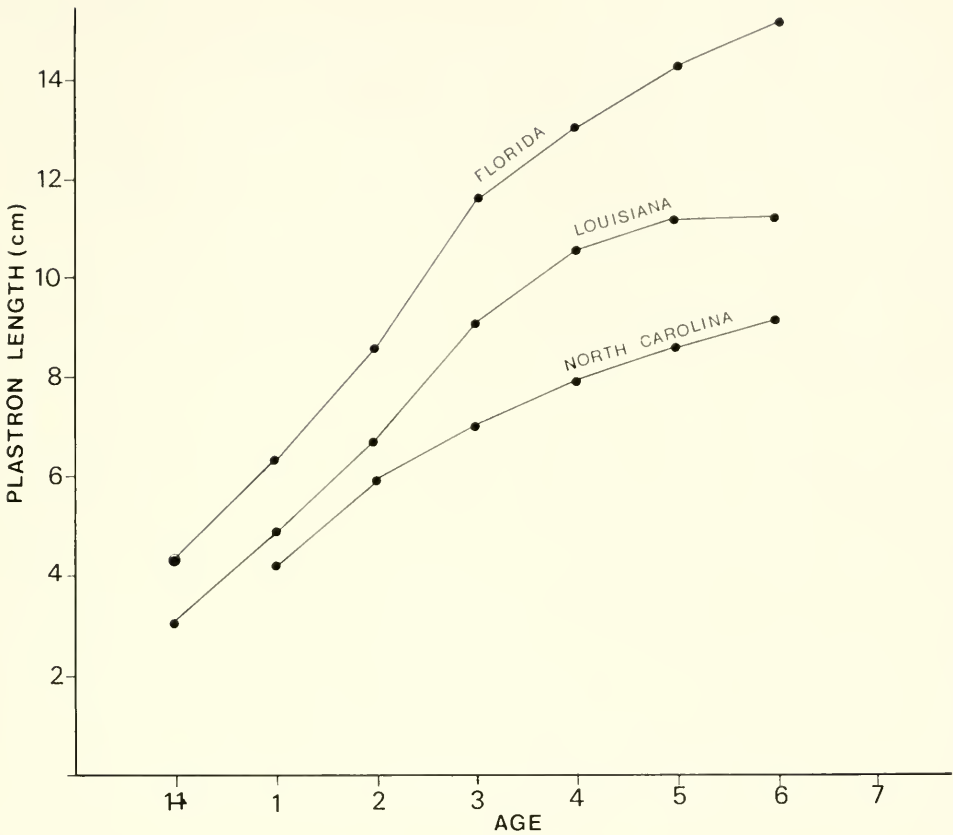


FIG. 4. Comparison of growth rate of *Malaclemys* from different parts of the range (sexes combined). See text for data sources.

(mollusks), so their growth may have been somewhat affected. The differences in Fig. 4 may reflect the longer activity and growing season of *M. t. tequesta*, which at Merritt Island is active from mid-February to late November (Seigel, unpub. data), whereas North Carolina captives were only active from May to October (Hildebrand 1932). No data on the activity season of Louisiana terrapins are available, but from a climatic viewpoint, it is probably more similar to Florida than North Carolina.

The smallest female showing evidence of sexual maturity (oviducal eggs or corpora lutea) was 13.5 cm PL, and all females > 14.0 cm PL were mature. Fig. 2 shows that most females reach 13.5–14.0 cm by age four, but that some may not attain maturity until age five. The smallest male considered mature (based on secondary sexual characteristics and enlarged testes) was 9.1

cm PL, and all males > 9.5 cm PL were considered mature. According to Fig. 2, males may reach this size as early as the second year of life, but most probably do not mature until age three. Hildebrand (1932) suggested that sexual maturity in *Malaclemys* was related to size rather than age, and my results support this idea. Table 1 shows the size and age at maturity for *Malaclemys* from different parts of the range. Size at maturity is rather uniform for both sexes, while age at maturity is more variable.

Bury (1979) summarized the data on growth and sexual maturity for freshwater, mainly north-temperate turtles, and made the following conclusions: 1) males often mature earlier and at a smaller size than females; 2) growth is most rapid before maturity is reached; 3) in temperate regions, individuals in southern populations mature earlier than northern conspecifics; 4) sexual

TABLE 1. Size and age at sexual maturity for male and female *Malaclemys terrapin* from different parts of the range.

Subspecies (locality)	♀ size (plastron length) and age (yrs) at maturity	♂ size (plastron length) and age (yrs) at maturity	Authority
<i>terrapin</i> (New Jersey)	13.2 cm/? yrs	—	Montevecchi and Burger (1975)
<i>terrapin</i> ¹ (North Carolina)	13.7 cm/7 yrs	9.0 cm/5 yrs	Hildebrand (1932)
<i>pileata</i> × <i>littoralis</i> (Louisiana)	16.0 cm/6 yrs	9.9 cm/3 yrs	Cagle (1952)
<i>tequesta</i> (Florida)	13.5 cm/4–5 yrs	9.5 cm/2–3 yrs	This study

¹ Captive population.

maturity is usually related to attaining a certain size rather than a certain age. The data from subtropical *Malaclemys* appear to conform closely to these patterns.

Sexual Dimorphism.—The sexes of *M. t. tequesta* are highly dimorphic, both for external characters and body size. Male terrapins have smaller, narrower heads, darker carapacial markings, and larger carapacial keels than females. In addition, adult males have long, thick tails, with the vent posterior to the margin of the carapace, while adult females have short, narrow tails with the vent beneath the overhanging carapace. The mean PL and weight of 113 Indian River females was 15.4 ± 1.00 cm, and 886 ± 193 g. The same measurements for 13 Indian River males were 10.4 ± 0.69 cm, and 283 ± 50.9 g. Using the terminology of Fitch (1981), *M. t. tequesta* has a FMR (female to male ratio) for length and weight of 148 and 313, respectively. Thus, while females are ca. 1.5 times male length, they are >3 times male weight. Fitch (1981) reported that other turtle species showed similar variation in FMR between length and weight.

Berry and Shine (1980) and Fitch (1981) reviewed sexual size dimorphism in turtles and other reptiles, and related such dimorphism to intrasexual competition and divergent reproductive strategies. The greater body size of female *M. t. tequesta* probably evolved as a means to increase reproductive potential, since clutch size is positively correlated with body size in *Malaclemys* (Montevecchi and Burger 1975; Seigel 1980c). Large males on the other hand, would gain no reproductive advantage over smaller males, because male combat for mates is apparently absent in *Malaclemys* (Seigel 1980b). How-

ever, small body size permits males to mature at a younger age than females, possibly increasing lifetime reproductive potential.

Population Structure.—The size class structure of Indian and Banana river females, and that of Indian River males are shown in Figs. 5 and 6. Too few Banana River males were captured for analysis. The age structure of Indian River terrapins is shown in Fig. 7. There is a noticeable lack of small or immature individuals in both populations. The under-representation of small terrapins is probably the result of sampling error which favored adults. Small *Malaclemys* (<9 cm PL) were rarely seen at either study site, and it seems likely that behavioral differences exist between adults and juveniles that reduce the probability of capturing small terrapins. Hurd *et al.* (1979) advanced a similar hypothesis to explain the lack of small individuals in a Delaware population of *M. t. terrapin*, but also noted that local habitat destruction may have caused "catastrophic mortality" among young terrapins. No evidence for such habitat destruction exists at Merritt Island (at least recently), and I suggest that sampling error, rather than heavy mortality, is sufficient explanation for the lack of immature individuals.

The population size structures of Indian and Banana river females are significantly different (Mann-Whitney *U* test, $P < 0.01$), with the most striking differences reflected in the 17.0 cm and larger size classes (Fig. 5). Thirty-one percent of the female turtles from the Banana River were >17.0 cm PL, compared to only 3% of the Indian River terrapins in the same size range. Conceivably, these differences could be artifacts of the different sampling techniques used, but this seems

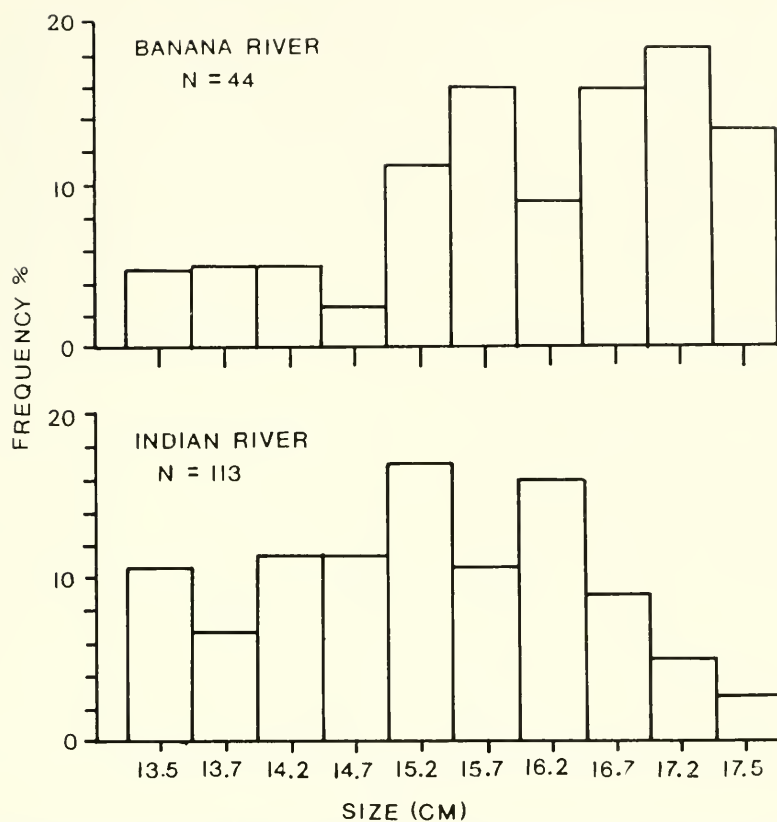


FIG. 5. Size structure of female *Malaclemys* from the Indian and Banana rivers 1977–1979. Size distributions did not differ between sampling periods (Mann-Whitney U test, $P > .10$), so data are combined for presentation.

unlikely, since both techniques were effective in capturing large individuals and it was in the larger size classes that most of the differences between the populations were found. Gibbons (1967) found that local populations of *C. picta* may vary widely in size structure, reflecting differences in feeding habits, food quality and growth rates. I was unable to determine if Indian and Banana river *Malaclemys* grew at different rates, but qualitative analysis of stomach contents from females from the two sites showed no striking differences (Seigel, unpub.), and it seems improbable that feeding habits varied sufficiently to account for the differences in size structure seen in Fig. 5. An alternative hypothesis is differential mortality. Elsewhere (Seigel 1980a) I have shown that Indian River females are subject to raccoon predation during the nesting season. No comparable predation was observed along the Banana River. Each time an Indian River

female nests, there is a small but definite risk of encountering a predator and being eliminated from the local population. Because *M. t. tequesta* may nest up to three times/year (Seigel 1980c), the probability of Indian River females surviving many nesting seasons may be low. This may result in a lower proportion of females surviving to reach the larger (i.e. older) size classes that might otherwise occur in the absence of predation. The under-representation of larger females in the Indian River when compared to the Banana River might be a reflection of the higher mortality rate among mature Indian River females.

Sex Ratio.—The ratio of females/males for Merritt Island *Malaclemys* is shown in Table 2. Ratios varied seasonally, but were always significantly different from unity (binomial distribution, $P < 0.05$). The samples showing the least skewed ratios (March–April) were taken during

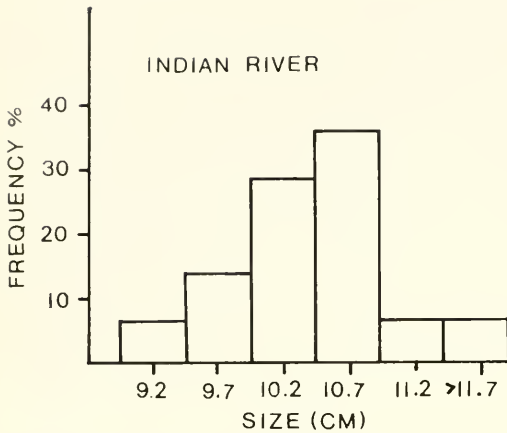


FIG. 6. Size structure of male *Malaclemys* from the Indian River, 1977-1979. Differences in size structure between sampling periods were insignificant (Mann-Whitney U test, $P > .10$), so combined data are shown.

the spring mating season (Seigel 1980b), at a time when males reach their greatest representation in local populations. The 5:1 ratio taken at this time probably represents the best estimate of the "true" sex ratio in this population. Hildebrand (1932), Hurd *et al.* (1979), and Yearicks *et al.* (1981) have also reported female-biased sex ratios in *Malaclemys*, although Cagle (1952) noted the opposite trend in offshore populations from Louisiana.

The skewed sex ratios in Merritt Island *Malaclemys* are not the result of sampling bias or investigator error as suggested by Gibbons (1970) for other studies where the sex ratio was not 1:1. The different sampling techniques used, as well as the number of populations examined, probably precluded most bias due to sampling error, and the distinct sexual dimorphism in *Malaclemys* (see above) greatly reduced the chances of mistaking juvenile males for females, as Gibbons (1970) suggested. Bury (1979) found that of 39 studies of sex ratio in freshwater turtles, skewed ratios were reported in only 13 (33%). Assuming no bias due to sampling error, cases of skewed sex ratio such as that of *M. t. tequesta* are in the minority. Such skewed ratios may be the result of differential juvenile mortality (which has been neither confirmed or rejected), or temperature-modified sex determination during incubation, for which extensive evidence exists (see Bull and Vogt 1979; Yntema 1979 and references

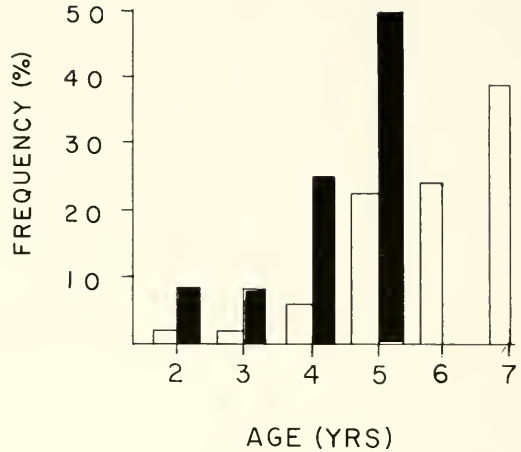


FIG. 7. Age structure of 12 male and 107 female *Malaclemys* from the Indian River, based on age-size relationships calculated from growth annuli. Males > 5 years old, and females > 7 years old, could not be accurately aged, so they are included with the oldest classes. Males are represented by shaded bars, females by open bars.

therein). If skewed sex ratios among adult turtles are a reflection of incubation temperatures, it remains to be determined if such ratios occur fortuitously (depending on the nest site chosen by the female) or if these ratios have been selected for by such factors as resource abundance, as was suggested by Nichols and Chabreck (1980) for *Alligator mississippiensis*.

Population Size.—Schnabel population size estimates and 95% confidence limits (Overton, 1969) for the Indian and Banana rivers were 404.7 (95% C.L. = 182.8-790.5) and 212.5 (95% C.L. = 58.7-627.3), respectively. The wide variability in the confidence limits are probably a result of two factors: 1) a low recapture rate which did not exceed 50% until the last sampling period, and 2) the apparent ability of *Malaclemys* to freely move into and out of the study area for short time periods (due to the lack of natural

TABLE 2. Sex ratio (females/males) of Merritt Island *Malaclemys* during different sampling periods.

Study site	Sampling period	Sex ratio	N
Banana River	February-November	9:1	47
Indian River	February-November	10:1	99
Indian River	March-April	5:1	26

barriers restraining movement). Plummer (1977a) found that temporary movements of *Trionyx muticus* out of his Kansas study site greatly increased the variability of his population size estimates. Although *Malaclemys* at Merritt Island showed relatively long-term (ca. 18 months) fidelity to a particular area (Seigel 1979), it is probable that short-term movements took place at both study sites, so the above estimates may be somewhat biased.

These population estimates and the size limits of the two sampling areas were used to construct density estimates. The Indian River sampling area covered 2.27 acres, yielding a density of 178.3 individuals/acre; the Banana River sampling area was 1.62 acres, yielding a density of 131.1 individuals/acre. These figures are somewhat higher than most reports of density in freshwater turtle populations (Bury 1979), but are not as high as the 239 individuals/acre reported by Ernst (1971) for *C. picta*. Biomass estimates, based on the above figures and wet body weight were 390.0 kg/ha for the Indian River, and 355 kg/ha for the Banana River. Both the density and biomass estimates may be somewhat inflated as a result of a) an arbitrary and possibly unrealistically low estimate of the population boundaries, and/or b) the tendency of *Malaclemys* to form large aggregations during the breeding season (Seigel 1980b). However, it seems clear that Merritt Island *Malaclemys* may attain a considerable density and biomass in local areas, at least during certain times of the year.

SUMMARY

The growth rates, age at maturity, population size and population structure of the Florida east coast terrapin, *Malaclemys terrapin tequesta* were studied from 1977 to 1979 at the Merritt Island National Wildlife Refuge, Brevard County, Florida. Data from two areas (Indian and Banana rivers) are presented. Growth was most rapid immediately after hatching, declining to <5%/year in mature turtles. Females matured at a plastron length of 13.5–14.0 cm, at an age of 4–5 years. Male terrapins reached maturity at a plastron length of 9.0–9.5 cm, at an age of 2–3 years. Female terrapins attain a much larger body size than do males, with a mean FMR (female to male size ratio) of 148 for length and 313 for weight. Such dimorphism probably reflects divergent reproductive strategies between the sexes; females

benefit from large body size via increased reproductive potential, whereas males attain only a small body size, but reach maturity earlier than females. The two study populations differed significantly in size structure, with the Banana River population having relatively more individuals in the larger size classes. This may reflect higher mortality among Indian River females. The sex ratios of both populations were significantly different from 1:1, with females outnumbering males by at least 5:1. Schnabel population size estimates for the Indian and Banana rivers were 404.7 and 212.5, respectively, and it appears that *Malaclemys* may attain a considerable density and biomass in local areas.

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An Ecological Study of the Cricket Frog, *Acris crepitans*

RAY D. BURKETT

INTRODUCTION

The cricket frog, *Acris crepitans*, is a useful subject for population studies since it is generally abundant throughout most of the year and tends to form separate and distinct populations. It occurs in a variety of habitats, such as along lakes, pond, rivers, streams and occasionally temporary ponds or rain pools and even relatively dry stretches of intermittent streams. Most *Acris* aggregate on relatively level, bare areas at the water's edge, avoiding steep, vegetation-covered slopes in most instances. Cricket frogs venture into water away from the shore line only when mats of algae are present on the surface.

Earlier knowledge of the ecology of *Acris* was based mainly on short notes summarized by Wright and Wright (1942). More recent studies include those by Turner (1960b) and Ferguson *et al.* (1965) on *Acris gryllus*; and those by Pyburn (1958, 1961a, 1961b), Blair (1961), Ferguson *et al.* (1967), Bayless (1969b), Labanick (1976), and Johnson and Christiansen (1976), on *A. crepitans*. Nevo (1973a, 1973b) has studied both species and Bayless (1969a) studied sympatric populations of both species.

Some comparisons were made with populations of *Acris* from other locations, but the main objective of this study was to determine if there were any differences in the ecology of populations of cricket frogs in different habitats separated by only a few kilometers.

DESCRIPTION OF STUDY AREAS

Populations of *Acris* were studied in and near Lawrence, Douglas County, Kansas, in the fall of 1961, and from fall 1963 through spring 1966. Two populations were studied intensively by capture/recapture and toeclipping: one in a wooded pond and stream at the University of Kansas Natural History Reservation (KUNHR), about 11 km northeast of Lawrence, and the other in an open reservoir and 11 rectangular ponds at the University Fish Laboratory (FL) on the southwestern part of the campus. The Kansas River lies between the two populations as a possible barrier to gene flow.

The pond at the Reservation was created by the construction of an earthen dam impounding water on its northeastern side. Water overflowing the pond drains down a stream to the southwest and into a small creek that empties into the Kansas River about four km east of Lawrence. The pond has a maximum circumference of about 435 m. The northeastern end of the pond is shallow and swampy with numerous willows (*Salix*) along its edge. Honey locust (*Gleditsia triacanthos*) borders much of the northern edge and northwestern edge of the dam. The southeastern end of the pond is almost always shaded by large oaks (*Quercus velutina*), elms (*Ulmus americana*) and ash (*Fraxinus americanus*). Much of the northwestern edge of the pond and dam are bordered by small trees, shrubs, herbs and grasses. Algae are common in the pond in a zone from about 0.3 to 0.9 m from shore. For a detailed description of the Reservation see Fitch (1952, 1965) and Fitch and McGregor (1956).

At the Fish Lab the reservoir is on a south-facing slope and the 11 ponds are located about 90 m south of the reservoir. Each pond is drained through pipes that empty into a small stream south of the ponds. The stream continues south until it reaches the Wakarusa River, which enters the Kansas River about 11 km east of Lawrence. The reservoir fluctuates considerably in depth since water is used to fill the ponds. The maximum circumference of the reservoir during my study was about 365 m, and the minimum 230 m. The only trees around the reservoir are small saplings of *Populus* and *Salix*, which occur in about equal numbers.

METHODS

A total of 2492 frogs were captured at the Natural History Reservation, and 1077 were captured at the Fish Laboratory. Owing to the large numbers of individuals that were sometimes present, frogs were marked serially rather than individually. Areas (not exceeding 100 m long and 4.5 m wide) were marked off at each locality. All individuals captured in each area were given a unique mark for that area and date. Frogs captured during the initial sampling period and sub-

TABLE 1. Estimated reproductive output for *Acris crepitans* in two populations in northeastern Kansas. See text for explanation.

Location	Year	Approx. no. in pop. in May	Approx. no. of females	Estimated no. of eggs laid (200–275 per female)
KUNHR				
Pond	1964	90	27	5400–7425
	1965	318	95	19,000–26,125
Stream	1966	100	30	6000–8250
Fish Lab				
Ponds	1965	68	32	6400–8800
Reservoir	1965	47	22	4400–6050
	1966	24	11	2256–3025

sequently recaptured, were given an individual mark on the third recapture. Frogs found unmarked at the second or subsequent sampling periods were given a unique mark. The place of capture, precise to the nearest meter, was recorded whenever frogs were given individual markings and during subsequent recaptures. Whenever new groups were being marked, they were captured in an area of pond-margin up to 6 m in length, then released in the center of the area.

RESULTS AND DISCUSSION

Breeding Season

The breeding season of *Acris* varies somewhat with geography and weather. Periods of calling near Austin, Texas have been reported as early as 30 January and as late as 10 September (Blair 1961). Smith (1961) stated that in Illinois calling occurs from late April until late summer; in Iowa, Johnson and Christiansen (1976) reported calling from mid-May until late July. In this study, large choruses were heard as early as late April in 1965 and mid-May in 1964 and 1966, and as late as 23 June 1964. Calling ceased by the last week in July. Each year calling began in the daytime; but later, as temperature increased, calling also occurred at night.

Observation of gravid and post-partum females indicates that most spawning occurred from late May to early July. Eggs became fully developed by about mid-April, and almost all females remained gravid until the end of May. Post-partum females first appeared in the populations on 6 June 1964, 31 May 1965 (KUNHR) and 29 June 1965 (FL). In the 13 July 1965 sample (KUNHR), some females were fully gravid, but most had only a few eggs remaining in one or both oviducts. One female containing only a few eggs was found as late as 3 August, and it appears that females may either retain a few eggs, or mate at least twice during the breeding season, laying a portion of their eggs each time they mate. In Kansas, however, there is no second breeding involving young-of-the-year as reported by Pyburn in Texas (Blair 1961).

Metamorphosed young first appeared about 10 July, and incompletely metamorphosed frogs still retaining tails were observed as late as 29 September. Larval development generally requires from five to ten weeks in northeastern Kansas (Burkett 1969), and transformation into frogs takes about two days (Wright and Wright 1942).

In northern Texas, I have found motile sperm in young males in early September. In the Kansas populations sperm were grouped in clumps in late September, but by early October nearly all males had well-formed sperm. A few males also develop chin spotting in the fall, but the vocal pouch is formed in late March or April, preceding the breeding season. These findings are in contrast to Brenner's (1969) conclusions that *Acris* must overwinter before attaining sexual maturity.

Sex Ratio and Reproductive Potential

Tadpoles and juveniles of *Acris* are easy to sex if dissected, as the testes are well formed and black. The sex ratio in newly metamorphosed *Acris* was found to be about four females per male, but in frogs over three months old, males usually were predominant. From September until the following July, males averaged between

FIG. 1. Growth rate of two populations of *Acris crepitans*, illustrated by combined samples for each month. Range, mean, one standard deviation, and two standard errors are indicated for each sample. Numbers above or below each line indicate sample size. April to July samples are subdivided to indicate males, left; entire sample, center; and females, right.

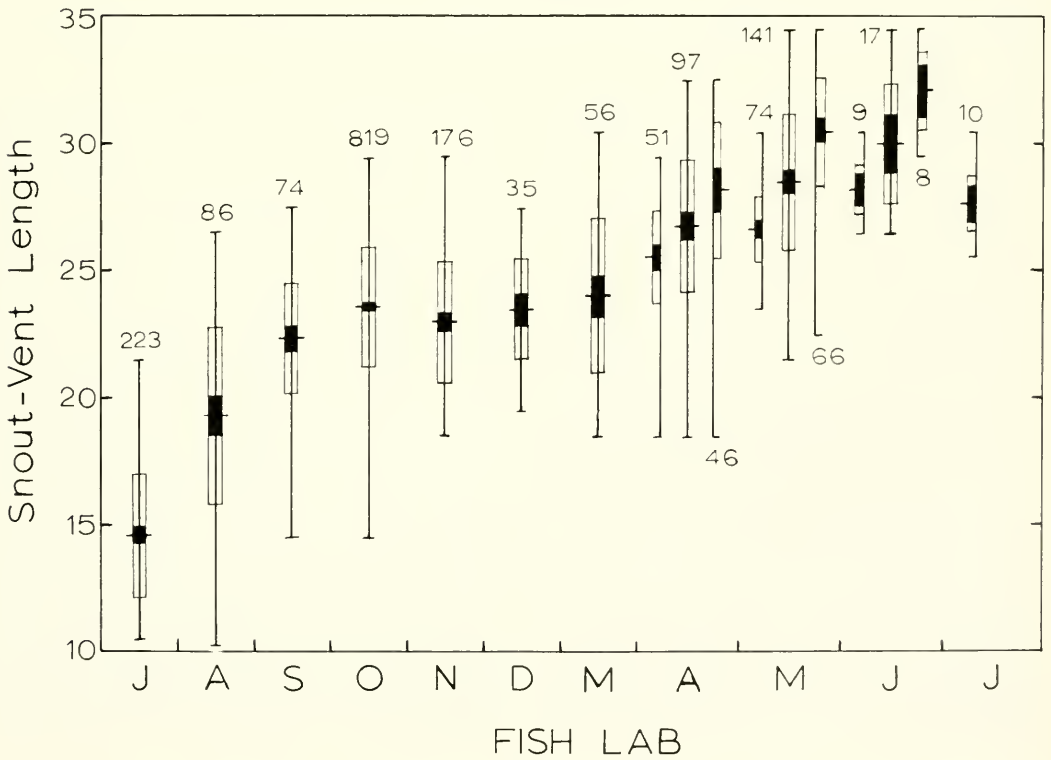
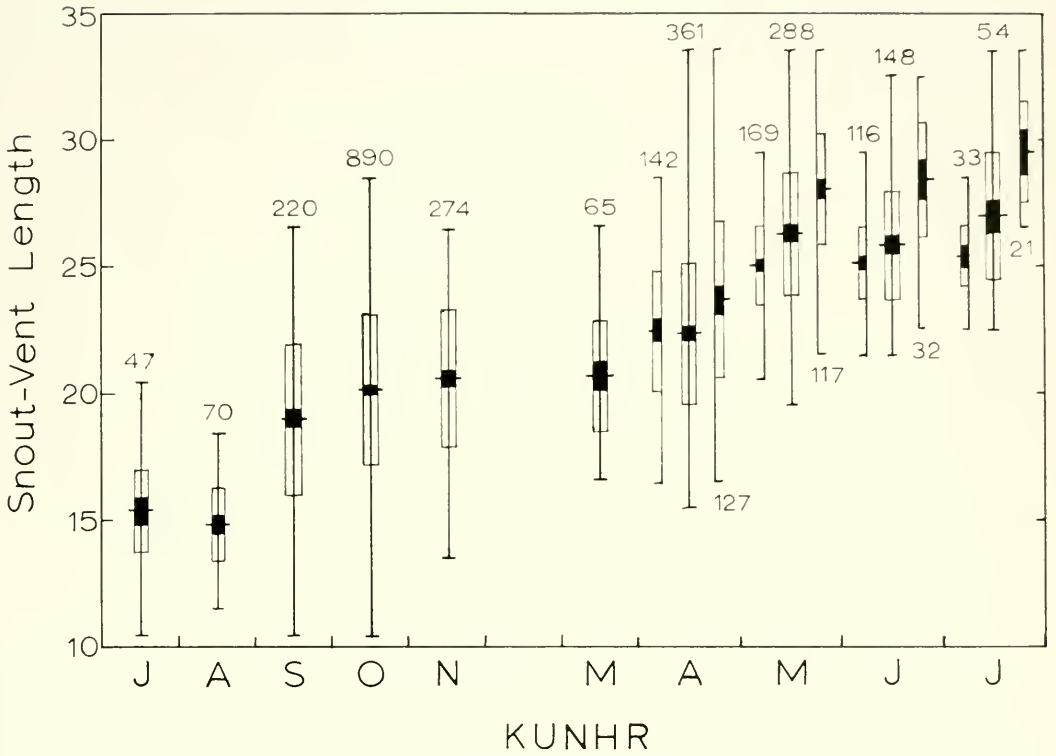


TABLE 2. Stomach contents of four samples of *Acris crepitans*. Abbreviations are the same as in Table 3. The average number of items per frog was calculated as the total of each item divided by the total number of frogs in each sample and not by the frequency for each item. Thus it represents the average for the sample, not the average of those frogs feeding on a particular category.

Location	KUNHR		RET		Fish Lab			
	Date	9/25/65	10/3/65		9/22/65		10/15/65	
Number in sample	38		34		28		22	
Percent of sample containing food	94.8		94.2		89.3		100	
Food item	Average no. of items per frog	Percent freq. of occurrence	Average no. of items per frog	Percent freq. of occurrence	Average no. of items per frog	Percent freq. of occurrence	Average no. of items per frog	Percent freq. of occurrence
Coleoptera	0.18	15.8	0.85	58.9	0.32	25	0.68	27.3
Collembola	13.16	71.0	0	0	0	0	0	0
Diptera	0.74	47.4	1.00	58.9	0.32	25	0.32	13.6
Hemiptera	0.05	5.3	0.32	23.6	1.11	32.2	0.23	13.6
Homoptera	1.26	44.8	0.18	14.7	0.32	14.3	0.18	18.2
Hymenoptera	0.29	13.2	0.65	41.2	0.67	35.8	0.46	27.3
Lepidoptera	0.32	26.4	0.09	8.8	0.07	7.1	0	0
Orthoptera	0	0	0	0	0.07	3.6	0	0
Unidentified Insect	0.11	10.5	0.26	20.6	0.29	14.3	0.77	45.5
Arachnida	0.11	7.9	0.35	29.4	0.36	35.8	0	0
Crustacea	0.05	5.3	0	0	0.07	7.1	0.05	4.6
Total	16.3		3.71		3.57		2.68	
	4.43*							

* If 10 Collembola = 1 other item.

47 and 78% of samples. The overall percentage for males (in a sample of 2131 frogs) was 57.6, which is highly significant (Chi-square. $P < .01$) in its deviation from the expected 1:1 ratio, as were most of the monthly samples. Whether or not this difference is real or the result of differences in behavior of the sexes is unknown. Adult males comprised 53% of the samples from April through June at the Fish Lab and 100% in July, whereas at the Reservation males ranged from 53% in April to between 59 and 87% from May through July. Pyburn (1958) obtained a ratio near 1:1 in a sample of 152 *Acris* from Texas in April 1954. He found more males than females at night but obtained more females than males on the following morning, and stated that females probably moved away from the water at night. Almost all of my own samples were obtained during the day, and I caught the frogs by moving slowly along the edge of ponds and streams. Most frogs were seen and captured only after they had hopped in an attempt to escape, but many were captured that had not yet moved as I approached. No differences in behavior between sexes were noticed. Females may tend to remain motionless, relying on their cryptic coloration to escape detection. However, a more likely possibility is that

females, because of their larger size, may be more sluggish and more easily seen and, hence, are preyed upon more often than males. Thus, the percentage of males may actually increase as time elapses.

Estimates of the number of frogs in each breeding population may serve as a guide for determining recruitment into the following year's population. Values obtained for the sex ratio in May and June (30% females at the Reservation and 47% at the Fish Lab) and number of eggs laid per female (200 to 275) were used in calculating reproductive output (Table 1). Number of eggs per female is based upon figures reported by Smith (1956) and Wright and Wright (1942). At the Fish Lab the estimate for 1966 is probably much lower than it should be. Further sampling might have indicated the presence of a larger population. The population figures in Table 1 represent the number of frogs known to be alive in early May and are probably conservative, but they are not out of line with estimates (discussed below) made by other methods. However, if most spawning occurs in late May or June, there would be fewer females, and these estimates might approximate the reproductive output for the two populations.

TABLE 3. Relationship between number of metacercariae and size of frogs in four samples of *Acris crepitans*. KUNHR = University of Kansas Natural History Reservation; RET = Rockefeller Experimental Tract; Fish Lab. = University of Kansas Fish Laboratory. Average size (in mm) of each sample is given in parentheses below the date of collection.

Location and date of collection	Size range of frogs (in mm)	Number of frogs in sample	Number of metacercariae total (range)	Average number of metacercariae per frog
KUNHR 25 Sept. 1965 (15.85)	12.5-14	8	243 (4-107)	30.4
	14.5-16	18	461 (0-80)	25.6
	16.5-18	9	221 (1-73)	24.6
	18.5-20	4	51 (3-26)	12.8
RET 3 Oct. 1965 (19.72)	16.5-18	5	103 (1-49)	20.6
	18.5-20	16	226 (0-79)	14.1
	20.5-22	9	68 (0-25)	7.6
	22.5-24	4	11 (0-11)	2.8
Fish Lab. 22 Sept. 1965 (22.77)	18.5-20	2	0	0
	20.5-22	14	0	0
	22.5-24	7	0	0
	24.5-26	2	0	0
	26.5-28	3	0	0
Fish Lab. 15 Oct. 1965 (23.43)	18.5-20	1	0	0
	20.5-22	7	0	0
	22.5-24	7	1	0.14
	24.5-26	5	29 (in 1 frog)	5.8
	26.5-28	1	0	0
	28.5-30	1	0	0

Growth

There are two periods of rapid growth in *Acris*: from July until late September (juvenile period) and from March through the breeding season (adult period). Fig. 1 shows composite growth estimates for the entire study period for the Reservation and Fish Lab populations. Although size was about the same at metamorphosis, the growth and maximum size of frogs at the Fish Lab were greater than at the Reservation.

Estimates of density (measured as frogs/meter of shoreline) usually indicated about three to four times as many frogs at the Reservation than at the Fish Lab (Fig. 2). With greater density, there is less food per individual, unless food density is proportionately greater. Unfortunately, no estimates of prey density were made. Examination of digestive tracts showed that most frogs in both populations fed regularly, as nearly every individual examined had a full stomach (Table 2). One outstanding difference in the samples was the utilization of Collembola in the Reservation population. Collembola were extremely abundant at the Fish Lab but were not used by any of the frogs in these samples, whereas Collem-

bola were not observed at the Reservation, but were eaten by 71% of the frogs there. Perhaps this finding indicates that there is much more competition for food at the Reservation, and a secondary food source must be utilized. Johnson and Christiansen (1976) found Collembola in 19% of the cricket frogs sampled in Iowa, but did not relate food preference to frog population density. Labanick (1976) also found the use of Collembola in Indiana, and stated that prey selection was a minor factor compared to prey availability. The lower density of frogs at the Fish Lab may result in more food per frog, and consequently, less expenditure of energy in seeking prey.

Other factors may have influenced growth rates in the two populations. Examination of frogs revealed large numbers of metacercariae of a fluke, probably *Zeugorhynchis megacystis* (Stewart 1960) in the abdominal cavity of 97.5% of the sample from the Reservation. Metacercariae were found in 47.1% of a sample of frogs from the nearby Rockefeller Experimental Tract (RET), and in only 9.1% of frogs from the Fish Lab. Frogs from the RET averaged 19.4 mm in length, approximately the same size as frogs from the Reser-

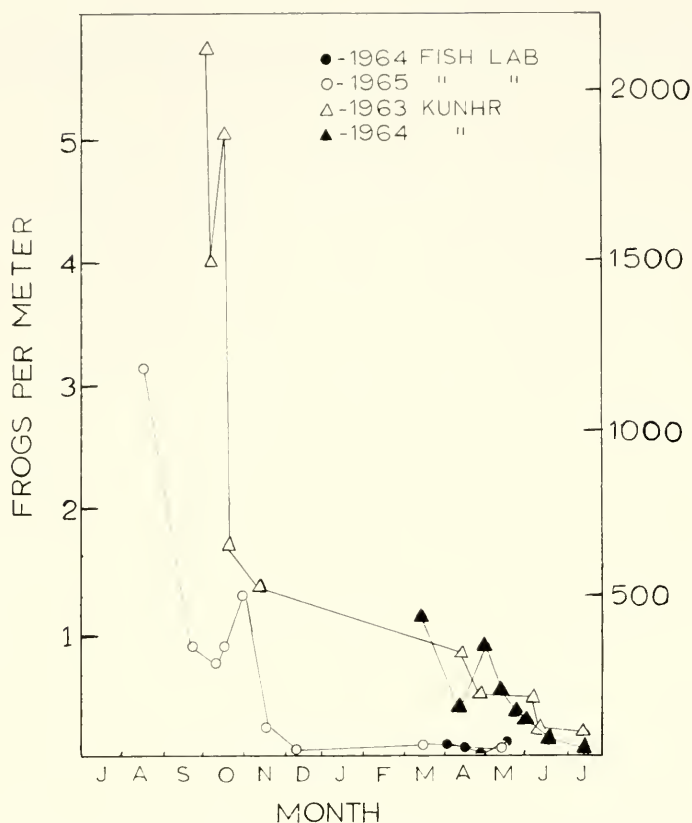


FIG. 2. Estimates of density of frogs per meter of shoreline (left), and population estimates (right) at the University of Kansas Natural History Reservation and University of Kansas Fish Laboratory. Estimates of population size assume equal inhabited areas for both sites.

vation at this time of year (late September and early October) but were much smaller than frogs found at the Fish Lab. An inverse relationship was found between the number of metacercariae and frog body size (Table 3). Owing to higher densities and (perhaps) increased competition for food, frogs at the Reservation may have been more susceptible to fluke infestations than frogs at the Fish Lab.

Estimation of Post-Metamorphic Density and Survival

The MLP (minimum living population) is the minimum number of individuals known to be alive at any one time, and can be calculated because the approximate age of all frogs is known. It is based on the number of individuals captured in any sample plus all previously marked indi-

viduals captured in later samples. The MLP, then, serves as a basis for comparing other estimates of population numbers; if those estimates are lower than the MLP, they are known to be too low; if higher, accuracy of the estimates is more difficult to interpret. Since the MLP is based upon number of individuals captured, it reflects degree of activity of the frogs as well as effort of the collector(s).

Several methods were used to estimate the size of the populations throughout each season. In most instances population estimates were lower than the MLP and were therefore invalid, or they were extremely high and believed to be unreliable according to calculations based on other methods. The Modified Lincoln Index (to reduce positive bias) produced more usable results than did the Schnabel or Haynes methods (see Smith 1974). The MLP and most reliable estimates are

TABLE 4. Population estimates of two populations of *Acris creptians*. MLP—minimum living population at beginning of specified period; D—estimate based on density along shore line (no. frogs/meter); H—Hayne method of estimating population; MLI—modified Lincoln index; S—Schnabel method of estimating population. See text for further explanation.

Location	Date	MLP	Population estimate(s)	
KUNHR Pond 1963	Sept.	1260	1700 H-32,000 MLI	
	Early Oct.	956	1105 D-2307 MLI	
	Late Oct.	633	943 S	
	Nov.	230	267 D-359 LI	
	Apr.	170	360 D	
	May	92	172 LI-238 D	
	June	86	112 MLI	
	July	27	36 MLI	
	Early Sept.	256	375 H	
	Late Oct.	240	} 227 MLI	
Oct.	120			
Pond 1965	Mar.	423	437 S-585 H	
	Apr.	411	500 MLI	
	Early May	318	—	
	Late May	163	470 MLI	
	June	91	214 MLI	
	July	20	—	
	Early Oct.	553	900 H-1200 MLI	
Stream 1965	Late Oct.	335	453 MLI	
	Nov.	216	294 D	
	1966 Apr.	93	—	
Fish Lab Ponds 1965	Mar.	115	165 H-202 MLI	
	Apr.	100	147 MLI	
	May	68	86 D	
	June	14	22 D	
	July	5	18 D	
	Aug.	1	—	
	Oct.		825 D	
	Dec.		275 D	
	1966 Apr.		40 D	
			20 D	
Reservoir 1965	Apr.	75	—	
	May	47	62 MLI	
	June	5	—	
	July	4	—	
	July-Aug.	887	3390 MLI	
	Sept.	695	1039 S	
	Early Oct.	649	705 MLI	
	Late Oct.	492	707 S	
	Nov.	163	677 S	
	Dec.	86	606 S	
	1966	Mar.	66	—
		Apr.	30	—
		May	24	30 D

listed in Table 4. Also, estimates of the populations based upon density are indicated by the numbers on the right side of Fig. 2.

In samples taken before mid-September, there was a very low percentage of recaptures, resulting in high population estimates. Either the popu-

lation was extremely large or an unusually high mortality rate occurred in juveniles. If the former were true, estimates of density would have been much higher, since more frogs would have been captured per meter of shoreline. The latter possibility appears more likely for the following rea-

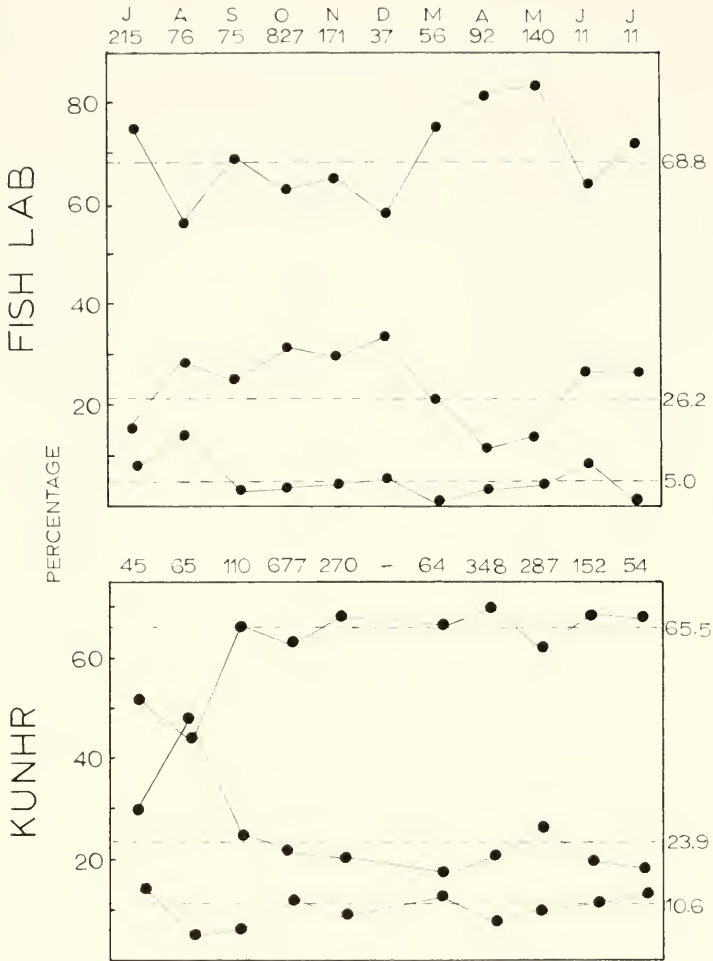


FIG. 3. Frequency of the three color morphs (gray = top, brown = middle, green = bottom) for combined samples of *Acris crepitans* at the University of Kansas Natural History Reservation and University of Kansas Fish Laboratory. Letters at top indicate month; numbers indicate sample size. Broken lines and numbers on right side indicate average values for each color morph.

sons: 1) small, young frogs are more susceptible to desiccation than larger frogs because of a higher surface/volume ratio; 2) increased density at the time of metamorphosis may have attracted predators that normally feed on a wider variety of species; 3) the young of most predators appear at approximately the same time, resulting in heavier predation on small frogs; 4) greater density at the time of metamorphosis may enhance the spread of disease; and 5) cricket frogs tend to jerk violently when held, in an attempt to escape. Injuries were noticed occasionally, and in many instances these frogs were not recap-

tured. It is likely that small frogs received more fatal injuries due to handling than did large frogs.

Of the above possibilities, the first three are probably more important in accounting for the rapid disappearance of young frogs in late summer and early autumn. Although most metamorphosis occurred in July and August, causing a population peak at that time, few juveniles were marked during those months because most field work was concerned with the study of adults. Vegetation became dense at that time, especially at the Reservation pond, causing parts of it to become inaccessible and allowing more frogs to

TABLE 5. Comparison of percentage of frogs having different colored vertebral stripes in populations from northeastern Kansas. The average is followed by the extremes in parentheses, then the number in the sample.

	Fish Lab (open)		Reservation (wooded)		Combined samples from other populations			
					(open)		(wooded)	
Green	5.0 (0-15.0)	86	10.6 (6.2-15.6)	219	5.8 (0-12.1)	7	11.4 (6.7-15.0)	4
Brown	26.2 (9.5-35.2)	450	23.9 (18.5-49.2)	495	24.8 (11.9-45.5)	29	14.3 (13.3-15.0)	5
Gray	68.8 (56.5-84.2)	1154	65.5 (44.6-70.2)	1358	69.4 (42.5-83.3)	81	74.3 (70.0-80.0)	26

escape detection. Furthermore, increased rainfall, high temperature and the usual swarms of arthropod pests resulted in decreased efficiency in collecting.

Due to rapid recruitment of young into the population and rapid mortality of adults during the latter part of the breeding season, composition of the population shifts constantly at that time. The change from adult populations to those consisting almost entirely of juveniles takes less than a month. Those frogs that metamorphose early grow rapidly, and since metamorphosis continues for over two months, the range in size of young frogs in any sample is large. Thus, samples taken in autumn do not show distinct size classes, even though a few adults may be present. By September, more favorable conditions for collecting revealed what appeared to be the end of a trend in high mortality rate. The number of frogs marked in autumn and recaptured in spring was extremely low, indicating that winter weather contributes appreciably to mortality.

Comparison of the population estimates at both localities indicates that the Reservation population is considerably larger than the Fish Lab (Reservoir) population (5000 to 26,000 egg/year compared to 2000 to 6000/year respectively). Recruitment at the Fish Lab ponds and swamp probably equal that at the reservoir. In both populations, approximately 50% of the frogs alive in early September die before mid-October. Almost 95% do not survive winter, and the survivors are reduced even more as the breeding season progresses. Less than 0.1% may live into the following September or October.

This general life pattern, consisting of annual turnover, differs from the pattern in most vertebrate animals that have been studied. Even among anurans, most common species live through more than one breeding season as adults, and a breeding population consists of animals representing several age classes, such as in the study by Turner (1960a) on *Rana pretiosa*. How-

ever, in populations of *Acris crepitans* in Kansas, only one age class is represented in a breeding population, and those members of a population that survive to breed have all been exposed to relatively similar conditions. This species is ideal for studies of both life patterns, since young-of-the-year may mature and reproduce before the end of the breeding season in central Texas (Pyburn *in* Blair 1961), and some adults survive through two breeding seasons in southern Louisiana (Bayless 1969a). It is not surprising to find such wide variation in the life pattern of *Acris crepitans*, since this species occupies an extensive geographical range. Under most circumstances natural selection can be expected to favor rapid development, and the sooner an organism matures, the better are its chances of reproducing before it dies. However, the climatic conditions are such in Kansas that sufficient growth and maturation cannot occur (at least in females) before winter. The production of sperm by young males in early autumn is of questionable value since it seems unlikely that any adult females would be gravid at that time. If mating did occur, development of tadpoles could not occur before winter, and chances of survival would be nil. With the relatively short breeding season and the sudden appearance of large numbers of young in northern Kansas, death of the adults removes one of the main sources of possible intraspecific competition for food and may allow for more rapid growth of the young through an increased food supply for each individual.

Mortality

The causes of mortality between populations may be the same (i.e., desiccation, predation, parasitism, winter kills and natural death), but the specific interactions of each of these are probably unique to each population and also from year to year within a population. Since tadpoles are difficult to find, the causes of mortality of

TABLE 6. Number of captures of 2244 cricket frogs in the 1964 and 1965 year classes at the University of Kansas Fish Lab and Natural History Reservation. Elapsed time in months is given in parentheses below the heading for each year class.

Number of captures per frog	Fish Lab				KUNHR				Total	Percent
	1964 (7)	Percent	1965 (10)	Percent	1964 (11)	Percent	1965 (7)	Percent		
1	157	82.6	511	61.0	455	68.5	424	76.6	1547	68.9
2	25	13.2	244	29.2	162	24.4	92	16.7	523	23.4
3	4	2.1	58	6.9	43	6.5	28	5.1	133	5.9
4	2	1.0	20	2.4	4	0.6	8	1.4	34	1.5
5	2	1.0	3	0.4	0		1	0.2	6	0.3
6	0		1	0.1	0		0		1	0.04
Total	190		837		664		553		2244	

perhaps more than half the population often remain obscure. Savage (1962) stated that the larvae of dragonflies often feed on tadpoles, and he quoted incidents of predation on tadpoles by frogs and leeches. Turtles, such as *Chelydra serpentina* often were seen at the Fish Lab and probably feed upon *Acris* tadpoles and adults.

Numerous predators at both locations feed upon frogs. On one occasion, I saw a large aquatic spider (*Dolomedes sexpunctatus*) attack and kill a young *Acris*. On other occasions, fish (*Microp-terus salmoides*) were observed feeding on *Acris* that had jumped into the water to escape capture by me. Although catfish were numerous at the Fish Lab ponds, predation by them on *Acris* was not observed. The presence of a large bullfrog population at the Reservation undoubtedly accounted for much of the predation on *Acris* at that site. Smith (1977) reported that 80% by volume of the food of large frogs at the Reservation (and other nearby ponds) consisted of small frogs. The relatively large size at metamorphosis in *Acris* probably serves to reduce or completely eliminate cannibalism which is common in other frogs such as bullfrogs. *Nerodia sipedon* and *Thamnophis sirtalis* appear to be the most abundant of several species of snakes that prey upon both populations of *Acris*. The efficiency of some snakes in capturing *Acris* (1 frog in 4.5 minutes) was noted in the behavior of *Thamnophis proximus* in Texas by Wendelken (1978). Killdeer, common grackles and red-winged blackbirds are common at the Fish Lab and often were seen foraging along the water's edge. Fitch (1958) observed both great blue herons and green herons feeding on *Acris* at the Reservation. Fitch also noted heavy predation on leopard frogs, cricket

frogs, chorus frogs, bullfrogs and American toads by raccoons. In addition, opossums commonly prowl along the edge of the pond at night and may prey upon *Acris*.

Polymorphism

The middorsal area of *Acris* may be green, rust-colored, some shade of brown, or gray; but in most frogs the area is indistinguishable from the background color, which is some shade of brown, gray, olive, or nearly black. Small spots or larger blotches of green may be present. The background color and green spots seem to be controlled by chromatophores and may change considerably under different conditions. Frogs on a dark substrate become darker than the same individuals on a light substrate. Bayless (1969a) stated that the color of *Acris* (especially *A. crepitans*) in southeastern Louisiana depends on sex and breeding activity of the individual.

The green vertebral stripe is almost always noticeable from a distance, being fairly wide and running almost the entire length of the body and including a rostral spot. In some frogs the stripe is short and narrow, and may be absent on the head. The brown or rusty stripe, however, is highly variable and sometimes divided into two small brown spots. At times it is barely distinguishable from the ground color, especially if it is light brown and narrow. A gray stripe is rarely present; other individuals have what appears to be a faint grayish-brown area (not a stripe) slightly lighter than the ground color. On a few individuals, both green and brown are present, and on most it is absent.

The genetic basis of the vertebral stripe was

TABLE 7. Distances moved between captures by cricket frogs in the populations of 1963, 1964, and 1965 (A, B, and C, respectively) at the University of Kansas Natural History Reservation.

A. 1963 KUNHR population		
Distance moved in meters	Number of frogs	Percent
0-7.7	53	45.3
7.8-23.0	29	24.8
23.1-38.2	14	11.9
38.3-53.4	7	6.0
53.5-68.7	9	7.7
68.8-83.9	3	2.6
84.0-99.1	2	1.7
Sample avg. = 20.1 m		

B. 1964 KUNHR population

Distance moved in meters	Elapsed time in weeks											Total no. of frogs	Percent
	2	3	4	5-6	7-8	9-10	11-16	26	30	35	39		
0-3.8	17	22	11	8	6	0						64	40.6
3.9-11.4	8	3	12	6	1	3						33	20.9
11.5-19.3	2	5	2		2	0						11	7.0
19.5-27.2	2	2	8		4	2						18	11.4
27.5-35.2	0	0	0		1							1	0.6
35.3-43.1	0	0	0		0							0	0
43.2-51.1	1	1	0		1							1	0.6
51.2-58.9	1	0	1	1	2		1					6	3.8
59.0-66.9	1	1	0		0							2	1.3
67.0-74.8	1	2	0		2	1	1					7	4.4
74.9-82.7	1	0	0		0							1	0.6
82.8-90.6		2	1	1	1							5	3.2
90.7-98.6					0					1		1	0.6
98.7-106.5					0							0	0
106.6-114.4					1							1	0.6
114.5-122.0								1	1			2	1.3
137.2									1			1	0.6
152.4									1			1	0.6
167.7									1			1	0.6
213.4									1		1	2	1.3
Avg. = 25.0													

C. 1965 KUNHR population (stream only)

Distance moved in meters	Elapsed time in weeks				Total no. of frogs	Percent
	1	2	3	4		
0-7.7	48	22	10	1	81	51.0
15.2	16	2	3	0	21	13.2
23.0	8	6	3	0	17	10.7
30.5	6	4	0	1	11	6.9
38.2	1	4	1	0	6	3.8
45.7	4	2	1	0	7	4.4
53.4	2	2	1	0	5	3.1
61.0	1	0	0	1	2	1.3
68.7	1	1	1		3	1.9
76.2		1			1	0.6
83.9		1			1	0.6
91.4		1			1	0.6
99.1-106.6		0			0	0
114.4		1			1	0.6
122.0		0	1		1	0.6
152.4		0			0	0
160.1		1			1	0.6

Avg. = 19.5

studied by Pyburn (1961a, 1961b), but is still not fully understood. Following the precedent set by Pyburn, but using "brown" instead of "red," I shall refer to only three classes of vertebral stripe: green, brown and gray. Frogs bearing any trace of a brown stripe or spots were included in the brown category.

Frequencies of these colors in each population

were recorded at each sampling and were combined into monthly totals and the percentage of each color calculated. Populations differ from one another in the percentage of frogs having vertebral stripes of each color. Also, variation occurs within each population at different times of the year, but I did not note differences associated with sex or breeding activity. Instead, the pro-

TABLE 8. Movements of cricket frogs in the 1965 University of Kansas fish laboratory population. Only the last place of capture is recorded for frogs captured several times.

Area first captured	Length of shore line (m)	Area recaptured					Ponds and swamp	Total no. of frogs	Percent
		1	2	3	4	5			
1	94.5	82	2	0	6	5	4	99	26.7
2	67.1	12	20	3	0	3	0	38	10.2
3	61.6	12	0	8	5	4	0	29	7.8
4	80.8	19	1	6	59	43	3	131	35.3
5	50.3	11	0	0	2	58	3	74	20.0
Total number of frogs		136	23	17	72	113	10	371	
Percent		36.7	6.2	4.6	19.4	30.4	2.7		

portion of green frogs increased when water levels were highest and vegetation was abundant. Data for the different years were combined, and the proportion of each color morph was calculated for each population (Fig. 3). Gray was far more common than the others, and green was the least common. In open situations the proportion of green frogs usually was considerably lower than in wooded areas, where the proportions of green and brown were approximately equal (Table 5).

The fact that green-striped frogs may at times change color and appear gray introduces a source of error into estimates of frequencies of green and gray. Experimental evidence indicates that drying of the skin may be responsible for a color change from green to gray (Pyburn 1961a). Contrary to my findings, Pyburn found that the proportion of green-striped frogs was highest at the

peak of the breeding season. Nevo (1973b) found a correlation between color of the substrate and frequencies of the three color morphs.

When water levels were lowest, gray-striped frogs were most abundant; and brown- and green-striped frogs were more easily seen by me at these times than were gray morphs. Predators with color vision probably would have detected the brown- and green-striped frogs more easily; hence, these individuals may have been at a selective disadvantage on bare soil.

Green spots or blotches have been noted on frogs of all three color morphs. These spots may be present at one time and absent the next. It is not known whether all *Acris* have the ability to develop green spots, but certainly a large percentage of them do. The spots may serve to protect brown and gray morphs to the same extent

TABLE 9. Comparison of distance moved with amount of rainfall in the 1965 year class of the University of Kansas Natural History Reservation and Fish Lab populations of cricket frogs. Movements between autumn and spring were excluded.

Mm of rainfall	KUNHR		Fish Lab	
	Distance in meters average (range)	No. in sample	Distance in meters average (range)	No. in sample
0	22.0 (0-65.5)	61	11.6 (11.3-15.9)	4
0.5	—	20	32.6 (0-129.6)	4
1.3	16.5 (0-48.8)	20	—	
2.0			12.2	1
3.3			15.6 (0-71.7)	21
3.8			1.5	1
10.2			1.8 (0.6-3.0)	2
10.7			12.2 (0.3-36.6)	3
13.2	16.8 (0.6-74.4)	20	42.4 (0.9-120.4)	11
14.0	—		1.5	1
14.5	22.6 (0-122.0)	46	6.1	1
81.8	—		16.5 (0-32.9)	2
	Sample avg. = 20.7		Sample avg. = 20.7	

that green morphs are protected on certain back-grounds.

Movements

Of 2244 of the frogs marked, a total of 1547 (68.9%) were not recaptured, and the remaining 697 were recaptured from one to five times (Table 6). Because of few multiple recaptures it was impossible to establish "preferred" activity ranges of individuals, as shown by Pyburn (1958). However, preferences for certain areas around the ponds are indicated to some extent by patterns of distribution along their shores.

Dispersal occurred in all directions during and following rains. On one occasion several *Acris* and one bullfrog were found in a small roadside puddle more than a quarter mile west-northwest of the Reservation pond, which was the closest permanent body of water. Movements discussed hereafter refer only to movements within the study areas, and were measured as distance moved around the ponds between two successive captures.

Movements were compared in relationship to distance, time, habitat, rainfall and sexual differences. Most frogs tended to remain in fairly small areas; nearly 50% of the recaptures were within 7.6 m of the previous place of capture (Table 7). The number of frogs moving greater distances steadily decreased. Since group markings were used on most samples in autumn, the time interval between captures could not be determined for the 1963 year class at the Reservation. In the 1964 year class at the Reservation, 63% recaptured remained in the area of the pond where they were originally captured (<30 m), 21% moved to adjacent areas, and 16% moved to more distant areas. Movements of more than 90 m in this population usually involved frogs moving from the stream to the pond. These movements occurred during the breeding season and may have been in response to calling. Average movements recorded in the three year classes were: 1963—20.1 m; 1964—25 m; 1965—19.5 m. In the 1965 year class of the Fish Lab population (Table 8), 61% of the recaptured frogs remained in the area of the pond where originally captured, 24% moved to an adjacent area, and 15% moved to more distant areas. Large aggregations at the southwest corner of the reservoir, where soil was almost always damp, indicated

that most distant movements were toward more favorable microhabitats.

As time elapsed, the distance moved by most frogs gradually increased (Table 7B and C). However, many of the longest movements occurred over extremely short periods of time. Pyburn (1958) made similar observations in Texas. Comparisons of distance moved with amount of rainfall between captures is given in Table 9. Although greater distances usually were moved after rain, the majority of frogs were still captured within 7.6 m of the site of previous capture. The average distance moved by frogs from both populations was 20.7 m. Rainfall alone cannot account for long movements; relative humidity, temperature conditions and breeding activity are also important.

SUMMARY

Populations of cricket frogs, *Acris crepitans*, were studied near Lawrence, Kansas. The two major study areas consisted of a pond and stream in woodland habitat (Reservation) and a reservoir and eleven ponds in grassland habitat (Fish Lab). *Acris* is usually the most abundant anuran near Lawrence, being active from March until November or December.

Most spawning occurs from late May to early July, and newly metamorphosed frogs are found between mid-July and late September. The sex ratio varied from about four females per male in juveniles to 53% or more males in adults, indicating higher mortality rates in females. The percentage of males was usually higher in the Reservation population. Estimates of reproductive potential indicate an average annual production of from 5000 to 26,000 eggs at the Reservation pond compared to about 2000 to 6000 at the Fish Lab reservoir and about 7000 at the Fish Lab ponds.

Average life expectancy is about four months, about 5% of the population survives the winter, and complete population turnover occurs in about sixteen months. Density was greater at the Reservation, suggesting that the wooded habitat there is more favorable than the grassy habitat at the Fish Lab.

Two periods of rapid growth were observed: from July until late September and from March through July. Size and growth rate of females exceeded those of males at all ages, and the Fish Lab population contained frogs that were con-

siderably larger than individuals in the Reservation population. The small size of individuals at the Reservation was attributed to inhibition of growth by heavy infestations of metacercariae and to greater competition for food.

Three classes of vertebral stripe coloration were distinguished: green, brown and gray. In all populations sampled, gray morphs were predominant (usually accounting for more than 60% of the sample), while brown morphs were less common (about 25%); in open areas green morphs comprised nearly 5%, and in wooded areas, about 10%.

Most frogs occupied shore lines having muddy, beach-like areas, and in dry periods they tended to remain in these areas. However, following rains and in mild, humid weather, they dispersed in all directions; movements of more than 100 meters were not uncommon. Nearly half of the recorded movements were less than 8 m, and recorded movements of entire year classes averaged between 19 and 25 m. Movements at the Fish Lab tended to be greater than those at the Reservation, probably as a result of division of the habitat at the Fish Lab into several separate ponds.

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Female Reproduction in an Arkansas Population of Rough Green Snakes (*Opheodrys aestivus*)

MICHAEL V. PLUMMER

INTRODUCTION

Because of the kinship between lizards and snakes the tendency when reviewing certain aspects of snake ecology is to compare them to lizards (e.g., Fitch 1970; Turner 1977). However, while lizards "... may well become paradigmatic for ecology as a whole" (Schoener 1977), such is hardly true for snakes. Indeed the nocturnality, secretive nature, great vagility, and frequent periods of inactivity of most snakes make them less of an ideal subject than the conspicuous, mostly diurnal lizards. Reviews of reproductive ecology in lizards and snakes (Fitch 1970; Turner 1977) clearly reveal the need for more information on the latter.

Although highly cryptic, *Opheodrys aestivus* is a non-secretive, diurnal arboreal snake that is abundant, has low vagility, and is easily collected (Plummer 1981). Consequently, some of the attributes of lizards that contribute to successful study also make this snake species a favorable subject. *Opheodrys aestivus* ranges from southern New Jersey to southern Florida, west to eastern Kansas and Texas, and south to southern Tamaulipas, Mexico (Conant 1975). In this paper I report on female reproduction from a population in the central part of the species' range.

METHODS

Female *O. aestivus* (N = 167) were collected May 1977–October 1979 from a population at Bald Knob Lake in White County, Arkansas. Snout–vent length (SVL) and body weight were measured. Cloacal smears were made on 43 snakes during April–October 1979 and were examined for sperm under 100× magnification. One hundred and twenty-seven snakes were preserved and autopsied for reproductive condition. Forty gravid snakes, collected 14 June–14 July 1979, were returned to the field after their clutches were deposited in the laboratory. Observations were made on snakes in the field which were not collected. Autopsy included counting and measuring with vernier calipers or an ocular

micrometer, ovarian follicles, corpora lutea, and oviducal eggs. The diameter of the oviducts was measured at their approximate midpoint. Coelomic fat bodies were removed, blotted, and weighed to the nearest .01 g. Percent body fat (fat (g)/body wt. (g) × 100) was used to control for size-induced variation in fat body weight. In the laboratory snakes were housed in a 1.1 W × 4.9 L × 2.8 H m cage. A thin layer of moist wood shavings was maintained on the floor. Ten 30 × 30 cm plywood boards were placed on the floor under which clutches were deposited. The cage was maintained at 28 ± 2°C and on a 14L:10D photoperiod. Crickets and water were provided *ad libitum*. On the day of oviposition females and eggs were measured, weighed, the eggs were individually marked with a felt-tipped pen, and each egg was incubated individually on top of a thin layer of moist vermiculite in a small glass jar at 28°C. Some eggs were sacrificed immediately following oviposition in order to stage the embryo according to Zehr (1962). On the day of emergence from the egg hatchlings were weighed, measured (SVL) and sexed. They were returned to the field at a later date. Data are reported as mean ± 1 SE.

RESULTS

Sexual Maturity and Mating.—The presence of oviducal eggs, corpora lutea, enlarged ova, or convoluted oviducts indicated sexual maturity. Most snakes mature between 36–40 cm SVL (Table 1). The largest immature was 45.0 cm whereas the smallest mature measured 33.5 cm. Immature snakes had straight, narrow (0.5–1.5 mm), ribbon-like oviducts and follicles <3.0 mm in diameter with greater interfollicular distance than mature snakes.

Sperm were present in most mature females in spring but were not detected in other parts of the year (Table 2) indicating that mating is limited to spring. No sperm was found in any females <35.0 cm SVL.

Ovarian Cycle.—In adults follicles measuring 1–5 mm in greatest diameter were present in

TABLE 1. *Ophedryx aestivus*: size at sexual maturity of females.

SVL (cm)	N	No. mature (%)
>45	50	50 (100)
41–45	47	46 (97.9)
36–40	30	29 (96.7)
31–35	16	2 (12.5)
<31	19	0 (0)

TABLE 2. *Ophedryx aestivus*: Presence of cloacal sperm in females (>35.0 cm SVL) at different times of the year.

Period	Snakes (N)	Snakes (N) with cloacal sperm (%)
Apr–May	10	8 ¹ (80.0)
Jun–Aug	16	2 ² (12.5)
Sep–Oct	17	0 (0)

¹ Spermatozoa extremely abundant.

² Only 3 spermatozoa detected in 2 samples from each of 2 snakes collected in June.

ovaries throughout the sampling period (Fig. 1). Follicles measuring 1–3 mm proliferate in post-reproductive females in July and August and increase in size to a maximum 5 mm by October. Two snakes collected in mid-February had a mean of 9 follicles measuring 1–3 mm and 9.5 follicles measuring 3–5 mm. The February data are similar to the September–October data and indicate that very little follicular activity occurs over winter. Vitellogenesis resumes in spring. Rapid yolk-ing and enlargement to approximately 15–25 mm occur in May and oviducal eggs are present from late May to early July.

In 8 pre-ovulatory females which contained enlarged (>12 mm) follicles the mean number in the left and right ovaries was $2.6 \pm .26$ and $3.6 \pm .38$, respectively. Fourteen of 23 post-ovulatory females (60.1%) had a disparity in the corresponding number of corpora lutea and oviducal eggs on each side. In 10 snakes extrauterine transfer of ova involved only 1 ovum and in 2 snakes movement of 2 ova was involved. A significantly greater number of ova moved from the left ovary to the right oviduct than vice versa ($\chi^2 = 7.14$, $P < .01$). Reciprocal transfers, of course, could not be detected. The average number of oviducal eggs in the left and right oviducts was $2.2 \pm .15$ and $4.1 \pm .23$, respectively. It appears that the right oviduct, which is longer than the left, receives more ova because of greater ova production by the right ovary and because of greater extrauterine transfer from the left ovary.

Oviposition dates in the laboratory from females collected 14 June–14 July 1979 were 1–7 July (N = 11); 8–15 July (N = 18); 16–23 July (N = 11). Oviposition in 1978 apparently occurred earlier (Table 3) or perhaps laboratory stress caused a delay in oviposition in 1979. Snakes collected in 1979 seemed to be delayed in follicular enlargement and ovulation as determined by palpation.

Body fat (Fig. 1, Table 4) is the greatest in early

spring and late fall and least in June. Two February females averaged 8.3 (range = 5.3–11.4). These data indicate that fat is not depleted in overwintering snakes. However, the significant reduction of fat during secondary vitellogenesis and ovulation from late May to June ($t = 9.27$; $P < .001$) suggests that energy needed for these processes is derived from fat reserves. Although the pattern of fat cycling resembles that in juveniles (Table 4), an abrupt significant decrease in fat is not evident. Additionally, mature females have more fat overall than do juveniles ($t = 3.17$, $P < .01$).

Clutch Size.—The number of eggs in a clutch was determined by counting the eggs actually deposited (42 snakes), by counting oviducal eggs (28 snakes), or by counting enlarged (>12 mm) ova (8 snakes). Clutch size in 77 snakes was $6.1 \pm .21$ (range 3–10). Estimates of clutch size by these methods are subject to some error. Enlarged, atretic follicles (N = 4) were present in the ovaries of 3 snakes which had oviducal eggs. Additionally, 11 unfertilized, unshelled ova were deposited singly and separate from clutches among the 40 laboratory snakes. The relative number of enlarged follicles that do not terminate as a part of an actual clutch, therefore, appears to be small. This fact along with the fact that only 8 of 77 clutch size estimates were based solely upon number of enlarged ova probably has not biased the clutch size estimate greatly. Clutch size averaged $6.3 \pm .59$ eggs based on number of enlarged follicles which is not significantly different from the total estimate ($t = .20$; $P > .50$).

No evidence was seen which indicated that more than 1 clutch was produced in a given year.

Incubation and Hatching.—Of 180 eggs laid and incubated in the laboratory, 161 (89.4%) were fertile. One hundred forty-five (90.0%) of the fertile eggs hatched. Of 19 infertile eggs, 18 (94.7%)

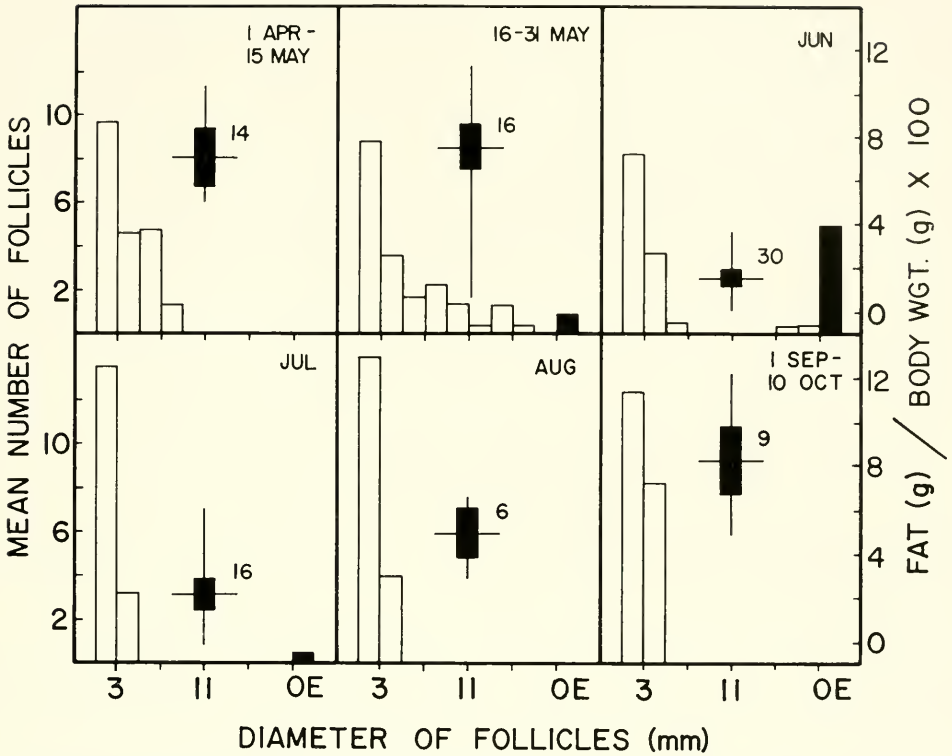


FIG. 1. *Opheodrys aestivus*: Number of various sized follicles and amount of body fat in mature females at different times of the year. The horizontal lines of the dicegrams are means; vertical lines are ranges; rectangles delimit 95% confidence limits. OE = oviducal eggs.

were either partially or totally unshelled. For totally shelled eggs the modal embryonic stage (Zehr 1962) at oviposition was 25 (N = 37, range 21–27). The range of stages in a single clutch of 7 eggs was 25–26. For partially shelled eggs or those that were inviable at or soon after oviposition (determined by the rapid loss of tonicity and growth of mold) the mode was 18 (range = 14–19; N = 10). Statistics relating to egg size are given in Table 5.

Incubation ranged 36–43 days and averaged

39.2 ± .12 (N = 142). Hatching occurred 9–30 August in the laboratory. Hatchlings were seen in the field on 31 August and on 10 September in 1978.

Statistics relating to hatchling size are summarized in Table 5. Of 141 hatchlings, 67 (47.5%) were males. Sex ratio is not significantly different from 1:1 ($\chi^2 = .35$; $P > .50$). Male hatchlings weigh about the same as females (1.37 ± .023,

TABLE 3. *Opheodrys aestivus*: Number of snakes (>35.0 cm SVL) determined to be gravid by palpation in the field during various times in 1978.

Period	Snakes (N)	No. gravid (%)
5–20 Jun	39	39 (100)
22–30 Jun	32	20 (62.5)
2–7 Jul	29	11 (37.9)
12–31 Jul	50	0 (0)

TABLE 4. *Opheodrys aestivus*: Percent body fat of juvenile females and adult females. Data are $\bar{x} \pm 1$ SE (N) fat (g)/body weight (g) × 100.

Period	Juvenile	Adult
Apr–15 May	4.1 ± 1.17 (5)	7.2 ± .62 (14)
16–31 May	1.7 ± .11 (2)	7.9 ± .57 (16)
Jun	2.1 ± .49 (9)	1.9 ± .20 (30)
Jul	2.3 ± .34 (9)	2.3 ± .38 (16)
Aug	2.4 ± .54 (7)	5.1 ± .57 (6)
Sep–Oct	3.2 ± .42 (6)	8.6 ± .77 (9)

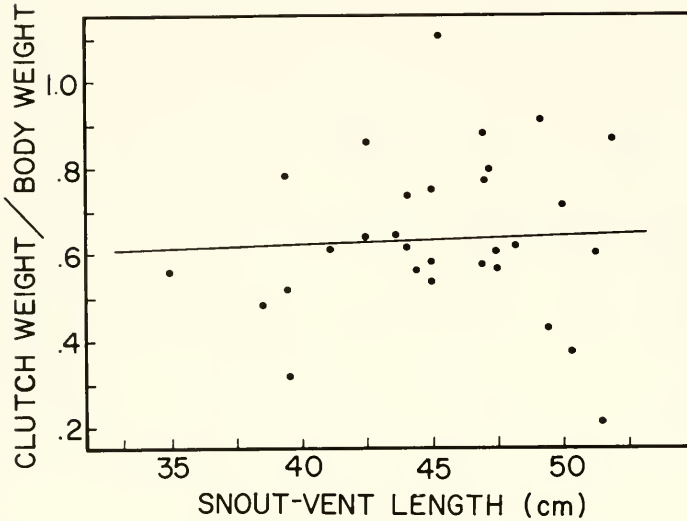


FIG. 2. *Ophedryx aestivus*: The relationship of clutch weight/post-reproductive body weight and snout-vent length for snakes collected in 1979. The regression equation is $\bar{Y} = .001X + .588$ ($r = .024$, $P > .75$).

1.36 ± 0.23 g; $t = .01$, $P > .90$) and have about the same SVL ($13.9 \pm .10$, $14.0 \pm .10$ cm; $t = .02$, $P > .90$).

Reproductive Effort.—Reproductive effort of a female is that organism's total investment in a current act of reproduction (Pianka 1976). In snakes reproductive effort has been crudely estimated using the ratio of clutch weight to non-reproductive female weight (C/B) (Clark 1970; Fitch 1975; Pianka and Parker 1975; Shine 1977). Because in *O. aestivus* there is no parental care (egg brooding or oviducal retention) most of the reproductive investment should be contained in the egg itself and therefore the ratio C/B should be representative of reproductive effort (but see Vitt and Congdon 1978). The risks involved in transporting the enlarged ova and eggs in the maternal body are assumed to be negligible. In *O. aestivus* C/B averages .64 and does not change with body size (Fig. 2). Less than .06% of the variation in C/B is explained by body size. Larger

snakes produce both larger eggs and larger clutches (Fig. 3). There is a possible trend toward smaller eggs with increasing clutch size (Fig. 4) although there is great variation ($r^2 = 1.7\%$) and the regression is not significant. Larger eggs produce significantly larger hatchlings (Fig. 5).

DISCUSSION

Ophedryx aestivus appears to have a typical female reproductive cycle for a temperate oviparous snake. From the limited data available for a comparison of geographic variation in reproductive attributes, other reports appear to conform with this population. In southern Louisiana Tinkle (1960) and in Illinois Morris (1982) found similar results in *O. aestivus* with regard to size at sexual maturity, the ovarian cycle, and reproductive potential. Apparently, mating is limited to spring in this population although fall mating may occur in other populations (Richmond 1956).

TABLE 5. *Ophedryx aestivus*: Egg and hatchling statistics. All data are expressed as $\bar{x} \pm 1$ SE (N); range.

	Wgt. (g)	Max. width (cm)	Max. length (cm)	SVL (cm)
Shelled eggs	$1.62 \pm .015$ (190); 1.17–2.26	$9.9 \pm .04$ (190); 8.4–11.9	$24.8 \pm .23$ (190); 16.2–34.2	— —
Hatchlings	$1.37 \pm .016$ (144); .82–1.76	— —	— —	$13.9 \pm .07$ (144); 10.7–16.1

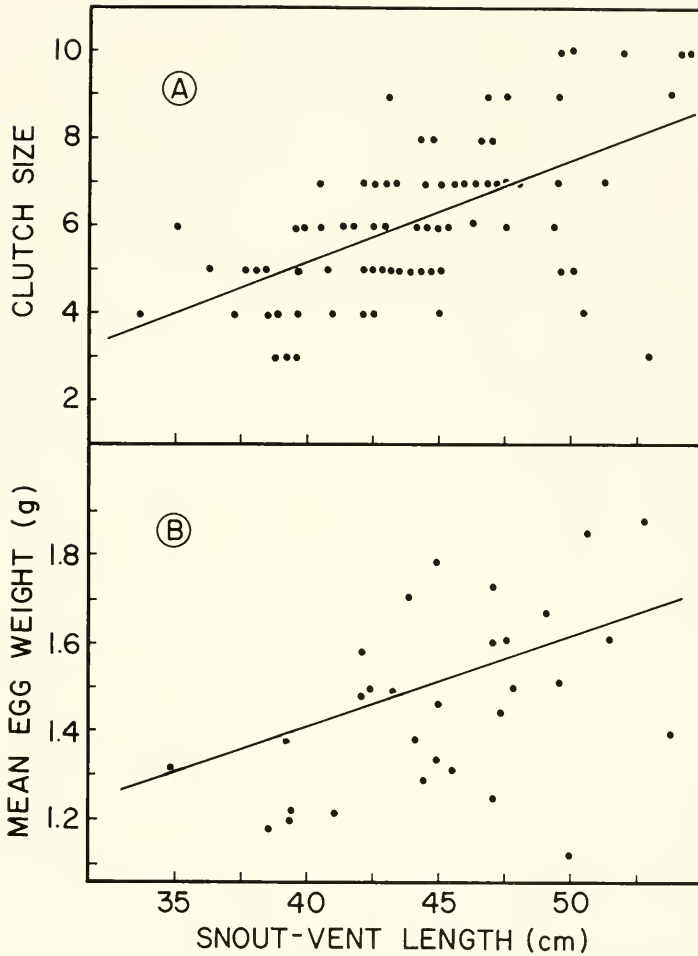


FIG. 3. *Ophedryx aestivus*: A. The relationship of clutch size and snout-vent length. The regression equation is $\hat{Y} = .23X - 4.1$ ($r = .58$, $P < .001$). B. The relationship of egg weight and snout-vent length. The regression equation is $\hat{Y} = .02X + .61$ ($r = .46$, $P < .05$).

McCauley (1945) observed mating behavior on 18 May of a captive male *O. aestivus* directed toward a female *O. vernalis*. The data on egg and hatchling size, clutch size, and dates of oviposition and hatching of several anecdotal reports (Conant 1938; Conant and Downs 1940; McCauley 1945; Curtis 1950; Guidry 1953; Carpenter 1958; Sabath and Worthington 1959; Smith 1961; Anderson 1965; Webb 1970; Mount 1975; Morris 1982; and others summarized in Wright and Wright 1957) generally are similar to the present report. The greatest differences are in time of oviposition and in incubation time. Since the timing of these probably is dependent

upon phenological events and temperature, respectively, it is not surprising that they are so variable. The extremely wide variation in oviposition dates (17 June–28 August) and subsequent hatching in southeastern Texas (Guidry 1953) suggests the possibility of multiple clutching.

Seemingly, enlargement of follicles to the 5 mm stage occurs throughout the activity season and could be described as primary vitellogenesis (*sensu* Aldridge 1979). The rapid enlargement from the 5 mm follicle to ovulatory size is confined to late April and May and may be described as secondary vitellogenesis (*sensu* Aldridge 1979).

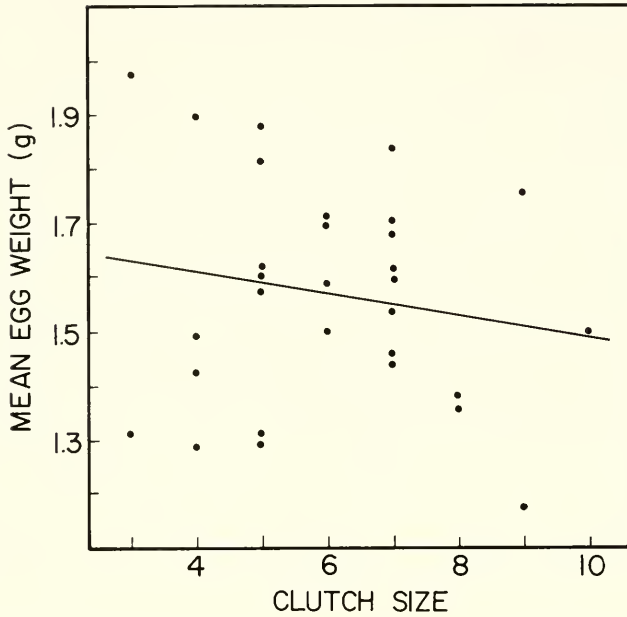


FIG. 4. *Ophedryx aestivus*: The relationship of egg weight and clutch size. The regression equation is $\hat{Y} = -.014X + 1.65$ ($r = -.13$, $P < .50$).

Aldridge (1979) described Type I secondary vitellogenesis in which rapid yolking of ova is confined to spring and Type II secondary vitellogenesis in which rapid yolking begins in late summer and fall, becomes dormant in winter, and resumes in spring. He classified *O. aestivus* as having a Type II pattern based upon Tinkle (1960). My interpretation of Tinkle (1960) is that of a Type I pattern, as is that of the present study. Although not mentioned by Aldridge, I suspect that intraspecific vitellogenic patterns might vary geographically.

Differential production of ova by left and right ovaries and extrauterine transfer of ova are probably simple consequences of space limitations. Shine (1977) stated that it is difficult to see how extrauterine transfer would affect clutch size and embryonic survivorship and therefore would be of doubtful selective importance. However, because in snakes the right oviduct is longer than the left, production of ova by the left ovary beyond that which the left oviduct can accommodate probably would result in greater follicular atresia were it not for differential extrauterine transfer to the right oviduct.

The decision to stage the embryos at ovipo-

sition was prompted by the data of Blanchard (1933) for *O. vernalis*, who found incubation to vary from 4 to 23 days. This species is a possible example in the evolutionary transition from oviparity to viviparity (Packard *et al.* 1977) with a relatively short incubation period and a presumably wide range in the degree of embryonic development at oviposition. *Ophedryx aestivus*, however, has little variation in embryonic development at oviposition and has an incubation period similar to many other oviparous colubrids (Fitch 1970).

Determination of oviposition dates in the field by palpation assumes that each mature female breeds annually. This apparently is the case as all 39 females palpated 5–20 June in 1978 were gravid (Table 3), all 40 mature females collected for the laboratory oviposited in 1979, and all 125 females autopsied April–July (1977–1979) were in breeding condition or had evidences of recent oviposition. The annual ovarian cycle is correlated with an annual fat cycle which presumably provides much of the energy needed for reproduction. Energy, in the form of stored fat reserves or as an outcome of foraging success, has been implicated as the major factor in the control of

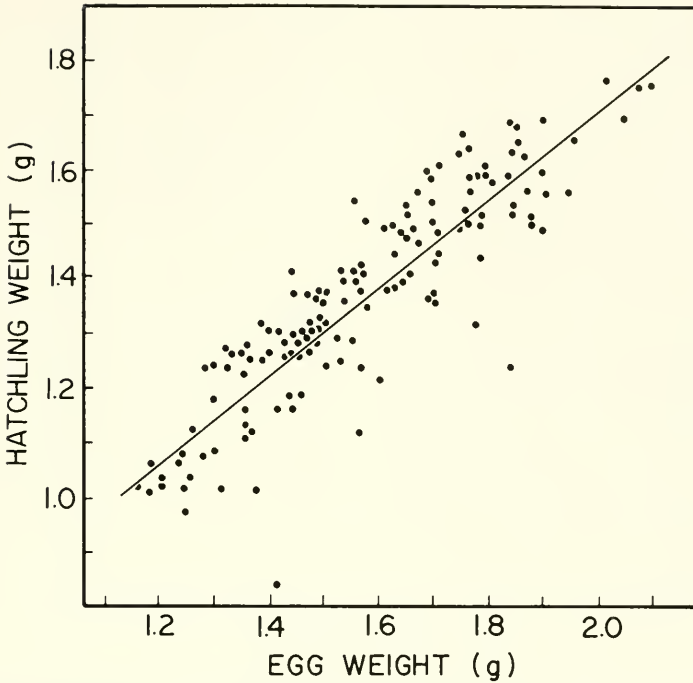


FIG. 5. *Opheodrys aestivus*: The relationship of hatchling weight and egg weight. The regression equation is $\hat{Y} = .79X + .115$ ($r = .85$, $P < .001$).

frequency of female reproduction in several snakes (summarized in Wharton 1966; Gibbons 1972).

Production of equal numbers of male and female hatchlings of similar size and weight is in accordance with Fisher's sex ratio theory and is the usual situation in snakes (Shine and Bull 1977).

Because metabolism decreases with body weight in snakes (Galvao *et al.* 1965) proportionally more energy may be available for reproduction. The risks involved when time and energy are allocated to reproduction may decrease survivorship and therefore the expectation of future progeny (reproductive value). Therefore, a younger snake with a higher expectation of future progeny might be expected to devote less time and energy to reproduction than an older snake which has less expectation (Pianka and Parker 1975; Pianka 1976). Tests of this hypothesis in snakes have shown diverse results. In *Carphophis vermis* (Clark 1970) C/B increases with body size (=age). In *Diadophis punctatus* (Fitch 1975), *Masticophis taeniatus* (Pianka and Parker 1975),

and *O. aestivus* (present study) C/B remains constant with body size. In *Notechis scutatus* and *Pseudechis porphyriacus* (Shine 1977) C/B decreases with body size. Pianka and Parker (1975) and Pianka (1976) suggested that correlations between reproductive effort and reproductive value might be greater in multiple-brooded species than in single-brooded species where proximal factors such as resource availability might have a greater effect. In all of the above studies the snakes were single-brooded. However, in a study of annual reproductive variation in *O. aestivus* (Plummer 1983) it was shown that C/B and other reproductive attributes did not vary between years in which snakes stored greatly different quantities of lipids. Even if reproductive effort remains constant with age (as in *O. aestivus*), the absolute energy allocated to reproduction actually increases. The increased energy available in *O. aestivus* is reflected in the production of larger eggs and larger clutch sizes (Fig. 3). Fecundity in snakes is often related to body size (Fitch 1970; Shine 1977; Aldridge 1979; present study). Shine (1978) found that in about 66% of species (including *O.*

aestivus) females attain a larger body size than males. Shine suggested that one reason for this disparity was that selection has favored large body sizes in the females because of greater fecundity. Another reason for increased body size might be that larger snakes produce larger eggs which produce larger hatchlings (Fig. 5). In general, larger hatchlings should enjoy higher survivorship and be better competitors (Pianka 1976). In the lizard *Sceloporus undulatus* (Ferguson and Bohlen 1978) larger hatchlings from late broods enjoy greater survivorship than do smaller hatchlings, but larger hatchlings from early broods have survivorship similar to smaller hatchlings. Although to my knowledge there are no comparable data for snakes, if female fitness was increased by producing larger eggs then selection should favor either larger parental body size or decreased clutch sizes (Pianka 1976).

Smith and Fretwell (1974), Pianka (1976), and Stewart (1979) discuss models which predict that with a constant reproductive effort, an increased female size may result in either larger clutches or larger sized eggs. These models assume a negative correlation between clutch size and egg weight. In *O. aestivus* there is no statistical relationship between clutch size and egg weight (Fig. 4). Although the correlation between SVL and egg size is not strong ($r = .46$), it appears that in this population correlates of female body size are selection for increased clutch size as well as for increased egg size.

SUMMARY

Various aspects of female reproduction in *Opheodrys aestivus* were examined by specimen autopsy and from the study of living snakes in the field and in the laboratory. These snakes mature at 36–40 cm SVL and breed annually thereafter. Ovarian follicles measuring 1–5 mm in diameter are present in mature snakes throughout the year. Rapid yolkling of follicles occurs in the spring and ovulation begins in late May. Extra-uterine transfer of ova is common. One clutch is produced per year ($\bar{x} = 6.1$ eggs). Coelomic fat bodies cycle annually and presumably provide energy for vitellogenesis and ovulation. Oviposition occurs in late June and July. Ninety percent of the eggs laid were fertile and 90% of fertile eggs hatched in the laboratory. At oviposition the modal embryonic stage (Zehr 1962) was 25

(range 21–27). Incubation averaged 39 days. The sex ratio of hatchlings was not significantly different from 1:1. Male and female hatchlings are similar in length and weight. Reproductive effort ($\bar{x} = .64$) did not change with body size. Larger females produce both larger clutches and larger eggs. Larger eggs produce larger hatchlings.

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Clutch Size in *Iguana iguana* in Central Panama

A. STANLEY RAND

INTRODUCTION

Iguana iguana, laying up to 6 dozen eggs in a single clutch, is one of the most prolific lizards in the new world. Prized as food and heavily hunted in many parts of its range, its conservation and the possibilities for sustained yield harvesting have been discussed (Fitch *et al.* 1983). Though reproductive potential is important in any understanding of population dynamics, only one detailed study of the number of eggs which female iguanas produce has been published, Fitch and Henderson (1977) for Nicaragua. The present paper describes the size and weight of clutches produced by female iguanas and their relation to female size in Panama. The clutch size and reproductive investment in *Iguana iguana* is compared with that described for other lizards.

MATERIALS AND METHODS

Clutch size data were collected from females caught during the nesting season, late January to early March, between 1968 and 1980 in the vicinity of Panama City and Gamboa, Republic of Panama. Some females were caught and allowed to nest in a large outdoor enclosure, others were killed or found as fresh road kills and the eggs removed from the oviducts. The sample was not randomly selected from the population, rather, because of my interest in the relationship between female size and clutch size, the few females deliberately shot were selected because they were very large or very small. The following measurements were taken on 30 females: snout-vent length (SVL), female wet weight without eggs, clutch wet weight before significant hydration and clutch size (number of eggs). In some cases clutch volume, clutch dry weight (oven dried at 105°C) were also measured.

Regressions were compared using covariance (Snedecor 1956).

RESULTS

The results from examination of females with oviductal eggs are given in Table 1. Sizes of these

animals were not distributed normally nor do they suggest that the population can be divided into age classes. Even though animals were collected to emphasize the extremes, only one female was below 300 mm SVL. Because sampling was not random, ranges are probably more accurate representations of the population than are means. Female weight is closely correlated with SVL ($N = 30$, $r = 0.86$, $P < .001$) (Fig. 1) particularly if logs of both are plotted ($N = 30$, $r = 0.91$, $P < .001$).

Number of eggs per clutch ranged from 9 to 71 ($N = 30$, mean = 40.6) and was closely positively correlated with female size. The correlation of egg number with SVL ($N = 30$, $r = 0.78$, $P < .001$) (Fig. 2) is about equal to that with female weight ($N = 30$, $r = 0.79$, $P < .001$). A better predictor of the number of eggs that a female will lay, and one that can be used in the field, is her weight before she has laid her eggs (i.e., her own body weight plus the weight of her clutch) ($N = 28$, $r = 0.88$, $P < .001$) (Fig. 3).

The weight of 28 clutches ranged from 84 to 1086 g (mean = 538 g) and is closely correlated with female size ($N = 28$, $r = 0.83$, $P < .001$). Mean egg weight per clutch (clutch weight/number of eggs) ranged from 9.3 to 16.0 g ($N = 28$, mean = 13.1). Eggs within a clutch appear quite uniform in size. Larger females tended to lay larger eggs but the correlation of mean egg weight to SVL, though significant ($N = 28$, $r = 0.55$, $P < .01$), is not as high as the correlations already cited. The single very small female with her very small eggs contributes greatly to this correlation; if she is excluded the correlation is lower ($N = 27$, $r = 0.35$, $.01 < P < .05$).

The water content of the eggs varied little, 57–67% ($N = 11$, mean = 62.3%). There was no significant correlation of water content either with egg weight or female size.

The percentage that the clutch contributed to the combined weight of female and clutch (relative clutch mass of Vitt and Congdon 1978) ranged from 19.7 to 39.9% ($N = 28$, mean = 30.3%). It shows a weak positive correlation with female SVL ($N = 28$, $r = 0.30$, $.01 < P < .05$) which depends heavily on the single small fe-

TABLE 1. Clutch size in Panamanian *Iguana iguana*.

Female		Number of eggs	Clutch weight in g	Mean egg weight in g	Relative clutch mass ¹	Expenditure per egg ²	Percent water in clutch	
SVL in mm	Wt. in g							
224	289	9	83.7	9.3	22.5	2.5	62.8	
304	843	26	371.0	14.3	30.6	1.2	61.9	
310	814	26	315.6	12.1	27.9	1.1	65.8	
316	910	26	319.0	12.3	26.0	1.0	61.8	
320	774	25						
320	994	24	293.1	12.2	22.8	0.9	57.5	
330	1042	35	433.3	12.4	29.4	0.8	61.9	
331	1136	40	476.1	11.9	29.5	0.7	64.2	
340	907	30	407.8	13.6	31.0	1.0		
340	1114	46	558.6	12.1	33.4	0.7		
340	883	37						
340	836	30	415.3	13.8	33.2	1.1		
350	1219	29	464.9	16.0	27.6	1.0		
350	1141	48	635.4	13.2	35.8	0.7		
350	1019	35	462.7	13.2	31.2	0.9		
350	1246	53	614.5	11.6	33.0	0.6		
353	1322	56	693.0	12.4	34.4	0.6	67.0	
359	1422	46	551.1	12.0	27.9	0.6	59.9	
360	886	42	462.0	11.0	34.3	0.8		
363	1341	42	568.1	13.5	29.8	0.7	62.0	
370	902	46	585.6	12.7	39.4	0.9		
380	1299	24	319.0	13.3	19.7	0.8		
390	1369	28	445.1	15.9	24.5	0.9		
390	1937	54	662.4	12.3	25.5	0.5		
390	1639	56	742.7	13.3	31.2	0.6		
397	1784	59	724.1	12.3	28.9	0.5		
410	2306	69	926.1	13.4	28.7	0.4		
410	1639	56	742.8	13.3	31.2	0.6		
410	1721	49	717.2	14.6	29.4	0.6		
430	1636	71	1085.8	15.3	39.9	0.6		
N =	30	30	28	28	28	28	11	
\bar{x} =	354.2	1212.3	40.6	538.4	13.1	30.3	0.7	62.4

¹ Percent relative clutch mass = clutch weight/(female weight + clutch weight) × 100.

² Percent expenditure per egg = relative clutch mass/number of eggs × 100.

male; if she is excluded r falls to 0.14 ($P < .05$). The percentage that a single egg represented of the combined weights of female and clutch (expenditure per egg) varied from 0.4 to 2.4% ($N = 29$, mean = 0.7%). It also shows a correlation with female weight ($N = 29$, $r = 0.37$, $P < .01$).

DISCUSSION AND CONCLUSIONS

In any lizard an upper limit to the possible volume of its clutch is set by the space available within the female for eggs. Two sorts of observations suggest that most gravid female iguanas have reached this limit. First, most have their abdomen distended and on dissection are found to have their body cavity packed with eggs with no extra space, even for food. Second, most points

in Fig. 2, relating clutch weight to female length, lie close to the regression line, and there are only a few females that have a smaller clutch weight than their length predicts. Since most females produce as large a clutch as there is space for, it seems probable that clutch size usually is not limited by food availability.

Iguana clutches in Nicaragua were measured by Fitch and Henderson (1977). Table 2 shows that, comparing the population in Nicaragua with that in Panama, the slopes of the various regression lines are not significantly different ($P < .05$), but that the elevations of some of them are. Compared with those in Panama, female iguanas in Nicaragua of the same size have lower body weights and lay lighter clutches. They also lay fewer and smaller eggs. These differences balance

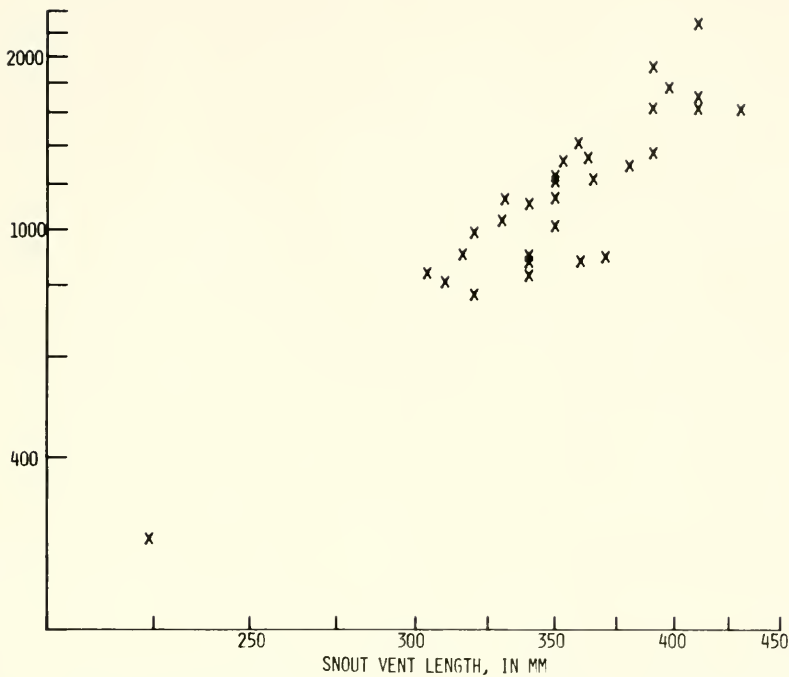


FIG. 1. The relationship between weight and snout-vent length in Panamanian iguanas.

so that females of the same weight in two populations lay about the same number of eggs but have a lower total clutch weight in Nicaragua. The relative clutch mass and the investment per egg is not significantly different between the two populations.

No other equally extensive data on *Iguana iguana* clutch sizes has been published. Hirth (1963) reported SVL and clutch size for 7 females from Tortuguero, Costa Rica (Fig. 2). These clutch sizes are intermediate between those of Panamanian and Nicaraguan females of similar sizes. This suggests the possibility of a geographical trend in reproductive strategies that would be worth exploring. However, it does not appear to continue into South America. Hoogmoed (1973) reports clutch sizes from 24 to 57 in Surinam. Muller (1972) reports clutches from 14 to 70 at Santa Marta, Colombia, and egg weights averaging 13.0 g (12.4–14.0). Detailed comparison with South American populations awaits more data.

Wiewandt (1983) has compared reproductive patterns among iguanine lizards. He distinguished three groups of genera on ecological grounds: 1) those in mainland deserts of tem-

perate North America (*Dipsosaurus* and *Sauromalus*); 2) those on dry subtropical islands (*Cyclura*); and 3) those in mainland tropical areas (*Iguana* and *Ctenosaura*). The mainland tropical group grows the most rapidly, matures earliest, and has the largest clutch sizes and the lowest ratio of egg weight to female weight.

In *Iguana iguana*, though its eggs are small relative to female size, the weight of its total clutch, relative to that of the female, is about the same as it is for the three other iguanine species for which Wiewandt gives data (*Sauromalus obesus*, *Cyclura carinata* and *Cyclura coronuta stejnegeri*). The marine iguana of the Galapagos was not classified in his scheme but is extreme within the iguanines in having very few, very large eggs with a high investment per offspring but a low investment per clutch (Carpenter 1966).

Wiewandt attributes the reproductive pattern in *Iguana iguana* and *Ctenosaura similis* to the relatively high predation pressure on young lizards in these species. Tinkle *et al.* (1970) have reviewed the reproductive strategies of a wide taxonomic and geographical representation of lizards. That survey included few iguanines, or other large tropical herbivorous lizards and it is

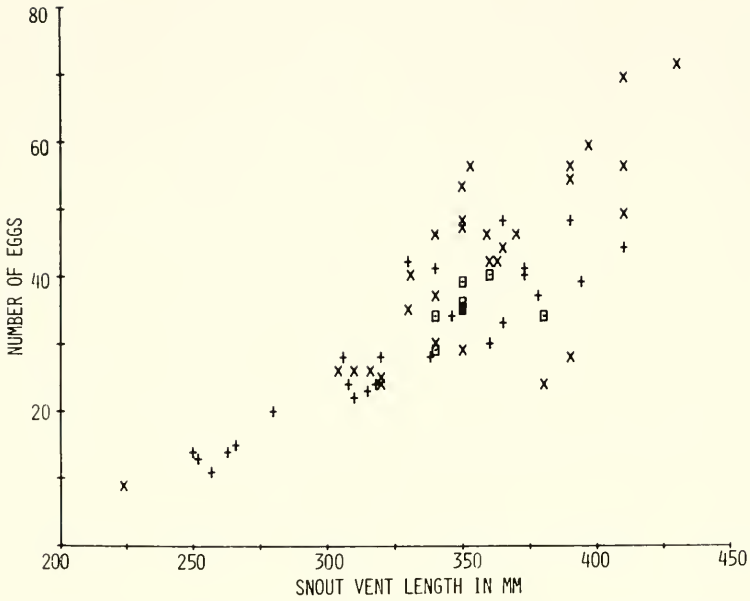


FIG. 2. The relationship between clutch size and snout-vent length in iguanas from Panama (X); Nicaragua (+) (Fitch and Henderson 1977), and Tortuguero, Costa Rica (□) (Hirth 1963).

interesting to compare our data with their results. Tinkle *et al.* recognize two different reproductive strategies among lizards: those that mature during their first year and lay more than one clutch

per season, and those that delay maturation for more than a year and lay only a single clutch per year. *Iguana iguana*, and most iguanines (see Wiewand for possible exceptions) clearly fall into

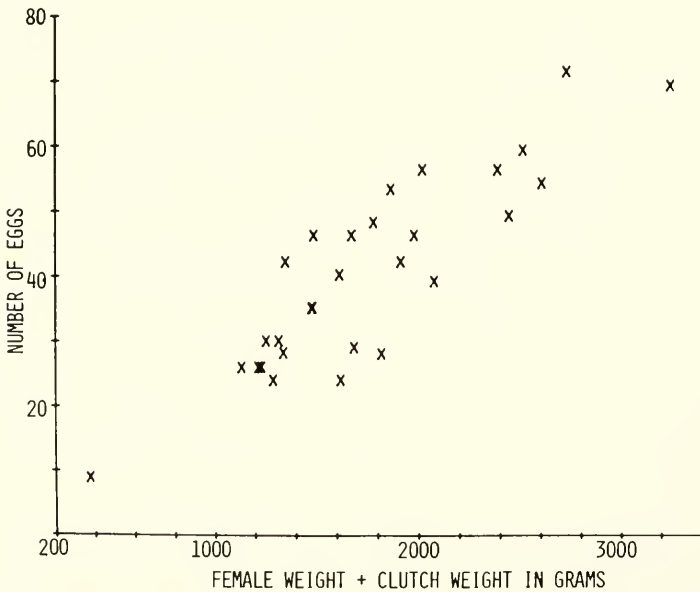


FIG. 3. The relationship, in iguanas from Panama, between clutch size and the weight of the female plus the weight of her clutch.

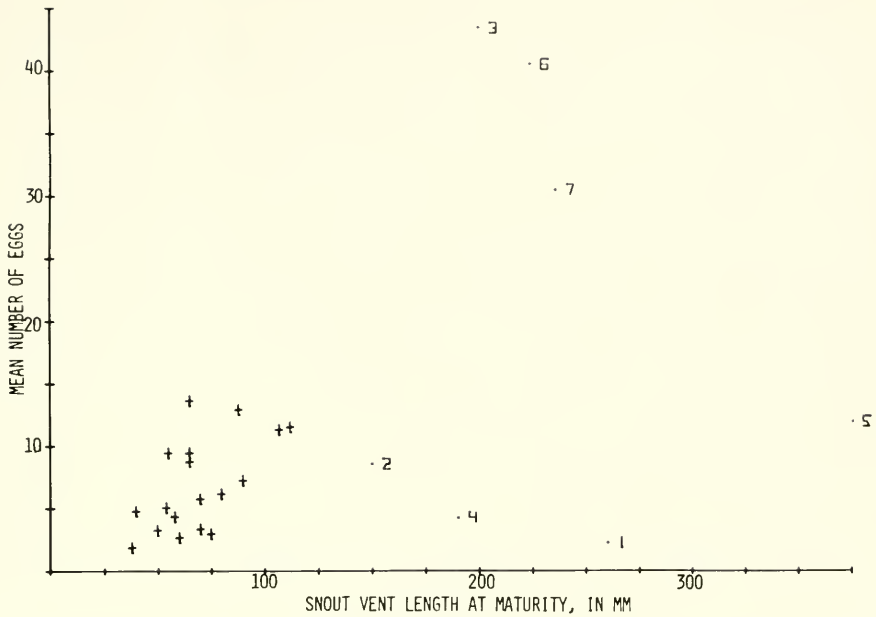


FIG. 4. The relationship between clutch size and minimum snout-vent length at maturity. + = single brooded iguanas (Tinkle *et al.* 1970). 1 = *Amblyrhynchus cristatus*, (Carpenter 1966), 2 = *Sauromalus obesus*, 3 = *Ctenosaura similis*, 4 = *Cyclura carinata*, 5 = *Cyclura coronuta stejnegeri* (2-5, Wiewandt 1983), 6 = *Iguana iguana* from Panama, 7 = *Iguana iguana* from Nicaragua (Fitch and Henderson 1977).

the second group. In contrast to the largely tropical iguanines, most of Tinkle *et al.*'s single brooded species are temperate in distribution.

Fig. 4 plots the relationship between minimum size at first reproduction and mean clutch size for the species that Tinkle *et al.* included in their single brooded group as well as the data for *Iguana iguana* from Panama and Nicaragua and 4 other iguanines. As Wiewandt noted, *Amblyrhynchus cristatus*, *Cyclura carinata* and *C. coronuta stejnegeri* and *Sauromalus obesus* have few eggs for their size. Fig. 4 shows that *Ctenosaura similis* and *Iguana iguana* have clutches close to but still slightly below those predicted from the smaller lizards. We do not have enough data to plot other iguanines but those for which we do have some data (*Brachylophus faciatus*, *Sauromalus varius* and *S. hispidus*, *Conolophus subcristatus*, and *Iguana delicatissima*) all seem to have clutch sizes below those of *Iguana iguana* and *Ctenosaura similis* and those of the smaller, single brooded lizards.

Number of eggs per clutch is an important parameter in a reproductive strategy. It is not, however, a very good index of reproductive effort (Tinkle and Hadley 1975; Vitt and Congdon

1978); in part, because a female iguana expends a great deal of energy in traveling to a nest site, digging a nest burrow, defending it, filling the burrow and returning to her home range (Rand and Rand 1976). Even for the clutch itself, clutch mass or calorific content is a better measure of reproductive effort than is number of eggs. We do not have calorific data for iguanas but Ballinger and Clark (1973) and Vitt (1978) have shown that calorific content per unit weight is quite constant for the eggs of a variety of numbers of lizards. Vitt (1978) has shown that the ratio of calorific content of clutch to calorific content of female is similar to the ratio of wet weight of clutch to wet weight of female. That our ratio of dry to wet weight of iguana eggs lies within the range that Vitt reported for other lizards is support for our assumption that iguana eggs are probably not too different from other lizards in calorific content per unit wet weight.

For *Iguana iguana*, in Panama, wet clutch weight averages 30.3% of the total wet weight of female and clutch (relative clutch mass); this is close to the mean of 27.7% that Vitt and Congdon (1978, Table 2) give for 17 much smaller North American iguanid lizards. Not surprising-

TABLE 2. A comparison between clutch sizes of *Iguana iguana* from Panama and Nicaragua.

	N	r	Panama	
			a	b
X = Snout-vent length (mm) Y = female weight (g)	30	.86**	-1872	8.708
X = log snout-vent length Y = log female weight	30	.91**	-9.62	2.841
X = snout-vent length Y = number of eggs	30	.78**	-59.4	.282
X = snout-vent length Y = clutch weight	28	.83**	-936	4.141
X = snout-vent length Y = mean egg weight	28	.55**	6.34	.0186
X = snout-vent length Y = relative clutch mass ¹	28	.30*	18.2	.033
X = snout-vent length Y = expenditure per egg ²	28	.84**	3.59	-.008
X = female weight Y = number of eggs	30	.80**	6.10	.0284
X = female weight Y = clutch weight	28	.82**	35.8	.4054
X = female + clutch weight Y = number of eggs	28	.89**	1.70	.0222

¹ Relative clutch mass = clutch weight/(female weight + clutch weight).

² Expenditure per egg = relative clutch mass/number of eggs.

³ Panama minus Nicaragua.

* = significant at the 5% level.

** = significant at the 1% level.

ly, *Iguana iguana*, which is an arboreal, highly cryptic herbivore, has a relative clutch mass above that for active foragers and more like that of the sit-and-wait predators. Because *Iguana iguana* clutch size is so much larger, the investment per offspring, relative to female size, is much smaller than in the other iguanids that Vitt and Congdon report.

That the relative clutch mass is larger in large females than small ones in both Panama and Nicaragua (Table 2) suggests that *Iguana iguana* behaves in accord with the general prediction by Williams (1966) that, within a species, relative reproductive effort should increase with age because as an animal ages there is less cost to future reproduction from a high effort at the present age. Pianka and Parker (1975) develop this idea and discuss the conditions under which an animal should modify its current reproductive effort in order to maximize its total lifetime reproductive value, and discuss some examples both of

reptiles which increase their relative reproductive investment with age and those that do not seem to do so. In these iguanas, the greatest difference in relative reproductive effort is between very small females and all the rest. Differences between moderate and large females are much less strong. Until we have some estimates of growth and mortality for iguanas at different ages we cannot interpret the selective pressures that have produced the observed patterns and evaluate the relevance of Williams' suggestion and Pianka and Parker's model to the evolution of iguana reproductive biology. Certainly other factors such as body shape and the ability to acquire or process resources may change with female size and influence relative clutch mass.

SUMMARY

In *Iguana iguana* from Panama the number of eggs and the weight of a clutch laid by a female

TABLE 2. Continued.

N	r	Nicaragua		F values comparing		Differences in adjusted means ¹
		a	b	Slopes	Elevations	
24	.93**	-1490	7.113	1.79	9.49**	164
24	.96**	-10.4	2.945	0.12	14.59**	.159
24	.90**	-41.5	.2170	1.75	4.17*	4.48
24	.90**	-724	3.158	2.39	19.38**	127
24	.69**	-1.39	.0349	2.95	25.02**	2.15
24	.45*	9.92	.049	0.31	3.87	
24	.89**	3.19	-.007	0.77	0.44	
24	.81**	8.20	.0256	0.24	0.10	
24	.85**	-16.1	.3901	0.04	4.07*	67.5
24	.82**	8.01	.019	0.78	0.59	

are closely correlated with both her length and her body weight. The latter two variables are also closely correlated. Egg weight, relative clutch mass, and expenditure per egg all correlate positively with female size.

Iguanas from Nicaragua (Fitch and Henderson 1977) show similar relationships between these variables; though females from Nicaragua tend to be lighter and to lay fewer and smaller eggs than do females of equal length in Panama. Relative clutch mass and relative egg size are about the same in the two populations.

Compared with other lizards, *Iguana iguana* has a clutch size which is only a little below that predicted for its size at reproductive maturity from the relationship between these variables seen in other, much smaller lizards. The clutch weight, as a percentage of female size is also not very different. Among its close relatives *Ctenosaura similis* is like *Iguana iguana* but *Cyclura*, *Sauromalus*, *Amblyrhynchus*, and *Conolophus* seem to have fewer eggs than predicted on the basis of size at maturity.

ACKNOWLEDGMENTS

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Are Anuran Amphibians Heavy Metal Accumulators?

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INTRODUCTION

Concern about heavy metals in the environment has increased recently, partly as a result of increased awareness of their potential effects, and also because of the prospect of expanded use of fossil fuels in processes that release metals. From time to time amphibians have been examined as possible indicators of contamination by heavy metals. Their habitats, abundance, and ease of sampling have made them convenient subjects for such purposes.

There have been indications that amphibians may be unusual in their ability to accumulate metals. A survey of the copper content of the livers of a wide range of vertebrate species (Beck 1956) indicated extremely high levels (up to 1640 ppm) in *Bufo marinus*; average copper concentrations in livers were generally much lower in other species, although one species of marine fish had higher average concentrations. Surprisingly high concentrations of lead in the livers of some frogs from a remote and apparently uncontaminated area were reported by Schroeder and Tipton (1968). Gale *et al.* (1973) found up to 1590 ppm (dry weight) of lead in tadpoles from a contaminated area and these results suggest that they have a much greater ability to concentrate environmental lead than do the other species sampled. The iron content of one sample of *Rana catesbeiana* tadpoles analyzed in our own laboratory reached the startling level of 19,000 ppm (dry weight).

It is the purpose of this paper to present data from our own work at the Patuxent Wildlife Research Center (PWRC) and information from the literature in order to ascertain whether the concentrations of metals in amphibians fall outside the normal range of variation of other animals. This paper will assemble data which may bear on the questions of whether amphibians are particularly susceptible to heavy metal pollution, whether they can accumulate levels which may be hazardous to their predators, and whether they can be of value as monitors of heavy metal contamination.

METHODS

Adult amphibians collected at the Patuxent Wildlife Research Center were generally obtained from the Island Marshes, artificial habitats built for waterfowl management, or they were picked up on service roads on wet nights. Larval amphibians and fish were captured by seine or dip net from Harding Spring or Mabbott ponds; both are shallow, moderate-sized artificial ponds surrounded by wooded areas. The research center is not known to be contaminated by heavy metal residues. Iron is naturally abundant in the soil and groundwater. Possible alteration of Harding Spring Pond by runoff from a nearby landfill has led us to undertake a program monitoring organochlorine and heavy metal levels in certain animals found in different areas of the center. A sample of 10 leopard frogs (*Rana pipiens*) obtained from the National Fish and Wildlife Health Laboratory, Madison, Wisconsin was also analyzed for heavy metal levels.

Tissue samples were homogenized in a blender and a 5 g portion was weighed into a crucible for heavy metals analysis. A separate 5 g portion was weighed into a round-bottom flask to determine mercury levels. Digestion for mercury analysis used the method described by Monk (1961). Mercury was determined by cold vapor atomic absorption spectrophotometry using the method of Hatch and Ott (1968) with a Coleman model MAS-50 mercury analyzer. The lower limit of reportable residues was 0.02 ppm. The sample used to determine other metals was dried in an oven and then charred in a muffle furnace where the temperature was raised to 550°C at the rate of 100%/hr and left overnight. The cooled ash was dissolved over a hot plate in approximately 2 ml of concentrated nitric acid and 1 ml of concentrated hydrochloric acid, transferred to a 50 ml polypropylene centrifuge tube, and diluted with dionized water. Analysis was by flame atomic absorption spectrophotometry with a Perkin-Elmer model 703 equipped with a deuterium arc background corrector, an AS-50 autosampler, and a PRS-10 printer. The lower limit of reportable

TABLE 1. Cadmium in amphibians.

Sample	Area	Tissue	PPM		N	Reference
			Wet weight	Dry weight		
Tadpoles (sp.)	Pb contaminated	Whole body		1.4–3.0	8 pools	Gale <i>et al.</i> 1973
	Uncontaminated	Whole body		1.1	1 pool	Gale <i>et al.</i> 1973
Tadpoles (<i>R. catesbeiana</i>)	Uncontaminated	Whole body	0.16–0.24	1.2–2.0	5 pools	PWRC ¹
(<i>R. clamitans</i>)	Uncontaminated	Whole body	0.10–0.19	1.0–1.8	2 pools	
Toads (<i>Bufo</i> spp.)	Uncontaminated ²	Whole body	0.15–4.0	0.72–26	4	PWRC
		Livers	0.08–0.13	0.64–1.1	2	
		Kidneys (pooled)	1.9	6.1	1 pool	
		Carcasses	0.19–7.3	0.68–25	12	
Frogs (<i>Rana</i> spp.)	Uncontaminated	Whole body	0.10–0.36		11	PWRC
Adult amphibians (<i>Triturus</i> , <i>Rana</i> , <i>Pelobates</i> , <i>Bufo</i>)	Contaminated by Zn mill downwind	Whole body		10.7	1	Dmowski and Karolewski 1979
	protected area	Whole body		1.3–14.4	8	Dmowski and Karolewski 1979
	Uncontaminated	Whole body		0.3–1.4	11	Dmowski and Karolewski 1979

¹ Unpublished data, Patuxent Wildlife Research Center.

² Some of these animals were captured on or near highways; these local sources of contamination may explain the high levels of cadmium found in some samples.

residues was 0.1 ppm. Recoveries of all metals from fortified chicken livers ranged from 81 to 116%. Residues were not corrected for percent recovery.

All concentrations are on a whole body, wet weight basis unless stated otherwise. Tadpoles analyzed at Patuxent Wildlife Research Center were prepared in pools of at least 10 individuals each; variability among pools was relatively low. Most reports in the literature do not have estimates of variability. Indications that variability may be extreme, however, have led us to use ranges rather than means for comparative purposes.

RESULTS AND DISCUSSION

Metal Residues Reported in Amphibians

Arsenic.—Concentrations of arsenic in livers of adult *Rana*, *Bufo*, and *Bombina* collected in an apparently uncontaminated area (Byrne *et al.*

1975) averaged 0.164 ppm; they averaged 0.079 ppm in an area known to be contaminated with mercury. These concentrations are within normal levels for most organisms (Schroeder and Balassa 1966) and are considerably lower than levels found in many freshwater animals (Wagemann *et al.* 1978).

Cadmium.—Levels in lead-contaminated areas (Gale *et al.* 1973) generally exceeded those recorded in apparently unpolluted areas. Cadmium concentrations in tadpoles (Table 1) analyzed in our laboratory are about an order of magnitude higher than the concentrations found in a variety of fish species in New York (Lovett *et al.* 1972) and approximately twice the levels found in fish from the same areas. Concentrations of cadmium in livers and kidneys of toads and carcasses of frogs (Table 1) generally fall within the ranges reported for other animal materials by Fleischer *et al.* (1974). Carcass and whole-body concentrations in toads (up to 7.3 ppm wet weight) exceeded levels reported in oth-

TABLE 2. Copper in amphibians.

Sample	Area	Tissue	PPM		N	Reference
			Wet weight	Dry weight		
Tadpoles (sp.)	Uncontaminated	Whole body		8	1 pool	Gale <i>et al.</i> 1973
	Pb contaminated	Whole body		17-48	8 pools	
Tadpoles (sp.)	Pb contaminated	Whole body		169	1 pool	Jennett <i>et al.</i> 1977
Tadpoles (<i>Rana catesbeiana</i>)	Uncontaminated	Whole body	1.4-3.2	12-19	5 pools	PWRC ¹
<i>R. clamitans</i>	Uncontaminated	Whole body	0.93-1.2	8.8-12	2 pools	
Adult (<i>Rana temporaria</i>)	Uncontaminated	Whole body	53.1-207.1	159.9-845.1 ²	106	Pasanen and Koskela 1974
Adult (<i>Rana</i> , <i>Bufo</i> , <i>Bombina</i> , <i>Triturus</i> spp.)	Hg contaminated	Liver	4.0-318.9	13.8-1099.7	24	Bryne <i>et al.</i> 1975
Adult (<i>Bufo</i> , <i>Hyla</i> , <i>Limnodynastes</i>)	Uncontaminated	Liver		10-1640	21	Beck 1956
Adult (<i>Bufo marinus</i>)	Uncontaminated	Liver		367-2091	6	Goldfischer <i>et al.</i> 1970
Adult (<i>Bufo</i>)	Uncontaminated	Whole body	2.1-5.0	9-20	4	PWRC
Adult (<i>Rana</i>)	Uncontaminated	Whole body	1.2-3.5	9.0	11	PWRC
Adult (<i>Rana catesbeiana</i>)	Uncontaminated	Blood	0.5-5.9		40	Sarata 1938
		Plasma	0.3-1.5		11 pools	
		Liver		10-29	40	
		Fat		0.4-1.4	40	
		Eggs		0.19-0.26	2	

¹ Unpublished data, Patuxent Wildlife Research Center.

² Means; highest single observation was 1367 ppm.

er terrestrial animals from uncontaminated areas (Table 1).

Cobalt.—Bullfrog tadpoles had up to 12,760 pCi/g (dry weight) of cobalt-60 after treatment of an experimental pond (Brungs 1963). The level in tadpoles before treatment was 12 pCi/g. Amounts in the flesh of treated adult bullfrogs ranged up to 105 pCi/g, or less than 1% of the maximum levels in the larvae. Amounts of cobalt-60 taken up by the tadpoles exceeded those in various species of fish and invertebrates.

Tadpoles collected from a presumably uncontaminated area were analyzed in our laboratory; they averaged 1.92 ppm of cobalt in *R. catesbeiana* tadpoles and 0.38 ppm in *R. clamitans* tadpoles. A mixed species group of adult anurans averaged 2.1 ppm (range 0.73-3.2). Higher levels were found in the carcasses when kidneys and carcass remainders were analyzed separately.

Copper.—Copper levels may be strikingly high

in adult anurans, but they are highly variable, even in contaminated areas (Table 2). Copper in the livers of *Bufo marinus* is sequestered in lysosomes where it is unable to damage the hepatocytes (Goldfischer *et al.* 1970). These authors stated that similar levels in adult humans (not contained in lysosomes) would result in serious or fatal damage to the liver. This association with lysosomes explains how toads can tolerate high copper burdens, but does not explain how they accumulate such concentrations in apparently uncontaminated habitats (Table 2). Liver levels of copper up to 3000 ppm have been reported in sheep on a diet with copper-molybdenum imbalances and exceedingly high liver levels of copper have been found in Bedlington Terrier dogs with a hereditary and fatal liver disorder (National Research Council 1977). The high levels of copper found in some amphibians may likewise indicate unusual dietary or metabolic

TABLE 3. Lead in amphibians.

Sample	Area	Tissue	PPM		N	Reference
			Wet weight basis	Dry weight basis		
Tadpoles (sp.)	Uncontaminated	Whole body		28	1 pool	Gale <i>et al.</i> 1973
	Pb contaminated	Whole body		36–1590	8 pools	
Tadpoles (sp.)	Pb contaminated	Whole body		4139	1 pool	Jennett <i>et al.</i> 1977
		Eviscerated		93–213	2 pools	
Tadpoles (<i>R. catesbeiana</i>)	Uncontaminated	Whole body	2.5–3.2	14–23	5 pools	PWRC ¹
(<i>R. clamitans</i>)	Uncontaminated	Whole body	1.4–1.5	14–15	2 pools	
Frogs (<i>Rana</i> spp.)	Uncontaminated	Whole body	0.88–3.2	1.6–11	11	PWRC
Toads (<i>Bufo</i> spp.)	Uncontaminated	Carcass	21	0.73–75	3 pools	PWRC
		Kidneys	4.9	15	1 pool	
		Livers	2.1–2.6	19–21	2	
Adult frogs (<i>Acris</i> , <i>Bufo</i>)	Uncontaminated	Whole body		3.5 ²	14	Rolfe <i>et al.</i> 1977
	Pb contaminated	Whole body		3.7–3.0 ²	31	
Frogs (<i>Rana</i> spp.)	Uncontaminated	Livers		1.0–31.3	—	Schroeder and Tipton 1968
		Kidneys		1.3–10.2	—	
Adult amphibians (<i>Triturus</i> , <i>Rana</i> , <i>Pelobates</i> , <i>Bufo</i>)	Contaminated by Zn mill downwind protected area	Whole body		461	1	Dmowski and Karolewski 1979
	Uncontaminated	Whole body		46–202	8	
		Whole body		0	11	

¹ Unpublished data, Patuxent Wildlife Research Center.

² Means.

influences. Levels of copper in tadpoles are within the normal range of concentrations reported in various animal materials by National Research Council (1977).

Chromium.—Tadpoles collected on the Patuxent Wildlife Research Center averaged 3.8 ppm (*R. catesbeiana*) and 1.6 ppm (*R. clamitans*). Chromium concentrations in adult *B. americanus*, *B. woodhousei*, *R. sphenoccephala* ranged from 1.8 to 5.4 ppm. A single individual had 56 ppm, but it also had an unusually high concentration of nickel and the sample may have been contaminated during homogenization. Ten *R. pipiens* averaged 0.48 ± 0.12 ppm. Pooled samples of *B. woodhousei* carcasses and kidneys had 0.66 and 0.95 chromium. The levels of chromium reported in amphibians are higher than

the representative levels given by Schroeder *et al.* (1962b) for a variety of animals.

Iron.—Singh (1978) studied seasonal variation in the iron content of the serum of *Rana tigrina*. Averages were 0.99 ppm for males and 0.93 ppm for females. Levels tended to be highest during the breeding season. Concentrations were similar to those in humans, greater than those in fish, but less than those of laying fowl. A pooled sample of several species of adult frogs analyzed at Patuxent averaged whole body levels of 90 ppm. Kidneys (180 ppm) contained more than carcasses (21 ppm). Tadpoles accumulated large body burdens of iron; *R. catesbeiana* larvae averaged 2600 ppm and *R. clamitans* 500 ppm. There is little published information about iron in wild animals, but these levels are several or-

TABLE 4. Mercury in amphibians.

Sample	Area	Tissue	PPM (wet weight basis)	N	Reference
Amphibian spawn	Uncontaminated	—	0.0002–0.012	6	Byrne <i>et al.</i> 1975
	Hg contaminated	—	0.365	1	
Newt larvae	Hg contaminated	Whole body	0.18, 0.22	2	Byrne <i>et al.</i> 1975
Tadpoles (sp.)	Hg contaminated	Whole body	0.41, 0.49	2	Byrne <i>et al.</i> 1975
Tadpoles					
(<i>R. catesbeiana</i>)	Uncontaminated	Whole body	0.05–0.10	5 pools	PWRC ¹
(<i>R. clamitans</i>)	Uncontaminated	Whole body	0.04–0.10	2 pools	PWRC
Frogs (<i>Rana</i> spp.)	Uncontaminated	Whole body	<0.01–0.14	11	PWRC
Toads (<i>Bufo</i> spp.)	Uncontaminated	Whole body	0.04–0.14	4	PWRC
Adult amphibians	Uncontaminated	Muscle	0.04–0.48	19	Byrne <i>et al.</i> 1975
(<i>Bufo</i> , <i>Rana</i> , <i>Bombina</i> , <i>Triturus</i>)					
Adult amphibians	Hg contaminated	Muscle	1.39–2.85	9	Byrne <i>et al.</i> 1975
(<i>Bufo</i> , salamander)					
Frogs (<i>Rana</i> spp.)	Hg contaminated	Carcass	<0.10–0.18	4	Dustman <i>et al.</i> 1972
		Liver	0.28–0.74	4	
Frogs (<i>Rana</i> , <i>Bufo</i> , <i>Bombina</i>)	Uncontaminated	Liver	0.07–2.3	16	Byrne <i>et al.</i> 1975
	Hg contaminated	Liver	1.2–16.2	8	

¹ Unpublished data, Patuxent Wildlife Research Center.

ders of magnitude higher than levels reports in humans or in foods of animal origin (National Research Council 1979).

Lead.—High levels of lead in tadpoles from contaminated waters of Missouri's New Lead Belt are reported by Gale *et al.* (1973) and Jennett *et al.* (1977). But Rolfe *et al.* (1977) could not detect elevated lead levels in adult anurans from an area near a highway which presumably received lead from automotive exhausts. Despite this negative evidence, it is thought that elevated lead levels in some of the PWRC samples (Table 3) might have resulted from the proximity of the collection sites to highways. The range of concentrations found in adult frogs falls within the range reported in humans (Schroeder and Tipton 1968) and levels seem to be close to those found in small mammals (Getz *et al.* 1977). The data indicate little tendency for lead to be preferentially stored in liver, kidney, or carcass. Other authors have not found lead to be concentrated in particular tissues (Schroeder and Tipton 1968; Getz *et al.* 1977). When lead contaminated earth-

worms were fed to *Xenopus laevis*, animals consuming up to 170 µg/day accumulated up to 81 ppm (dry weight) in the kidneys and 31 ppm in the liver (Ireland 1977); relatively greater amounts of lead are stored in soft tissues in *Xenopus* than in *Peromyscus*.

Mercury.—Reports of mercury in amphibians are summarized in Table 4. An extensive study by Byrne *et al.* (1975) surveyed mercury levels in a number of species of amphibians in both contaminated and uncontaminated areas. Dustman *et al.* (1970) reported much higher concentrations of mercury in predatory birds and fish than in amphibians from a contaminated area. Higher concentrations of mercury have been reported in amphibians collected from other contaminated areas but they do not seem to concentrate mercury as much as some other species.

Nickel.—Levels of nickel of 2.7 ppm for *R. catesbeiana* and 0.9 ppm for *R. clamitans* were found in tadpoles from the Patuxent Wildlife Research Center. Specimens of adult anurans analyzed ranged between 0.9 and 2.9 ppm, with a

TABLE 5. Zinc in amphibians.

Sample	Area	Tissue	PPM		N	Reference
			Wet weight basis	Dry weight basis		
Tadpoles (sp.)	Untaminated	Whole body		62	1 pool	Gale <i>et al.</i> 1973
	Pb contaminated	Whole body		160–1090	8 pools	
Tadpoles (sp.)	Zn contaminated	Whole body		2808	1 pool	Jennett <i>et al.</i> 1977
		Carcass (without GI tract)		240–256	2 pools	
Tadpoles (<i>R. catesbeiana</i>)	Untaminated	Whole body	9.7–15	60–86	5 pools	PWRC ¹
Tadpoles (<i>R. clamitans</i>)	Untaminated	Whole body	3.7–6.0	33–59	2 pools	
Adult amphibians (<i>Bufo</i> , <i>Rana</i> , <i>Bombina</i> , <i>Triturus</i>)	Untaminated	Liver	11.0–28.3	38–98 ²	20	Byrne <i>et al.</i> 1975
	Hg contaminated	Liver	20.0–33.4	69–115 ²	4	
Adult frogs (<i>Rana temporaria</i>)	Untaminated	Liver	12.2–24.6	45.0–90.7	106	Pasanen and Koskela 1974
Adult toads (<i>Bufo</i> spp.)	Untaminated	Whole body	25–94	85–460	4	PWRC
		Carcass (pool of 10)	84	300	1 pool	
		Kidneys (pool of 10)	39	120	1 pool	
Adult frogs (<i>Rana</i> spp.)	Untaminated	Whole body	6.2–31	130	11	PWRC
Adult amphibians (<i>Triturus</i> , <i>Rana</i> , <i>Pelobates</i> , <i>Bufo</i>)	Contaminated by Zn mill downwind protected area	Whole body		534	1	Dmowski and Karolewski 1979
		Whole body		56–206	8	
	Untaminated	Whole body		104–301	11	

¹ Unpublished data, Patuxent Wildlife Research Center.

² Calculated on the basis of average percent moisture given by the authors.

single specimen containing 27 ppm (see account on chromium). Ten leopard frogs (*R. pipiens*) averaged 1.39 ± 0.13 ppm. Pooled kidneys and carcasses of *B. woodhousei* each had 0.76 ppm nickel. Levels of nickel in wild species are poorly known, but the levels reported here seem to be within representative levels reported by Schroeder *et al.* (1962a).

Zinc.—Levels of zinc in amphibians (Table 5) show little variation between tadpoles and adults or between background and metal-contaminated areas except in an area directly contaminated by

zinc (Dmowski and Karolewski 1979) and in tadpole samples from lead-contaminated areas (Gale *et al.* 1973; Jennett *et al.* 1977) which show definite evidence of elevated levels. Zinc concentrations in whole tadpoles were about 10 times those in fish and in eviscerated tadpoles were about double those in fish (Jennett *et al.* 1977). Zn-65 reached approximately 60,000 pCi/g (dry weight) in bullfrog tadpoles inhabiting an artificially contaminated pond (Brungs 1963), a level close to that found in carp and higher than in mollusks or bluegills. Levels in adult bullfrogs

TABLE 6. Other elements in amphibia.

Element	Sample	Area	Tissue	PPM		N	Reference	
				Wet weight	Dry weight			
Bromine	Adult amphibians	Uncontaminated	Livers	2.6-15.1		3	Byrne <i>et al.</i> 1975	
		Hg contaminated	Livers	1.35-1.59		2		
Calcium	Adult <i>R. temporaria</i>	Uncontaminated	Livers	48.9-67.3	176.0-259.6 ¹	106	Pasanen and Koskela 1974	
Iodine	Adult amphibians	Uncontaminated	Livers	0.076-0.145		3	Byrne <i>et al.</i> 1975	
		Hg contaminated	Livers	0.049-0.092		2		
Magnesium	Tadpoles <i>R. catesbeiana</i>	Uncontaminated	Whole body	58-160		5 pools	PWRC ²	
	<i>R. clamitans</i>	Uncontaminated	Whole body	14-29		2 pools		
	Adult <i>R. temporaria</i>	Uncontaminated	Livers	81.0-170.4	315.1-663.8 ¹	106		Pasanen and Koskela 1974
Manganese	Tadpoles <i>R. catesbeiana</i>	Uncontaminated	Whole body	14-42		5 pools	PWRC	
	<i>R. clamitans</i>	Uncontaminated	Whole body	1.1		2 pools		
	Tadpoles (sp.)	Uncontaminated	Whole body		710	1 pool		Gale <i>et al.</i> 1973
		Pb contaminated	Whole body		262-5650	8 pools		
Selenium	Adult amphibians	Uncontaminated	Livers	0.069-0.077		2	Byrne <i>et al.</i> 1975	
		Hg contaminated	Livers	3.2-4.7		2		

¹ Means.

² Unpublished data, Patuxent Wildlife Research Center.

(≈4000 pCi/g) were much higher than those in turtles but less than half the levels found in crayfish.

Other Elements.—Bromine, calcium, iodine, magnesium, manganese, and selenium have been reported in amphibian tissues (Table 6) but either the potential threat posed by the materials seems remote or there is little comparative information. Manganese was present at higher levels in tadpoles than in crayfish or small fish from waters contaminated with lead (Gale *et al.* 1973). Selenium levels also may be higher in areas contaminated by mercury than in areas not contaminated by mercury (Byrne *et al.* 1975).

Other Radionuclides.—There is some information on radionuclides in addition to those (Co-60 and Zn-65) discussed earlier. Radioactive cesium has been reported in a single mixed species

sample of amphibians in the food of green herons by Dobby *et al.* (1977). The sample contained 0.2 pCi/g (wet weight) of Cs-134 and Cs-137 and was from an area polluted by radioactive wastes. Bullfrog tadpoles which originally averaged 33 pCi/g (dry weight) of cesium-137 contained 21,000 pCi/g after the experimental addition of radionuclides (Brungs 1963). Adult bullfrogs contained 426 pCi/g. Brungs also found that tadpoles accumulated 7923 pCi/g of strontium-85 but that adult frogs accumulated only 521 pCi/g in their flesh. Both Cs-137 and Sr-85 were accumulated to higher levels in tadpoles than in other animals but were accumulated less by adult frogs than by most aquatic animals. *Rana temporaria* tadpoles take up more yttrium-90 (a breakdown product) than they do the parent strontium-90 material from treated water (Lucas

and Pickering 1958). Pendleton and Hanson (1958) looked at cesium-137 uptake in a variety of organisms following addition of 6 pCi/ml of the radionuclide to the water of a concrete-lined pond. They analyzed concentration factors after approximately 90 days when levels of Cs-137 in the water had apparently stabilized. They found high concentrations in bullfrog tadpoles, with the bulk of the material stored in the gut fraction. Still higher levels were found in spadefoot toad (*Scaphiopus hammondi*) tadpoles and adult bullfrogs.

Comparison of Anuran Amphibians with Other Animals

Brungs (1963) published a number of useful comparisons of the abilities of aquatic animals to take up radionuclides. The highest recorded tissue levels of Co-60, Zn-65, Sr-85, and Cs-137 were all recorded in tadpoles. Somewhat lower levels were found in pelecypods (Co-60, Zn-65, Sr-85) and gastropods (Cs-137). Concentrations in bluegill sunfish and carp tended to be much lower except for Zn-65 and Sr-85 which tended to accumulate in bone. One possible explanation for the high body burdens in tadpoles is their relatively large gut capacity and the chance that a large part of the metals recorded was in the gut cavity and had not actually been assimilated. Separate analyses of gut and the remainder of the carcass confirmed the presence of high levels in the gut fraction, but, with the exception of Sr-85, body remainders still had greater accumulations than most other animals.

Also of interest is the fact that the highest levels of radioactivity in tadpoles occurred relatively soon after exposure; other species usually took longer to reach maximum levels and they maintained high levels longer than did the tadpoles. Brungs suggested that the high levels of radionuclides recorded were the result of the vertical distribution of the contaminants in the experimental ponds and the tendency of tadpoles to feed on fine sediments. Shortly after addition to the aquatic system, the radionuclides become attached to fine particles and settle to the bottom. Tadpoles consume them there and accumulate high levels before various processes had distributed the contaminants more generally throughout the system. Support for the assertion that feeding habits rather than physiological factors produced the high levels observed in tadpoles is

seen in Brungs' data on adult bullfrogs; they accumulated much lower levels of all the metals than did tadpoles, and less than detritivores such as crayfish.

Relatively high concentrations of Cs-137 were found in tadpoles in ponds experimentally dosed by Pendleton and Hanson (1958), but the levels were lower than those reported in sunfish, shrimp, and adult frogs. These comparisons were based on data collected some months after the addition of Cs-137 to the system. The authors stated that tadpoles are among organisms which take up the metal rapidly, accumulating it faster than do adult fish, frogs, or seed plants, but Pendleton and Hanson (1958) did not present specific data on the speed of uptake by tadpoles. The apparent differences between these results and those of Brungs are due to the different time spans between dosing and observation; both the relative amounts of Cs-137 in tadpoles compared to other animals and its absolute concentrations declined as the time after dosing approached 80 days (Brungs 1963).

Most of the lead, zinc and copper in tadpoles from a lead-contaminated area were in the gut (Jennett *et al.* 1977). However, concentrations in the rest of the body tended to be higher than those in fish from the same waters. These results support the idea that the uptake of the metals is through the diet. Comparison of tadpole gut and contents with those of bass and bluegills indicates an approximate 10-fold greater concentration of the three metals in the amphibian samples, also supporting Brungs' (1963) contention that feeding habits produce the higher levels in amphibians.

Getz *et al.* (1977) compared lead in different freshwater animals in urban and rural areas. They pointed out that lead levels were higher when the animals (fish and invertebrates) were more closely associated with silt substrata; analyses showed that the uppermost layers of sediment were highest in lead. Getz *et al.* (1977) concluded that physical contact with silt and the direct ingestion of lead in silt and detritus were important in uptake. They believed that food chain concentration did not occur.

Pooled samples of tadpoles of two species, and fish collected from two nearby ponds, are compared in Fig. 1. These results do not closely correspond to those metal levels reported by Gale *et al.* (1973) and Jennett *et al.* (1977) nor the radionuclides documented by Brungs (1963) be-

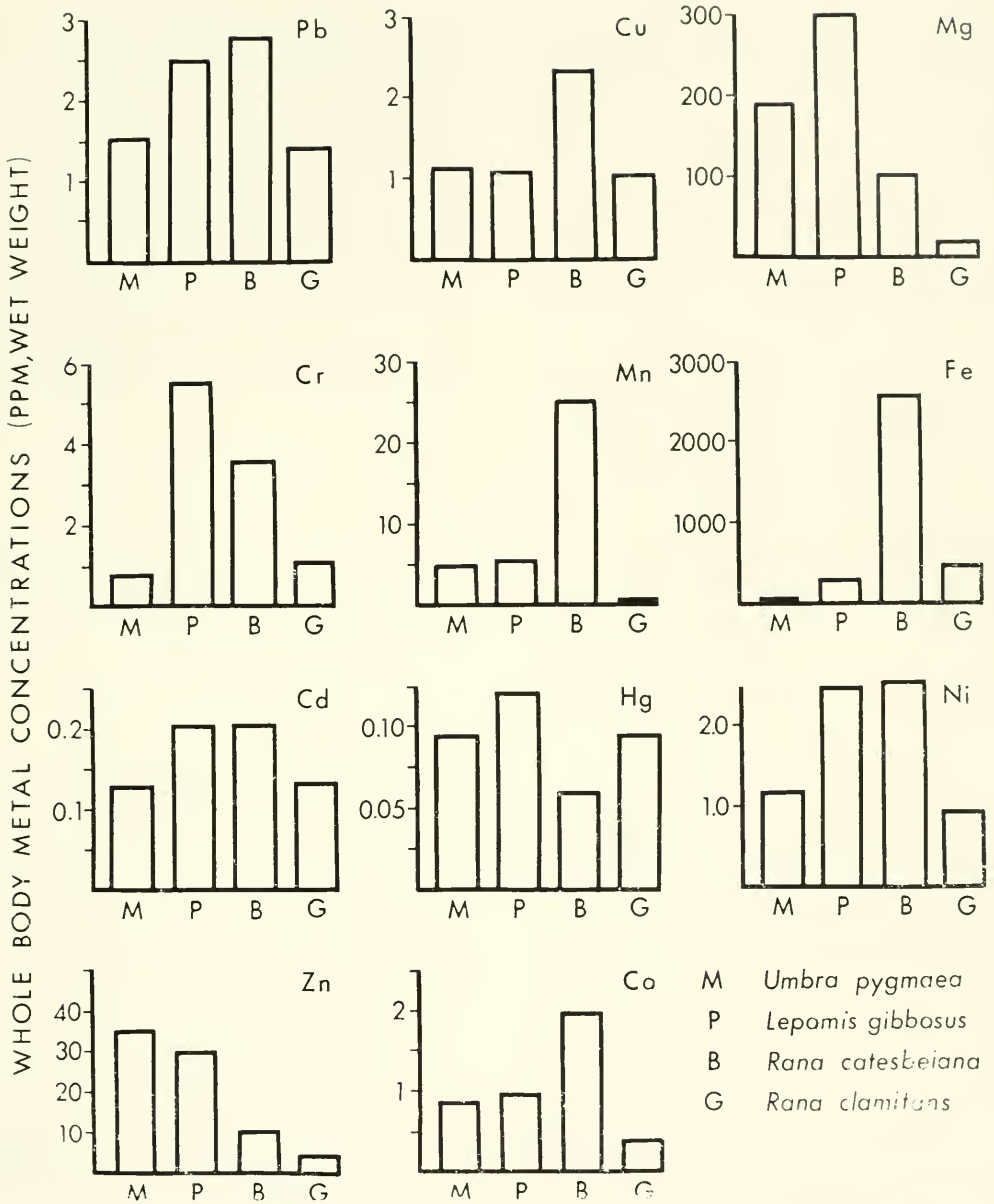


FIG. 1. Levels of metals detected in pooled samples of fish and amphibians collected from two ponds at the Patuxent Wildlife Research Center. Altogether, mudminnows (*Umbra pygmaea*) were represented by four pools, bullfrogs (*R. catesbeiana*) by five pools, green frogs (*R. clamitans*) by two pools, and pumpkinseed sunfish (*Lepomis gibbosus*) by seven pools. Pools of the first three species ranged from five to 50 individuals each; sunfish were of various sizes and each sample was comprised of from one to several individuals. Arithmetic means are shown.

cause the concentrations in tadpoles are not consistently higher than those in fish. Levels in bullfrog tadpoles are higher than those in fish in 6 of the 11 metals, but green frog tadpoles contain

levels lower than the fish in all but one of the metals. Zinc shows a trend opposite to that seen in the other studies and, with the exception of iron and manganese, the differences between

groups of animals are much less than those reported earlier. The concentrations of metals reported in Fig. 1 seem to show some real differences, but they indicate that conditions favoring the uptake of specific metals do not always result in the greatest uptake occurring in tadpoles.

Presumably the availability of metals to the different animals and their potential for uptake are influenced by the habits of the animals (see Steinwascher 1978, 1979) and the distribution of the metals within the environment. Distribution of metals in the ponds seems to differ from that in the systems examined by other authors, perhaps because our areas were essentially uncontaminated and had stable levels of most of the metals rather than a single treatment (Brungs 1963) or a continuous (Jennett *et al.* 1977) influx of contaminants. The result would be a greater dispersion of the metals and less tendency for tadpoles to accumulate them. This apparent tendency for tadpoles to selectively take up contaminants which have only recently entered an aquatic system, or which enter on a more or less continuous basis, would seem to make them good indicators of environmental contamination.

CONCLUSIONS

1) Adult amphibians of certain species can accumulate extremely high levels of copper in the liver. It seems likely that dietary imbalances or metabolic factors, rather than high environmental levels, result in this accumulation. It has been shown that some anurans are protected from these high copper levels, but individuals with such accumulations may be toxic to their predators. There is little evidence that adult amphibians can concentrate other metals to a greater extent than other vertebrates.

2) Tadpoles accumulate high levels of certain metals, including lead, zinc, copper, cobalt, cesium, strontium, iron, and manganese, because of their contact with them in sediments and suspended particles. There is extensive literature, not reviewed here, on the toxic effects of metals on amphibians and other aquatic vertebrates which indicates that these organisms are susceptible to poisoning by metals. Doubtless their unusual powers of accumulation can sometimes result in metals in tissues reaching toxic levels.

3) The apparent tendency for tadpoles to pick up metals from surface sediments might make

them excellent indicators of contaminated environments. Metals transported into an aquatic ecosystem would first collect in sediments where tadpoles could accumulate them, as has been suggested in the case of lead (Getz *et al.* 1977; Jennett *et al.* 1977). Residual metals in uncontaminated areas, or those which have been in the ecosystem for some time, should tend to become more widely dispersed (Brungs 1963) and to produce patterns similar to those seen in samples analyzed in our laboratory. Thus because of their apparent tendency to selectively accumulate those metals adsorbed to surface sediments, it might be possible to use tadpoles to identify ongoing contamination.

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Part III
Feeding and Behavior

Energetics of Sit-and-Wait and Widely-Searching Lizard Predators

ROBIN M. ANDREWS

INTRODUCTION

The foraging tactics of insectivorous lizards, like those of most other predators, appear to be dichotomous (Pianka 1978). In North America, iguanid lizards exemplify the "sit-and-wait" tactic in which prey are sought passively from a fixed perch site. Sight of a moving prey item elicits ambush or pursuit. Teiid lizards, on the other hand, exemplify the "widely-searching" tactic in which prey are sought actively while the lizard moves through the habitat. These two tactics may represent a fundamental means of partitioning the food niche (Pianka *et al.* 1979). Each tactic apparently gives maximal foraging efficiency (in time or energy units) under conditions of varying prey abundance (Norberg 1977) or structural configuration of the habitat (Stamps 1977).

The sit-and-wait and the widely-searching tactics are each associated with an "adaptive syndrome" of predator characteristics (Eckhardt 1979). In addition to characteristics strictly related to foraging, the adaptive syndromes of iguanid and teiid lizards differ markedly in several ways. Iguanids have more stereotyped responses to novel items in their environment than do teiids (Regal 1978). Iguanids are strongly territorial, teiids lack home range defense (Stamps 1977). Iguanids escape predators by cryptic behavior and, once discovered, by the use of known routes to hiding places. In contrast, teiids rely on rapid flight to escape their predators (Vitt and Congdon 1978; Schall and Pianka 1980). Clutch size per unit body weight is higher for iguanids than for teiids (Vitt and Congdon 1978).

Although many aspects of the adaptive syndromes of sit-and-wait and widely-searching predators have been described, the energetic costs and benefits of each tactic are unknown. For example, the low searching costs of the sit-and-wait tactic are often associated with relatively low preferred body temperatures. Sceloporine and anoline iguanids have preferred body temperatures of 35°C or less even in well insulated environments (Blair 1960; McGinnis 1966; Andrews, unpublished data; Huey and Webster 1976; Ben-

nett and Gorman 1979). In contrast, (macro) teiids such as *Cnemidophorus* not only have high searching costs (Bennett and Gleeson 1979), but their foraging tactic is associated with preferred body temperatures of about 40°C (Asplund 1970; Schall 1977; Bennett and Gorman 1979). Thus, for many iguanids (notable exceptions are desert lizards such as *Holbrookia* and *Callisaurus*), the metabolic cost of foraging is low compared to that of teiids not only because of the low levels of activity associated with the sit-and-wait tactic but because of low activity temperatures.

The major objectives of this study were to answer two questions: 1) What are the relative energy intakes of lizards using sit-and-wait and widely-searching tactics when both forage in the same habitat? 2) Does the proportional allocation of assimilated energy to production and metabolism differ for lizards using the sit-and-wait tactic and the widely-searching tactic?

LIZARD SUBJECTS AND FIELD SITES

Field studies were conducted in the Chiricahua Mountains of Arizona. The lizard subjects were *Sceloporus jarrovi* (viviparous, Goldberg 1971) and *Cnemidophorus exsanguis* (parthenogenetic, Cole and Townsend 1977). These species are an ideal pair for comparative studies of feeding behavior and energetics. First, they are broadly sympatric in oak-pine-juniper woodland. Second, they are of similar size; females of both species reach a maximum weight of about 20 g. Third, their ecology is comparatively well known (Simon 1975; Congdon 1977; Schall 1977; Ruby 1977; Ballinger 1979).

Observations were made from 11 July to 8 August 1979. At this time, the fat reserves of both species are increasing rapidly (Goldberg 1972; Schall 1978). Since energy stored by female lizards prior to winter inactivity contributes directly to the development of offspring or eggs that will be produced the following spring (Hahn and Tinkle 1965; Gaffney and Fitzpatrick 1973), energy available for fat storage is directly related to the reproductive effort of both *S. jarrovi* and *C. exsanguis*. Moreover, adult *S. jarrovi* females,

TABLE 1. Prey items used in laboratory feeding experiments, their dry weights, ash contents, and proportional representation in the feeding regimes of the lizard subjects.

Prey taxa	Dry wt. (%)	Ash (%)	<i>S. jarrovi</i>	<i>C. exsanguis</i>
Coleoptera			59	61
<i>Tenebrio molitor</i> , adult	34.0	5.1		
<i>Dermestes caninus</i> , adult	38.4	4.4		
<i>Dermestes caninus</i> , larvae	43.4	2.5		
<i>Phyllophaga</i> sp., adult	28.6	6.1		
<i>Chaulognathus pennsylvanicus</i> , adult	25.3	4.9		
Lepidoptera (various moths)	34.0	4.4	37	16
Orthoptera				
<i>Blattella germanica</i> , adult male	31.0	6.7	4	23

at least, allocate large amounts of energy to growth during the summer and fall (Tinkle and Hadley 1975). Since body size is related to clutch size (Vitt and Congdon 1978; Ballinger 1979), the energy available for growth is directly related to reproductive effort.

Observations were made at two sites. Site A was located in North Fork Canyon immediately west of the Southwestern Research Station (SWRS) at 1650 m elevation. The study area extended for 3 km along North Fork Creek (and a gravel road). Both *S. jarrovi* and *C. exsanguis* were found in the open woodlands along the creek and in the more sparsely wooded hillsides. However, individuals of both species were most abundant near the creek and most observations were made there. Site B was located in Cave Creek Canyon 7 km SW of Portal. The site was bisected by the South Fork of Cave Creek. Although *S. jarrovi* was abundant, *C. exsanguis* was not found in this well shaded riparian forest.

METHODS

Faecal and Urinary Production by Free-ranging Lizards

Lizards were captured by hand or by noosing. They were placed individually in plastic bags and taken to the SWRS where they were held in a screened open-air laboratory for 48 h before release at the place of capture. Scats produced during this period were collected, their faecal and urinary portions were separated, dried at 65°C for 48 h, and then weighed to the nearest 0.1 mg. Mean maximum and minimum temperatures in the laboratory during the study were 32°C and

16°C, respectively. Mean maximum and minimum temperatures outside of the laboratory (SWRS weather records) were 31.5°C and 11.5°C, respectively.

Relation Between Faecal and Urinary Production and Food Intake

In order to estimate the food intake of free-ranging lizards, the relation between faecal and urinary production and food intake was determined in my laboratory at Virginia Polytechnic Institute and State University (VPI and SU) in June and July 1980. Lizards were individually caged in 20 gal. aquaria. Temperatures during the experiments were set to simulate field conditions in July. Night (12 h) temperatures were 16°C and day temperatures were 26°C. Heat lamps suspended over one end of each cage allowed the lizards to thermoregulate normally from 0900 to 1500 h. Lizards were fed a pre-weighed quantity of live insects each morning for 3 days. The ratio of live to dry weight for each prey type or species used was determined for representative individuals (Table 1). About noon at the end of the 3 d feeding period, lizards were placed in plastic bags. The urinary and faecal material produced in the following 48 h were treated the same as that produced by field-collected lizards.

Prey items used for the feeding experiments were selected on the basis of what lizards were eating in the field (see Results). One-half of the faecal material produced by lizards collected on Site A was used to determine prey taxa and size. Each faecal pellet was softened in a detergent-water solution and gently teased apart. Prey taxa were identified from their chitinous remains and

their lengths were estimated roughly at 5 mm intervals.

A major assumption of this method of estimating food intake is that lizards are active every day and that they defecate regularly. From observations made near my site B. Simon and Middendorf (1976) found that the percent of adult *S. jarrovi* active every day was 75% in July and 100% in August. Thus, the assumption of daily activity is probably valid for *S. jarrovi* but has not been tested for *C. exsanguis*. Observations on *S. jarrovi* and *C. exsanguis* maintained in large cages under simulated field conditions suggest that defecation occurs at least every morning following the attainment of preferred body temperatures (see also Cowles and Bogert 1944).

Ash contents of faeces, urinary wastes, and the various prey types used in the laboratory experiments were measured by heating samples for 1 h at 550°C in an ashing oven. The mass of all materials is presented as ash-free dry weight.

Activity Periods and Body Temperatures

Any lizard seen was considered active. Because *S. jarrovi* individuals were readily found during all daylight hours. I assumed that their activity period potentially spanned 10–12 h. In contrast, *C. exsanguis* individuals were encountered most frequently in the morning. To define the activity period of *C. exsanguis*, a series of 30-minute censuses was conducted on 3 and 4 August. All individuals encountered while I slowly walked about 2 km through site A were counted.

Body (cloacal) temperatures (T_b) were measured immediately after capture with a Schultheis quick-reading thermometer. Temperatures of lizards which avoided capture for more than a minute were not taken to avoid bias. Shaded air temperatures were taken at 1 m and at 1 cm above the place where the lizard was first seen.

RESULTS

Food Intake by Free-ranging S. jarrovi and C. exsanguis

Various species of beetles made up about 60% of the insects eaten by lizards in the feeding experiments and moths and cockroaches made up the other 40% (Table 1). This particular feeding regime was similar to the natural diets of the two

TABLE 2. Prey items of *Sceloporus jarrovi* and of *Cnemidophorus exsanguis* in July–August 1979. Proportion of total prey is given for each species followed by modal length category in parentheses.

Prey taxa	<i>S. jarrovi</i>	<i>C. exsanguis</i>
Coleoptera (adults)	.306 (5–10)	.189 (5–10)
Formicidae	.518 (<5)	.500 (5–10)
Lepidoptera (adults)	0.0	.122 (10–15)
Hymenoptera (adults)	.082 (5–10)	0.0
Araneida	.023 (<5)	.067 (<5)
Orthoptera	.023 (10–15)	.078 (10–15)
Miscellaneous*	.047 (<5)	.044 (5–10)
	85	90

* *S. jarrovi*: 4 Homoptera-Hemiptera; *C. exsanguis*: 2 Homoptera-Hemiptera, 1 mantid, 1 Chilopoda.

lizard species (Table 2). Judging by both frequency and size, beetles were probably the most important component of the diets of both *S. jarrovi* and *C. exsanguis*. Orthoptera were probably the second most important component of the diet of *S. jarrovi* and Lepidoptera were probably the second most important component of the diet of *C. exsanguis*. Ants were not used in the feeding experiments although they comprised about half of the items eaten by both species in the field. Because of their small size (bulk) their contribution to total energy intake was probably low. Using stomach contents to evaluate the diet of *C. exsanguis* in New Mexico, Medica (1967) also found the major items (by volume) to be beetles and Lepidoptera, with Hymenoptera (mostly ants) to be relatively unimportant.

Food intake of field-collected *S. jarrovi* and *C. exsanguis* females was estimated as

$$I_f = F * CFF^{-1} * W^{-0.83}$$

and

$$I_u = U * CFU^{-1} * W^{-0.83}$$

where I_f and I_u are the respective estimates of food intake based on faecal and urinary production, F and U are faecal and urinary production (mg dry wt) during the 48 h of confinement, respectively, CFF and CFU are the factors which convert F and U to food intake for faecal and urinary production, respectively, and $W^{-0.83}$ is live body weight in g raised to a power of 0.83 to adjust for weight specific metabolic rates (Ben-

TABLE 3. Daily food intake (I_f and I_u) of *S. jarrovi* and *C. exsanguis* based on production of faecal and urinary material (see text for details).

Species and site	$\ln I_f \pm SE$ ($\text{mg} \cdot \text{g}^{-0.83} \cdot \text{d}^{-1}$)	$\ln I_u \pm SE$ ($\text{mg} \cdot \text{g}^{-0.83} \cdot \text{d}^{-1}$)
<i>S. jarrovi</i> —A	2.58 ± 0.122	*
<i>S. jarrovi</i> —B	2.72 ± 0.067	*
<i>C. exsanguis</i> —A	3.06 ± 0.128	2.94 ± 0.097

nett and Dawson 1976). This latter procedure eliminated a positive and significant relationship between I_f or I_u and W .

CFF and CFU were determined as

$$\text{CFF} = F_{\text{lab}}/I_3$$

and

$$\text{CFU} = U_{\text{lab}}/I_3$$

where F_{lab} and U_{lab} are the respective production of faeces and urine during the 48 h confinement following the laboratory feeding experiments and I_3 is the food intake on the final (3rd) day of the feeding experiments. I_3 was used to determine CFF and CFU because correlations between F and I_3 for both species and between U and I_3 for *C. exsanguis* were statistically significant ($P < 0.05$). Correlations between F or U and summations of food eaten on the last 2 days and the total 3 days of the feeding experiments were generally not significant, and all had lower correlation coefficients (r) than did the correlations between F and I_3 and U and I_3 . Since neither CFF nor CFU varied as a function of lizard weight for either species ($P > 0.05$), mean values were used to estimate food intake. Respective mean values ($\pm SE$) for *S. jarrovi* and *C. exsanguis* were $\text{CFF} = 0.56 \pm 0.053$ and 0.24 ± 0.024 and $\text{CFU} = 0.21 \pm 0.027$ and 0.19 ± 0.027 . Natural log transformations were used to normalize the I_f and the I_u data for statistical analyses. Some female-sized male *S. jarrovi* were included in the analyses (5 of 9 and 9 of 29 individuals on Sites A and B, respectively) since the faecal production of these males did not differ from females on either site ($P > 0.05$, two-tailed t -tests). Although individuals were captured at various times during the day (see below), regression analyses indicated that time of capture was not related to food intake ($P > 0.05$).

Differences in I_f and I_u among the *C. exsanguis* females and the two populations of *S. jarrovi*

(Table 3, Fig. 1) were statistically significant ($P < 0.05$, analysis of variance). *A posteriori* tests showed that *C. exsanguis* females had a significantly ($P < 0.05$) greater I_f and I_u than both the *S. jarrovi* populations, and that the *S. jarrovi* populations did not differ from one another for either I_f or I_u ($P > 0.05$, Duncan's multiple range tests). Therefore, in subsequent analyses the data for *S. jarrovi* females have been combined. The two estimates of food intake for *C. exsanguis* differed by only 4% on a ln scale (Table 3) and by only 11% on an arithmetic scale. Since the correlation between U and I_3 for *S. jarrovi* was not statistically significant, I_u was not determined.

Activity Periods and Thermoregulation

Sceloporus jarrovi and *C. exsanguis* differed considerably in the apparent length of their activity periods. I made observations from about 0800 to 1730 h with comparable times spent in the field in the morning and in the afternoon. The number of *S. jarrovi* individuals observed in the morning and the afternoon was very similar. In contrast, *C. exsanguis* individuals were active primarily in the morning; only 3 of 37 individuals collected were caught in the afternoon. The census data also indicated that peak activity was in the morning (Table 4).

Body temperatures of *S. jarrovi* were dependent on weather conditions (Figs. 2 and 3). On site A where temperatures were measured under sunny conditions, *S. jarrovi* individuals maintained relatively constant T_b s (Mean $\pm SE = 34.2 \pm 0.36^\circ\text{C}$). In contrast, on site B about one-half of temperature measurements were taken under overcast or intermittently cloudy conditions. At these times, T_b s averaged $31.1 \pm 0.61^\circ\text{C}$. During sunny conditions T_b s averaged $35.8 \pm 0.34^\circ\text{C}$.

Body temperatures of *C. exsanguis* were independent of ambient temperatures (Fig. 1), averaging $40.0 \pm 0.31^\circ\text{C}$. The one individual with a T_b of 34°C had probably just emerged from a burrow.

DISCUSSION

During the July–August study period, *S. jarrovi* females, using sit-and-wait tactics, had a significantly lower intake of food than did *C. exsanguis* females which were using widely-searching

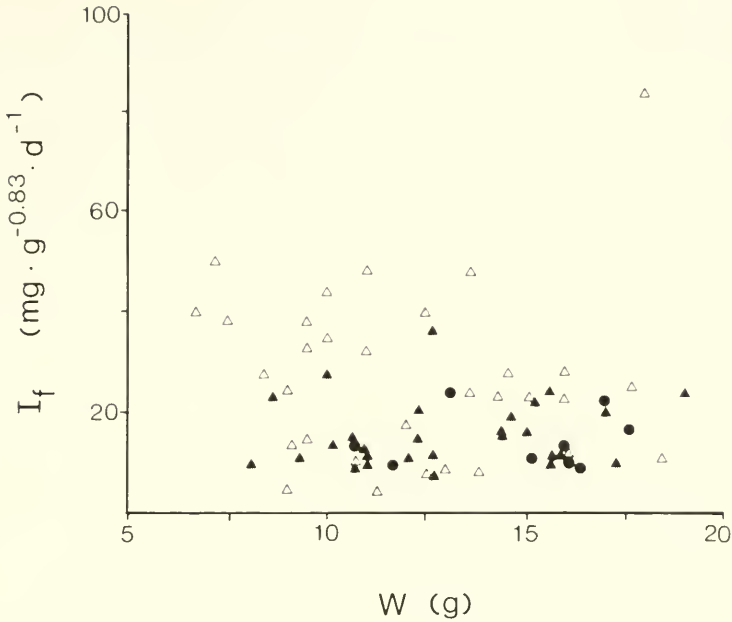


FIG. 1. Food intake based on faecal production (I_f) of field-collected *Sceloporus jarrovi* (Site A, filled circles, and Site B, filled triangles) and *Cnemidophorus exsanguis* (Site A, open triangles) as a function of body weight.

tactics. The result is particularly interesting in that *S. jarrovi* was active more than twice as long as *C. exsanguis*. Moreover, since lizards were foraging in the same habitat, individuals of both species potentially had the same kinds and abundances of prey available to them. Thus, the widely-searching tactic appears to be more efficient both in terms of time spent and energy acquired.

In order to compare the energy that *S. jarrovi* and *C. exsanguis* females have available for production, I_f and I_u were partitioned into their major components as

$$I = R + P + FU$$

where I is food intake, R is metabolism, P is production, and FU is the combined faecal and urinary wastes. The energy value of food intake was determined as 1 times 5800, the mean caloric value for a variety of insects (Griffiths 1977). Digestion and assimilation efficiencies of small insectivorous lizards are quite similar (Harwood 1978; Johnson and Lillywhite 1979). Therefore, FU was estimated as 20% of I for both *S. jarrovi* and *C. exsanguis* (Johnson and Lillywhite 1979; Andrews and Asato 1977). The parameters used

to estimate field metabolism of a 12 g *S. jarrovi* female are from Table 3 and Appendix A, Table 1, of Congdon (1977). Since his Ash Spring site and my sites were located within a few km of one another, I have used his July–August determinations directly. The field metabolism of *C. exsanguis* was estimated from metabolic data collected on *Cnemidophorus murinus*, a West Indian species. Metabolic rates of *C. murinus* were determined under standard conditions for both resting individuals and for individuals moving

TABLE 4. Numbers of *Cnemidophorus* individuals seen during 30 min censuses conducted on 3 and 4 August 1979. Shaded air temperatures 1 m above ground are shown for the time the census was begun. Both days were sunny.

Census period	T (°C)	N
800–830	23	2
930–1000	27	6
1030–1100	27	6
1100–1130	27	5
1200–1230	29	2
1400–1430	28	1
1700–1750	29	0

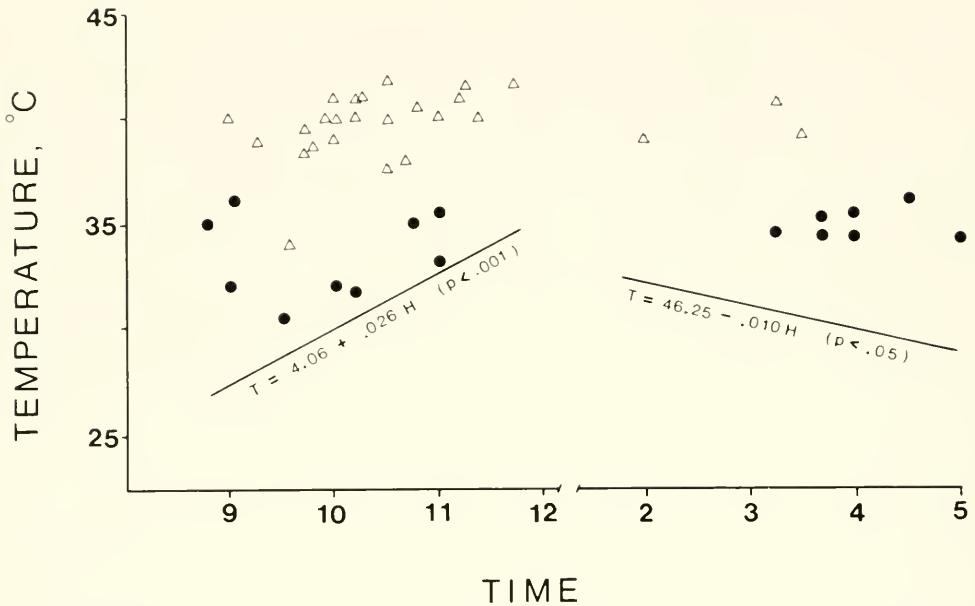


FIG. 2. Body temperatures of *Sceloporus jarrovi* (filled circles) and of *Cnemidophorus exsanguis* (open triangles) on site A as a function of time. Regression lines represent the relationship between shaded air temperature at 1 m for each lizard capture site and time (in hours, e.g., 1200, 1300, etc.).

at speeds at which foraging normally takes place (Bennett and Gleeson 1979; Bennett and Gorman 1979). In order to extrapolate their results to *C. exsanguis*, I adjusted metabolism for differences in body weight using $b = 0.705$ as the exponent in the relationship between metabolic rate and weight and I adjusted for differences in temperature using a Q_{10} of 2.64 (both values from Bennett and Gorman 1979). Judging from field observations of activity periods, the daily progression of soil temperatures in *Cnemidophorus* burrows, and the body temperatures of two individuals observed in burrows during the day, I calculated metabolism assuming an individual to be active 4 h at 40°C, inactive for 6 h at 27°C (day), and inactive for 14 h at 22°C (night). In addition, since the metabolic rates determined for *C. murinus* were measured on fasted individuals, I applied a correction factor of 1.8 (day) and 1.6 (night) for inactive individuals to account for the additional metabolic increment due to recent feeding (Andrews and Asato 1977).

Energy budgets of *S. jarrovi* and *C. exsanguis* females were similar in their proportional allocation of food energy to metabolism (59 versus 54–61%) and production (22 versus 19–26%) (Table 5). However, because of the lower abso-

lute caloric intake of *S. jarrovi* these females allocated 71% fewer calories to metabolism and 60–90% fewer calories to production than did *C. exsanguis* females.

The prediction that widely-searching lizard predators might have a greater proportion of their energy budgets allocated to metabolism appears to be incorrect, at least for the *S. jarrovi*-*C. exsanguis* comparison. The explanation involves activity patterns of the two species. Although locomotion of *Cnemidophorus* lizards is energetically costly (Asplund 1970; Bennett and Gleeson 1979), this activity by *C. exsanguis* was confined to a 3–4 h period in the morning. The rest of the day was spent in burrows and under rocks where body temperatures presumably approximated soil temperatures (27°C). In contrast, active *S. jarrovi* individuals maintained body temperatures of about 35°C for at least 8 h during the day. To some extent, then, the relatively low body temperatures of *C. exsanguis* when they were inactive during the day compensated for the high costs of activity and thermoregulation that were incurred over a relatively short period.

The greater absolute allocation of energy to production by *C. exsanguis* than by *S. jarrovi* females means that both growth and fat storage

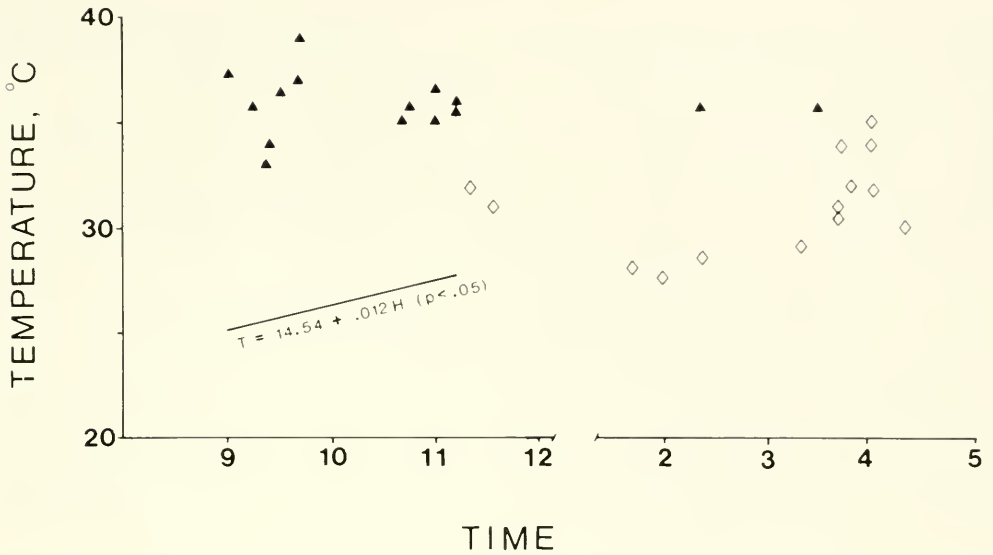


FIG. 3. Body temperatures of *Sceloporus jarrovi* on site B. Filled triangles represent temperatures taken under sunny conditions and open diamonds represent temperatures taken under overcast or intermittently sunny conditions. Regression lines as in previous figure (for sunny conditions only).

should occur at a greater rate for *C. exsanguis* than *S. jarrovi*. This prediction cannot be tested at present because of a lack of information on *C. exsanguis*. However, the prediction is at least consistent with the observation that *C. exsanguis* becomes inactive in late August or early September (Schall 1978; C. J. Cole, pers. comm.) while *S. jarrovi* females continue to fatten during September and October simultaneously with the initiation of yolk deposition (Goldberg 1972).

During the time frame of this study, the widely-searching tactic was more efficient than the sit-and-wait tactic. Even with a restricted foraging period, *C. exsanguis* individuals had a greater daily energy intake than *S. jarrovi* individuals. This result suggests several approaches for future

research. One concerns the conditions which would tip the balance to favor the sit-and-wait tactic. Theoretical models suggest seasonal or annual changes in prey availability may be involved (Norberg 1977). Another approach would be to examine possible trade-offs between energy intake and mortality. Widely-searching tactics may make lizards more conspicuous to predators than sit-and-wait tactics. Demographic studies may be useful to evaluate the adaptive syndromes of lizards using these two foraging tactics.

SUMMARY

Energy budgets were constructed for adult female *Sceloporus jarrovi* which use "sit-and-wait" foraging tactics and for adult female *Cnemidophorus exsanguis* which use "widely-searching" foraging tactics. Females of these species both have maximum sizes of about 20 g and both occur together in oak-pine woodlands in the Chiricahua Mountains of Arizona.

The objectives of the research were to determine the relative foraging success of these two lizard species and their allocation of food energy to metabolism and production.

Food intake during July and August 1979 was determined by measuring the faecal and urinary production of field-collected individuals during

TABLE 5. Energy budgets (cal/d) for 12 g female *S. jarrovi* and *C. exsanguis*. See text for explanation of how each compartment was estimated.

	<i>S. jarrovi</i>	<i>C. exsanguis</i>	
I	669 (I _p)	972 (I _p)	868 (I _u)
FU	-133	-194	-174
R	-387	-528	-528
P	149	250	166
R/I	59%	54%	61%
P/I	22%	26%	19%

48 h confinement. The relationship between food intake and faecal and urinary production was established by measuring the faecal and urinary production of lizards fed known quantities of normal prey items. Active metabolism was estimated from recently published studies on *Cnemidophorus murinus* and *S. jarrovi*.

Food intake of *C. exsanguis* females was significantly greater ($P < 0.05$) than that of *S. jarrovi* females. Respective food energy values calculated for 12 g females were 972 and 669 cal/d. Thus, the widely-searching foraging tactic was more efficient than the sit-and-wait foraging tactic. Although *C. exsanguis* and *S. jarrovi* had a similar proportional allocation of food energy to metabolism (54 and 59%) and to production (26 and 22%), *C. exsanguis* had a greater absolute allocation of energy to metabolism (528 versus 387 cal/d) and to production (250 versus 149 cal/d) than did *S. jarrovi*. Thus, the high metabolic cost of active foraging by *C. exsanguis* females was associated with a greater absolute allocation of energy to metabolism than for *S. jarrovi* females which foraged passively. The greater absolute allocation of energy to production by *C. exsanguis* than by *S. jarrovi* females suggests that both growth and fat storage should occur at a greater rate for *C. exsanguis* than *S. jarrovi*.

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Feeding Behavior and Diet of the Eastern Coral Snake, *Micrurus fulvius*

HARRY W. GREENE

INTRODUCTION

Snakes are prominent predators in many terrestrial, aquatic, and tropical marine communities, and exhibit some unusual morphological and behavioral modifications for this role. They rely heavily on chemical senses for locating food (Burghardt 1970; Chiszar and Scudder 1980) and their usual method of locomotion (lateral undulation) is energetically more efficient than tetrapody (Chodrow and Taylor 1973). Perhaps most importantly, these "limbless tetrapods" possess an extremely flexible jaw apparatus that permits the ingestion of large prey items without the assistance of limbs or mastication (Gans 1961). Although many species swallow prey alive and struggling, others immobilize it by constriction, venom injection, or a combination of these methods (Gans 1978; Greene and Burghardt 1978; Kardong 1980).

It is now clear that venom delivery systems comprise at least three grades of structural complexity and that these have evolved independently in several lineages of snakes (see Gans and Gans 1978; Savitzky 1978; 1980; Kardong 1980; Cadle, *in press*, for extensive discussion and reviews). Opisthoglyphs (many species of colubrids) possess enlarged, grooved teeth on the posterior ends of otherwise normal, elongate, toothed maxillae. Proteroglyphs (elapids and hydrophiids) have one or two enlarged, canaliculate, anterior teeth on each short, nonmobile or slightly mobile maxilla. Solenoglyphs (viperids and atractaspids) have a single, very elongate hollow fang on each highly movable maxillary bone. Studies on several solenoglyphs of the family Viperidae show that these snakes often strike and release prey, then relocate it before swallowing (e.g., Klauber 1956; Duellmeijer 1962; Nalleau 1966; Minton 1969; Kardong 1975; Chiszar and Scudder 1980). Although there are isolated notes on the feeding behavior of opisthoglyphs and proteroglyphs in the literature (e.g., Armitage 1965, Lambiris 1967, for African elapids), the only extensive accounts are for certain sea snakes (Voris *et al.* 1978; Radcliffe and Chiszar 1980).

With few exceptions (e.g., Shine 1977, for elapids; Voris *et al.* 1978, for hydrophiids), we also know very little about the dietary ecology of proteroglyphs. This general lack of descriptive studies on proteroglyphs, particularly terrestrial forms, hampers broader considerations of functional morphology, adaptive radiation, and community structure in snakes (cf. Arnold 1972; Rabb and Marx 1973; Kardong 1980; Savitzky 1980; Greene, MS).

In the present paper I provide a description of feeding behavior, an ecological characterization of the food habits, and a discussion of factors affecting diet composition in a venomous coral snake, *Micrurus fulvius*. This species occurs in the southeastern United States and northeastern Mexico, in habitats ranging from subtropical swamps and lowland forests to semiarid scrub (Wright and Wright 1957). It is a northern representative of an essentially Neotropical radiation of the cosmopolitan front-fanged family Elapidae (Roze 1967; see Savitzky 1978, and Cadle and Sarich 1981 for contrasting views on the relationships of coral snakes). Eastern coral snakes have been found crawling on the surface and in or under rocks, logs, stumps, litter, and burrows (Wright and Wright 1957; Gentry and Smith 1968). There is perhaps seasonal and geographic variation in diel activity, but these snakes are predominantly diurnal (cf. Neill 1957; Wright and Wright 1957; Jackson and Franz 1981). An average adult is ca. 50–85 cm long and weighs 20–55 g. Wright and Wright (1957), Shaw (1971), Campbell (1973), Greene (1973a, 1973b), Quinn (1979), and Jackson and Franz (1981) summarized some aspects of the biology of this species.

METHODS

Behavioral Observations.—Sixty-five complete feeding sequences on live and dead prey by four captive coral snakes were observed (one female, three males; total lengths 52.5–85.0 cm; from Dallas, Hidalgo, and Nacogdoches Counties, Texas). The snakes were individually housed in glass terraria that measured 32 × 32 × 62 cm

or $27 \times 32 \times 52$ cm. Each cage had a gravel substrate covered with leaf litter, a water bowl, and at least one large piece of bark for cover. Water was sprinkled over the leaves two or three times each week. The snakes were kept in a dark room that usually had a temperature of $22\text{--}24^\circ\text{C}$, but occasionally rose to 30°C . A 100 W bulb on top of the perforated metal cover of each tank raised the temperature at one end to ca. $24\text{--}26^\circ\text{C}$ for 10 hr each day. Observations were timed with a stop watch and recorded on audio tape or with a 35 mm camera and electronic flash.

Captive coral snakes were offered live or dead prey, as available, of the following species: *Anolis carolinensis*, *Eumeces tetragrammus*, *E. fasciatus*, *Scincella lateralis*, *Carphophis amoenus*, *Coluber constrictor*, *Diadophis punctatus*, *Elaphe obsoleta*, *Heterodon platyrhinos*, *Nerodia erythrogaster*, *N. rhombifera*, *Opheodrys aestivus*, *Sonora semiannulata*, *Storeria dekayi*, *Tantilla gracilis*, *T. nigriceps*, *Thamnophis proximus*, *Tropidoclonion lineatum*, and *Virginia striatula*. Live prey was released in a cage as far from the coral snake as possible. Dead prey was held with forceps ca. 20 cm from an active snake and jiggled to simulate prey movements; if there was no response, the prey was moved closer until it was seized.

Trail Following.—I used a modified version of the arena used by Gehlbach *et al.* (1971), consisting of an 80×80 cm piece of white duck cloth (28 strands/cm²) in a plastic swimming pool. An octagonal trail lane with segments 20 cm on an outer side and 1 cm wide was marked on the cloth with small, faint broken lines of indelible ink. Prior to an experiment a potential prey item was restricted to the trail lane by a portable 8 cm high cardboard alley and allowed to crawl around for one or two circuits. Then the prey animal and the cardboard alley were removed. Next a coral snake was confined in the center of the arena for three minutes in a bottomless 1-gal plastic jar. The snake was released by lifting the jar, and its behavior observed under a 60 W red light positioned so that the arena was very dimly lit. The cloth arenas were machine washed, rinsed, and dried after each test.

Diet Studies.—Museum specimens were opened with a ventral incision and the orientation of each prey item in the gut was recorded. The identity and approximate total length (TL) of each item was determined if possible, often

on the basis of a tail or a tail and posterior portion of a body, by comparisons with published information and intact reference specimens. Additional records were obtained from conversations or correspondence with collectors and from the literature (Matthes 1860; Hay 1893; Mitchell 1903; Strecker 1908; Schmidt 1932; Loveridge 1938, 1944; Klauber 1946; Ruick 1948; Minton 1949; Clark 1949; Telford 1952; Curtis 1952; Highton 1956; Martin 1958; Kennedy 1964; Myers 1965; Neill 1968; Chance 1970; Malloy 1971; Fisher 1973; Jackson and Franz 1981).

Snout-vent (SV), tail, and head lengths of preserved coral snakes were measured when possible. Because many museum specimens had damaged heads, SV was used for comparisons with prey TL. I estimated the weights of common prey items from published statements and from live measurements of four *Scincella lateralis*, one *Leptotyphlops dulcis*, three *Storeria dekayi*, three *Tantilla* sp., six *Tropidoclonion lineatum*, and eight *Virginia striatula*. The average total lengths of all snakes in east Texas were taken as the midpoints of the ranges for adults given in Conant (1975). In a few cases I weighed preserved coral snakes and intact prey after blotting them on paper towels.

I evaluated geographic variation in food habits by grouping records for Texas in four subsamples: "east Texas" (mixed deciduous and pine forests), "north central Texas" (tall grass-prairie-forest ecotone), "central Texas" (forested hill country of the Edwards Plateau and the extreme eastern edge of the Chihuahuan Desert), and "south Texas" (semiarid thorn scrub and subtropical forest, see Gould 1969, for vegetation regions). Records from elsewhere in the species range are grouped as "Florida" and "other" (Arkansas, Louisiana, South Carolina, and Mexico).

FEEDING BEHAVIOR

The description that follows incorporates published accounts (Grijs 1898; Ditmars 1907, 1912; Clark 1949) and my observations. Feeding behavior is discussed in six groups of sequentially and functionally related motor patterns to facilitate future comparisons with other snakes.

Encountering Prey.—Methods of encountering prey should be included in discussions of feeding behavior, because snakes use species-typical postures and strategies for obtaining food.

Prey might be located by some type of searching, trail following, "sitting and waiting," (Pianka 1966), or a mixed strategy (Tollestrup 1980; Chiszar and Scudder 1980): each of these techniques might be enhanced by behavioral or morphological specializations. For example, searching and trail following utilize stereotyped poking behavior (in coral snakes, see below) and highly specialized receptor systems (e.g., facial pits in boids and some viperids). "Sitting and waiting" is probably more efficient when accompanied by camouflage (Fitch 1960) or caudal luring (Greene and Campbell 1972).

When a coral snake had not fed for several days, it crawled slowly over the substrate and poked its head in and out of the leaf litter. This involved repeated forward and lateral head movements, and was accompanied by frequent tongue flick clusters. At times a snake crawled slowly beneath a large leaf or a small piece of bark and soon emerged from the opposite side, still moving its head from side to side and flicking its tongue. When a coral snake was searching, any movement of an object in the terrarium elicited pointing and, if it was not a large object, approach behavior. When an acceptable prey item caused the approach, it was seized and eaten. Unsuccessful attempts to capture prey were followed by more searching behavior.

F. R. Gehlbach (pers. comm.) observed similar crawling and poking movements by two free-living coral snakes on the Santa Ana Wildlife Refuge, Hidalgo County, Texas, one of which I later used for behavioral studies. Neill (1951) described what was perhaps foraging behavior by a coral snake in Clay County, Florida. The snake crawled rapidly, moved its head from side to side, and poked its head into the surface litter. Neill also stated that the snake's tail made "constant rapid, probing motions" in the leaves, and that at times "the hind part of the creature was thrown nearly as far forward as the head." He observed similar behavior in a captive snake, and suggested that the head and tail movements served to flush small reptiles and amphibians from cover. These observations suggest that crawling and head-poking in ground litter are motor patterns normally used by coral snakes to locate potential prey items. However, neither Gehlbach nor I observed use of the tail in foraging, and I doubt that it is a normal behavior, at least for coral snakes in Texas. The threshold

for tail waving, an important component of coral snake antipredator behavior (Gehlbach 1972; Greene 1973b), is often very low for this species (pers. obs.), and perhaps the snake observed by Neill was responding defensively to tactile or vibrational stimuli.

Several species of small snakes deposit chemical trails that serve as attractant pheromones (Burghardt 1970; Gehlbach *et al.* 1971), and there are indications that these trails release searching and trail following behavior by coral snakes. Once two small earth snakes (*Virginia striatula*) were kept in a jar of wet moss for several days before the snakes and moss were put in a coral snake's cage. The coral snake was crawling on the leaves and encountered the moss. It moved its head back and forth over the moss for approximately five minutes and frequently flicked its tongue. Then it crawled across the cage, generally following the route taken by one of the earth snakes. The coral snake soon found the prey in a corner and ate it. During staged encounters with ground skinks (*Scincella lateralis*), a coral snake frequently paused for several seconds in the exact spot where a skink had recently rested and pointed and tongue-flicked before searching again.

Experiments with coral snakes on cloth arenas provide additional evidence that they respond to prey trails. For two trails with each of two coral snakes, a small colubrid snake (adult *Storeria dekayi* or *Virginia striatula*) was allowed to crawl around the alley one time. In each case the coral snakes crawled away from the central release point, paused briefly and pointed at the trail, and moved off the cloth. A second block of trials used trails laid by a small snake or a skink (adult female *Eumeces fasciatus*) making four circuits of the octagon in five minutes. One coral snake responded to two snake trails with pointing and then escape behavior, but followed a skink trail for one complete circuit and two additional turns on the octagon. The other coral snake followed trails laid by *S. dekayi* (two trials) and *V. striatula* (one trial) for one complete circuit, seven lane segments, and three lane segments, respectively. It followed two lane segments of a skink trail before crawling off of the cloth. These observations suggest that known prey species can leave trails which are perceived and followed by coral snakes. Additional experiments using more coral snakes, more prey species, and more trials are required before comparisons with the exten-

sive study by Gehlbach *et al.* (1971) are warranted.

Trail following behavior was stereotyped and similar to that described by Gehlbach *et al.* (1971) for blind snakes, *Leptotyphlops dulcis*. A coral snake crawled slowly from the release site, pointed and flicked its tongue at the trail, then turned 90° and began following it. The snake's head remained elevated while it crawled, and there were frequent tongue-flick clusters. At each corner it overshot 2–4 cm, paused, pointed and tongue-flicked at the cloth, moved its head from side to side, turned back onto the trail, and resumed crawling. If a wire was jiggled on the cloth in front of a coral snake it pointed and approached rapidly.

The available captive and field observations imply that coral snakes actively search for prey, but the frequency and extent of foraging movements are unknown. There is no evidence that free-living coral snakes use a "sit and wait" strategy to ambush prey, but the behavior of captives suggests that they might. My snakes were frequently seen coiled with head raised and protruding from beneath the edge of a piece of bark or pile of leaves. Such snakes responded to nearby movements by pointing, tongue-flicking, and approaching.

Recognition and Approach.—Recognition of prey probably begins as soon as a coral snake points toward a stimulus, and incorporates visual and chemical cues. Captives approached any small movement, such as a wire jiggled in the leaves or a finger moved against the glass from outside of the terrarium. Larger moving objects, such as a hand or a piece of bark, usually elicited pointing and then rapid head withdrawal and crawling. This seemed especially likely if the object was moved suddenly.

Approach was accompanied by tongue-flick clusters, which evidently convey the necessary stimuli for seizing or avoiding a potential prey item. Coral snakes quickly approached to within 2 cm of large coleopteran larvae, cricket frogs (*Acris crepitans*), and newborn mice, but then withdrew without seizing them. Small live water snakes (*Nerodia* sp.) were also approached and rejected, and in most cases they had discharged the cloacal sac contents. However, rapid prey movements seemed to result in a quicker attack and to override aversive chemical cues. Dead *Nerodia* were usually refused when stationary or

pulled slowly but were attacked when pulled more rapidly. In 10 incomplete feeding sequences, a prey item was grasped and immediately released, or maneuvered for a short time and then released. This suggests that a coral snake continues to receive input from the prey after it is seized, perhaps via either oral sensory papillae (Burns 1969; Greene, unpublished) or the Jacobson's Organ (cf. Burghardt 1970).

Capture and Immobilization.—Approach was usually slow if the prey snake was moving slowly, and rapid if it crawled away quickly. Prey was seized with a quick forward movement of the anterior part or entire body of the coral snake, usually from a distance of several centimeters. In some cases a coral snake crawled parallel to a moving snake, flicked its tongue several times, and then seized the prey by turning its head sharply to the side and down.

Coral snakes have relatively small eyes (Marx and Rabb 1972) and apparently cannot strike very accurately. Live *Scincella lateralis* proved difficult for them to seize, perhaps because of the coral snakes' relatively poor vision and the skinks' small size and erratic escape behavior (Lewis 1951). Also, ground skinks seemed to perceive an approaching predator at a distance of several centimeters and often slipped away unseen. During 11 attempts on these lizards by a coral snake, I observed eight misses, two tail autotomies (skink escaped unharmed), and one capture. These were during staged confrontations on a 32 × 62 cm substrate of gravel and scattered leaves, and the only capture occurred when the snake trapped a skink in a corner. Small live prey snakes presented a slower and more elongate target, and were captured without difficulty; each of 23 attempts was successful.

Ditmars (1907) and Clark (1949) stated that *Micrurus fulvius* immobilizes its prey with venom before swallowing, but Ditmars (1912) remarked that the venom is of little value in subduing "cold blooded" animals. My observations indicate that this species typically holds prey at the point of seizure until paralysis and then begins pre-ingestion maneuvers (see below). Slight movements of the prey were sometimes seen even as the tail was swallowed, suggesting that it is immobilized but not immediately killed by the venom. Coral snakes usually dragged their prey a few centimeters backward or forward before pausing, seemingly in response to its struggles.

TABLE 1. Pre-ingestion latencies (in seconds) for coral snakes, *Micrurus fulvius*, dealing with live and dead prey. Ranges, means, standard deviations, and sample sizes are given.

Latency	Snake no. 4	Snake no. 5
Time between seizure and onset of pre-ingestion maneuvers (live prey)	290–595 (\bar{x} = 434.2 ± 132.5) N = 6	70–940 (\bar{x} = 400.9 ± 334.9) N = 8
Time between seizure and onset of pre-ingestion maneuvers (dead prey)	0–85 (\bar{x} = 28.6 ± 32.3) N = 10	0–290 (\bar{x} = 73.7 ± 86.5) N = 10
Time between last prey body movement and onset of pre-ingestion maneuvers	63–190 (\bar{x} = 99.2 ± 52.6) N = 5	0–152 (\bar{x} = 71.8 ± 73.3) N = 4

This tended to untangle a small, writhing snake, and it might also imbed the fangs more deeply. During envenomation, the temporal region of the coral snakes sometimes appeared shriveled; this was probably caused by contraction of the *M. adductor mandibulae externus superficialis*, which has been shown to force venom out of the main venom gland in an elapid, *Bungarus caeruleus* (Rosenberg 1967; see also Savitzky 1978).

In two instances a coral snake bit and quickly released an adult female *Eumeces fasciatus* that struggled violently. One of the skinks was immediately recaptured. The other lizard crawled slowly for several centimeters and went under a piece of bark. It was soon followed by the coral snake and regrasped. Both skinks subsequently made only feeble movements and were eventually eaten.

Pre-ingestion Maneuvers.—Coral snakes normally do not release prey prior to swallowing it. Pre-ingestion maneuvers are probably evoked by tactile and/or chemical cues (cf. Nalleau 1966) and inhibited by prey movements. If prey movements inhibit the coral snake, the time between seizure and the onset of pre-ingestion maneuvers should be longer with live prey than with dead prey. The mean pre-ingestion handling times with live and dead prey (Table 1) differed significantly for each of two coral snakes ($P < .01$, Mann-Whitney *U* test). If prey movements inhibit the snake, the time between the last prey movement and the onset of preingestion maneuvers should be similar for live and dead prey. These times were significantly different for one snake ($P < .01$, Mann-Whitney *U* test) but not for the other snake ($P > .90$). I interpret the large variances and the equivocal results of the last comparison

as resulting from individual differences and from the use of different sizes and species of prey in the feeding trials.

Captive and free living coral snakes almost always swallowed prey head first, and scale overlap on the prey item was used as a cue in locating its anterior end (Greene 1976). Alternating jaw movements, typical of snakes (Gans 1961), were used to shift along the prey's body prior to swallowing. In one instance a small stick in the mouth of a coral snake prevented it from shifting over a snake's snout to begin swallowing. The coral snake released the prey, removed the stick by jaw movements and rubbing its head on the substance, regrasped the prey by the snout, and swallowed it. In all other feeding sequences, prey snakes were not released before they were swallowed.

Swallowing.—After the prey's head had been shifted down the throat, it was swallowed by repeated series of alternating jaw movements. These were separated by brief pauses and accompanied by lateral movements of the entire head. According to McDowell (1970), *Micrurus* belongs to a group of elapids in which "the palatine is erected along with the maxilla during maximum protraction of the palate." This presumably occurs when a coral snake's head is rotated back and forth across a prey snake's long axis during swallowing movements. I could not observe the action of the palatine bones in live coral snakes, but frequently saw the maxillary fangs depress (and penetrate?) a prey snake's skin during swallowing.

During swallowing a coral snake sometimes rolled about its long axis, perhaps using the prey's inertia to achieve better contact between its teeth

TABLE 2. Continued.

Prey species	E (46)	N (15)	C (16)	S (19)	U (10)	F (57)	O (14)	T (177)
<i>Virginia striatula</i>	8	9	1	1				19
<i>V. valeriae</i>							2	2
<i>S. semiannulata</i> or <i>Tantilla</i> sp.		1	1	4				6
<i>S. dekayi</i> or <i>V. striatula</i>	5						2	7
Elapidae								
<i>Micrurus fulvius</i>	2					3		5
Viperidae								
<i>Agkistrodon contortrix</i>	2							2
Mammalia								
Rodentia								
Unidentified					1		1	2
Totals	60	17	17	25	13	67	22	221

and the prey's skin. As swallowing neared completion, lateral bends of the anterior part of the body moved the prey posteriorly in the gut. Sometimes the snake attempted to maneuver the prey's tail into its mouth by head rubbing or snout pushing against the substrate. As the prey's tail was swallowed, a coral snake usually raised its head almost vertically and two to ten centimeters from the substrate.

Post-ingestion Behavior.—Swallowing was always followed by tongue-flick clusters, and sometimes by yawns. These usually occurred prior to lowering the head, and were followed by searching behavior. Occasionally a snake rubbed its head on the substrate after swallowing was completed. After feeding, coral snakes always responded to small movements (e.g., a wire jiggled in leaves) by pointing, tongue flicking, and approaching. If another prey item was offered it was seized and eaten.

Discussion.—Snakes exhibit several behavioral grades of prey immobilization. Most nonvenomous colubrids probably rely on a weight advantage and simply grasp and swallow living prey. Some other colubrids and probably all boids use constriction to bring about immobilization by suffocation (Greene and Burghardt 1978). Many viperids and at least one sea snake release and then relocate relatively large prey before swallowing (Loop and Bailey 1972; Chiszar and Scudder 1980; Radcliffe and Chiszar 1980; Jacob and Greene, unpublished). *Micrurus fulvius* typically uses a variation on the simple colubrid pattern, in that prey is seized, held, and immobilized by venom injection and then swallowed.

Similar behavior occurs in other species of *Micrurus* (Greene 1973a) and in sea snakes of the genera *Enhydrina*, *Hydrophis*, and *Pelamis* (Pickwell 1972; Voris *et al.* 1978). However, *M. fulvius* (this paper), *M. frontalis* (Lankes 1928; Mertens 1956), and perhaps *M. lemniscatus* (Mole 1898; Lankes 1938) occasionally release prey if it struggles violently or if some other difficulty is encountered in the preingestion phase; they then resume maneuvers at the same stage in the feeding sequence. It is interesting to note that the variable feeding behavior of these *Micrurus* combines a simple pattern seen in colubrids and some proteroglyphs (seize, hold, swallow) with a more complex sequence obtaining in some proteroglyphs (Armitage, 1965; Lambiris, 1967) and in many solenoglyphs (strike, release, relocate, seize, swallow). Unlike Ditmars (1912), I do not imply that this pattern mirrors the phylogeny of colubrids, elapids, and viperids. Additional information on feeding in other species and on intergeneric and interfamilial relationships is required before these observations can be meaningfully applied to scenarios of snake evolution.

DIET ECOLOGY

Taxonomic Composition and Seasonal Variation.—Eastern coral snakes of all sizes are specialized tertiary consumers; snakes, amphisbaenians, and elongate lizards comprised 97% of 221 prey items from throughout the species range (Table 2). Seventy of 132 items (53%) in Texas snakes were colubrid or leptotyphlopoid snakes of

TABLE 3. Seasonal incidence of three prey types in coral snakes, *Micrurus fulvius*, from Texas. Number of coral snakes containing prey per season are in parentheses following months. Decimal fractions indicate contribution of each prey type to the total prey sample for each season.

Seasons	Skinks	Juvenile large snakes	Other prey	Total
Spring, March–May (33)	12 (.29)	2 (.05)	27 (.66)	41
Summer, June–August (16)	2 (.11)	3 (.17)	13 (.72)	18
Fall, September–December (33)	9 (.22)	10 (.24)	22 (.54)	41
Total (82)	23	15	62	100

the genera *Diadophis*, *Leptotyphlops*, *Sonora*, *Storeria*, *Tantilla*, *Tropidoclonion*, and *Virginia*; undoubtedly, some of the unidentified snakes also belonged to these genera. These secretive snakes are normally found in litter or beneath logs or rocks (Wright and Wright 1957; Kassing 1961; Clark 1964). *Diadophis*, *Sonora*, *Tropidoclonion*, and *Virginia* usually have TLs of 20–40 cm and weigh 3–10 g. *Leptotyphlops* and *Tantilla* are shorter (TL < 30 cm), more slender, and weigh less (1–3 g). Five coral snakes had also eaten green snakes (*Opheodrys aestivus*); these are relatively long arboreal snakes T (TL ≤ 80 cm), but no thicker than an adult *Tropidoclonion*.

Nine *Eumeces* made up 7% of the total Texas sample. The *E. fasciatus* were females or subadult males (TL ≈ 13 cm), and probably weighed 5–7 g (Fitch 1954). Adult *E. tetragrammus* (TL ≈ 12 cm) are more slender than *E. fasciatus* and probably weigh slightly less. Eighteen *Scincella lateralis* comprised 14% of the prey items, but this species probably makes only a small contribution to total prey biomass of *Micrurus fulvius*. Adult *S. lateralis* (TL ≈ 8 cm) weigh ca. 1 g, and only four records represent confirmed ingestion of an entire skink. In 12 cases only the tail was found; six of these had clearly been autotomized, and five others looked as if they had been also. It seems likely that in most cases the skinks escaped, and observations on captive encounters (see above) support this conclusion. The monthly distribution of 23 skinks (*Eumeces* and *Scincella*) in stomachs suggests that they are more frequently eaten in the spring and fall (Table 3).

Most of the other prey were young or subadults of large terrestrial snakes (*Elaphe*, *Lampropeltis*, *Salvadora*, *Thamnophis*, *Agkistrodon*). Aquatic snakes (*Nerodia*, *Thamnophis*), amphibians, and mammals were very rarely eaten, and the three items in the latter two classes might have been secondarily ingested.

Five *Micrurus fulvius* made up 2% of the total 221 items from throughout the species range. Curtis (1952) suggested that two males from Angelina County, Texas attempted to swallow a *Storeria dekayi* from opposite ends, and that the smaller coral snake was then eaten by the larger one. This seems unlikely, because it implies that two free-living coral snakes found a single item almost simultaneously and, more importantly, that one of them attempted to swallow the prey tail-first (cf. Greene 1976). Ardrey (1970) misrepresented Loveridge's (1944) account of cannibalism in *M. fulvius* and suggested it as an example of inability to control aggressive social behavior, an unsupported speculation. There is no evidence for size of sex as an explanation, since the following combinations of predator and prey were involved: two adult males had eaten other adult males, one adult male had eaten a juvenile male, one adult male had eaten a gravid female, and one adult female had eaten another adult female.

Geographic Variation.—Regional variation in the diet of *Micrurus fulvius* largely reflects the distributions of particular prey species (compare Table 2 with maps in Conant 1975), rather than shifts in the general size and type of prey taken. Each Texas subsample included small secretive snakes, skinks, and the young of large snakes. Coral snakes frequently ate small colubrids in each region: *Virginia* and *Storeria* in east Texas; these genera and *Tropidoclonion* in north-central Texas; and *Sonora*, *Storeria*, and *Tantilla* in the more xeric southwestern and southern parts of the state. An obvious exception is that predation on scincid lizards occurred more often in the mesic forests of the eastern parts of the state.

Eighty-nine items in 71 *Micrurus fulvius* from elsewhere in the species range (Table 2) are consistent with the Texas data. Forty small, secretive colubrids of the genera *Diadophis*, *Ficimia*,

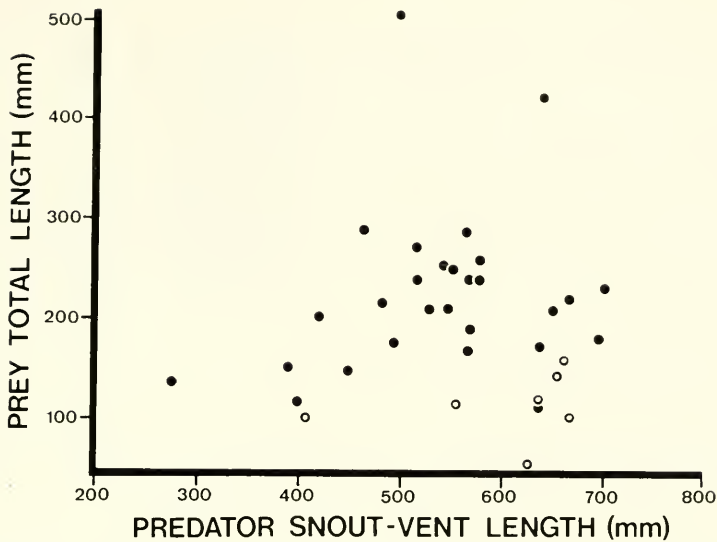


FIG. 1. Relationship between snout-vent length of coral snakes, *Micrurus fulvius*, and total length of prey. ● indicates snake prey and ○ indicates lizard prey.

Seminatrix, *Stilosoma*, *Storeria*, *Tantilla*, *Tropidodipsas*, and *Virginia* accounted for 45% of the sample. The remaining items included 12 limbless anguid lizards (14%), 12 scincid lizards (14%), five limbless amphisbaenians (6%), and 21 other snakes (22%). The only mammal was represented by a few hairs in a specimen from Tamaulipas, Mexico, and was perhaps secondarily ingested.

Predator/Prey Size Relationships.—Even very small coral snakes eat skinks and small colubrid snakes. Seven specimens from Texas (SV 25–29 cm) contained three *Scincella lateralis* (tails only), scales of an unidentified skink, one *Ophedryx aestivus*, one *Storeria dekayi*, and one *Virginia striatula*. A snake hatched in captivity began feeding on *S. lateralis* at an age of two months (Campbell 1973), and another very small captive also ate these lizards (Sochurek 1955).

Coral snake SV was positively correlated with prey TL (Fig. 1), although large coral snakes sometimes ate small prey. On some occasions *Micrurus fulvius* eats colubrids that are quite large (Matthes 1860; Mitchell 1903), but such meals are infrequent and can even be fatal (Neill 1968). If a 45 g adult *M. fulvius* ate a 9 g prey snake, the meal would equal 20% of the coral snake's weight. In six cases where adult coral snakes (23.5–64.1 g, \bar{x} = 41.5 g) and their prey could be

weighed, the items comprised 2–131% (\bar{x} = 41.7%) of the predators' weights.

Discussion.—My results demonstrate that throughout its range *Micrurus fulvius* feeds almost entirely on small snakes, elongate lizards, and amphisbaenians. Within these broad taxonomic, size, and shape limits, an interesting variety of prey are eaten. Factors that can affect diet composition include demographic, behavioral, and morphological characteristics of the predator and all of its potential prey species (Holling 1959; MacArthur and Pianka 1966; MacArthur 1972; Schoener 1971). These components are included in the concepts of availability and vulnerability, where "availability means that [particular] prey organisms are present, and vulnerability encompasses all physical and biological conditions that cause one species to be preyed on more heavily than another" (Hornocker 1970:29; availability is relative to the densities of particular prey populations as well as absolute in terms of their presence and absence). Demographic data on *M. fulvius* and its prey are lacking, but available information on the natural history of these animals suggests ways in which availability and vulnerability interact to determine the diet.

Small fossorial and terrestrial snakes are especially vulnerable to capture by coral snakes

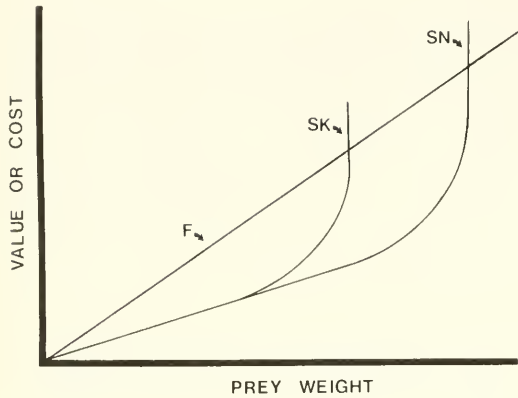


FIG. 2. Costs and benefits for coral snakes feeding on skinks (SK) versus snakes (SN). The straight line (F) indicates food value. See text for details.

because of their size, absence of effective anti-predator behavior, and preferred microhabitat. Predation on juveniles of larger species of snakes is presumably more restricted because of their seasonal availability in temperate climates (Table 3; Fitch 1970). Size, defensive capabilities, and microhabitat probably also influence coral snake predation on lizards. It appears that skinks are not as vulnerable as snakes because of their smaller total length, agility, and capacity for tail autotomy. Whiptails (*Cnemidophorus* sp.) are sympatric with *Micrurus fulvius* throughout its range, but these highly mobile lizards prefer hot, open areas (Fitch 1958) and are probably rarely encountered by coral snakes. Small iguanids (*Anolis* sp., *Sceloporus* sp.) are abundant in some places and anoles are sometimes accepted as food by captives (pers. obs.); however, these lizards are probably not important in the diet of coral snakes because they are largely arboreal and would not often be found by a foraging *Micrurus*.

What follows is a post hoc consideration of "ideal" prey size, "ideal" prey type, and two aspects of variation in the diet of *Micrurus fulvius* (see Appendix, Note 1). For this purpose, location costs include the energy expenditure and risk required to bring a snake within attack distance of its prey, and handling costs include the energy expenditure and risk involved in capturing and ingesting an item (these terms include search time and pursuit time, respectively, of MacArthur and Pianka 1966). Food value includes the energy and other nutritional factors present in a prey

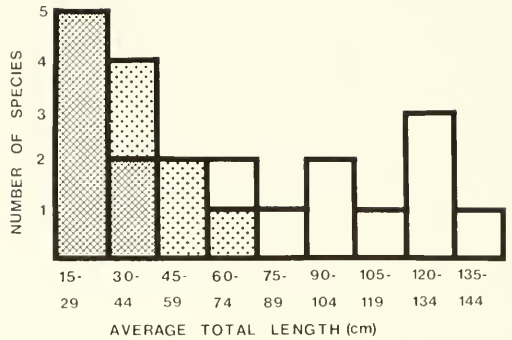


FIG. 3. Frequency distribution of average total length for snake species that are sympatric with *Micrurus fulvius* in eastern Texas. Cross hatching indicates species in genera frequently eaten by coral snakes. Stippling indicates species that are relatively unavailable (rare) or invulnerable (too stout). See text and Appendix Note 3 for details.

item; I assume that food value is a positive function of weight and equal on a per gram basis for all items (e.g., skinks versus snakes). The overall value of a prey item is thus some function of location costs, handling costs, and food value. Following MacArthur and Pianka (1966), I assume that prey items differ in terms of handling costs (due to differential characteristics of predator and prey), and that the addition of different prey types to the diet results in lower location costs (due to increased prey density). The overall value of a prey item increases as a function of weight (as does food value, Fig. 2) up to some point for a coral snake and then drops rapidly to zero. This is because as the diameter of the prey approaches and then exceeds the gape of the predator, ingestion will rapidly become difficult and dangerous (Appendix, Note 2). Ideally, coral snakes should take items that are to the left of but as close as possible to the food value-handling cost intercept in Fig. 2.

It is true that large coral snakes sometimes eat larger prey than do small individuals (Fig. 1), but large individuals also frequently eat small prey. Similar predator/prey size relationships have been demonstrated in a sea snake (Voris and Moffett 1981), males of a small, burrowing colubrid (Seib 1981), primitive snakes of the family Aniliidae (Greene 1983), and among small and medium size classes of a viperid (Beavers 1976). At least three factors might account for the fact that large

coral snakes sometimes eat small prey: (i) Because of the negative allometry of metabolic rate that obtains in most snakes (Bennett and Dawson 1976), an item of a particular relative weight might contribute proportionately more to the total energy budget of a large snake than it would to that of a smaller individual. Whether this is actually true for large and small coral snakes is not known. (ii) Occurrence of young individuals of large prey snakes is seasonally restricted, and they are thus not a predictable resource for coral snakes at all times of the year. (iii) The size configurations of terrestrial snake communities in temperate forests can be discontinuous; in east Texas they contain several species of very small, moderate, and large snakes, but very few medium-small species relative to adult *M. fulvius* (Fig. 3; Appendix, Note 3). In other words, because of (ii) and (iii), large coral snakes in the southeastern United States probably rarely encounter prey snakes proportionately as large as those eaten by small individuals.

Skinks are more heavy bodied than small snakes and as a result their food value-handling cost intercept occurs at a lower weight (Fig. 2). The disparity is increased by the lower vulnerability of skinks (see above and Viitt *et al.* 1977) and perhaps by their capacity for inflicting a powerful bite on the predator. In other words, skinks are probably more costly to handle than small snakes of equivalent weight and provide less food value than small snakes of equivalent handling cost. Ideally, coral snakes should add skinks to their diets only when location costs are reduced proportionate to the increased handling costs these lizards impose. This suggests an explanation for the increased predation on skinks in east Texas: quantitative data are lacking, but my field experience is that skinks are much more commonly encountered there than in other parts of the state where coral snakes occur. In any case, the stomach contents and behavioral observations certainly imply that *Micrurus fulvius* often attacks skinks and that these encounters frequently result in little or no net energy gain for adult coral snakes (three of 12 records of skink tails were for very small *M. fulvius*, for which they might have been proportionately large items). Either skinks (or skink tails) are proportionately more valuable than small snakes in per gram food value (cf. Clark 1971; B. E. Dial, pers. comm.) or the overall expectation of finding

"better" items is low enough to make them worth chasing in spite of the very low average payoff per attempt.

These considerations suggest that eastern coral snakes attack and sometimes eat substantial numbers of intuitively non-ideal prey (skinks, relatively small snakes). That they do so is perhaps surprising, because many snakes apparently feed infrequently on relatively heavy items (Greene 1983, MS) and such predators might be especially able to defer feeding until a highly profitable prey could be located. There are at least two plausible, non-exclusive reasons why *Micrurus fulvius* does not meet this prediction:

(i) Coral snakes might forage so as to minimize the time required to find and consume a given amount of food, rather than to maximize the intake of energy in a given time period or prey encounter (Schoener 1969; Morse 1980). In doing so they would reduce the time of exposure to predators and gain time for other activities, but the importance of either factor in coral snake biology is unknown.

(ii) According to MacArthur (1972:62), "an animal should elect to pursue an item if and only if, during the time the pursuit would take, it could not expect both to locate and to catch a better item" (MacArthur 1972:61. included "capture and eating" in "pursuit"). This paradigm underlies much subsequent literature on optimal foraging (e.g., Pyke *et al.* 1977; Krebs and Davies 1978; Morse 1980), although MacArthur (1972: 59) noted that it assumed "a fairly clear statistical expectation of the resources [a predator] will come upon." However, I suspect that location costs/item very greatly exceed handling costs/item for many terrestrial snakes (and perhaps some other predators), and that in most cases the predictability of finding a "better" item nearby is extremely low (see also Godley 1980). If this is true, MacArthur's formulation is trivial for such predators, at least in the practical sense of specifying the occurrence of a narrowly defined item in the diet.

I conclude that diet breadth in coral snakes is probably constrained primarily by naive feeding preferences and perhaps minor experimental modifications (Appendix, Note 4), by morphological factors (Appendix, Note 2), and by relative prey abundances (through their effects on encounter rates), rather than by more complex strategic "decisions" on an item by item basis

(Krebs and Davies 1978:23). The feeding rule for coral snakes seems to be, if it is an elongate reptile, not too large or dangerous, and can be caught, eat it.

SUMMARY

This paper reports the first extensive survey of feeding biology in a New World proteroglyphous snake, *Micrurus fulvius*. Foraging behavior was described on the basis of anecdotal field reports and detailed observations on four captive snakes. Literature records and stomach analysis of museum specimens provided information on 221 items from 177 coral snakes.

Eastern coral snakes used stereotyped head poking movements and chemical cues to search for prey and to follow prey trails. Visual and chemical stimuli elicited attack, and prey was held until it was immobilized by venom. Pre-ingestion movements were apparently inhibited by the prey's struggles and directed by scale overlap. Prey was almost always swallowed head first, by means of lateral shifts of the entire head of the coral snake and by unilateral jaw movements. Occasionally prey were bitten, released, relocated, and reeized before ingestion. This variable prey handling repertoire combines elements of a simple pattern seen in colubrids and some proteroglyphs with a more complex sequence seen in other proteroglyphs and some solenoglyphs.

Micrurus fulvius of all sizes feed almost entirely on small, terrestrial snakes, elongate lizards (especially scincids and limbless anguids), and amphisbaenians. Other lizards and the young of large colubrid and viperid snakes make up the remainder of the diet. Taxonomic variation in the diet largely reflects the distribution and seasonal availability of particular prey species, rather than shifts in the general types of prey taken. Large coral snakes sometimes eat larger prey than do smaller individuals, but they also continue to feed on relatively small items.

Behavioral observations and the diet analysis demonstrate that coral snakes often feed on two kinds of items, skinks and relatively small snakes, that are perhaps non-ideal in terms of average payoff per attack. These results and other considerations suggest that diet breadth in *Micrurus fulvius* might be constrained by naive prey preferences, morphological constraints, and relative prey abundance rather than by strategic "decisions" on an item by item basis.

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APPENDIX

Note 1.—Much of the recent literature on foraging theory is couched in terms of optimality, and some studies even purport to test an hypothesis that animals are feeding optimally. In practice, these approaches test feeding performance against constructs based on economic or design principles; in so doing, they usually assume that the animal is behaving optimally and set out to determine, via alternative models, how this is accomplished (Krebs and Davies 1978; Oster and Wilson 1978; Greene 1980). Maiorana (1978) referred to such hypothetical diet parameters as “ideal,” a more appropriate label than optimal in view of the procedures used in these studies.

Note 2.—The factors affecting gape in snakes are poorly studied, but probably include the elasticity of throat and neck skin, and the length and mobility of certain cranial elements (Gans 1961; Greene, MS). Circumstantial evidence suggests that coral snakes have relatively restricted gapes: they have fewer scale rows (15) than most snakes (implying less interscalar skin and consequently less capacity for stretching), relatively shorter quadrate bones, and relatively shorter mandibular elements than many other snakes (Marx and Rabb 1972; Greene, MS). As in most other elapids, the maxillae are greatly foreshortened and, at most, slightly mobile. Apparently the palatine and pterygoid bones are mostly restricted to anterior-posterior and

vertical movements (McDowell 1970), and this is also suggested by lateral movements of the entire head during swallowing (see above, and Frazzetta 1970). My casual observations of captive elapids (*Bungarus*, *Micrurus*, *Naja*, *Ophiophagus*, *Walternesia*) indicate that they have more difficulty swallowing prey of a particular relative diameter than do some snakes in other families (e.g., booids, viperids, *Attractaspis*, some colubrids).

Note 3.—The taxa in Fig. 3 and their average total lengths (to nearest cm) are: *Tantilla gracilis* (19), *Virginia striatula* (22), *V. valeriae* (22), *Storeria occipitomaculata* (23), *S. dekayi* (28), *Tropidoclonion lineatum* (30), *Diadophis punctatus* (31), *Cemophora coccinea* (44), *Ophedrys vernalis* (44), *Sistrurus miliaris* (45), *Lampropeltis triangulum* (49), *Heterodon platyrhinos* (68), *O. aestivus* (69), *Agkistrodon contortrix* (76), *L. calligaster* (92), *Elaphe guttata* (99), *L. getulus* (107), *Coluber constrictor* (112), *Farancia abacura* (120), *Masticophis flagellum* (130), *Crotalus horridus* (130), *Pituophis melanoleucus* (132), and *E. obsoleta* (145). The size structure of this assemblage is perhaps even more bimodal in terms of potential prey for *Micrurus fulvius* (average total length 64 cm) than Fig. 3 suggests; this is because several taxa of intermediate length are either rare in east Texas (*C. coccinea*, *O. vernalis*) or proportionately stout for their lengths (*A. contortrix*, *H. platyrhinos*, *S. miliaris*).

Note 4.—I attempted to test the responses of two newly hatched coral snakes (see Campbell 1973) to prey odors. Surface wash extracts were prepared by placing mealworms, newborn mice, a ground snake (*Sonora semiannulata*), or earthworms in a beaker of distilled water at 60°C for three minutes. The prey to water ratio was 3 g/10 ml. Extracts were stored frozen and warmed to room temperature before use. For testing, a sterile cotton swab was dipped in a vial of extract and then slowly moved to within 5 mm of the snout of a snake. Repeated attempts with each extract failed because the hatching coral snakes always responded to the swabs with rapid crawling and body thrashing. It nevertheless seems likely that *Micrurus fulvius* exhibits innate preferences for snakes and lizards, because these comprise almost all known natural prey for all sizes of coral snakes, and because such prey and a centipede are the only kinds that have been accepted by very small, naive coral snakes in captivity (Campbell 1973; Zegel 1975; see Burghardt 1970, and Arnold 1980, for reviews of the roles of naive preferences and experiential factors in the recognition of food by snakes).

The Role of Chemoreception in the Prey Selection of Neonate Reptiles

PENNIE H. VON ACHEN AND JAMES L. RAKESTRAW

INTRODUCTION

The role of chemoreception in the prey selection of neonate reptiles was the focus of our research on ten species of Kansas snakes and two species of Kansas lizards. Recent investigators, most notably Burghardt (1970b, 1971, 1973) have demonstrated innate chemical preferences in certain snakes and lizards for the kinds of prey normally eaten in the wild. However, such innate feeding preferences are subject to some degree of variation, including geographic variation paralleling those in the animals' natural diets (Burghardt 1970a; Arnold 1977). Furthermore, distinct polymorphism within local populations, even within broods, has been demonstrated, apparently serving to prevent overspecialization, thereby permitting better utilization of available food resources (Arnold 1977; Burghardt 1975; Gove and Burghardt 1975).

Elimination of visual and olfactory senses results in unaltered prey attacks in at least some kinds of snakes (Wilde 1938; Burghardt and Hess 1968; Burghardt 1970b). Snakes with vomeronasal nerve lesions fail to respond differentially to chemical cues (Halpern and Frumin 1979). Therefore, the primary receptor of this chemical information appears to be the vomeronasal system: the tongue, Jacobson's organ, and associated nerves. This system likely evolved as primitive lizards accidentally picked up chemicals with the tongue while drinking, eating, and mating. With increased sensitivity of Jacobson's organ and concomitant facilitating manipulations of the tongue, the system became proficient at responding to airborne chemicals (Gove 1979). Since the tongue transmits the chemical cues to Jacobson's organ, the number of tongue flicks elicited by an odoriferous object, as well as actual attacks, seem to be reliable measures of the reptile's interest in the object (Burghardt 1967).

Past works have dealt predominantly with naticines (Burghardt 1967, 1969, 1975; Burghardt and Hess 1968; Sheffield *et al.* 1968). While these snakes displayed a strong response when tested (many tongue flicks and attacks) others, such as

Lampropeltis getulus, appear to be less responsive to this methodology (Brock and Myers 1979). Exploration of saurian chemosensory mechanisms, although scant, has shown innate predisposition to chemical stimuli in some species of *Eumeces* (Loop and Scoville 1972; Burghardt 1973) and *Gerrhonotus* (Burghardt 1977).

The innateness of the behavior implies an evolutionary origin; thus one might expect a phylogenetic basis for the differential reliance upon this sensory system. Our objectives were to determine whether the chemoreceptive responses to prey odors that have been shown for some reptiles are of widespread occurrence in squamates and whether these responses differ among species and among higher taxa regardless of life histories.

METHODS

Subjects.—Twenty-three broods of snakes, representing ten species (one hundred and thirty-four individuals), and four broods of lizards representing two species (thirty-one individuals) were born in captivity to gravid females captured in central or eastern Kansas (Table 1). The females were kept in individual containers until parturition, and subsequently released. Each brood was housed collectively in the container in which they were born. The lizards and small snakes (*Storeria dekayi* and *Diadophis punctatus*) were kept in gallon jars in moist wood frass with moistened plastic wrap. Larger snakes were housed in wooden cages (30 × 30 × 60 cm) with screen fronts which held small water containers and open boxes full of wood frass. Experimental animals were maintained in a concrete building with natural lighting, temperature, and humidity.

Preparation.—A variety of prey animals were collected (Table 2). Although most investigators have followed Burghardt's extract preparation technique (1968), Carr and Gregory (1976) suggest that since reptiles presumably respond to odors emanating from the surface of the prey, rubbing a moistened cotton swab over the prey

TABLE 1. Data on reptiles at time of testing.

Species	Capture site of gravid female (Kansas county)	Brood size	Age (days)	Temp. (C)	Time (CDT)
<i>Eumeces fasciatus</i>	Johnson	6	4	31	1600
	Johnson	11	5	29	1430
<i>Ophisaurus attenuatus</i>	Johnson	3	<7	28	1400
	Johnson	11	<7	27	2000
<i>Coluber constrictor</i>	Johnson	5	8	22	1100
	Johnson	8	6	28	1400
<i>Lampropeltis calligaster</i>	Johnson	5	14	23	1630
<i>Diadophis punctatus</i>	Johnson	3	6	29	1630
	Johnson	1	5	29	1715
	Douglas	2	6	29	1745
	Johnson	1	7	28	1830
	Douglas	2	4	27	1845
	Douglas	2	6	26	1915
	Johnson	2	3	26	2000
	Johnson	4	3	25	2030
<i>Storeria dekayi</i>	Douglas	9	6	33	1500
	Douglas	15	4	32	2000
	Douglas	7	3	32	1330
	Douglas	12	5	38	1600
	Douglas	13	4	31	1400
<i>Thamnophis sirtalis</i>	Douglas	8	6	28	1530
	Douglas	7	6	27	1830
<i>Thamnophis radix</i>	Unknown ^a	8	4	28	1500
<i>Nerodia sipedon</i>	Douglas	5	5	23	1600
<i>Agkistrodon contortrix</i>	Douglas	5	<7	25	1600
<i>Sistrurus catenatus</i>	Unknown ^a	5	<7	25	1500
<i>Crotalus viridis</i>	Unknown ^a	5	<7	26	1300

^a Captured in central Kansas, county unknown.

surface results in an equally valid test. Therefore, cotton spindles (5 × 12 mm) were soaked in distilled water and rubbed over the surfaces of the live prey animals. These swabs were freshly prepared just before testing and rerubbed on the prey item every five minutes. Each cotton spindle was suspended on thread tied to a dowel. The investigator could thus manipulate the swab without being seen.

Ingestively naive reptiles less than fourteen days old were used since feeding responses can be modified by experience (Burghardt *et al.* 1973; Arnold 1978). While some individuals had already shed their natal skins, none were experiencing ecdysis at the time of testing. Each reptile was removed from its cage and placed in a straight-sided glass gallon container which was covered with cloth to prevent distracting visual stimuli. All individuals were tested in this container. A habituation time of five minutes was allowed. Each individual was presented a series

of prey swabs by slowly lowering the swab to within 2 cm of its snout, taking care to prevent accidental swab contact with the container. During each sixty second presentation, tongue flicks were counted, differentiating between those that touched the swab and those that did not. The number of attacks and the elapsed time before attack (attack latency) were also recorded. If no attacks or touching tongue flicks were made within thirty seconds, the swab was gently touched to the subject's snout once. The swab was removed immediately upon attack. Prey swabs were presented in random order, with a distilled water swab serving as a control. A one minute rest period elapsed between each presentation. Our results show no effects of desensitization or carry-over interest to successive stimuli due to order of presentation. The testing chamber was wiped out with distilled water after each experimental reptile was removed. Additional testing information can be found in Table 1.

Scoring.—Burghardt's tongue flick-attack score (1967), an arbitrary value system based on the number of tongue flicks and length of attack latencies, was used to calculate a "response profile" for each species (Table 2). This score is based on the assumption that an attack is a more significant response than any number of tongue flicks, and that a more desirable stimulus leads to an attack with a shorter latency than a less desirable stimulus. The formula for attacking reptiles is represented by:

$$\text{Score} = \text{base unit} + (60 - \text{attack latency})$$

The base unit is the maximum number of touching tongue flicks given by any individual of the experimental group tested to any of the stimuli in a sixty second trial. An attacking reptile was given a score identical to the base unit for that species plus the trial length minus the attack latency. A reptile which did not attack was given a score identical with the number of tongue flicks emitted towards the swab. Czaplicki (1975) found a high test-retest reliability when this scoring method was used ($r = .86$). To eliminate responses other than those elicited by swabs (e.g., exploratory tongue flicking), only those tongue flicks which touched the swabs were used.

RESULTS

In all species a preference was shown for one or more types of prey items over the control swab. Using the Wilcoxon Signed Ranks Test to investigate differences between the control and the most preferred swab (those with the highest tongue flick-attack score for each species), we determined that for four species the difference was significant ($P < 0.05$) (Fig. 1). In addition, *Diadophis punctatus* showed a significant response ($P < 0.03$) to a swab other than the one receiving the highest tongue flick-attack score. Although comparison was not possible with the Wilcoxon Signed Ranks Test for *Thamnophis sirtalis*, a paired *t*-test showed highly significant results ($P < 0.005$). Preferred stimuli generally corresponded to the prey species in the natural diet as indicated by food samples from the local population.

Lizards.—*Eumeces fasciatus* responded strongly to grasshoppers and spiders (Table 2). Although grasshoppers received the most atten-

tion, they are outnumbered two : one by spiders in stomach contents (Fitch 1954). Perhaps this is because as adults, most grasshoppers are too large for even an adult skink to subdue and ingest. Spiders and orthopterans combined comprise the bulk of the diet in the wild. Only 6% of the skinks attacked harvestman swabs, compared to 47% that attacked the grasshopper swab. Harvestmen constitute a minor food source in the local population.

Ophisaurus attenuatus likewise showed a strong response to spider ($P < 0.015$) and orthopteran swabs (grasshopper $P < 0.003$), (cricket $P < 0.003$). Orthopterans comprise 58% of their diet, spiders 12.5%, in a food sample of a local population (Fitch, pers. comm.). Although the cricket swab elicited as many attacks as the spider swab, the spider trials were characterized by shorter attack latencies and more tongue flicks.

Snakes.—*Coluber constrictor* showed minimal responses to all prey swabs. Of the three prey offered, worms are not included in their natural diets, mice are often eaten, but crickets are the most frequently consumed prey (Fitch 1963). The mouse swab elicited the strongest response, although that was negligible. No attacks were made on any swab.

Lampropeltis calligaster eats mainly small mammals and reptiles (Fitch 1978). While the mouse swab surprisingly aroused no more interest than the distilled water swab, the swabs of red sided garter snake and eastern yellow bellied racer did elicit some response as expected. Since ringneck snakes have been found in stomach and scat contents (Fitch 1978), it is somewhat surprising that ringneck swabs received so little attention (Table 2). No attacks were made.

The diet of local populations of *Diadophis punctatus* is composed almost exclusively of earthworms (Fitch 1975). While the earthworm swab did elicit the strongest response, the snail swab received almost as much interest and was significant at $P < 0.03$. No attacks were made.

Storeria dekayi showed an overwhelming preference for the earthworm swab ($P < 0.0001$), supporting Collins' (1974) assessment that locally they eat primarily earthworms. There was a weaker, but still significant ($P < 0.01$) response to the pond snail (Table 2).

Thamnophis sirtalis preys chiefly on mammals, frogs and worms (Fitch 1965). Fish are not well represented in the diet of the local popula-

TABLE 2. Tongue-flick attack (TFA) scores for 12 species of Kansas reptiles.

Prey swab	Number of attacks	Mean TFA score \pm SE
<i>Eumeces fasciatus</i> ($P < 0.023$, $N = 17$) ^a		
Distilled water	1	3.24 \pm 3.11
Harvestman (<i>Leiobunum vittatum</i>)	1	4.71 \pm 3.37
Differential grasshopper (<i>Melanoplus differentialis</i>)	8	16.41 \pm 5.16
House spider (<i>Achaeranea tepidariorum</i>)	3	8.71 \pm 4.79
<i>Ophisaurus attenuatus</i> ($P < 0.015$, $N = 14$) ^a		
Distilled water	0	0.43 \pm 0.20
Differential grasshopper (<i>Melanoplus differentialis</i>)	3	21.21 \pm 9.17
Cricket (<i>Acheta assimilis</i>)	5	26.21 \pm 8.46
Prairie wolf spider (<i>Lycosa rabida</i>)	5	28.36 \pm 9.59
<i>Coluber constrictor</i> ($t = 1.39$, $N = 13$, $P < 0.10$) ^b		
Distilled water	0	0.00 \pm 0.00
Cricket (<i>Acheta assimilis</i>)	0	0.15 \pm 0.10
House mouse (<i>Mus musculus</i>)	0	0.85 \pm 0.61
Earthworm (<i>Allolobophora caliginosa</i>)	0	0.15 \pm 0.15
<i>Lampropeltis calligaster</i> ($P < 0.18$, $N = 5$) ^a		
Distilled water	0	0.20 \pm 0.20
House mouse (<i>Mus musculus</i>)	0	0.20 \pm 0.20
Red-sided garter snake (<i>Thamnophis sirtalis</i>)	0	1.80 \pm 1.36
Eastern yellow-bellied racer (<i>Coluber constrictor</i>)	0	1.40 \pm 0.87
Prairie ringneck snake (<i>Diadophis punctatus</i>)	0	0.20 \pm 0.20
<i>Diadophis punctatus</i> ($P < 0.14$, $N = 17$) ^a		
Distilled water	0	0.71 \pm 0.37
Pond snail (<i>Physa hawni</i>)	0	2.06 \pm 0.52
Mealworm (<i>Tenebrio molitor</i>)	0	0.24 \pm 0.18
Earthworm (<i>Allolobophora caliginosa</i>)	0	2.59 \pm 1.27
<i>Storeria dekayi</i> ($P < 0.0001$, $N = 56$) ^a		
Distilled water	0	1.02 \pm 0.25
Pond snail (<i>Physa hawni</i>)	0	2.14 \pm 0.43
Earthworm (<i>Allolobophora caliginosa</i>)	0	12.46 \pm 1.90
Mealworm (<i>Tenebrio molitor</i>)	0	1.46 \pm 0.26
<i>Thamnophis sirtalis</i> ($t = 3.25$, $N = 15$, $P < 0.005$) ^b		
Distilled water	0	0.00 \pm 0.00
Bullfrog (<i>Rana catesbeiana</i>)	0	3.60 \pm 1.45
Earthworm (<i>Allolobophora caliginosa</i>)	5	25.00 \pm 7.70
Red shiner (<i>Notropus lutrensis</i>)	1	9.20 \pm 4.54
Mealworm (<i>Tenebrio molitor</i>)	0	1.87 \pm 1.27
<i>Thamnophis radix</i> ($P < 0.052$, $N = 8$) ^a		
Distilled water	0	0.50 \pm 0.27
Earthworm (<i>Allolobophora caliginosa</i>)	2	17.63 \pm 8.29
Red shiner (<i>Notropus lutrensis</i>)	0	5.25 \pm 0.84
Pond snail (<i>Physa hawni</i>)	3	20.63 \pm 10.09
House mouse (<i>Mus musculus</i>)	0	3.38 \pm 1.25
<i>Nerodia sipedon</i> ($t = 1.48$, $N = 5$, $P < 0.15$) ^b		
Distilled water	0	0.00 \pm 0.00
Red shiner (<i>Notropus lutrensis</i>)	0	3.20 \pm 1.85
Leopard frog (<i>Rana pipiens</i>)	0	4.40 \pm 2.98
Tree frog (<i>Hyla chrysoscelis</i>)	0	2.60 \pm 1.66
<i>Agkistrodon contortrix</i> ($t = 1.57$, $N = 5$, $P < 0.10$) ^b		
Distilled water	0	0.00 \pm 0.00
House mouse (<i>Mus musculus</i>)	0	1.00 \pm 1.00
Cricket frog (<i>Aceris crepitans</i>)	0	0.80 \pm 0.80
Prairie ringneck snake (<i>Diadophis punctatus</i>)	0	5.00 \pm 1.84
Western slender glass lizard (<i>Ophisaurus attenuatus</i>)	0	6.40 \pm 4.07

TABLE 2. Continued.

Prey swab	Number of attacks	Mean TFA score \pm SE
<i>Sistrurus catenatus</i> ($P < 0.110$, $N = 5$) ^a		
Distilled water	0	0.80 \pm 0.80
Bullfrog (<i>Rana catesbeiana</i>)	0	0.00 \pm 0.00
Prairie vole (<i>Microtus ochrogaster</i>)	0	3.20 \pm 1.53
White-footed mouse (<i>Peromyscus leucopus</i>)	0	0.80 \pm 0.49
House mouse (<i>Mus musculus</i>)	0	0.00 \pm 0.00
Fence lizard (<i>Sceloporus undulatus</i>)	0	2.20 \pm 1.74
<i>Crotalus viridis</i> ($P < 0.110$, $N = 5$) ^a		
Distilled water	0	0.40 \pm 0.40
Leopard frog (<i>Rana pipiens</i>)	0	3.80 \pm 3.80
Prairie vole (<i>Microtus ochrogaster</i>)	0	6.20 \pm 3.92
White-footed mouse (<i>Peromyscus leucopus</i>)	0	2.20 \pm 2.20
House mouse (<i>Mus musculus</i>)	0	11.20 \pm 6.11

^a Wilcoxon Signed Ranks Test between distilled water swab (control) and prey swab with highest mean TFA score.

^b One-sided paired *t*-test between control and swab with highest TFA score.

tion. The strong response to earthworm swabs (Table 2) corresponds to their natural preference. The comparisons between the earthworm swab and all other prey swabs were significant ($P < 0.05$). One might expect a higher response towards the frog swab as well. Perhaps frogs are not included in the juvenile diet, as the availability of small frogs is greatly reduced by the time the hatchling snakes are feeding.

Thamnophis radix feeds upon amphibians, worms, fish and rodents (Collins 1974). Gastropods are not known to be a regular food source. Consequently, the one unexpected result of our tests was the well defined preference for the snail swab (Table 2). Since snails are abundant and easily caught, their absence from the available samples of this snake's food is puzzling. Burghardt (1969), in testing *Thamnophis sirtalis* with slugs, found that although the snakes might attack the slug, they rejected it immediately and quickly learned to avoid it. Since ingestion could not be accomplished in our experiments, it is not known if snail rejection and subsequent aversion would follow. Another congener, *Thamnophis elegans*, displayed both geographic variation and intrapopulation polymorphism in its predisposition to eat slugs (Arnold 1977). In our study there was no bimodal distribution of feeding scores and therefore no polymorphic response to snails. Perhaps in this species juvenile prey preference differs from that of the adult. The earth worm swab also elicited a strong response ($P < 0.02$), as would be expected, since worms are

prominent in food samples. While the fish received a lower score, it was significant at $P < 0.01$.

Locally, *Nerodia sipedon* feeds on frogs and fish (Fitch, pers. comm.). While responses were made to all three stimuli, the swab from the leopard frog, one of the two most frequently consumed foods of local populations, (Fitch, pers. comm.) was the most preferred in these tests. No attacks were made (Table 2).

Agkistrodon contortrix eats rodents, frogs, certain insects, lizards and snakes (Fitch 1960). Fitch found that ringneck snakes comprised 8% of the adult's diet, but are one of the primary foods of the hatchlings. Accordingly, a high response was elicited by the ringneck swab, although the glass lizard swab scored a higher tongue flick-attack score. The glass lizard constituted 2% of food eaten, but house mice and cricket frogs were rarely taken. The strong response to the glass lizard (Table 2) may well indicate a preference for this prey, but the low percentage found in their stomachs may reflect the difficulty involved in catching such an evasive animal. No attacks were made.

Sistrurus catenatus is primarily a rodent eater, although frogs, lizards and snakes are also eaten (Fitch, pers. comm.). In this study, the prairie vole swab received the most tongue flicks, while the fence lizard swab attracted moderate attention (Table 2). No attacks were made.

Mammals are reported to be the common food for *Crotalus viridis* (Collins 1974). Frogs are not

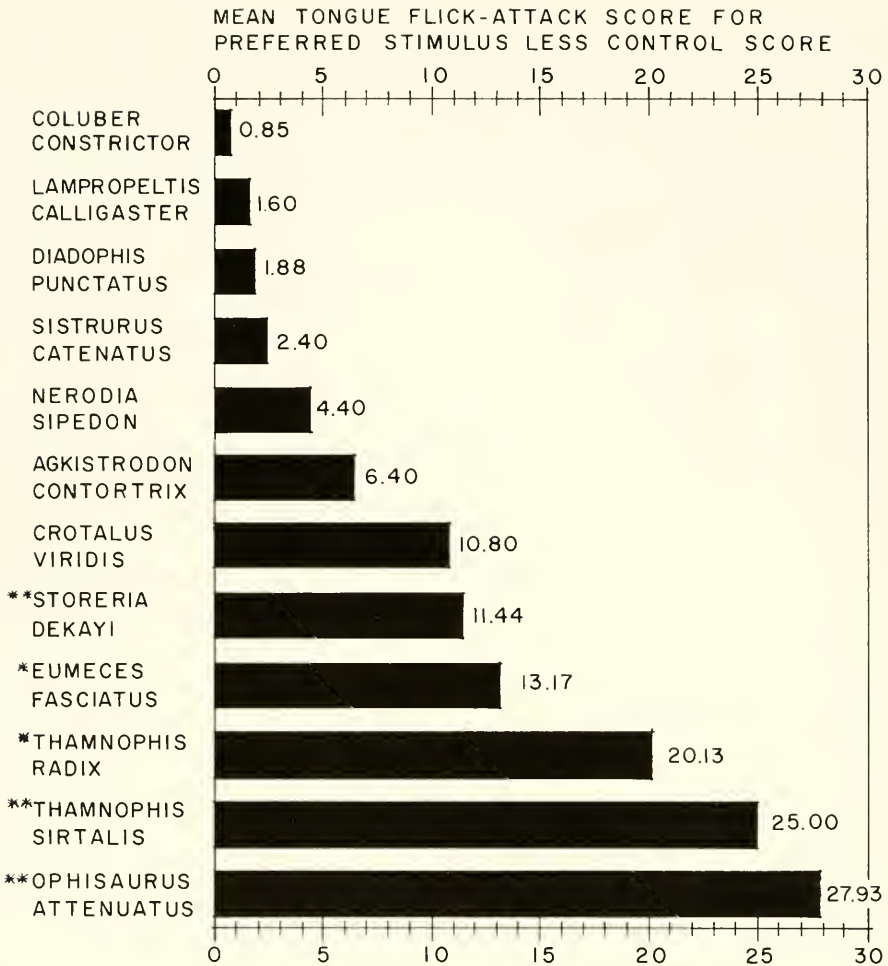


FIG. 1. The difference between the tongue flick-attack scores for the most preferred prey stimulus (the one with the highest tongue flick-attack score) and the distilled water control swab for twelve species of previously unfed Kansas reptiles. Levels of chemosensory dependence are indicated, tending to conform to subfamily groupings.

Probability values are from Wilcoxon Signed Ranks Test for all species but *Thamnophis sirtalis* for which a paired *t*-test was used (* = $P < 0.05$, ** = $P < 0.01$).

normally eaten. The house mouse swab elicited the greatest response in these tests. As was true of the other pit vipers tested, no attacks were made (Table 2).

DISCUSSION

Our experiments follow the general pattern of many previous investigators over the past two decades, but, in choosing potential prey species from which to obtain odoriferous test swabs, we

were guided, in most instances, by the results of large-scale food-habit studies on the same local populations from which our experimental neonates were drawn. Also notable are the large number of species and individuals tested, and the inclusion of species not tested before. It was hoped that the inclusion of ecologically diverse types of reptiles for study under the same experimental conditions would enhance the value of the results, allowing phylogenetic comparisons of chemoreceptive responsiveness.

In their test on six families of lizards, Bissinger and Simon (1979) noted that the difference in frequency of tongue extrusions in different families might indicate the relative importance of the vomeronasal system. Accordingly, mean responses to preferred prey swabs provide the basis for comparing each species' differential sensitivity to chemical cues. Fig. 1 shows the difference in the tongue flick-attack scores between the most preferred type of swab (the one receiving the highest tongue flick-attack score) and the distilled water control swab for each of the twelve species. These responses vary among the species and could represent the relative importance of chemoreception in the selection of prey. While only a tentative indication, this does suggest an interesting pattern. Ranked by their levels of selective chemical discrimination, the reptiles are generally arranged into subfamilies (based on Dowling's [1975] classification).

The three species with the lowest response scores, *Coluber constrictor*, *Lampropeltis calligaster*, and *Diadophis punctatus*, belong to the subfamily Colubrinae. *Coluber constrictor*, a snake of open grassland, appears to rely largely on sight (Collins 1974). Movement of nearly any small animal stimulates the racer to pursue and attack. Olfaction appears to play a minor role in the finding and capture of prey.

Diadophis punctatus is thought to depend on smell for prey detection, and its secretive life under rocks seems to confirm this. However, under the conditions of our experiments, the odor of its primary prey evoked little response, although a lower scoring swab did elicit a significant response.

Lampropeltis calligaster, unlike the natricines usually used in these works, is a constrictor. Other investigators using colubrid constrictors have found their responses towards test swabs differ somewhat from that of natricines. Brock and Myers (1979) were unable to find any significant difference between the control and prey swabs for ingestively naive *L. getulus*. However, Williams and Brisbin (1978) found that adult *L. getulus* had an innate preference for certain prey extracts despite restricted diets. Burghardt and Abeshaheen (1971), working with another colubrid constrictor, *Elaphe vulpina*, found that, in contrast to a garter snake's immediate attack and ingestion of prey, *E. vulpina* moved more deliberately and hesitantly, often taking several hours

to constrict and ingest the prey. Perhaps a sixty second trial is insufficient for such snakes.

The importance of the vomeronasal system to the Crotalinae seems not to be strongly associated with prey detection. Previous work on rattlesnakes (Chiszar and Radcliffe 1976; Chiszar *et al.* 1978) has demonstrated that visual or thermal signals are needed to elicit attacks and relatively few tongue flicks are emitted prior to striking. Once the strike has occurred, however, tongue flicking is initiated and continues while the snake trails the stricken prey and investigates the carcass, presumably to locate the head. Tongue flicking again commences after the prey is swallowed, perhaps to detect any remaining prey in the vicinity. However, rattlesnakes are able to detect prey solely by chemical cues (Cowles and Phelan 1958). The lack of any attacks by the crotalines that we tested supports the supposition that visual or thermal cues are necessary to elicit a strike, even though detection can be accomplished by odor alone.

The fourth snake in an intermediate position is a natricine, *Nerodia sipedon*. Unlike the other natricine tested, *N. sipedon* exhibited a relatively low degree of tongue flicking and made no prey attacks. Burghardt (1968) has reported similar findings for this species. Because this snake generally feeds in the water, volatile chemical cues may not be as useful as visual or tactile cues. Drummond (1979) suggests that this species responds to and integrates visual and chemical cues. Out of the water attacks can be elicited from experienced snakes by visual stimuli alone. When the snake is submerged, visual and/or mechanical stimuli are adequate. Attack frequency increases when diffuse chemical cues accompany visual ones. However, attack can be induced by chemical cues alone.

The three snakes with the highest response scores, *Storeria dekayi*, *Thamnophis sirtalis*, and *Thamnophis radix*, are terrestrial natricine non-constrictors that overpower, hold and swallow their prey. Their high response scores corroborate previous findings based on essentially the same testing technique (Burghardt 1967, 1969, 1970a, 1971; Burghardt and Hess 1968). Prey attacks were common and tongue flick activity was among the highest of all the snake species tested, suggesting a strong dependence on chemosensory methods of prey selection. Sheffield *et al.* (1968) note that prey attacks were always

preceded by at least one tongue flick that actually touched the swab, and we noted only two exceptions among the one hundred sixty-five individuals tested in this study. One *E. fasciatus* attacked a harvestman swab immediately upon introduction, and an *O. attenuatus* likewise attacked a cricket swab. These attacks were not surprising since many lizards are known to respond to visual cues, including movement. However, Chiszar *et al.* (1976) noted that juvenile *Thamnophis* flick their tongue more often than do adults. It is possible that other senses gradually replace some of the dependence on chemoreception during ontogeny (Burghardt 1969; Burghardt and Pruitt 1975). That would explain how a garter snake could catch swiftly moving prey such as a frog, which would seldom remain motionless to permit close approach and preliminary tongue flicks by the predator.

Lizards are generally thought to be less dependent on Jacobson's organ than snakes. Terrestrial lizards, however, usually have better developed olfactory/vomeranosal organs and concomitant decreased vision as compared with arboreal lizards (Gravelle 1980). *E. fasciatus* exhibited a relatively strong chemical preference when tested, placing it among the natricines in response scores. While Loop and Scoville (1972) found no differential tongue flicking or prey attack behavior in a congener, *E. inexpectatus*, our findings support the conclusion of Burghardt (1973) that there is innate chemical recognition of prey. Burghardt also noted, as we did, the very low rate of tongue flicking in *Eumeces* compared with snakes in similar tests.

Ophisaurus attenuatus displayed the highest level of response of all the species tested, both in terms of tongue flicks and attacks. This is consistent with the theory that those lizards showing a lack of elaborate visual communication use Jacobson's organ more frequently (Bissinger and Simon 1979). Furthermore, Gove (1979) demonstrates that the tongue flick pattern of these lizards are more similar to snakes than are most lizards.

Other studies, addressing different questions, have used techniques similar to those used here. However, future investigators should be aware of several problematic areas. One involves the arbitrary age at which the hatchlings are tested. Postnatal onset of hunger following absorption of stored yolk material may take a short or relatively long time in different species and indi-

viduals. Moreover, tests to date are based on adult food preferences. It is known that the young of some species prefer different prey than do the adults (Mushinsky and Lotz 1980). If more were known about juvenile diets, utilization of prey items which would generate maximum responses could be assured.

Furthermore, we tentatively conclude that various obscure inhibiting factors altered results to varying degrees, depending on the species and perhaps on the individual. The gentle momentary handling involved in transferring the animal to the experimental container may have involved psychological stress that resulted in suppression of the normal responses to food far beyond the five-minute adjustment period in some hypersensitive kinds. In the more secretive kinds that normally spend their time in burrows or beneath sheltering objects, the experimental container's lack of the necessary thigmotactic stimuli may have inhibited feeding behavior. Differential responses to light intensities and to temperatures may also have been involved.

Finally, most studies have not differentiated between tongue flicks which touched the swab and those which did not. To minimize the risk of confusing tongue flicks not directly stimulated by the odor of the swab, such as exploratory tongue flicks, only those flicks touching the swab were used. This measures response to chemicals of low volatility. Sheffield *et al.* (1968) showed that nonvolatile macromolecules were the attack stimulus for *Thamnophis*. Cowles and Phelan (1958) theorized that the external nares, receiving olfactory stimuli, were highly sensitive but of low discrimination, alerting the snake to visual stimuli of movements and initiating lingual air sampling and subsequent specific analysis by Jacobson's organ. In other words, olfaction conveys volatile information from a distance, while Jacobson's organ is most sensitive to proximal compounds of low volatility. Indeed either the tongue or lips must touch the object before an attack is released (Sheffield *et al.* 1968). Presumably then, touching tongue flicks are more significant indicators of interest than non-touching tongue flicks. Once the prey is inside the mouth, gustation mediates which prey are suitable for swallowing (Burghardt 1969). If prey moves on after detection, a snake may trail it utilizing Jacobson's organ. However, *Elaphe* (Burghardt and Abeshaheen 1971) and *Nerodia* (Dunbar 1979) have demonstrated discrimination of prey on the

basis of volatile chemical cues alone. In our tests, the constrictor *L. calligaster* displayed substantial discriminatory behavior when both touching and non-touching tongue flicks are considered. By contrast, only a weak response was made directly towards the swab. On the other hand, *N. sipedon*, similarly appraised on the basis of all tongue flicks made, responded more to the control than to the scented swabs. Clearly more investigation is needed to determine the most meaningful scoring procedure to use.

With some reservations due to the foregoing constraints, we conclude that purposeful tongue extrusions and attacks do consistently vary among species, the pattern generally following subfamily groupings. This may well suggest a phylogenetic relationship of the differential dependence on chemoreception in the selection of prey.

SUMMARY

Inexperienced young of two lizard and ten snake species from Kansas were presented with cotton swabs scented with body surface odors of various animals including the preferred prey species of each kind of reptile. Distilled water swabs were used as controls. The number of tongue flicks, attacks and attack latencies were recorded. In all cases a preference was shown for one or more prey swabs over the water control swab, generally corresponding to the diet of the local population. This supports earlier findings that suggest innate chemical preferences.

On the basis of tongue flicks and attacks, various levels of discriminatory behavior were recorded, suggesting the relative importance of chemoreception in prey selection for each species. The reptiles tested can be ranked according to their levels of responsivity to chemical stimuli. Tending to conform with subfamily groupings, the colubrinae show the lowest level of discriminatory behavior, natricines, the highest level for snakes, and crotalines, intermediate between the two. The saurian *Eumeces* ranks among the natricines, but *Ophisaurus attenuatus* responded above all the other species tested in exhibiting the highest effectiveness of this sensory modality.

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Ecology of Small Fossorial Australian Snakes of the Genera *Neelaps* and *Simoselaps* (Serpentes, Elapidae)

RICHARD SHINE

INTRODUCTION

Most of continental Australia is arid, but the herpetofauna of these enormous deserts is poorly known. Recent studies have clarified the taxonomy of Australian desert reptiles (e.g., Storr 1967, 1979; Greer 1979; Cogger 1979), but the ecology of these animals remains virtually unstudied. The present paper is based on dissections of snakes from museum collections, and describes the general biology and life-histories of several small snake species from the arid zone. These snakes belong to the genera *Neelaps* (two species) and *Simoselaps* (11 species); both Storr (1967) and Cogger (1979) suggest that these genera are closely related to each other.

All of the *Neelaps* and *Simoselaps* species are characterized by small body size (<50 cm snout-vent length), bright colouration, and fossorial habits. Five *Simoselaps* species show a pronounced upturned edge on the rostral scale, presumably as an adaptation to burrowing. In this regard, as well as in general appearance and habits, *Neelaps* and *Simoselaps* are strikingly convergent with small sand-dwelling snakes from other continents (e.g., *Chilomeniscus*, *Chionactis*, *Ficinia*, *Gyalopion* in North America; *Prosymna* and *Elapsoidea* in Africa).

Although *Neelaps* and *Simoselaps* species may be among the most abundant snakes over most of Australia, they have attracted little study. Storr (1967, 1979) recently has revised the group, describing several new species in the process. According to Storr (1967), *Neelaps* and *Simoselaps* are not sufficiently distinct to warrant generic separation; Storr considers that they belong to the single large genus *Vermicella* (together with the Bandy-Bandy, *V. annulata*). Cogger (1979) prefers to recognize the three genera separately. I follow Cogger's (1979) nomenclature in the present study, because of my subjective impression that *Vermicella* (*sensu* Storr) is too heterogeneous a group.

Geographic distributions of the *Neelaps* and *Simoselaps* species are given by Storr (1967, 1979) and Cogger (1979) and are briefly summarized

in Table 1. Within these two genera, at least five distinct "species-groups" are evident:

- (i) *Neelaps bimaculatus* and *N. calonotus* are slender unbanded species of south-western Australia.
- (ii) The *Simoselaps* "bertholdi group" (*bertholdi*, *anomala*, *littoralis*, *minima*) are all short heavy-bodied snakes with distinct yellow-and-black bands and lacking an upturned rostral (Fig. 1).
- (iii) The *Simoselaps* "semifasciatus group" (*semifasciatus*, *approximans*, *incinctus*, *roperi*) have less distinct bands along the body (*incinctus* lacks bands). The rostral has a sharply upturned, angular leading edge (Fig. 1).
- (iv) *Simoselaps australis* and *S. fasciolatus* may not be closely related to each other. Both species resemble *S. semifasciatus* in general shape and colour; *S. australis* has a sharp-edged rostral whereas *S. fasciolatus* does not.
- (v) *Simoselaps warro* is a rainforest species of northeastern Queensland, and is so aberrant that it is only doubtfully included in this genus (Storr 1979).

METHODS

I examined all specimens (N = 953) of *Neelaps* and *Simoselaps* in the collections of the Western Australian Museum, the South Australian Museum, the National Museum, the Queensland Museum and the Australian Museum. I took the following data from each specimen: (i) snout-vent length (SVL), measured by running a tape measure along the body; (ii) gut contents; (iii) reproductive maturity or immaturity (criteria were: males—large testes or opaque efferent ducts; females—gravid, large oviducts, or ovarian follicles >5 mm); and (iv) diameters of ovarian follicles or oviducal eggs, in mature females. Growth rates were estimated from seasonal distributions of body sizes; this method is explained in more detail below.

TABLE 1. Sample sizes, body sizes and sexual size dimorphism in *Neelaps* and *Simoselaps*.

Species	Geographic distribution	Total sample size	Adult ♂♂				Adult ♀♀			♂ ♀ SVL
			N	\bar{x} SVL (SE) (cm)	Range	N	\bar{x} SVL (SE) (cm)	Range	\bar{x} ♀ SVL	
<i>N. bimaculatus</i>	south-west Aust.	82	25	29.3 (.8)	23.0–40.3	22	33.6 (.9)	26.4–40.6	.87	
<i>N. calonotus</i>	south-west Aust.	80	30	20.5 (.2)	18.2–23.0	32	22.4 (.3)	18.6–25.1	.92	
<i>S. anomala</i>	north-west Aust.	18	8	16.6 (.6)	14.1–18.7	5	18.2 (.6)	15.9–19.4	.91	
<i>S. approximans</i>	central-west Aust.	24	9	27.8 (.9)	23.5–32.0	7	27.8 (1.4)	21.4–32.2	1.00	
<i>S. australis</i>	south-east Aust.	118	42	22.7 (.4)	17.0–29.0	31	27.5 (.7)	19.5–33.7	.83	
<i>S. bertholdi</i>	western Aust.	318	105	18.3 (.2)	14.3–22.5	98	20.8 (.3)	16.4–31.2	.88	
<i>S. fasciolatus</i>	south-west Aust.	46	18	25.8 (.6)	20.2–30.0	13	29.4 (1.0)	23.1–35.2	.88	
<i>S. incinctus</i>	central Aust.	8	2	24.8	21.4–28.1	2	26.5	23.3–29.6	.94	
<i>S. littoralis</i>	central-west Aust.	53	16	16.2 (.3)	14.3–18.1	16	24.0	16.7–35.4	.68	
<i>S. minima</i>	north-west Aust.	1	1	19.4	—	—	—	—	—	
<i>S. roperi</i>	north-west Aust.	9	1	25.5	—	4	28.2 (2.1)	25.5–34.4	.90	
<i>S. semifasciatus</i>	south-west and north-east Aust.	186	68	24.2 (.3)	19.2–33.6	74	27.1 (.5)	19.6–33.4	.89	
<i>S. warro</i>	north-east Aust.	10	3	29.0	24.0–36.2	5	33.5 (3.1)	25.6–40.9	.87	

RESULTS

Body Sizes.—Table 1 presents data on sample sizes, geographic ranges, SVL's and sexual size dimorphism. Most species, especially in the genus *Simoselaps*, are very small. Females exceed males in SVL in all species except *S. approximans*, where a small sample suggests that the sexes attain similar body sizes. The degree of female size superiority is greatest in *S. littoralis*, where adult males average less than 70% of the mean SVL of adult females. The degree of female size superiority is not correlated with mean adult SVL in an interspecific comparison (data from Table 1, $N = 12$, $r = .24$, n.s.)

Food Habits.—A total of 95 prey items were identified from *Neelaps* and *Simoselaps* stomachs (Table 2). Most of these items were scincid lizards (55.8%), with several pygopodid lizards (8.4%) and a surprisingly large number of squamate eggs (35.8%). Lizards were the only prey recorded in *Neelaps* species ($N = 18$), and in the *Simoselaps* "bertholdi group" ($N = 38$). *Simoselaps australis* and *S. fasciolatus* eat both lizards and squamate eggs, whereas squamate eggs appear to be the only prey type of the *S.* "semifasciatus group" ($N = 30$). All eggs in *Simoselaps* stomachs lacked recognizable embryos, suggesting that the eggs were eaten soon after oviposition. A single lizard was the only prey recorded for *Simoselaps warro*.

A comparison of the most abundant sauro-

phage (*S. bertholdi*) with the most abundant oophage (*S. semifasciatus*) revealed a clear difference in the frequency with which multiple food items were recorded. *Simoselaps bertholdi* almost always takes lizards singly (mean number of prey items per snake with food = 1.08, SE = 0.05, $N = 25$) whereas *S. semifasciatus* usually takes more than one egg at a time ($\bar{x} = 3.00$ items per snake with food, SE = 0.44, $N = 9$). These numbers are significantly different (Dice-Leras graphic test, $P < .01$).

Mode of Reproduction.—Oviducal eggs with thick shells were found in gravid females of *Neelaps calonotus* (W.A.M. 5666), *Simoselaps australis* (A.M. 1680), *S. bertholdi* (S.A.M. 291), *S. littoralis* (N.M.V. 824) and *S. warro* (A.M. 16697). No data are available for the other species, but oviparity (rather than viviparity) clearly is the mode of reproduction in most of the *Neelaps* and *Simoselaps* species.

Size at Hatching.—Where sample sizes are large (Table 1), SVL of the smallest specimen should be close to SVL at hatching. The behaviour of the snakes makes this particularly likely: recently-hatched individuals often disperse actively and are particularly likely to be collected. Fig. 2 shows that presumed SVL at hatching ranges from 7.0 cm (*S. littoralis*) to 14.2 cm (*N. bimaculatus*), and is highly correlated with mean adult body size in an interspecific comparison ($N = 9$, $r = .85$, $P < .01$; Fig. 2).

Sexual Maturity.—As would be expected from

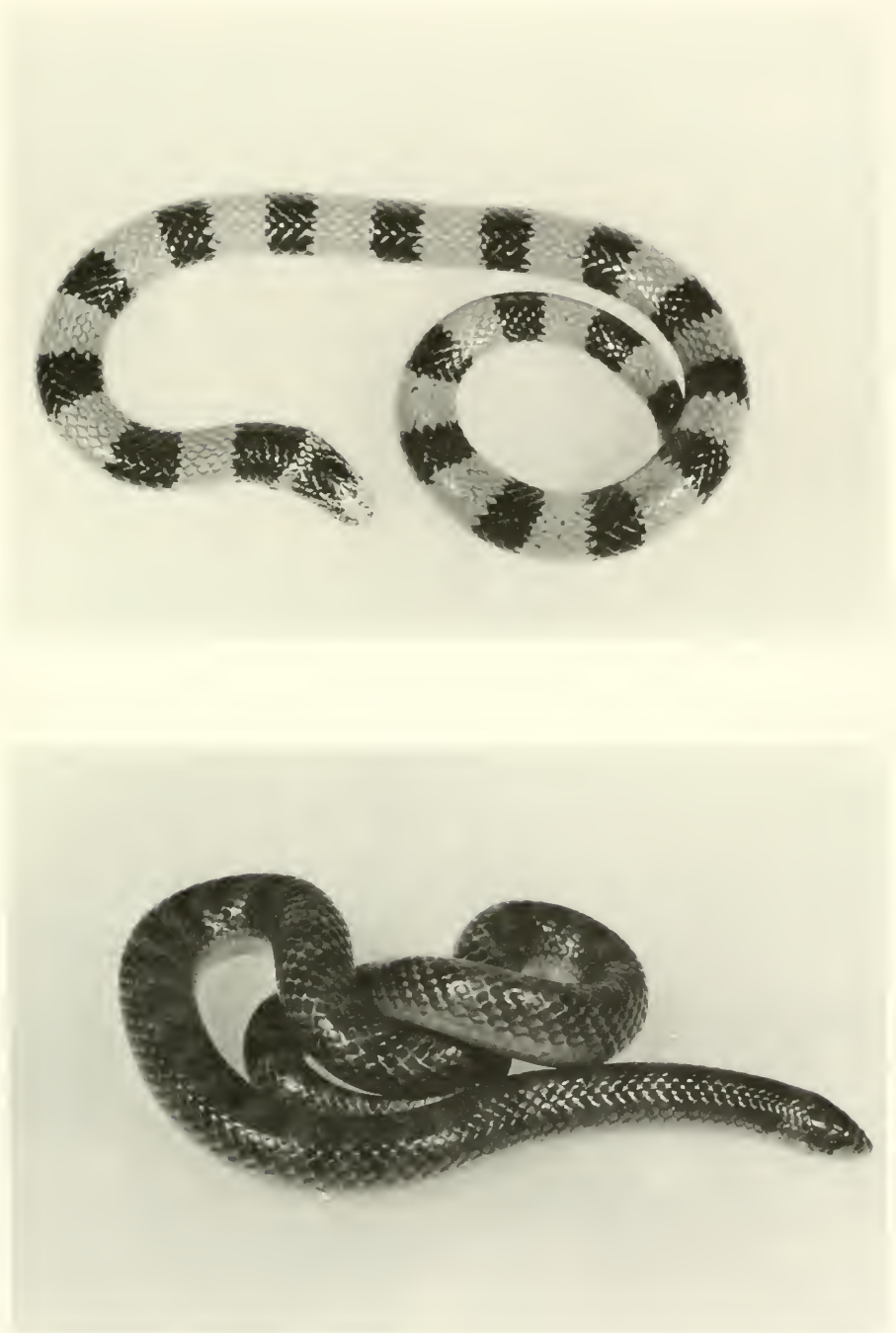


FIG. 1. *Simoselaps bertholdi* (upper) and *S. semifasciatus* (lower). Note the upturned edges to the rostral scale in *S. semifasciatus*. Photographs courtesy of H. G. Cogger.

TABLE 2. Prey items found in stomachs of *Neelaps* and *Simoselaps* species.

Prey items	<i>N. bimaculatus</i>	<i>N. calonotus</i>	<i>S. anomala</i>	<i>S. australis</i>	<i>S. bertholdi</i>	<i>S. fasciolatus</i>	<i>S. littoralis</i>	<i>S. minima</i>	<i>S. roperi</i>	<i>S. semifasciatus</i>	<i>S. warro</i>
Squamate eggs				3		1			3	27	
Unidentified skinks	1	2	2	1	8		3				1
<i>Ctenotus</i> sp.					3	3					
<i>Lerista</i> sp.	2	4			9		2	1			
<i>L. elegans</i>							1				
<i>L. lineata</i>		1									
<i>L. praepedita</i>		3									
<i>L. picturata</i>							1				
<i>Menetia</i> sp.					4						
<i>Morethia</i> sp.							1				
<i>Aprasia</i> sp.		4									
<i>A. repens</i>		1			3						
Total number of prey items:	3	15	2	4	27	4	8	1	3	27	1

the sexual size dimorphism in *Neelaps* and *Simoselaps*, males mature at smaller body sizes than do females (Table 1). The only exception to this trend is *S. approximans*; in this species, a single very small mature female is the reason for the discrepancy.

Growth Rates.—No direct data are available on this topic, but one may infer growth rates from seasonal distributions of body sizes of collected snakes (see Shine 1978a for examples and discussion of this method). The technique is suitable only for large samples, and I have chosen to apply it only to the two most common species (*Simoselaps bertholdi* and *S. semifasciatus*). A sample taken at a single instant in time should reveal discrete size-groupings which correspond to year-classes. One cannot combine samples taken throughout the year, as this would include individuals of intermediate body sizes. However, samples can be combined for that part of the year during which growth is slow or negligible; the gaps in the resulting size distribution reflect the growth occurring during the remainder of the year.

Fig. 3 shows data obtained in this way. In both *S. bertholdi* and *S. semifasciatus*, two size classes are presented among the immature snakes collected during the cooler (slow growth) part of the year. I infer that these two size classes represent year classes. In each case, the smaller individuals are first-year snakes (zero to seven months old) and the larger individuals are one year older (12 to 19 months old). These data suggest that in both species, sexual maturity begins at about 20

months of age (i.e., in the second spring after birth). It seems likely that many individuals, particularly females, require an extra year to attain maturity.

Seasonal Reproductive Timing.—Efferent ducts of mature males are opaque (indicating that they contain sperm—Shine 1977a) throughout the year in all the species examined. In mature females, ovarian follicles are small (<5 mm) during most of the year (Fig. 4). Vitellogenesis commences in late spring (Oct.–Nov.), ovulation in summer (Dec.–Jan.), and oviposition shortly thereafter. Data for one female *S. bertholdi* are anomalous, with enlarged follicles in autumn (May). The restricted time period over which gravid females were recorded (Dec.–Jan.) suggests that only a single clutch of eggs is produced annually.

Clutch sizes.—Fecundity data are summarized in Fig. 2 and Table 3. Clutch sizes are relatively small in all species, with most records from three to five eggs. Fecundity increases with maternal SVL in *Neelaps bimaculatus* ($P < .05$), and *Simoselaps bertholdi* ($P < .01$), but apparently not in *Neelaps calonotus* or *Simoselaps semifasciatus* ($P \gg .5$). Larger species produce larger clutches (Fig. 2).

Seasonal Abundance.—Snakes were collected throughout the year; Fig. 5 presents data for the two most common species. When these data are combined into frequency of collection in different seasons (spring, summer, autumn, winter), analysis shows that there is no significant seasonal variation in the number of snakes collected, either in *S. bertholdi* ($N = 117$, 3 d.f., $\chi^2 =$

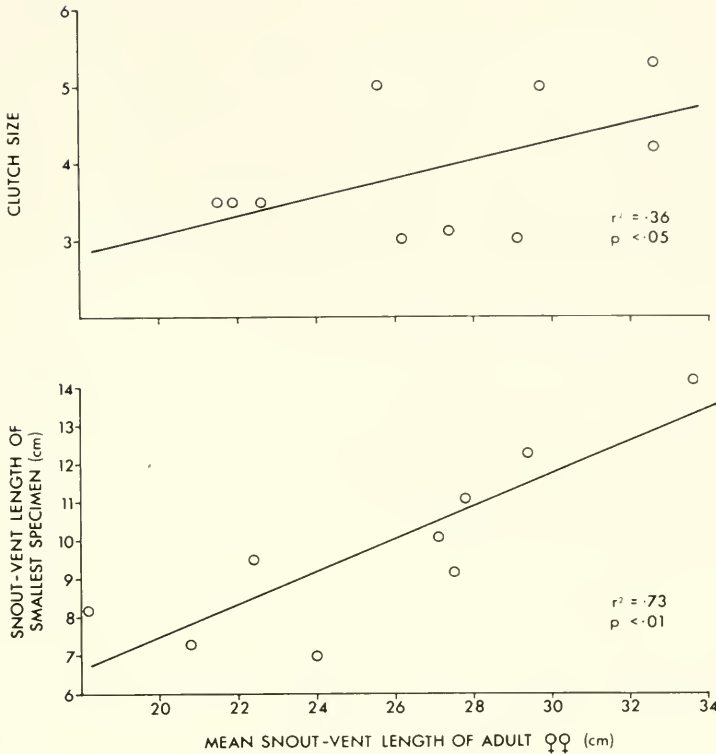


FIG. 2. Fecundity and inferred body-size at hatching in *Neelaps* and *Simoselaps* species.

3.99, $P > .20$) or *S. semifasciatus* ($N = 88$, 3 d.f., $\chi^2 = 7.73$, $P > .05$). Neither are the seasonal distributions of these two species different from each other ($N = 205$, 3 d.f., $\chi^2 = 3.45$, $P > .30$).

Data on feeding activity (the proportion of snakes containing food items) show a different pattern (Fig. 5). In both *S. bertholdi* and *S. semifasciatus*, feeding is most common in summer, and ceases during winter.

DISCUSSION

Body Sizes.—The tendency for females to grow larger than males in *Neelaps* and *Simoselaps* species is not unexpected. Females are the larger sex in most, but not all, of the small Australian elapids studied to date (females larger in *Cacophis*, *Furina*, *Drysdalia* and *Vernicella*; males larger in *Unechis*—Shine 1978a, 1980a, 1980b, 1981a, 1981b). Female size superiority is also the most common situation among snakes in general, and is correlated with the absence of male combat behaviour (Shine 1978b).

Food Habits.—Published literature generally

is in error on this subject. Glauert suggested that most *Simoselaps* species eat “insects and other small forms of life, including frogs and small lizards” (1957, p. 40). Kinghorn (1964) suggested that the diet of *Neelaps bimaculatus* consisted mainly of small insects. Mackay (1949) believed that *S. australis* fed on slugs, beetle larvae, and worms. McPhee (1979) noted that *S. semifasciatus* probably ate only insects. Worrell (1963) correctly asserted that *S. bertholdi* feeds on skinks. Gow (1976) suggested that *N. bimaculatus* feeds on insects, and that *S. australis* probably does also (as well as feeding on skinks). Gow (1976) credited *S. bertholdi* with feeding on insects, frogs and lizards, and recorded captive *S. warro* feeding on skinks. Storr (1967) speculated that the geographic distribution of *Neelaps* and *Simoselaps* was constrained by competition with lygosomine skinks. Data from the present study suggest that these lizards are food items rather than competitors.

The repeated assertion that these snakes feed on invertebrates (especially insects) is not supported by data in Table 2. Lizards are the only

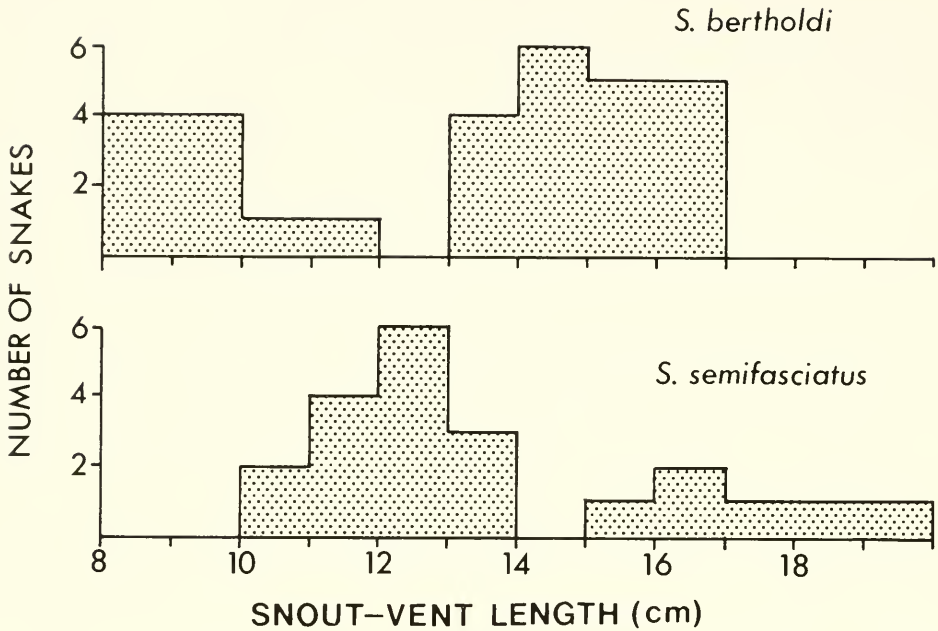


FIG. 3. Body-size distributions of juvenile *Simoselaps bertholdi* and *S. semifasciatus* collected during the "non-growing season" (April through October).

prey type of *Neelaps* and the *Simoselaps* "bertholdi group," and squamate eggs are the only prey taken by the *S. "semifasciatus group."* Studies on several other small Australian elapids have revealed an analogous situation: published literature is almost unanimous in suggesting that invertebrates are the main food items, but dissections show that lizards comprise the major portion of the diet. This is true in *Cacophis*, *Furina*, *Demansia*, *Unechis* and other groups (Shine 1977c, 1980a, 1980c, 1981a, 1981b).

The saurophagous *Neelaps* and *Simoselaps* species mainly eat fossorial lizards: skinks of the genus *Lerista* and pygopodids of the genus *Aprasia*. However, the heavy-bodied *Simoselaps* "bertholdi group" also take non-fossorial lizards. The skinks *Ctenotus*, *Menetia* and *Morethia* are surface-active forms; *Ctenotus* is a very large and robust prey for these small snakes. The inclusion of these prey items in the *S. bertholdi* diet may be related to the daily activity cycle of the snakes. Waite (1929), Worrell (1963) and Gow (1976) note that *S. bertholdi* may be active diurnally, unlike all the other (nocturnal) *Simoselaps* for which records are available. *Simoselaps ber-*

tholdi subdues its scincid prey by constriction, in the same manner as do pythons (Bush 1981).

The specialization of the *Simoselaps* "semifasciatus group" on squamate eggs was an unexpected finding. No other Australian snakes are known to feed predominantly upon eggs, although oophagy apparently is common in the large northern colubrid *Stegonotus cucullatus* (McDowell 1972 found squamate eggs in 6 of 18 stomachs with identifiable food; the rest contained lizards, mice, frogs and orthopterans). Occasional oophagy has been recorded in several other Australian elapids. These include small species such as *Cacophis harrietae* (N = 4 eggs), *C. squamulosus* (N = 9) (Shine 1980a), *Demansia olivacea* (N = 1), *D. psammophis* (N = 2) (Shine 1980c), and *Drysdalia coronoides* (N = 6) (Shine 1981a). Eggs have also been found in the stomachs of large species: *Austrelaps superbus* (N = 2), *Pseudechis porphyriacus* (N = 3) and *Pseudonaja textilis* (N = 8) (Shine 1977c). However, eggs form only a small part of the diet in all of these species.

In contrast, squamate eggs were the only food recorded in stomachs of *Simoselaps roperi* (N =

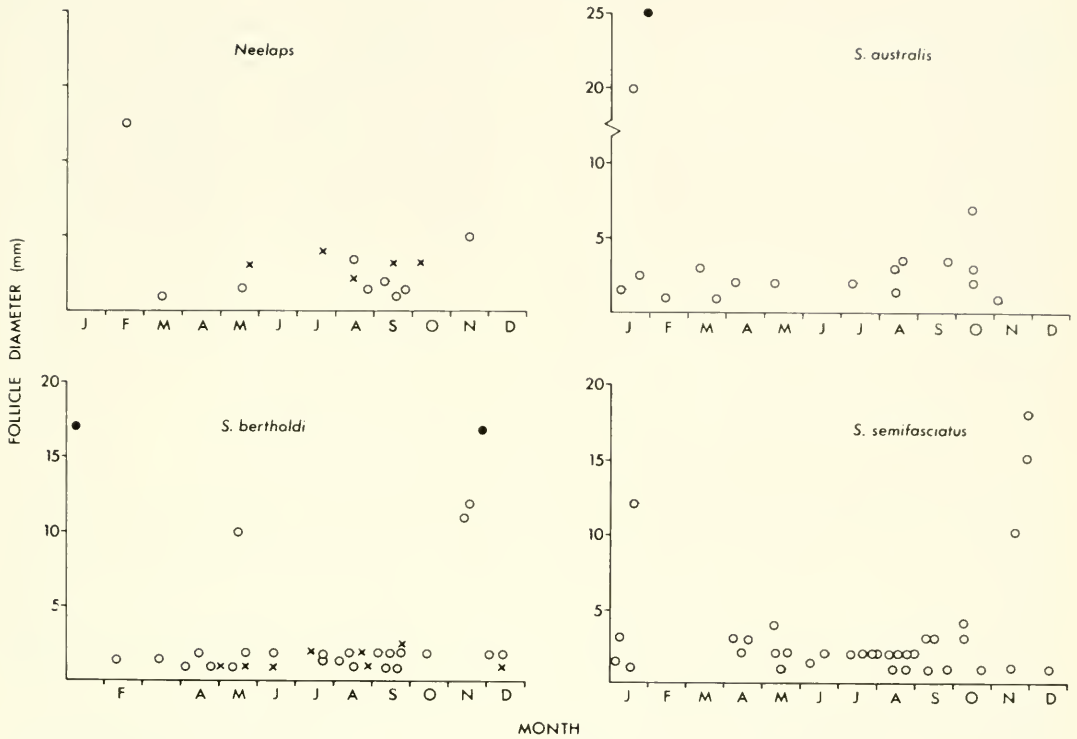


FIG. 4. Monthly variation in diameter of the largest ovarian follicle in mature female *Neelaps* and *Simoselaps*: in *Neelaps* graph, circles show *N. bimaculatus*, crosses show *N. calonotus*; in *S. bertholdi* graph, circles show *S. bertholdi*, crosses show *S. littoralis*. In all graphs, dots show oviducal eggs.

3) and *S. semifasciatus* (N = 27), were common in *S. australis* (3 of 4 food items) and present in *S. fasciolatus* (1 of 4 food items). The lack of recognizable embryos in all these eggs suggests that the oophagous *Simoselaps* raid nests soon after oviposition. Moll and Legler (1971) found that most predation on turtle nests occurred at this time, probably because predators can locate the nest more easily. Observations by Blair (1960) suggest that the snake *Salvadora lineata* preys chiefly upon squamate eggs from freshly-laid nests. However, some oophagous snakes take eggs at all stages of embryonic development (e.g., *Prosymna*—Broadley 1979; *Oligodon*—Wall 1921).

Snakes that feed primarily on squamate eggs may show morphological adaptations to this diet. A clear correlate of oophagy within *Neelaps* and *Simoselaps* is the shape of the rostral scale. The "shovel-nosed" species (i.e., those with an upturned angular edge to the rostral) are egg-eaters (*S.* "semifasciatus group," *S. australis*), whereas the snakes lacking this feature (*Neelaps* and other

Simoselaps) are saurophagous. A survey of published literature reveals the same general correlation among snakes in general, but there are many exceptions. Reptile eggs are an important dietary component of several "shovel-nosed" species (e.g., *Prosymna*—Broadley 1979; *Phyllorhynchus*—Klauber 1940; *Salvadora*—Blair 1960; *Oligodon*—Wall 1921), and an occasional component in others (e.g., *Rhinocheilus lecontei tessellatus*—Shaw and Campbell 1974; *Aspidelaps*—Branch 1979; *Heterodon*—Shaw and Campbell 1974). However, some "shovel-nosed" species do not feed on reptile eggs: *Lytorhynchus* is saurophagous (Minton 1966) and the extensive array of North American desert colubrids with upturned rostrals (e.g., *Chionactis*, *Chilomeniscus*, *ricimia*, *Gyalopion*) feed only on invertebrates (e.g., Shaw and Campbell 1974). Similarly, the upturned rostral is lacking from at least two snake species that feed mainly on squamate eggs (*Cemophora coccinea*—Palmer and Tregembo 1970; *Elapsoidea sundevalli*—Branch

TABLE 3. Fecundity of *Neelaps* and *Simoselaps* species: Table gives values to solve the equation $y = ax + b$ where $y =$ clutch size and $x = \text{♀ SVL (cm)}$. Regression fit by least squares.

Species	N	a	b	r^2	\bar{x} SVL ♀♀ (cm)	Clutch size	
						\bar{y} (SE)	Range
<i>N. bimaculatus</i>	10	.24	-3.60	.47	32.6	4.2 (.5)	2-6
<i>N. calonotus</i>	13	.10	1.17	.03	22.6	3.5 (.2)	2-5
<i>S. anomala</i>	2	—	—	—	17.1	2.5	2-3
<i>S. approximans</i>	2	—	—	—	29.1	3.0	2-4
<i>S. australis</i>	4	—	—	—	32.6	5.3 (.5)	4-6
<i>S. bertholdi</i>	11	.70	-11.56	.76	21.5	3.5 (.7)	1-8
<i>S. fasciolatus</i>	3	—	—	—	29.7	5.0 (0)	5
<i>S. littoralis</i>	2	—	—	—	21.9	3.5	3-4
<i>S. roperi</i>	2	—	—	—	26.2	3.0	2-4
<i>S. semifasciatus</i>	11	.00	3.00	.00	27.4	3.1 (.3)	2-5
<i>S. warro</i>	1	—	—	—	25.6	5	5

1979). These data suggest that (i) the upturned rostral has not evolved only for oophagy, but for burrowing in general; and (ii) specialized oophagy is possible without modification of the rostral.

Several snake species that feed on squamate eggs show adaptations of the dentition—the development of enlarged flat blade-like teeth which function to slit the egg-shell as it is swallowed. Such structures occur at the rear of the maxillary in the oophagous *Stegonotus* (McDowell 1972), *Prosymna* (Broadley 1979), *Oligodon* (Wall 1921) and *Cemophora* (Palmer and Tregembo 1970). Examination of *Simoselaps* shows a similar structure in *S. semifasciatus* (the egg-eater) but not in *S. bertholdi* (the lizard-eater). The posterior part of the maxilla in *S. semifasciatus* bears a single large tooth, triangular in lateral view but recurved at the tip. In *S. bertholdi*, the rear of the maxilla bears two smaller teeth, similar in shape to the rest of the dentition. These observations suggest that typical oophagous dentition has evolved within the genus *Simoselaps*. The development of enlarged blade-like teeth on the rear of the maxilla is an excellent example of convergent evolution in oophagous snakes.

How might the ecology of *Simoselaps* species be affected by the observed dichotomy in diets (saurophagy versus oophagy)? One might expect that the oophagous snakes could feed only during a limited time of year (when recently-oviposited eggs are available) whereas saurophagous snakes potentially have food available all year. If feeding was restricted to a short period, this could also affect the activity period of the snakes (which should be reflected in the numbers of specimens

collected at different times of the year). Data in Fig. 5 do not support these predictions. The most common saurophage (*S. bertholdi*) and oophage (*S. semifasciatus*) show similar seasonal patterns of feeding and "collectability." Both species feed most often in summer, less often in spring and autumn, and not at all in winter. The monthly range over which feeding was recorded was only slightly greater in *S. bertholdi* (Aug.–May) than in *S. semifasciatus* (Nov.–Mar.). Neither were the seasonal distributions of captures of the two species significantly different from each other or from a random assortment (see RESULTS).

Reproduction.—The only published reference to reproduction in these two genera is McPhee's (1979) note that *Simoselaps semifasciatus* probably is an egg-layer. My study confirms oviparity as the common, possibly exclusive, mode of reproduction in these snakes.

The seasonal timing of the female reproductive cycle in *Neelaps* and *Simoselaps* (Fig. 4) consists of vitellogenesis in spring and ovulation in summer. This pattern is the same as that found in all other temperate-zone Australian elapids studied to date (Shine 1977b, 1980a, 1980b, 1980c, 1981a, 1981b).

Neelaps and *Simoselaps* produce very small clutches, usually only three to five eggs. This low fecundity seems to be a function of the small adult size of these snakes, because (i) large species within these genera have the largest clutches (Fig. 2), and (ii) fecundity is much higher in most other (larger) Australian elapids (Shine 1977b, 1980a, 1980b, 1980c, 1981a, 1981b). The trend for larger species to produce larger offspring (Fig. 2) also

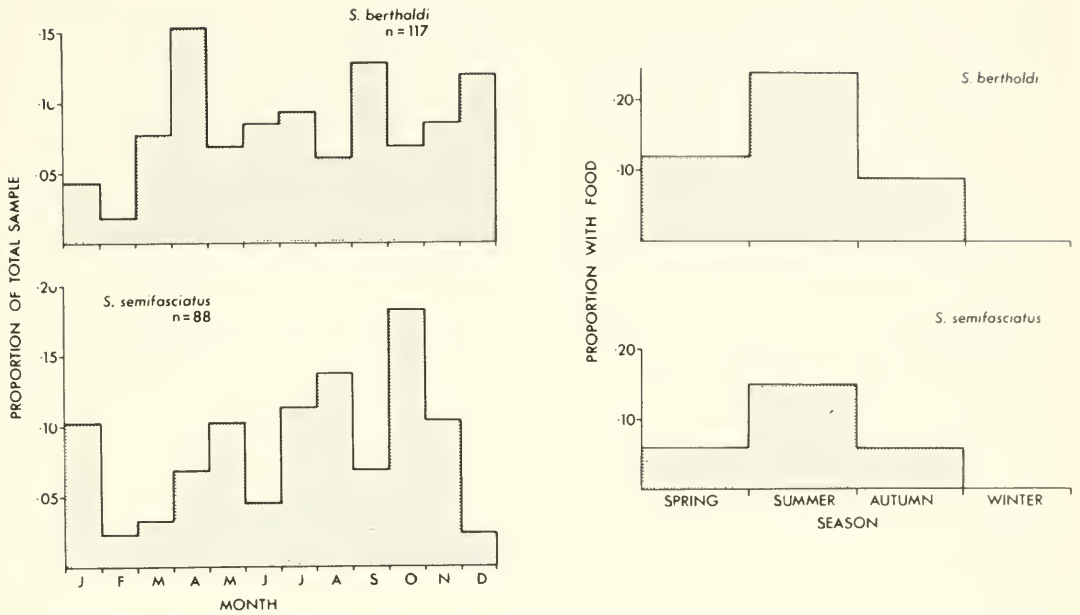


FIG. 5. Seasonal variation in numbers of snakes collected, and the proportion of these snakes containing food items, in *Simoselaps bertholdi* and *S. semifasciatus*.

is consistent with other studies on elapids (Shine 1978a).

The inferred age at sexual maturity (20 mo. to 32 mo.) in *S. bertholdi* and *S. semifasciatus* is lower than in many other snake species studied, but is similar to estimates for other small elapids (Shine 1978a, 1980a, 1981a, 1981b). Comparable data are lacking for arid-zone burrowing snakes of other continents (e.g., *Prosymna*, *Chionactis*): such a comparison would be instructive.

Overview.—The small burrowing snakes of the genera *Neelaps* and *Simoselaps* have undergone an impressive adaptive radiation in the desert and semi-desert zones of Australia. These snakes are strikingly convergent with many species in other continents, in morphology (general shape, colour, dentition, shape of the rostral scale), behaviour (nocturnal and fossorial habit) and diet (saurophagy and oophagy). Nonetheless, the differences between the Australian species and those of other continents are often substantial. For example, the North American desert colubrids that superficially resemble *Simoselaps* (e.g., *Chionactis*, *Chilomeniscus*, *Ficimia*, *Gyalopion*) in fact feed on entirely different prey types (invertebrates). The African genus *Prosymna* and the

Asian *Oligodon* are entirely oophagous (Wall 1921; Broadley 1979), whereas only a single species-group within *Simoselaps* specializes on squamate eggs as a food resource. Indeed, perhaps the most noteworthy aspect of the present study is the documentation of this clear dichotomy in food habits within *Simoselaps*. As the snakes of this genus have become specialized to predation upon different life-history stages of lizards (eggs versus adults), so they have evolved two distinct lines of adaptive radiation. Rostral scalation and maxillary dentition have changed in concert with feeding behaviour, so that two lineages clearly may be distinguished within this superficially homogeneous group of small desert snakes.

SUMMARY

Small brightly-coloured snakes of the genera *Neelaps* and *Simoselaps* have radiated widely in the arid and semi-arid zones of Australia. Dissections of 953 museum specimens yielded data on food habits, body sizes, sexual size dimorphism, mode of reproduction, seasonal schedules of reproduction, clutch sizes and inferred growth rates. A clear dichotomy in food habits is ap-

parent: scincid and pygopodid lizards are the only prey taken by *Neelaps* species and by the *Simoselaps bertholdi* species-group, whereas the *Simoselaps semifasciatus* species-group feeds exclusively on squamate eggs. Oophagy is common also in *S. australis*, and recorded in *S. fasciolatus*. Oophagous species show adaptations of scalation (upturned edges of the rostral for burrowing) and dentition (flat blade-like posterior maxillary teeth for slitting egg-shells). Feeding occurs only in the warmer months of the year, in saurophagous as well as oophagous species.

At least five of the thirteen species studied are oviparous. In mature females, vitellogenesis commences in spring, with ovulation in summer. Fecundity is low (mean clutch sizes 2.5 to 5.3), and is correlated with mean adult body size in an interspecific comparison. Body size at hatching also increases with mean adult body size. Females attain larger body sizes than males, and mature at larger sizes. Analysis of body-size distributions suggests that sexual maturity is attained at 20 to 32 months of age.

ACKNOWLEDGMENTS

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Scaphiodontophis (Serpentes: Colubridae): Natural History and Test of a Mimicry-Related Hypothesis

ROBERT W. HENDERSON

Snakes of the sibynophiine colubrid genus *Scaphiodontophis* Taylor and Smith are relatively rare in collections and are something of a curiosity since they possess two enigmatic characteristics: all taxa have extremely long tails and exhibit a high incidence of tail injuries; and one of two basic color patterns exhibited by members of the genus has coral snake-like banding restricted to the anterior portion of the body. In addition, they have peculiar hinged, shovel-like teeth (Savitzky 1981).

The purposes of this paper are first to summarize what is known about the natural history of *Scaphiodontophis* and, second, to test a hypothesis related to coral snake mimicry.

Note.—*Scaphiodontophis* taxonomy has long been in a chaotic state. However, an unpublished dissertation by Morgan (1973) dealing with the entire colubrid subfamily Sibynophiinae has clarified the situation. Morgan recognized two monotypic species of *Scaphiodontophis*: *S. annulatus* (including *S. carpincinctus* and *S. zeteki* listed by Peters and Orejas-Miranda [1970]) and *S. venustissimus*. I follow Morgan's (1973) classification in this paper.

NATURAL HISTORY

Habitat.—*Scaphiodontophis* ranges from southern Tamaulipas, México to northern Colombia. *S. annulatus* is primarily a rainforest inhabitant (Alvarez del Toro 1960; Duellman 1965; Martin 1955; Neill and Allen 1959; Stuart 1935, 1958; Wilson and Meyer 1982). It has also been taken in dense scrub forest (Duellman 1965), pine savanna and parkland (Henderson and Hoevers 1975), coffee groves (Slevin 1939; Taylor and Smith 1943), banana plantations (Roze 1969) and citrus groves (McCoy 1970). It is a leaf litter species (Alvarez del Toro 1960; Henderson and Hoevers 1975; McCoy 1970; Slevin 1939; Taylor and Smith 1943; J. Wright, *in litt.*) and may also be subterrestrial (Neill and Allen 1959). *Scaphiodontophis venustissimus* is found in wet lowlands (Scott 1969), occurs in leaf litter (Taylor 1954) and is also "fossorial" (Scott 1969).

Food and Feeding Behavior.—Both species of *Scaphiodontophis* are stenophagous, apparently feeding almost exclusively on scincid lizards of the genus *Sphenomorphus* in nature (Alvarez del Toro 1960; Landy *et al.* 1966; Scott 1969; Stuart 1948; Taylor and Smith 1943; pers. observ.), but also taking *Gymnophthalmus* (Teiidae) and *Eumeces* (Scincidae) (Alvarez del Toro, *in litt.*).

I observed a captive *S. venustissimus* prowling on the leaf litter-covered floor of its cage during the day. It fed readily on *Anolis* and on at least one occasion captured the anole from below while the snake was under the leaf litter and the anole was on top of the litter. The captive *S. venustissimus* constricted an anole on one occasion and Alvarez del Toro (1960) observed constriction of larger prey by *S. annulatus* from Chiapas, México. Subduing prey by constriction is probably uncommon in *Scaphiodontophis* and prey is usually swallowed alive and with incredible speed (Alvarez del Toro 1960; R. W. Van Devender, *in litt.*; pers. observ.). I recorded amount of time necessary for prey (*Scincella lateralis*) ingestion by a 41.0 cm SVL *S. annulatus* with a stopwatch on eight occasions. The watch was started as soon as the snake grasped the lizard and it was stopped when the lizard's body (tails were removed immediately prior to feeding) was no longer visible. Mean time of ingestion for six lizards between 40–47 mm SVL was 7.73 ± 2.09 sec (2.8–16.9), but the four fastest times had a mean of 4.87 ± 0.91 sec (2.8–7.2). Two skinks 52 mm SVL took 5.2 sec and 20.5 sec for ingestion. One 45 mm SVL skink which did not have its tail removed, was grabbed by the tip of the tail. The snake worked its way to the lizard's snout and then swallowed it head first; the entire episode took 10.0 sec. All lizards were swallowed head first.

Defensive Behavior.—The only display observed in *Scaphiodontophis* has been tail and body thrashing. J. W. Wright (*in litt.*) observed it in *S. annulatus* in the field in northern Guatemala. An *S. annulatus* "was found in a fallen bush that was overgrown with herbs and grasses along with a considerable amount of leaf litter. My attention



FIG. 1. *Scaphiodontophis venustissimus* from Limon, Costa Rica. (Photo by R. W. Van Devender.)

was called to the snake because of the noise it was making. I heard the thrashing right up to the point of close inspection. . . . The banded portion of the snake was elevated for at least a third of the length of the body and was visible above the bush. The head and neck remained motionless. The posterior more unicolor part of the snake was undulated and thrashing in the bush. The thrashing was not like the tail fluttering (=rattling) of some snakes, as much of the body moved as well." Likewise, I have observed that *S. annulatus* is always inoffensive and never offers to bite, but it does have a peculiar response to tactile stimuli: the body is vigorously twitched and both ends of the body are thrashed about. It never failed to startle me! R. W. Van Devender (*in litt.*) has observed similar behavior in *S. venustissimus*. This may be comparable to the tail thrashing in *Clelia clelia* described by Greene (1973).

Reproduction.—Alvarez del Toro and Smith (1958) reported a clutch of four *S. annulatus* eggs laid on 16 June and hatched on 15 August 1956 in Chiapas, México. W. F. Pyburn (*in litt.*) collected three *S. annulatus* eggs from beneath a

rotting log in Veracruz, México on 3 August 1964. One egg was opened on 14 September and it contained a living male snake of 11.4 cm SVL; a second egg was opened on 9 October and it contained a living snake 11.5 cm SVL. The third egg hatched on 12 October and the snake was 16.7 cm SVL and 4.5 g. The number of anterior bands in the "hatchlings" was variable (2 with 2 bands, 1 with 4 bands). A specimen of *S. venustissimus* from Limon Prov., Costa Rica had a clutch of three eggs; the gravid snake was 43.5 cm SVL (Carl S. Lieb, *in litt.*).

TEST OF A CORAL SNAKE MIMICRY-RELATED HYPOTHESIS

Smith (1975, 1977) found that wooden dowels painted from end to end with coral snake colors and pattern and presented to naive, laboratory reared individuals of two species of neotropical reptile-eating birds (motmots and kiskadees) caused avoidance and alarm, and the birds would not peck at them. Dowels painted with coral snake colors but in stripes rather than rings, and those



FIG. 2. *Scaphiodontophis annulatus* from Honduras. (Photo by L. W. Porras.)

painted in rings but not with coral snake colors, did not cause alarm and were attacked by the birds with little or no hesitation. Likewise, when only the end-third of a dowel was painted with coral snake colors and pattern, the birds attacked the dowel but directed their pecks at the unpainted end. Other end-third models, in color and pattern combinations as for the solid models, had pecks directed mostly or entirely at the painted ends.

The *S. venustissimus* (Fig. 1) pattern has black bands bordered by yellow bands and red interspaces; this pattern typically covers the entire length of the body and the tail. The venter is yellowish and marked with small dark spots. *S. venustissimus* almost invariably exhibits this pattern. In *S. annulatus* (Fig. 2) banding is frequently restricted to the anterior part of the body or to the entire body but not the tail. The pattern is of yellow-bordered black bands (range of 2 to 18 triads [Morgan 1973]) with red interspaces. Those portions of the body and/or tail which do not exhibit triads are of a drab grey or brown

ground color with 3 rows of dark spots, giving the impression of stripes. Again, the venter is unpatterned.

Scaphiodontophis has an extremely long tail. Mean tail length expressed as a percentage of SVL in male and female *S. annulatus* is 86.3 (78.0–96.2) and 69.1 (58.2–92.6), respectively; in *venustissimus* it is 67.3 (60.1–72.0) in males and 56.7 (52.3–60.2) in females (Morgan 1973).

Greene (1973) suggested that "the tail of any escaping animal generally trails the body, and thus would be more likely to be grasped by a pursuer than any other part." Assuming that tail damage is predator inflicted (see below) and since *S. annulatus* is a living example of Smith's (1975, 1977) "end-third" model and *S. venustissimus* a living example of her "solid ring" model, I hypothesized that if the coral snake color pattern does confer some selective advantage, then snakes with the *S. venustissimus* pattern should show a significantly lower incidence of tail injuries than snakes with the *annulatus* pattern.

Methods.—Forty-eight preserved specimens of

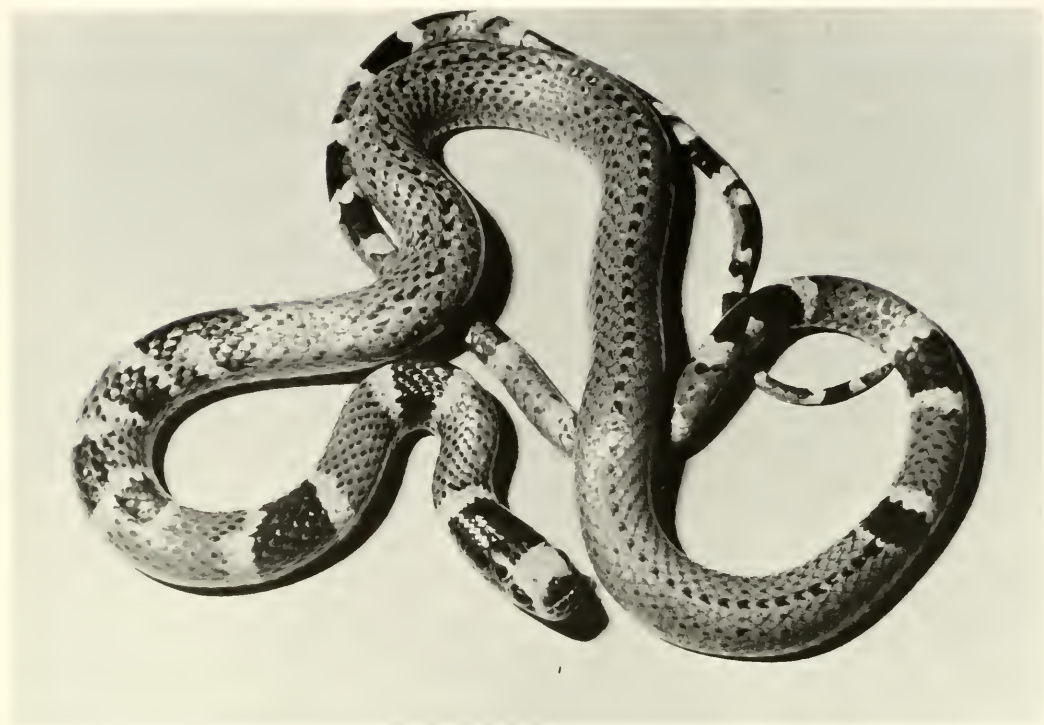


FIG. 3. *Scaphiodontophis venustissimus* from Palmar Sur, Puntarenas, Costa Rica. (Photo by R. W. Van Devender.)

Scaphiodontophis with an *S. annulatus* pattern, and 29 specimens with the *venustissimus* pattern, were examined for tail injuries. A few *S. annulatus* were banded the entire length of their body and tail. These specimens were regarded as having the *S. venustissimus*-type pattern. Two specimens I examined had a "dugandi" pattern (Roze 1969; Henderson 1983) in which the anterior portion of the body is banded, the posterior portion is not banded, but the tail is banded (Fig. 3). These specimens were discounted from the statistical treatment. An additional number of snakes was examined but disregarded because their tail injuries appeared recent (i.e., the posterior end of a caudal vertebra was exposed) and therefore may have been collector-inflicted. Also, some juveniles known to have been hatched in captivity were also discounted. A dissecting microscope was used to examine tails in which damage was not obvious, but with which the possibility existed that a minor injury may have occurred.

Results.—Twenty-seven of 48 (56.3%) snakes with the *S. annulatus* pattern had sustained tail

injuries while 15 of 29 (51.7%) with the *S. venustissimus* pattern had suffered tail injuries. Using a chi-square contingency table, the incidence of injured vs. uninjured tails in *S. annulatus*-patterned and *S. venustissimus*-patterned snakes was compared. Differences were found to be not significant ($P > .05$, $\chi^2 = 0.1494$, 1 d.f.).

DISCUSSION

Scaphiodontophis venustissimus resembles a coral snake, primarily *Micrurus nigrocinctus* (Dunn 1954; Hecht and Marien 1956; Savage and Vial 1974). *S. annulatus* is, however, enigmatic in that individuals frequently have banding restricted to the anterior portion of the body. Perhaps, as suggested by Echternacht (1973) mimicry may just be in a developmental stage "in some species of the *S. venustissimus* and *S. annulatus* groups. . . ." A. H. Savitzky (*in litt.*), however, suggests that "*Scaphiodontophis* shares a common ancestor with *Simophis*. If so, the mimetic pattern is probably primitive (and,

TABLE 1. Ratios of tail length to SVL and total length in snakes various adaptive zones as compared to male *Scaphiodontophis annulatus*.

	Genera species**	Tail length/SVL**	Genera species***	Tail length/total length***
<i>S. annulatus</i> *	1/1	\bar{x} = .863 (.780-.962)	1/1	\bar{x} = .451 (.397-.537)
Terrestrial	9/13	\bar{x} = .269 (.119-.398)	13/22	\bar{x} = .223 (.118-.538)
Arboreal/terrestrial	2/5	\bar{x} = .491 (.342-.548)	3/6	\bar{x} = .332 (.238-.378)
Arboreal	5/8	\bar{x} = .467 (.305-.656)	6/10	\bar{x} = .345 (.243-.429)
<i>Micrurus</i>	1/2	\bar{x} = .079 (.053-.106)	1/7	\bar{x} = .102 (.062-.160)

* Data from Morgan (1973).

** Data, exclusive of *Scaphiodontophis*, from Duellman (1979).

*** Data, exclusive of *Scaphiodontophis*, from Dixon and Soini (1977).

therefore, is being lost in the partially banded morphs of *Scaphiodontophis*." It is also possible that, although derived, the *S. annulatus* pattern is a response to strong selective pressures—an adaptation to a specific problem. Morgan (1973) considered *S. annulatus* primitive to *S. venustissimus*, primarily on the basis of geographic distribution.

Tail length in *Scaphiodontophis* is extreme. Using data presented by Duellman (1979) for male snakes at Santa Cecilia, Ecuador, in which he provided the maximum size (SVL and tail length) for each species, I found no species to have a tail length/SVL ratio comparable to *Scaphiodontophis* (Table 1). Likewise, Dixon and Soini (1977), in a study of Iquitos, Perú region snakes, presented tail/LOA (=total length) ratios for most species (including some of the same species as Duellman 1979) (Table 1). Interestingly, only one species, *Dendrophidion dendrophis*, has a higher tail/LOA ratio than *S. annulatus*. According to Duellman (1979), *D. dendrophis* is diurnal, terrestrial and exhibits an extremely high incidence of broken tails.

Little has been published on the incidence of tail breaks in tropical snakes. Zug *et al.* (1979) reported frequency of tail injuries in three neotropical species. *Coniophanes fissidens* (diurnal, leaf litter dweller) has "a high frequency of broken tails" (about 30% of their sample) and it appeared that "females and males (were) usually subjected to equal predation pressure." *Dipsas catesbyi*, a nocturnal, arboreal species had fewer than 1% of the sample with broken tails. Another

nocturnal, arboreal species, *Imantodes cenchoa*, showed 6% incidence of tail breaks in mature females and a 10% incidence in mature males. Myers (1967) found that 29.4% of 192 *Rhadinaea flavilata* had incomplete tails. *R. flavilata* is a small, nocturnal (?), terrestrial species. Myers (1974) also found that an even higher percentage of stub tails occurred in long-tailed species of the *R. lateristriga* group of *Rhadinaea*. He found that few specimens of the long-tailed, diurnal *R. decipiens* "have complete tails when collected" and he suggested it may be due to conflicts with predators. Looking at tail injuries in four snake species that perform tail displays and one that does not, Greene (1973) found incidences of tail injuries ranging from 0–51.9% in species with tail displays, and no injuries in the species lacking a caudal display. Gehlbach (1972) found that the incidence of tail injuries in coral snakes and unrelated taxa of various color patterns and behaviors depended on whether or not they performed tail displays. Incidence of injuries in the various groups ranged from 3.8% in coral snakes (*Micrurus fulvius* and *Micruroides euryxanthus*) to 7.8% in potential coral snake color mimics lacking defensive tail displays. Vitt and Hulse (1973) found a 14.3% incidence of tail scars on a small sample of *Micruroides euryxanthus*. The high, but unspecified, incidence of tail breaks noted by Duellman (1979) in *Dendrophidion dendrophis* has already been mentioned. Two species of Hispaniolan tree snakes (*Uromacer*) had tail injuries at an incidence of 10–11% (Henderson *et al.* 1981).

Do these data suggest that long-tailed snakes are more susceptible to predation? Possibly, but alternatively it suggests that such species are more successful at escaping conflicts with predators than are short-tailed species (i.e., snakes with shorter tails exhibit fewer tail injuries because fewer escaped with only a broken tail—most were killed by the predator). Arboreal snakes with prehensile tails (such as *Dipsas catesbyi* and *Imantodes cenchoa*) may show a low incidence of tail breaks because the tail is usually wrapped around a branch making it more difficult for a predator to grab. Also, prehensile tails may be mechanically less susceptible to breaking, and perhaps these snakes are more likely attacked in the head region; injuries thus become more serious and escape less likely. Being nocturnal may also decrease the incidence of predation.

The frequency of broken or regenerated tails in lizards has been used as an indicator of predation intensity (e.g., Brooks 1967; Parker 1972; Parker and Pianka 1975; Schall and Pianka 1980; Vitt *et al.* 1977), although Schoener (1979) and Jaksic and Fuentes (1980) have suggested that tail break frequency might be a better indication of predator efficiency. Pianka (1970) found that there was a positive correlation between tail breaks in *Cnemidophorus tigris* and number of potential predators in northern to southern samples. Some size class samples show tail breakage incidence at 100% (e.g., Clark [1971] for *Scincella lateralis*). Taylor and Smith (1943) attributed the high incidence of stub tails in *Scaphiodontophis* to disease, but Taylor later (1954) reported that *S. venustissimus* apparently breaks its tail deliberately when restrained by it. On three occasions he grabbed a snake by the tail and three times the tail broke. He experienced the same result when attempting to catch another *S. venustissimus*; the tail broke off in his hand and the snake escaped. I have observed no indication of tail disease in preserved specimens of *Scaphiodontophis* and therefore attribute the high incidence of caudal damage to encounters with predators. I believe that the extremely long tail and the ability to autotomize the tail are anti-predator adaptations.

Tail autotomy allows the attacked snake an opportunity to escape a potential predator. Since there is no tail regeneration in snakes (but see Sharma 1980), any portion of the tail lost is gone forever. To compensate for this, *Scaphiodontophis*, and possibly other snake species (e.g., *Den-*

drophidion dendrophis and *Rhadinaea decipiens*), have evolved a tail long enough to sustain several predator-inflicted breaks. If a predator were to grab a *Scaphiodontophis* near the base of the tail, that may be the only attack the tail (and the snake) could sustain. Liner (1960) found that the tail of a *Pliocercus elapoides* "was given off like that of a lizard" when he tried to pick it up caudally. Wilson (1968) examined caudal vertebrae in *P. elapoides* and described a fracture plane on the expanded transverse processes. He also found very shallow grooving on the transverse processes of "a few caudal vertebrae" from a single specimen of *S. zeteki nothus* (= *S. annulatus*). (Morgan [1973], however, found no evidence of a fracture plane in the caudal vertebrae of *Scaphiodontophis*, and found that tail breaks had always occurred between successive vertebrae.) In Wilson's opinion "this grooving of the transverse processes of the caudal vertebrae of *Pliocercus* and perhaps *Scaphiodontophis* is a point of sufficient weakness that allows the vertebrae to break when the snake is seized by the tail. The selective advantage of this adaptation seems obvious. As in lizards, the essential portion to the animal survives while the tail remains behind to occupy a predator."

Although the results of the chi-square test do not support my hypothesis (i.e., *Scaphiodontophis* with the *venustissimus* pattern do not have an obvious selective advantage over those with the *S. annulatus* pattern), other interpretations of the data are feasible. If predation pressure on leaf litter rainforest snakes is high, as the incidence of incomplete tails in *Scaphiodontophis* suggests, then each of the two color patterns, in conjunction with the easily broken tail, may have selective value. (One does not have to have an advantage over the other.) For *S. venustissimus* it is obvious: it mimics a venomous coral snake in color and pattern. Coral snakes and their look-alikes are preyed upon by birds (Howell 1957; Pough 1964; Skutch 1971; Smith 1969) and mammals (Jackson 1979) despite having aposomatic patterns. Since these snakes are going to be preyed upon despite their aposomatic colors and pattern, a tail which can be easily autotomized can only be advantageous.

Alternately, *Scaphiodontophis annulatus* is essentially bi-patterned, whereas *S. venustissimus* is uni-patterned. Since *S. annulatus* is bi-patterned, a predator has the option of choosing which pattern to attack: a dull-colored, striped



FIG. 4. *Scaphiodontophis annulatus* (41.0 cm SVL) from Honduras in a typical diurnal posture. (Photo by R. W. Henderson.)

pattern, or a brightly colored banded pattern. I suggest that the predator would more often attack the dull, striped pattern and Smith's (1975, 1977) experiments support this: naive birds would attack a dowel if the coral snake pattern was restricted to only one end of it. A predator does not have to make a choice with a uni-patterned snake and it may just as likely grab the snake at mid-body or at the head as at the tail (although I suspect the caudal region is more frequently grabbed than more anterior regions). Thus, *S. venustissimus* exhibits a high incidence of tail injuries because it has an autotomizeable tail and is able to escape conflicts with would-be predators. In addition, the coral snake pattern, even without benefit of a tail display (Gehlbach 1972) may inhibit and confuse a predator and cause it to go for the tail. *S. annulatus* exhibits a high incidence of tail injuries because a predator must make a choice between attacking two patterns and most likely will go for the dull posterior pattern which ends with a tail that is easily autotomizeable. Other leaf litter snakes may be exposed to similar predation pressure as *Scaphio-*

dontophis, but because they lack tail autotomy, they are killed by the predator, rather than being able to escape minus only a portion of their tail.

In conclusion, I offer three possible functions of observed behavior, incidence of tail damage and color pattern in *Scaphiodontophis*:

1) *Scaphiodontophis* (*annulatus* and *venustissimus*) exhibit a high incidence of broken tails because they are adapted to autotomy and are exceptionally long in order to sustain several breaks. Color pattern in both species is potentially confusing and/or inhibitive to potential predators.

2) An alternative interpretation of pattern function in *Scaphiodontophis* is based on the antipredator strategies of flight and defense, and on the phenomenon of flicker fusion (Jackson *et al.* 1976). Brattstrom (1955) suggested that the coral snake pattern conceals the bearer by a disruptive effect when it is immobile and, when fleeing, the banded pattern prohibits the predator from shifting focus rapidly forward to maintain the snake in its field of vision and the snake may therefore escape. Jackson *et al.* (1976) concurred with

Brattstrom (1955) that a regularly banded pattern "may represent a compromise between the strategies of disruptive concealment and generation of a deflective illusion during flight." *Scaphiodontophis annulatus* bears a pattern that can be regularly or irregularly banded anteriorly and is essentially striped posteriorly. According to Jackson *et al.* (1976), a striped pattern is associated more with flight than defense, and they came to the conclusion that "The aposematic-mimetic functions might be most useful with predators, like birds, that can perceive color . . . , while the disruptive-deflective effect might be of greatest value against color-insensitive mammalian predators. . . ."

Observations of captive *S. annulatus*, even in relatively small enclosures where there is not opportunity for prolonged movement, have illustrated to me the confusing effect of the pattern. Even with *a priori* knowledge of the appearance of *S. annulatus*, it takes several seconds to determine where the head is and whether the snake is coming or going. In addition, I have observed captive *S. annulatus* on numerous occasions with only the banded part of the body exposed and the rest of it under a cover object (Fig. 4). I believe, like Jackson *et al.* (1976) and as stated by Pough (1976), that ". . . a pattern of brightly colored crossbands can be both cryptic and conspicuous depending on the light conditions, the visual capacity of the predator involved, and the behavior of the snake."

3) Finally, Wright's field observations of *S. annulatus*, along with its unusual color pattern, suggests a function of tail thrashing apart from defense. *Sphenomorphus cherriei* is apparently the primary prey species of *Scaphiodontophis*, and it would not be surprising that such extreme stenophagy would give rise to anatomical and possibly behavioral characteristics adapted to *Sphenomorphus* predation. Savitzky (1981) has noted a number of anatomical peculiarities in *Scaphiodontophis* which apparently are adaptations for swallowing hard-bodied prey (i.e., scincid lizards). *Sphenomorphus cherriei* is, like *Scaphiodontophis*, a rainforest, leaf litter inhabitant (Fitch 1973; Stuart 1958; pers. observ.) and much of its activity occurs beneath the leaf litter (Fitch 1973). Fitch (1973) noted that a collector could flush *Sphenomorphus* by "trampling" through the litter. Could Wright (*in litt.*) have been watching a *Scaphiodontophis* trying to flush prey

by thrashing its tail through the leaf litter? Although the moving tail could attract the attention of potential predators (as it did Wright), the long autotomizeable tail, which would be the part of the snake most likely attacked, is adapted to sustain such attacks. The motionless, coral snake-patterned head would attract less attention and is mimetically colored.

SUMMARY

Snakes of the sibynophiine colubrid genus *Scaphiodontophis* have remarkably long tails (up to 96% of SVL in males) and they exhibit a high incidence (>50%) of broken tails. *Scaphiodontophis venustissimus* has coral snake-like colors and pattern the entire length of the body and tail, but *S. annulatus* usually has the coral snake colors and pattern restricted to the anterior one-half (or less) of the body. Preserved *S. venustissimus* exhibit fewer tail injuries, but not significantly so, than *S. annulatus*. Assuming that the tail injuries are predator inflicted, the incidence of injuries in the two species suggests that the coral snake pattern and colors confer no selective advantage to *S. venustissimus* over *S. annulatus*. I conclude that the patterns of both snakes are confusing and inhibitory to potential predators: in *venustissimus* because it is a coral snake mimic, and in *annulatus* because it is bi-patterned and a predator must choose which pattern to attack (most likely the non-coral snake-like posterior). The tails of both species are autotomizeable and potentially able to sustain several breaks. Another potential function of the color and pattern of *Scaphiodontophis* is as an anti-predator strategy of flight and defense. Finally, the long tail, at least in *S. annulatus*, may be useful in flushing scincid lizard prey from leaf litter substrate.

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Dominance in Snakes

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Dominance behavior has been suggested by a number of observers as an explanation for a function of combat rituals in snakes. Other reported types of behavioral actions which by their nature could be interpreted as relating to dominance are: territoriality, rivalry or competition, winning and defeat, submission, pursuit and chase, flight or avoidance, strength and weakness and physically overcome. It is not my aim to review all of the literature using these terms, but significant references will be cited below.

Confusion or uncertainty arises from the lack of criteria for measuring or determining dominance in snakes, and what the functions of dominance might be. Recent definitions of dominance infer this behavior should indicate priority for resources such as food, a mate, a territory (Wilson 1975; Brown 1975). Good evidence for priority use of a resource in snakes is scarce or wanting.

The criteria or behaviors used by observers to judge dominance vary with the group being observed; what may be used for lizards, birds or mammals, may not apply for snakes. The operational definition I shall use for dominance behavior in snakes is as follows: Dominance is an interaction between two snakes in which one individual performs certain actions (physical or otherwise) which ultimately causes the other individual to avoid these actions (subordinate).

Interactions between snakes are difficult to observe in the field, although the potential is there for certain species patiently observed. In captive snakes the evidence for social dominance is more direct and easily observed.

Social behaviors are known to occur for snakes during the interactions of courtship and mating, combat rituals, and possibly, parental care and could be associated with different types of aggregations such as feeding, communal nesting, denning and other hibernation groupings, and cover concentrations. The spacing of adults of certain species and their tendency to have limited activity or home ranges (Seibert and Hagen 1947; Stickel and Cope 1947; Fitch 1949; Carpenter 1952; Barbour *et al.* 1969) suggests that snakes

may interact in the field. But while these studies show limited movement of certain species of snakes, few indicate interactions in the field between individuals. Kennedy (1965) and Bennion and Parker (1976) recorded interactions between male *Masticophis* and Andren (1975) and Volsoe (1944) have observed males showing aggression related to breeding sites in *Vipera berus*. Combat rituals are the most easily recognized agonistic interactions between male snakes (Carpenter and Ferguson 1977).

What must be involved in snake interactions which may result in the dominance of one individual? There must be species recognition between conspecifics. I believe the evidence is good that an individual snake recognizes its own species, especially after tongue contact—implicating the vomeronasal modality or channel for this recognition (Noble and Clausen 1936; Kubie *et al.* 1978; Devine 1976). Sex recognition must also occur and this appears to be rapid between conspecifics and accomplished by chemical cues (Noble 1937; Froese 1980), perhaps sometimes visually. Individual recognition or identification involves the ability of one member of a species to identify an individual conspecific. There is no satisfactory evidence that a snake distinguishes one conspecific individual from another, though I see no reason they could not accomplish this by detecting individual differences in chemical or visual cues. Individual recognition is considered important in establishing social hierarchies in groups of birds and mammals. The observations of Barker *et al.* (1979) strongly suggest that individual recognition occurred in the formation of a hierarchy in a captive group of four males and one female *Python molurus*.

Combat Rituals.—Over the past few years I have observed many interactions in captivity between conspecific male snakes. I believe I recognize dominance as a result of most of these interactions whether or not actual combat rituals occurred. Numerous descriptions of combat rituals are available from the literature (Carpenter and Ferguson 1977) and I will use aspects of those descriptions which relate to the establish-

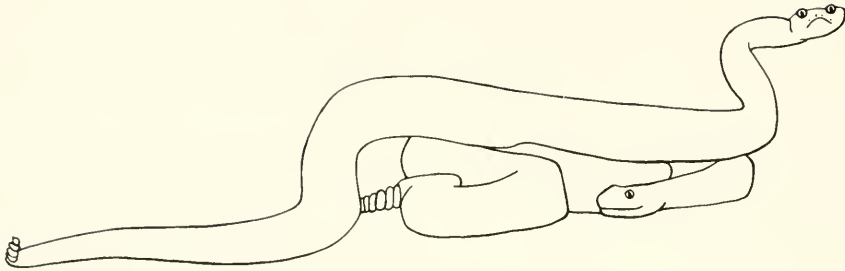


FIG. 1. Dominant male crawling over subordinate male in submissive posture. *Crotalus viridis*.

ing of physical superiority and those behaviors which indicate a dominant-subordinate relationship between two snakes.

During a combat ritual between two conspecific male snakes, one, or both individuals attempt to obtain a higher or superior position by assuming a posture with the head and anterior trunk higher in display than his adversary (*Crotalus*—Carpenter *et al.* 1976; *Sistrurus*—Carpenter 1979), or over that of his adversary (hovering) (*Lampropeltis*—Carpenter and Gillingham 1977; Murphy *et al.* 1978). The snake in the superior position then attempts to force his adversary down by quickly looping around him and pushing or throwing (topping) him down (*Crotalus*, *op. cit.*) or by lowering the hovering head and anterior trunk down on the anterior region of his adversary (*Lampropeltis*, *op. cit.*) forcing the lower snake down and pinning his anterior region to the substrate. These actions are obvious physical attempts by one individual to force another into a lower posture.

When one individual has been forced to a lower or prostrate posture (head and anterior trunk) the superior snake may then return to the solicitation display (Carpenter *et al.* 1976) of the combat ritual with the other again rising in response and repeating attempts at topping. Such actions may continue for an hour or more with numerous topping bouts. During these bouts it appears that the more aggressive snake keeps his posterior trunk region over some posterior part of the other snake.

Often after a combat ritual has been proceeding for sometime one individual attempts to crawl away from the contact with the other, sometimes becoming hyperactive and violently thrashing away. Following these attempts to move away, the superior snake (dominant) follows or pursues the fleeing snake (subordinate). In captive situ-

ations the area for flight is small so that the dominant can easily reestablish contact. The dominant may again perform the solicitation display before the subordinate with the latter sometimes rising in response. If the subordinate does not respond but takes a low posture, usually coiling against a wall of the chamber, the dominant then crawls over (Fig. 1) and may lie on the subordinate (Fig. 2). If the subordinate tries to flee or move away, the dominant will continue to crawl over or lie on top of him. If the subordinate raises his head, the dominant may respond by moving over his head region, as if forcing him to maintain his submissive (negative) posture (Fig. 3). Each time the subordinate shows activity, the dominant may crawl away, and when the subordinate again becomes active, the dominant will start to return at which time the subordinate will try to avoid the approach of the dominant by fleeing, only to be pursued by the dominant, the subordinate attempting to climb the sides of the chamber. When contact is again made, between the two males, the subordinate may again attempt to flee or again assume the submissive posture.

During many of my attempts to induce combat rituals in a variety of male snakes, no tendency to perform a ritual was exhibited, or only one individual might rise to a solicitation posture. In such instances, the non-responder, or one of the individuals, appears to act subordinate, assuming a submissive posture without overt physical contact, or may actively try to avoid the other which appears to be dominant. From these actions it appears that dominance may occur without contact between two males.

OBSERVATIONS OF DOMINANCE

The following brief summaries are from unpublished notes on complete videotapes of the

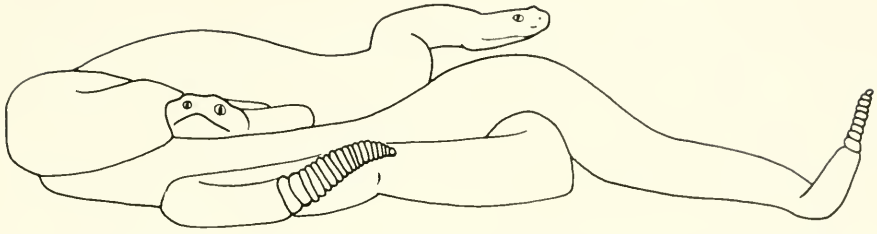


FIG. 2. Dominant male *Crotalus viridis* lying on subordinate male *Crotalus molossus*.

interactions of staged encounters between paired male snakes.

Lampropeltis getulus holbrooki.—After initial contact the larger male continued to follow the smaller male, crawling over him, hovering and pushing down on his anterior region. The smaller male tried to escape or avoid the larger male and at times assumed a submissive coil with his head flat, vibrating his tail when pinned by the larger male. The subordinate male burrowed completely beneath the sand.

Lampropeltis getulus holbrooki.—The larger of the two males on first contact immediately hovered over the smaller male which tried to avoid contact. The larger male persisted in crawling over, hovering and attempting to pin the smaller male which tried to flee. They separated and when the larger male returned and continued his dominance actions, the smaller male at times vibrated his tail rapidly. The smaller male finally burrowed under the sand and escaped.

A second, smaller, male, when introduced, was immediately approached rapidly by the larger male and crawled upon, the smaller male trying to flee to a corner where he backed up body loops against the sides of the chamber. After separating, the smaller male fled from approach of the larger male.

Lampropeltis calligaster.—A male *L. c. calligaster* placed with a slightly smaller female showed no courtship actions for a period of 12 min at which time a smaller male was added. Over the next 50 min the larger male continually pursued, bit and crawled over the smaller male, biting him four times and hovering over and pinning him six times before he was removed, but directed no actions towards the female. A slightly smaller male *L. c. rhombomaculata* was then introduced and within 35 sec the larger male had crawled over the smaller male with the smaller male crawling away pursued by the larger

male. The larger male hovered and pinned the smaller male within 2½ min and then persisted during the 35 min they were together, intermittently, in pursuing, crawling over, hovering and pinning the smaller male, until he was removed. Over this time the larger male bit the smaller male 11 times, some bites lasting over 30 sec. During these long bites, the smaller male was shaken vigorously. The larger male (dominant) exhibited no overt actions towards a second female added at this time. The smaller male (subordinate) remained active during the entire episode moving about the chamber, climbing the sides and pushing its rostrum against the glass front of the chamber.

Crotalus atrox.—After approximately 10 min of combat ritual, the more aggressive male performing solicitation displays appeared dominant when the other male ceased to display, tried to escape, was pursued, and then assumed a submissive coil with the dominant crawling over him.

Sistrurus miliarius.—The initiator made contact with the other male which jerked in response, then the initiator crawled over the other which assumed a loose coil with head down. They separated and as the initiator again made contact the other violently thrashed away pursued by the initiator. The initiator crawled over the fleeing male. The submissive male lay coiled and when contacted waved his tail vertically.

Sistrurus catenatus.—On contact one male immediately assumed a submissive coil, head down. As the superior male moved back and forth over the coiled male, the inferior male waved his tail. If the submissive male moved from his coil, he immediately assumed a submissive coil again when contacted by the now dominant male, the former tail waving. The dominant moved away and then back over the subordinate male several times.

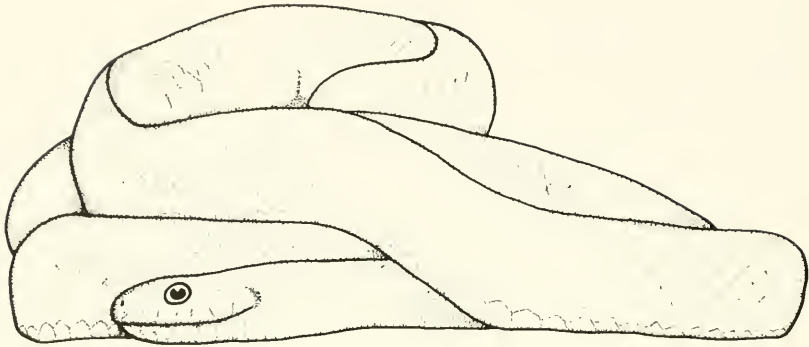


FIG. 3. Submissive (negative) posture of a male *Lampropeltis getulus holbrooki*.

Bothrops godmani.—On first approach, one snake bit the other. As the two males crawled over each other, one rose to a solicitation display. The biter's actions appeared dominant as he crawled over and lay on the other. The subordinate crawled off and was pursued by the dominant which displayed and kept himself higher than the subordinate. The dominant continued his display actions while crawling over the subordinate, with the subordinate finally thrashing violently to escape, only to be pursued and crawled upon by the dominant.

Vipera lebentina.—One male, after performing solicitation display persistently, crawled over and lay upon the other which assumed a coil (submissive posture) with its head down.

Crotalus triseriatus.—After nearly one hour of continuous combat ritual between two males (a female also present) with no apparent superior male, one bit the other, and a few seconds later the one bitten first bit and held onto the other for 3 to 4 sec. After this reciprocal biting episode, all displaying ceased and both males lay quiet with no further interaction.

Crotalus v. viridis.—One male initiated the combat ritual with solicitation displays, the other responded, but soon moved off, pursued by the initiating male. They again displayed intermittently and the initiator started to crawl over the other male, which tried to retreat (violently) and then assumed a submissive coil with the now dominant initiating male crawling back and forth over the subordinate.

Crotalus viridis.—The lighter male persistently followed and crawled over the darker male. When the darker male tried to move from contact he was pursued by the light male. The darker male

assumed a submissive coil in a corner with the lighter male crawling over him.

This light male (*C. viridis*) was then matched with a larger male *Crotalus molossus*. The *C. viridis* immediately crawled over the *C. molossus* which coiled with its head down and waved its tail (no rattling). The *C. viridis* stayed on top of the *C. molossus*, crawling back and forth and at times rising to display. The *C. molossus* tried to crawl away but the *C. viridis* stayed on top of him and persisted in crawling back and forth, the *C. molossus* responding by vertical tail waving.

When placed with a second male *C. molossus*, the *C. viridis* immediately crawled over him as he assumed a submissive coil. Then when a male *Agkistrodon contortrix* was placed with the *C. viridis*, the latter crawled over this new male, but the *A. contortrix* did not form a submissive coil and did not appear to respond to the dominance actions of the *C. viridis*.

A male *Agkistrodon piscivorus* was then placed in the chamber with the *C. viridis*. The *C. viridis* immediately performed a solicitation display and persisted in displaying for some time finally eliciting a solicitation display response from the *A. piscivorus*. In two topping attempts, the *C. viridis* appeared dominant, forcing the *A. piscivorus* down. At one time the *A. piscivorus* waved his tail as the *C. viridis* crawled over him. It appeared that the *A. piscivorus* was trying to avoid the persistent actions of the *C. viridis*.

OBSERVATIONS BY OTHERS

Published records of species for which dominance, dominance-like behavior, submissive behavior and territoriality have been stated, sug-

gested or inferred follow. A brief reference is made to my interpretation of each account.

Boidae.—*Python molurus* (Barker *et al.* 1979). Dominance with linear hierarchy. Combat ritual with spur gouging and escape. Individual recognition. *Sanzinia madagascariensis* (Carpenter *et al.* 1978). Dominance-subordination resulting from combat ritual with spur gouging.

Colubridae.—*Elaphe obsoleta bairdi* (Brecke *et al.* 1976). Combat ritual with strong rivalry. *Elaphe o. obsoleta* (Rigley 1971). Combat ritual suggesting dominance as a result. *Coronella austriaca* (Andren and Nilson 1976). Males bite while fighting. *Coluber viridiflavus* (Guibe and Saint Girons 1955). Combat ritual with the victor first to mate. *Lampropeltis triangulum* (Shaw 1951). Flight by subordinate after combat ritual. *Lampropeltis getulus holbrooki* (Carpenter and Gillingham 1977). As a result of a combat ritual one male exhibited dominance actions, the other male subordinate behaviors. *Lampropeltis mexicana alterna* (Murphy *et al.* 1978). Dominance as a result of combat ritual. *Lampropeltis pyromelana* (Martin 1976). Aggression with biting and chasing. *Masticophis f. flagellum* (Kennedy 1965). Territoriality and dominance proposed from aggression on mating area. *Pseudaspis cana* (Fitzsimons 1962). Males fight vigorously with gashing bites. *Ptyas mucosus* (McCann 1935). Territoriality suggested in contest for supremacy.

Elapidae.—*Demansia textilis* (Fleay 1937, 1951). Dominance was indicated with the "weaker" subordinate retreating, the "stronger" male intimidating rivals. *Pseudechis porphyriacus* (Fleay 1937, 1951). Territorial "right" suggested from combat ritual.

Crotalidae.—*Agkistrodon piscivorus leucostoma* (Perry 1978). Suggests territoriality and dominance from combat ritual. *Crotalus adamanteus* (Wagner 1962). During combat ritual the dominant has more stamina. *Crotalus atrox* (Jenni 1966). Dominance apparent for victory and defeat clearly defined as result of combat ritual. *Crotalus atrox* (Foree 1949). Territoriality suggested. *Crotalus cerastes* (Lowe and Norris 1950). Territoriality suggested and discussed as a result of combat ritual. *Crotalus horridus atricaudatus* (Sutherland 1958). Dominance a possible result of combat ritual. *Crotalus lepidus klauberi* (Carpenter *et al.* 1976). Dominance apparent result of combat ritual. *Crotalus ruber* (Shaw 1948). Dominance apparent from the result of rivalry in combat ritual. *Crotalus v. viridis* (Thorne 1977).

Social domination and territoriality suggested from combat ritual. *Sistrurus miliarius* (Carpenter 1979). Dominance as a result of combat ritual.

Viperidae.—*Vipera* sp. (Prior 1933). Territoriality suggested. *Vipera aspis* (Nauulleau 1970). Territoriality suggested. *Vipera berus* (Andren 1975). Indicates winner and loser, with chasing, in combat rituals. *Vipera berus* (Volsoe 1944). Dominance suggested, with winner of combat ritual pursuing female. *Vipera berus* (Guibe and Saint Girons 1955). Territoriality suggested.

There are many other descriptions of combat rituals in the literature but these observers did not record the consequences or conclusions of interactions or were possibly not aware that dominance might be occurring.

DISCUSSION

In a recent paper (Carpenter 1977) I discussed the role of different signal channels in communication between snakes, stressing the importance of tactile actions in agonistic and courtship interactions. Tactile and visual communication appear to play the significant roles in determining dominance and subordination in snakes. The chemical senses may also be important.

The actions employed in combat rituals and other agonistic interactions involving contact (tactile) signals are tongue flicking, crawling over, dorsal crawl, lying on, pinning, topping, pushing down, entwining, spur use and biting, and are apparently used in determining dominance. Visual signals are those of vertical or oblique displays, hovering, pursuit, and perhaps approach.

The subordinate snake signals its submission by avoiding the dominant, thrashing on contact, fleeing (retreat), tail waving, submissive (negative) posture, and sometimes burrowing, which are visual signals. If the subordinate raises his head (visual) or begins to move (tactile or visual) these are signals to which the dominant will respond. The submissive posture fits the criterion for submissive postures in other animals, that is, offering the lowest or smallest profile.

I believe the evidence is strong that in many instances the interplay of these agonistic signals results in individual male snakes becoming dominant and their adversaries becoming subordinate.

What is the function of individual dominance in male snakes? The resources over which male

snakes might compete are a mate, food, and space. The strongest evidence of possible competition for a mate is in *Vipera berus*. A male having localized and identified a reproductive female will fight with, and repeatedly chase off, other males (Andren 1975; Volsoe 1944), with possible temporary territoriality. The evidence for competition for food and space is less evident, though combat rituals are noted in the presence of food (Shaw 1951; Sutherland 1958). Since many of my observations occurred in the absence of a female or food, dominance does occur in the absence of these resources.

We need to know more about mating strategies in snakes and how these may relate to dominance. Shine (1978) provided data that "reveals a high correlation between the occurrence of male combat, and sexual dimorphism in which the male is the largest sex" and states "These results strongly support the hypothesis that large male size is an adaptation to intrasexual competition." Dominance is a natural consequence of intrasexual male competition. We need evidence of a resource reward for dominance.

What are the taxonomic relationships of dominance? Since combat rituals have been observed in the Boidae, Colubridae, Elapidae, Crotalidae and Viperidae, this spread suggests that dominance is likely to be a phenomenon occurring in all groups of snakes. The fact that it is recorded mostly for the larger species of snakes may be due to the difficulty, or lack, of observing the smaller species.

For those species where aggregations are common and multiple courtships occur (two or more males courting a female at the same time, i.e., some natricine colubrids), it appears that combat rituals do not occur and that dominance is not likely to occur.

Is there individual recognition between male snakes and is this a necessary attribute of dominance (this is suggested in *Python molurus* by Barker *et al.* 1979, where a linear hierarchy occurred)?

When does the onset of dominance interactions occur, i.e., at a certain size, age, sexual maturity? Most combat rituals have been observed in large (presumably sexually mature) males.

The establishment of dominance, whether by combat rituals or other dominance actions, appears to fulfill the ritualistic function of gaining superiority without significant physical harm. The

general lack of biting during combat rituals and dominance-subordinate encounters supports this.

Certain of the actions seen performed by the dominant, i.e., the dorsal crawl and crawling over, are similar to the actions performed by a male courting a female, and a courted female may assume a submissive posture, or retreat and be chased by a male. The similarity of these subordinate actions by a male to those of a courted female may provide communication signals that lead the dominant male to homosexual action, i.e., aligning next to the subordinate male and attempts to tail search and effect intromission, though chemical signals should direct otherwise.

Is dominance related to larger size? This appears to be true for the *Lampropeltis getulus holbrooki* observed, but more detailed measurements of size and weight are needed to verify this assumption. The observations of *Crotalus viridis* indicate that this male dominated larger males of different species (perhaps an artifact of captivity).

The determination of the existence and significance of dominance as a social factor in naturally occurring populations of snakes will be difficult. I hope that my observations will create an awareness of this phenomenon of dominance by other herpetologists and stimulate them to watch for this behavior in the field.

SUMMARY

The existence of dominance-subordinate relationships between individual conspecific snakes has been suggested by observers recording combat rituals, mostly from captive encounters. Using an operational definition of dominance in snakes based on one snake exhibiting superiority through various actions over a subordinate which in turn performs certain actions, I believe the evidence is clear that dominance does occur in certain species.

The dominant male performs actions such as displaying higher and attempting to force his opponent to remain lower by forcing him down, by topping or pinning and then persistently crawling over or lying on the subordinate male; biting is very infrequent. The subordinate snake shows its submission by avoiding, fleeing, tail waving or assuming a submissive posture. The dominant will pursue the subordinate if it flees and will respond to movements from the submissive posture, repeating its dominant actions.

A series of observations of male encounters for nine species of snakes all indicate dominance-subordinate relationships using the above behaviors. Literature records for 25 species of snakes suggest the occurrence of dominance-like behavior.

The evidence that dominance functions to give priority for a resource has not been adequately demonstrated, and is often observed in the absence of food, a mate, and in a confined space.

Dominance and dominance-like behavior have been observed in five different families of snakes (Boidae, Colubridae, Elapidae, Crotalidae, Viperidae). More information will be needed to determine if different mechanisms are used in determining dominance in these and other groups. The dominance actions of snakes are likely to be related to the behaviors used in combat rituals, while subordinate behaviors are likely to be more similar between families.

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An Experimental Study of Variation in Habitat Selection and Occurrence of the Deermouse, *Peromyscus maniculatus gracilis*

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INTRODUCTION

Habitat selection has important consequences at the levels of both the individual and the population. Many organisms must actively select the type of habitat in which to live from a variety of accessible choices. The choice of a particular habitat exposes the organism to a specific set of selective pressures that can profoundly affect its survival and breeding success (Partridge 1978). Variations in habitat selection may lead to modifications of gene frequencies at the population level (Doyle 1975).

A positive correlation between the spatial distribution of a population and a specific habitat type does not provide sufficient evidence that individuals are actively choosing that habitat (Klopfer 1969). Habitat occurrence may also be affected by external factors such as predation (Kettlewell 1959, 1965), interspecific competition (Sheppe 1961; Turner 1961), intraspecific competition (Kluyver and Tinbergen 1953), or by internal morphological or physiological constraints (Bursell 1960; Klopfer 1969). Habitat selection and its relationship to habitat occurrence must therefore be verified experimentally (Meadows and Campbell 1972).

Experimental studies that test the relationship between habitat selection and habitat occurrence usually allow animals to select a specific habitat or model of the habitat from several choices under controlled conditions. The relationship between habitat selection and occurrence has been experimentally verified and reviewed in vertebrate species of fish (Sale 1969; Casterlin and Reynolds 1978), amphibians (Wiens 1970, 1972), reptiles (Kiestler *et al.* 1975), birds (Klopfer 1965; Hildén 1965), and mammals (Harris 1952; Wecker 1963; Fitch 1979).

Patterns of habitat selection may vary within and among populations of a species or even subspecies. Intrapopulation variation in habitat selection has been documented experimentally in plankton (Doyle 1975, 1976) and in mice (Fitch 1979). Interpopulation variation in habitat se-

lection has not been extensively studied. Miller (1973) reported that prairie deer mice (*Peromyscus maniculatus bairdi*) from North Dakota selected a simulated forest habitat corresponding to their natural habitat; in Michigan, where *P. m. bairdi* occurs only in grassland habitats, individuals selected that simulated habitat in favor of forest. Little information is available, however, on variations in habitat selection among local or regional populations occupying the same biome.

The purpose of this study was to investigate the local variations in habitat selection among two populations of the woodland deer mouse, *Peromyscus maniculatus gracilis*, in relation to observed differences in habitat occurrence. Habitat occurrences of populations were first verified in a forest habitat and an open lichen-grass habitat 36 kilometers apart by trapping studies. Animals from each site were then allowed to choose between simulated forest and open habitat models under controlled laboratory conditions. These laboratory tests were needed to establish whether variations in habitat occurrence reflected real differences in habitat selection or whether they indicated acceptance of suboptimal habitats because of competition.

The woodland deer mouse occurs throughout the northeastern United States and southeastern Canada from Pennsylvania north to southern Quebec and from western Manitoba east to Maryland (Hall and Kelson 1959). In Michigan, *P. m. gracilis* is widely distributed throughout the Upper Peninsula, on many islands in Lake Michigan, and as far south as Missaukee County in the lower peninsula of the state (Burt 1946).

This subspecies is generally restricted to woodland habitats and occurs most commonly in upland deciduous associations of maple, birch, and beech in northern Michigan (Dice 1925; Blair 1941). In New York, *P. m. gracilis* is restricted to woodland habitats even in forest-grassland ecotonal areas (Klein 1960). Harris (1952) reported that *P. m. gracilis* from the Upper Pen-



FIG. 1. General map of Michigan showing the location of the Kingston Plains (see 1) and the Cusino Wildlife Refuge (see 2).

insula of Michigan consistently selected simulated forest models in preference to grassland models under controlled laboratory conditions.

Fitch (1979) discovered a population of *P. m. gracilis* inhabiting an open lichen-grass habitat in the Kingston Plains, Alger County, Michigan, approximately 36 kilometers from the Cusino Wildlife Refuge, where Harris (1952) obtained his animals. In the present study, trapping was done in both study areas to confirm patterns of habitat occurrences, and animals from both localities were then tested for habitat selection.

STUDY AREAS

Cusino

The Cusino Wildlife Refuge is located in the southern part of Alger County, Michigan, approximately 47 kilometers south of Lake Superior (Fig. 1). The region is characterized by lowland swamp conifer habitats, upland associations

of hardwoods, and infrequent man-made clearings. Most of the forests in this part of the Upper Peninsula were logged over in the late 1800's and are now secondary growth.

Lowland swamp conifer habitats are characterized by associations of northern white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), and balsam (*Abies balsamea*). Alder (*Alnus rugosa*), Labrador tea (*Ledum groenlandicum*), and wintergreen (*Gaultheria procumbens*) are found commonly in this habitat.

The upland hardwood forests have associations of striped maple (*Acer pensylvanicum*), sugar maple (*Acer saccharum*), and American beech (*Fagus grandifolia*). Elderberry (*Sambucus pubens*), bedstraw (*Galium* sp.), and bracken fern (*Pteridium aquilinum*) are commonly found in upland forests.

Man-made clearings are dominated by bluegrass (*Poa nemoralis*) and orange hawkweed (*Hieracium aurantiacum*).



FIG. 2. Open habitat in the Kingston Plains characterized by lichen-grass associations in the study grid. Partially buried logs and stumps served as shelter areas for *P. m. gracilis*.

Kingston Plains

The Kingston Plains is located in the north-eastern corner of Alger County, Michigan, approximately 11 kilometers south of Lake Superior (Fig. 1). This area, approximately 28 square kilometers in extent, was once a well-developed upland red and white pine forest (Jenkins 1942). From 1880 to 1890, the Plains area was extensively logged, and in 1890 a major fire burned over the area. This fire and subsequent fires destroyed the organic soil layer and exposed rubicon sand (Veatch *et al.* 1929).

Much of the Kingston Plains is still characterized by open, well-drained expanses of old charred tree stumps and occasional snags with vegetational associations of lichens, grasses, and ferns (Fig. 2). Small, shallow lakes occur in lowland areas, and small isolated enclaves of pine, maple, and birch are found in some parts of the Kingston Plains. Attempts have been made to reforest small sections with red and white pine, but have met with limited success due to the marginal soil conditions.

Open habitats are characterized by common associations of hair cap moss (*Polytrichum commune*) and lichens (*Cladonia mitis*, *Cladonia alpestris*, and *C. rangiferina*) interspersed with sparse clumps of hair grass (*Deschampsia flexuosa*) and *Festuca rubra*. Blueberry (*Vaccinium* sp.), bracken fern (*Pteridium aquilinum*), sourdock (*Rumex* sp.) and orange hawkweed (*Hieracium aurantiacum*) are common in open habitats.

Small isolated woodlots have associations of red maple (*Acer rubrum*), white pine (*Pinus strobus*), American beech (*Fagus grandifolia*), and white birch (*Betula cerulea*).

MATERIALS AND METHODS

Determination of Habitat Occurrence

Habitat occurrence in *P. m. gracilis* was determined by setting out transects of Sherman live-traps in three habitat types (swamp conifer, upland hardwood, and open field) at Cusino and two habitat types (woodlot and open lichen-grass

TABLE 1. Vegetation used in simulating forest and open habitat models in compartments.

Habitat model	Plant species	Approximate surface area or density in compartment	
Open	<i>Cladonia mitis</i> , grey lichen <i>Cladonia rangiferina</i> and <i>C. alpestris</i> , lichen } <i>Deschampsia flexuosa</i> , hair grass <i>Pinus strobus</i> , white pine (stumps and logs)	30% of surface area 60% of surface area 10% of surface area	
	Forest	<i>Pinus strobus</i> , white pine (stumps and logs) <i>Acer rubrum</i> , red maple (leaves) <i>Acer rubrum</i> , red maple (saplings) <i>Betula cerulea</i> , white birch (saplings) <i>Pinus strobus</i> , white pine (seedlings)	10% of surface area 90% of surface area .43 per sq. m .43 per sq. m .43 per sq. m

associations) in the Kingston Plains. Traps were set in transect lines at 10-meter intervals and baited with a mixture of rolled oats and peanut butter. Each habitat type was sampled for four consecutive nights with 50 traps each night, for a total of 200 trap nights. Transects were moved each night in order to sample other areas within each habitat. Trapping was done between 15 August and 20 September 1973.

Information on size, weight, sex, reproductive condition and estimated age was taken on all captures. Males captured from Cusino upland forest habitat and from Kingston open habitat were marked and returned to the laboratory for habitat selection tests. Several females from these habitats were also marked and returned to the laboratory in the hopes of establishing breeding colonies. The remaining females were marked and released.

Determination of Habitat Selection

Test Apparatus.—The test apparatus used in this study to determine habitat selection was the same as that used by Fitch (1979) to evaluate differences between animals captured from Kingston Plains forest and open habitats. Single animals were placed in one of four pens, each measuring 2.44 m × 1.83 m × 1.52 m. Each pen was divided by a plywood partition into two equal compartments each measuring 1.83 m × 1.22 m. A Plexiglas runway (24 cm × 7 cm × 7 cm) mounted 30 cm above the floor connected the compartments. Movements between compartments and total time spent in each compartment were measured by a treadle equipped with a mercury switch installed inside the runway. The run-

way was connected to the floor of each compartment by a sloping, wire mesh causeway.

Structural vegetation characteristically found in forest and open habitats during the autumn season was used to create a habitat model in each compartment. Species of plants used in the compartments and their approximate surface areas are listed in Table 1. All species used were either dominant or very common in their respective habitats. Ground cover in open habitat compartments was dominated by associations of lichen, grass, and bracken ferns (Fig. 4). Forest compartments had short red maple, beech, birch, and white pine saplings as well as red maple seedlings and leaf litter (Fig. 3). One small stump and three pieces of logs were placed in both open and forest habitat compartments.

Each compartment was provided with a nest-box, running wheel, water bottle, and wire container of food as described by Fitch (1979). Water was supplied in each compartment by a 100-ml graduated cylinder that was upended and attached to the outside wall so that only the metal drinking tube protruded into each compartment. Food (Purina Mouse Breeder Chow) was placed in a 6-mm wire mesh container that was suspended in one corner of each compartment.

Each pen was illuminated by two 20-watt fluorescent tubes attached to overhanging cross-beams parallel to the center partition. The rest of the test room was poorly illuminated in order to emphasize habitat cues within the pens. An artificial light cycle of 14 hours light and 10 hours dark was maintained by means of an automatic timer. A faint illumination of 0.01 footcandles was provided during the dark period.

All time-related dependent variables were re-



FIG. 3. Forest habitat compartment. Note runway, wire mesh causeway, and natural forest vegetation.



FIG. 4. Open habitat compartment. Note runway, wire mesh causeway, and natural vegetation from lichen-grass associations in the Kingston Plains.

TABLE 2. Dependent variables used to measure habitat selection for simulated forest and open habitat models.

Variable	Unit of measurement
Initial habitat choice	Habitat compartment first entered after release from central runway
First night compartment time	Percent of time spent in each compartment
Second night compartment time	Percent of time spent in each compartment
Third night compartment time	Percent of time spent in each compartment
Average night compartment time	Percent of time spent in each compartment

recorded by a 12-volt Esterline Angus Event Recorder in order to analyze both the distribution of time and the total time spent in each compartment.

Dependent Variables.—Five different dependent variables were chosen on the basis of pilot studies to measure habitat selection (Table 2). These variables included a time-independent variable, the initial habitat selected by each animal as it was released from a central area. This initial choice was defined as the first habitat that each animal actually entered.

The other four variables were time-dependent and measured the amount of time that each animal spent in each of two habitat compartments on each of three succeeding nights. *Peromyscus* are nocturnal; therefore, time spent in each compartment during the dark hours of the light cycle should more clearly reflect active selection of habitats than that spent during light hours.

Experimental Procedure.—The mouse to be tested was placed in the central runway and plastic transparent doors at either end of the runway were closed. The mouse was allowed to habituate to the runway for 15 minutes after which time the runway doors were pulled up from outside the pen. The animal was then free to enter either compartment via the wire causeways. Tests were usually begun between 1600 and 1700 hours during the light-on period. Usually the causeways were explored several times before a compartment was actually entered. The initial habitat choice was defined as the first compartment substrate upon which the animal placed all four feet and tail.

Individuals remained in the pens for the following 3 nights and 2½ days. Nestboxes were checked once daily, during daylight hours, to verify the animal's position. At the end of each test period, the animal was removed from the enclosure.

Ten animals from each habitat were placed in each pen prior to the tests in order to distribute scent equally in all habitat compartments. Individuals from each habitat were assigned randomly to specific pens to reduce potential population olfactory effects. Potential position effects within the room were reduced by orienting habitat compartments of the pens in opposite directions. Variations in behavior due to age and sex effects were avoided by using males at least 90 days of age as test subjects. Seasonal effects were avoided by using mice captured during the fall season.

Habitat selection was tested for 12 individuals from Cusino upland forest habitat and 12 individuals from Kingston Plains open lichen-grass habitat.

Statistical Analyses.—A Chi square contingency test was used to test for differences in the proportions of individuals that initially chose habitat compartments that were either different from or similar to those natural habitats in which they were trapped.

The four time-dependent variables were recorded in terms of the percentage of time spent in the compartments that modeled open habitats. The percentage data were transformed to arcsin values in order to conform to a normal distribution for statistical tests (Sokal and Rohlf 1969).

One-sample *t*-tests were used to evaluate the magnitude of habitat selection differences within Cusino and Kingston Plains sample groups for each time-dependent variable. Within these two groups, habitat selection was defined as the statistical difference between the group mean of the percentage time spent in open habitat compartments and a theoretical value of 50% (arcsin = 45), which indicated no specific selection of habitats. An *a priori* alpha significance level of .05 was set for each test.

TABLE 3. Summary of *P. m. gracilis* captures in relation to trapping effort in various habitat types in the Cusino Wildlife Refuge and the Kingston Plains, Alger County, Michigan.

Area	Habitat type	Number of trap nights	Number of captures per 100 trap nights
Cusino	Grassy fields	200	0
	Swamp conifer	200	3
	Upland hardwoods	200	9
Kingston Plains	Open lichen-grass	200	21
	Small woodlots	200	24

Differences in habitat selection between Cusino and Kingston Plains group means were evaluated by two-sample *t*-tests for each time-dependent variable.

RESULTS

Habitat Occurrence

Habitat occurrences of *P. m. gracilis* in the three habitats sampled in the Cusino Wildlife Refuge and the two habitats sampled in the Kingston Plains are summarized in Table 3 in terms of the numbers of individuals captured in each habitat per 100 trap nights.

At Cusino, *P. m. gracilis* were captured most frequently in upland hardwood forest habitats and less commonly in swamp conifer habitats. No individuals were captured from grassy field habitats, even though mice were captured in adjacent forest habitat transects. Both upland hardwood and swamp conifer habitats contained populations of *P. m. gracilis* with reproductively active adults. These patterns of habitat occurrence were similar to those reported by Blair (1942) in Alger County, Michigan.

In the Kingston Plains, *P. m. gracilis* were captured in both the small woodlot habitats and the open lichen-grass habitats (Table 3). These results were especially interesting because of the rather narrow range of habitats previously identified for this subspecies and because Harris (1952) had suggested that *P. m. gracilis* might have an innate preference for forest habitat. Kluyver and Tinbergen (1953) have suggested that individuals might be forced into less optimal and possibly less preferred habitats if density were

TABLE 4. Chi square analysis of the numbers of individuals that initially chose habitat compartments either different or similar to those natural habitats in which they were trapped.

Habitat compartment selection	Item	Habitat occurrence		
		Cusino forest	Kingston open	Totals
Forest	Observed	10	1	11
	Expected	5.5	5.5	
Open	Observed	2	11	13
	Expected	6.5	6.5	
	Totals	12	12	24
χ^2 3 df		13.6		
$P < .005$				

high in more optimal areas. In the Kingston Plains, however, similar numbers of individuals were captured from both habitat types and reproductively active adult animals were captured from both habitats.

Habitat Selection of Wild Caught Individuals

Cusino.—Of the 12 individuals captured from Cusino forest habitat, 10 individuals selected forest habitat models and 2 selected the open habitat models in initial habitat choice tests (Table 4). Group means for all time-dependent variables differed significantly ($P < .05$) from a mean of 50% (Table 5). Thus, significant numbers of animals from Cusino selected forest habitat compartment models. The two individuals that initially selected open habitat models exhibited less clear-cut habitat selection during subsequent nights, based upon the percentage time spent in forest and open habitat models.

Kingston Plains.—Of 12 animals captured from open habitats in the Kingston Plains, 11 selected open habitat models and 1 selected a forest habitat model in initial choice tests (Table 4). Group means for all time-dependent variables differed significantly ($P < .05$) from a mean of 50% (Table 5). Therefore, significant numbers of animals captured in Kingston Plains open habitats selected open habitat models. The individual that initially selected a forest model did not demonstrate a strong preference for either habitat model during subsequent nights.

Cusino versus the Kingston Plains.—The proportions of individuals from Cusino and Kings-

TABLE 5. Results of a one-sample *t*-test of within group means for four time-related variables for animals captured in Cusino forest and Kingston open habitats. Each column lists the arcsin transformation of group-mean percentages. Probabilities listed are in relation to significant departures from 50% utilization of open habitat compartments.

Habitat occurrence	Sample size	Time in open habitat compartment			
		1st night arcsin \bar{x}	2nd night arcsin \bar{x}	3rd night arcsin \bar{x}	Average nights arcsin \bar{x}
Cusino forest	12	30.2***	32.9***	28.3***	30.6***
Kingston open	12	56.3**	53.4**	54.3*	54.7**

*** *P* < .001.
 ** *P* < .01.
 * *P* < .05.

ton Plains initially choosing habitat models either different from or similar to the habitats in which they were captured differed significantly (*P* < .005) from one another in a Chi square test (Table 4). Thus, significantly greater numbers of individuals chose habitat models of the habitats in which they were captured. Differences between group means of animals captured in Cusino forest habitat and Kingston Plains open habitat were significant (*P* < .001) for all time-related measures (Table 6). Thus, the group means of animals captured from Cusino forest habitats and Kingston Plains open habitats were significantly different from no choice and from one another for all dependent variables tested.

Habitat Selection of Laboratory-Reared Offspring

Every effort was made to establish breeding laboratory colonies of *P. m. gracilis* from Cusino and from the Kingston Plains study areas. However, *P. m. gracilis* is known to breed poorly under laboratory conditions. Three offspring were eventually obtained from animals captured in Kingston Plains open habitats and two offspring were produced by individuals captured in Cusino forest. All five offspring were reared under laboratory conditions and were not exposed to hab-

itat cues until they were actually tested in habitat model compartments. The same testing procedure was used for these animals as was used for their parents.

In each case, the offspring initially selected the habitat model compartment that was similar to the habitat from which its parents were captured. All offspring also spent more time in that habitat compartment on subsequent nights. Unfortunately, sample sizes are too small for statistical analyses, but it is interesting that all offspring in all tests of dependent variables selected the habitat type that their parents had chosen and in which they had been captured.

DISCUSSION

Habitat Occurrence

The woodland deer mouse is usually found within a well-defined and narrow range of forest habitat types (Blair 1942; Dice 1925; Harris 1952; Klein 1960). The discovery of high population densities of *P. m. gracilis* in an open lichen-grass habitat in the Kingston Plains, Alger County, Michigan is therefore a major exception to the general pattern of habitat occurrence of this subspecies in mainland areas.

This subspecies sometimes occupies a greater

TABLE 6. Results of a two-sample *t*-test among group means for four time-related variables for animals captured in Cusino forest and Kingston open habitats.

Time-related variable	df	<i>t</i> -value	Significance
1st night compartment time	22	6.48	<i>P</i> < .001
2nd night compartment time	22	5.40	<i>P</i> < .001
3rd night compartment time	22	5.53	<i>P</i> < .001
Average night compartment time	22	6.20	<i>P</i> < .001

variety of habitats on islands than in adjacent mainland areas (Grant 1970; Hatt *et al.* 1948; Ozoga and Phillips 1964). These island populations were hypothesized to be under less predation and competition pressure than populations of *P. m. gracilis* in the nearest mainland areas.

Predation and competition pressures are probably lower for *P. m. gracilis* in the Kingston Plains than in surrounding regions of continuous forest (Fitch 1979). In open lichen-grass habitats, old charred tree stumps provide shelter, and avian and mammalian predator populations are low. Potential competitors such as the meadow vole (*Microtus pennsylvanicus*) and the red-back vole (*Clethrionomys gapperi*) may restrict the distribution of *P. m. gracilis* in some areas of northern Michigan (Manville 1949; Ozoga and Verme 1968). Both species, however, were extremely rare in the Kingston Plains, at least at the time of this study.

In contrast, potential predators such as the red-tailed hawk (*Buteo jamaicensis*) and the great horned owl (*Bubo virginianus*) were sighted and heard on numerous occasions in the Cusino area. Potential competitors such as *Microtus pennsylvanicus* and *Clethrionomys gapperi* were captured frequently in open grassy habitat and swamp conifer habitat, respectively.

Habitat Selection

Patterns of habitat occurrence as established by trapping studies were directly related to patterns of habitat selection as established by laboratory habitat model selection tests based upon five dependent variables. Group means of individuals captured from Cusino forest and Kingston Plains open habitats were significantly different from one another and from no active choice for all dependent variables measured.

Patterns of habitat selection established in this study for animals captured from the Cusino forest habitat are consistent with the results reported by Harris (1952). Although sample sizes of laboratory-reared offspring were unfortunately too small for statistical analyses, the trend was to select forest habitat models similar to those selected by their parents. Harris (1952) reported similar results and hypothesized that habitat selection might involve an innate preference for the parental habitat. Wecker (1963) confirmed

that innate preferences for the parental habitat existed in a closely related taxon, *Peromyscus maniculatus bairdi*.

The results of these studies make the differences in patterns of habitat selection between Cusino and Kingston Plains populations especially interesting. These populations are only 36 kilometers apart and yet differ in their patterns of habitat occurrence and habitat selection. Innate patterns of habitat selection may also differ between the two populations.

The Kingston Plains has been available for colonization by *P. m. gracilis* for approximately 80 years in its present form. At present, conditions such as shelter availability, and lack of predation and competition pressures seem favorable to colonization. An interesting question is: how was it colonized?

Fitch (1979) has noted that individuals captured from woodlot and open habitats in the Kingston Plains selected habitat models in the laboratory that most closely resembled habitats in which they were captured. However, the two habitats were not isolated from one another and there was sufficient movement of individuals between the habitats to indicate that populations were not isolated. Therefore, polymorphic variation in habitat selection seems likely within the Kingston Plains population, with one segment of the population occupying open habitats and the other occupying forest habitats in small woodlots.

Polymorphic variation may occur less commonly within the Cusino population. The two wild caught individuals from Cusino that selected open habitat type model compartments might be examples of such variation. Such animals might colonize open habitats in the Cusino area if they encountered the same favorable qualities that existed in the Kingston Plains open habitats. In the Cusino area, however, such animals may be less frequent in the population because they are under greater selective pressures from competition and predation when they enter open habitats.

SUMMARY

Unusual patterns of habitat occurrence were discovered in woodland deer mice, *Peromyscus maniculatus gracilis*, that inhabited ecologically disturbed habitats of the Kingston Plains, Alger

County, Michigan. Patterns of habitat selection and occurrence of the Kingston Plains population were compared with those of a population of *P. m. gracilis* occurring in forest habitat within the Cusino Wildlife Refuge, 36 kilometers to the south. The following results were obtained:

- 1) Habitat occurrence of *P. m. gracilis* was tested by live-trapping in three habitat types in the Cusino Wildlife Refuge and two habitat types in the Kingston Plains.
- 2) Capture rates in Cusino habitats were highest in upland forest and no animals were captured from open grassy fields. In the Kingston Plains, capture rates were equally high in both small woodlots and in open lichen-grass habitats. Capture rates per 100 trap nights were approximately two times higher in both Kingston Plains habitats than in Cusino upland forest habitats.
- 3) Significant numbers of individuals from Cusino forest and Kingston Plains open habitats selected habitat models simulating the habitats from which they had been captured. Habitat selection was measured by one dependent variable independent of time and four time-dependent variables.
- 4) Group means of individuals captured from Cusino forest habitat and from Kingston Plains open habitat were significantly different from no choice of habitats for all time-dependent variables.
- 5) Group means of individuals from Cusino forest habitat differed significantly from those of individuals from Kingston Plains open lichen-grass habitat for all dependent variables.
- 6) Laboratory-reared offspring from individuals captured in Cusino forest and Kingston Plains open habitats selected habitat models simulating those habitats in which their respective parents were captured.

Different patterns of habitat selection and occurrence were discovered in populations of *P. m. gracilis* only 36 kilometers apart. A hypothesis concerning the colonization of the Kingston Plains was presented.

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It is with great pleasure that I dedicate this study of habitat selection and occurrence to an excellent scientist, friend, and father, Henry S. Fitch. The substance of this volume in his honor bears testimony to the effects which his enthusiasm, originality, and high standards have had upon family, students, and colleagues alike. His characteristic research studies, sometimes referred to as "Fitchian Ecology," have contributed greatly to the eventual integration of the fields of natural history and theoretical ecology.

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Part IV
Systematics and Biogeography

Herpetogeography in the Mazatlán-Durango Region of the Sierra Madre Occidental, Mexico

ROBERT G. WEBB

Interest in studying the distribution of amphibians and reptiles along a transect in southern Sinaloa and adjacent Durango, México, began in June of 1955 when I first crossed the Sierra Madre Occidental. At that time the rough, narrow, unimproved road from Villa Unión, Sinaloa to Ciudad Durango, Durango, used mostly by busses and trucks, was virtually impassable in the rainy season. Now, a paved road (Highway 40), completed in November 1960, provides for year-round transportation along a scenic route; especially impressive is the rough barranca country that straddles the border of the two Mexican states. The paved highway affords the opportunity to collect amphibians and reptiles in what would otherwise be relatively inaccessible habitats. The highway also crosses the Sierra Madre in a region of its highest elevation and thus traverses a maximum diversity of habitats. The purpose of this report is to record the known kinds of amphibians and reptiles, to ascertain the kinds of distributional patterns along the transect based on the occurrence of each species in each major faunal region, and to relate these patterns to major herpetofaunal assemblages.

DESCRIPTION OF TRANSECT

The transect of the Sierra Madre Occidental is oriented in a generally northeast-southwest direction in southwestern Durango and southern Sinaloa, and coincides with Highway 40 that meanders for approximately 296 km (184 mi) between Durango, Durango and Villa Unión, Sinaloa (Fig. 1). About 1 km south of Villa Unión Highway 40 joins the coastal Highway 15, which in turn continues some 22.5 km (14 mi) northwest to Mazatlán. The total route of 320 km (198.5 mi) may be traveled in six hours under normal driving conditions.

Physiography and Climate

From Durango on the Mesa del Norte of the Mexican Plateau at an elevation of about 1905 m (6250 ft) the highway ascends through mon-

tane pastures cut by arroyos (crossing two of them at Río Chico and Mimbres) to the broad, irregular plateau that forms the crest of the Sierra Madre. Here, the general elevation of the undulating transect route is about 2438 m (8000 ft) with peaks near 2804 m (9200 ft). The highway then drops approximately 2347 m (7700 ft) in 104.5 road km (65 mi) over an airline distance of about 35 km (22 mi) in descending the steep, mostly west-facing slopes to the coastal lowlands of Sinaloa. The highway in the initial stages of this descent winds along the upper slopes of barrancas that mostly have a southern exposure. These south-facing slopes are cut by spectacular barrancas and canyons and show the most rugged topography of the transect. Just before El Palmito, the highway crosses the Durango-Sinaloa state line, which also marks the juncture of the Central and Mountain Time Zones. Farther west at Loberas, where the Pacific Ocean may be seen on clear days some 96.5 km (60 mi) away, the highway crosses a ridge and begins its switchback route on westerly exposed slopes. The Tropic of Cancer (23°27'15") intersects Highway 40 about 0.7 km east of Santa Rita. The descent is rapid to Santa Lucía, less so to Chupaderos, after which the highway traverses gently rolling foothills to the relatively flat coastal lowlands (Fig. 2).

The entire area is west of the Continental Divide so that all drainage is westward into the Pacific Ocean. The eastern slopes of the Sierra Madre are drained by the Río del Tunal, a large tributary of the Río Mezquital. Most of the high plateau of the Sierra Madre is drained by tributaries of the Río de Acaponeta (to the south) and the Río del Presidio (to the north). Watercourses on the western slopes drain into the Río del Baluartes or the Río del Presidio. Large tributaries intersecting Highway 40 generally have some water throughout the year.

Climates vary from an arid-tropical in the coastal lowlands of Sinaloa to a cool-temperate on the Mexican Plateau. In both places (vicinities of Mazatlán and Durango), rainfall, usually in the afternoons, is heaviest and temperatures are highest in summer and fall months. The driest

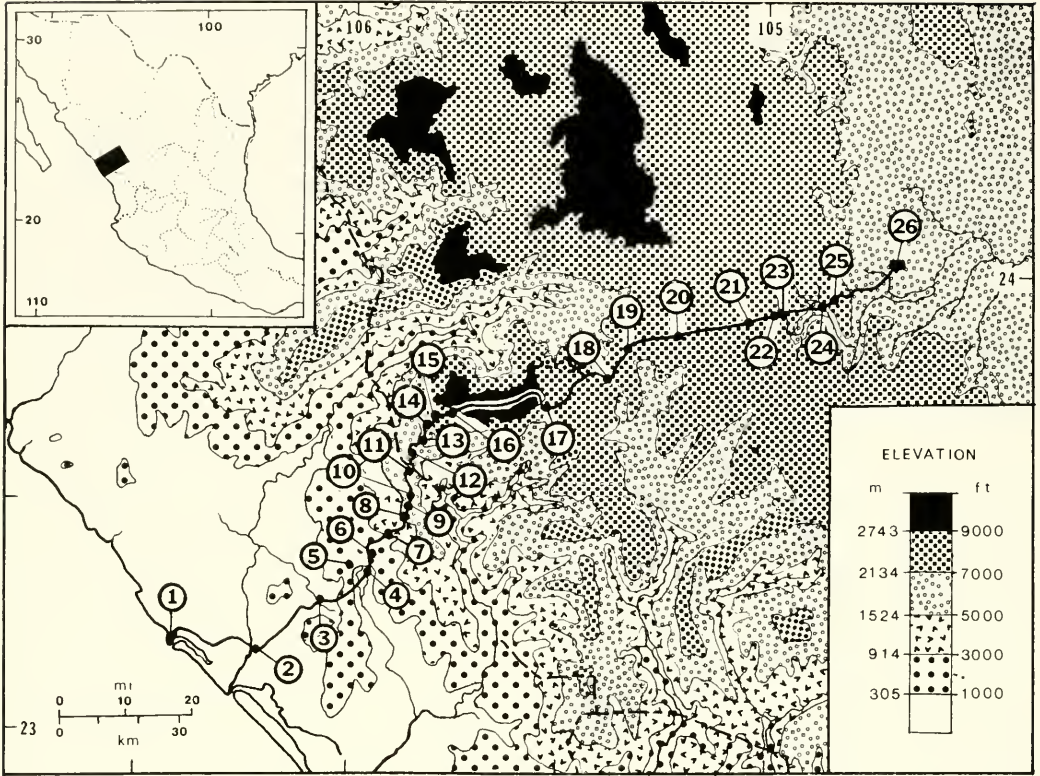


FIG. 1. Topographic map showing transect across Sierra Madre Occidental and spatial relationships of localities mentioned in text. The numbered localities, identified in gazetteer and arranged west to east, are: 1. Mazatlán. 2. Villa Unión. 3. Concordia. 4. Chupaderos. 5. Pánuco. 6. Copala. 7. Santa Lucía. 8. Potrerillos. 9. Santa Rita and El Batel. 10. Loberas. 11. El Palmito. 12. Revolcaderos. 13. El Espinazo. 14. Los Bancos. 15. Buenos Aires and Puerto Buenos Aires. 16. La Ciudad. 17. Las Adjuntas. 18. El Mil Diez and El Salto. 19. Estación and Hacienda Coyotes. 20. Llano Grande. 21. Navios. 22. Rancho Santa Barbara. 23. Mimbres. 24. Río Chico. 25. Metates. 26. Tapias and Durango.

months are generally March through May. Mazatlán has more rain (annual average about 86.4 cm or 34 in.) and higher temperatures (annual average about 24°C or 75°F) than Durango (48.3 cm or 19 in., and 17°C or 63°F). At Durango about 83% of the total rain falls from mid-June into October, most of it in July (12.5 cm or 4.9 in.), August (9.1 cm or 3.6 in.), and September (10.2 cm or 4.0 in.). The lowest average monthly temperatures are 10 to 11°C (53 to 54°F) in December and January, whereas the highest are 20 to 22°C (69 to 72°F) from May through August. In winter, cold northerly winds may drop temperatures below freezing. At Mazatlán, about 86% of the annual rainfall occurs in the months of July through October, most of it in August (24.4 cm or 9.6 in.) and September (27.2 cm or 10.7

in.). Occasional west coast tropical cyclones account for deluge rainfall in the Mazatlán-Villa Unión area—e.g., 32.0 cm (12.6 in.) of rain fell in 24 hours on 12 September 1968 at Siqueros (ca. 30 km NE Mazatlán; Schmidt 1976:22). Near Mazatlán, the lowest average monthly temperature is 19°C (67°F) in January, February, and March, whereas the highest temperatures are 26 to 27°C (79 to 81°F) from June through October.

Warm, moisture-laden, westerly winds sweep inland from the Pacific Ocean and precipitate most rain on the highest parts of the Sierra Madre that are often shrouded in clouds and where hail storms are not infrequent. This highest part of the Sierra Madre provides for the extremes of orographic precipitation in Sinaloa. Schmidt (1976:20) notes that the mean annual precipi-

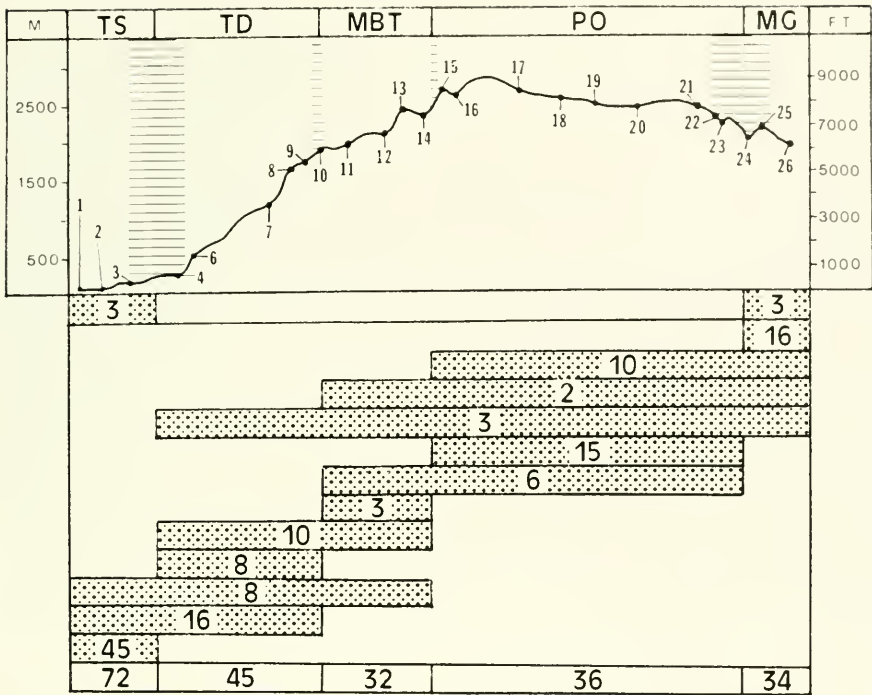


FIG. 2. Transect-highway profile showing localities (numbers identified as in Fig. 1, Pánuco omitted), elevations, herpetofaunal regions (TS, Thorn-Scrub; TD, Tropical-Deciduous; MBT, Mixed Boreal-Tropical; PO, Pine-Oak; MG, Mesquite-Grassland; shaded areas are approximate extent of transition zones), and kinds of distributional patterns (with included number of taxa for each pattern). The bottommost line indicates the total number of taxa in each region.

tation of 155.4 cm (61 in.) at Pánuco is the highest in the entire state of Sinaloa, and that 234.4 cm (92 in.) for El Palmito in 1958 is the wettest on record for the state. Average annual temperatures are lowest in the boreal Durango highlands (about 10°C or 52°F at El Salto) where snow may occur for about one third of the year, persisting as small patches in shaded places into June.

The most abrupt climatic change occurs between the pine-oak forest and mixed boreal-tropical habitats. This change was most dramatic when experienced in the winter month of February 1961 just westward of Puerto Buenos Aires. A cold, windy, wintery climate prevailed on the east side of the Sierra Madre and in the pine-oak forest highlands, but changed to a warm, sunny, spring-like climate in the adjacent mixed boreal-tropical where most herbs and shrubs were in flower. The latter conditions persisted with decreasing altitude to the coastal lowlands of Sinaloa.

HERPETOFAUNAL REGIONS

Biogeographic studies are necessarily based on field work and the collection of specimens. The highway-transect has been well traveled, so that localities of collection are relatively well represented. I have traveled the transect route many times. Personal field work and observations prompt the recognition of five ecologic regions. These regions seem to correlate well with the distribution of the herpetofauna, each having endemic species.

The distribution of the herpetofauna is analysed in terms of these five herpetofaunal regions, which are designated from east to west: Mesquite-Grassland, Pine-Oak, Mixed Boreal-Tropical, Tropical-Deciduous, and Thorn-Scrub. The approximate geographic extent of these regions along the transect is depicted in Fig. 2. Descriptive comments concerning these faunal regions are provided by Baker and Greer (1962, Duran-

go), Crossin (1967, Mixed Boreal-Tropical in Sinaloa), Smith (1971, Tropical-Deciduous), and Hardy and McDiarmid (1969, Sinaloa). Hardy and McDiarmid (1969) utilized Holdridge's classification and terminology of bioclimate in their herpetofaunal study of Sinaloa, recognizing in the transect area (from east to west) the Lower Montane Dry Forest, Subtropical Dry Forest, Tropical Dry Forest, and Tropical Semiarid Forest. The Lower Montane Dry Forest corresponds to the Mixed Boreal-Tropical, the Subtropical Dry Forest to the Tropical-Deciduous (here considered somewhat more extensive), and the Tropical Semiarid Forest to the Thorn-Scrub. The Tropical Dry Forest, not recognized, is here considered to be a transitional zone between the Thorn-Scrub and Tropical-Deciduous.

Mesquite-Grassland (Fig. 3)

The western part of the Mesa del Norte of the Mexican Plateau in Durango is climatically a grassland of mixed and short grasses, especially grama grasses (*Bouteloua*). This grassland has been modified by agrarian development and grazing of livestock, permitting an invasion of shrubby components. In most places the vegetation consists of a low grassy cover, often sparse with bare soil exposed, with scattered herbs, mesquite (*Prosopis*), huizache (*Acacia farnesiana*), prickly pear (*Opuntia*), and occasionally juniper and cholla. The relatively level terrain is interrupted by scattered low hills with rock outcroppings. Foothills of the Sierra Madre have a rather open scrub cover of catclaw (*Acacia*), leatherplant (*Jatropha*), some grasses, occasional prickly pears and sotol (*Dasylyrion*), and a large tree-yucca (*Yucca*).

The eastern terminus of the transect is in the Mesquite-Grassland at Durango, at an elevation of approximately 1905 m (6250 ft). Immediately after leaving the city westward, the highway rises through the *Yucca*-foothill zone, which extends for about 8 km (5 mi) to an elevation of about 2103 m (6900 ft), where a rocky landscape, having thin dark soils largely concealed by a cover of grasses and scrub oaks, is transitional to the Pine-Oak through a montane savanna or woodland.

This transitional, open wooded area consists of scattered tall pines, scrub oaks, juniper (*Juniperus*), pinõn pine (*Pinus cembroides*), and

manzanita (*Arctostaphylos*), with grasses common, and sotol, maguey (*Agave*), and prickly pears in some places. Bare ground, rarely exposed, is covered with grasses, pine needles, oak leaves, and loose rock. The terrain is hilly, rocky, and dissected by numerous canyons. Level areas are extensively cultivated, mostly in corn, and grazed by livestock. The highway dips into two canyons having tributaries of the Río Mezquital, the Río Chico and Río Mimbres. Riparian flora, best developed along the Río Chico, is principally of large willows (*Salix*), alder (*Alnus*), buttonbush (*Cephalanthus*), smartweed (*Polygonum*), a small sedge (*Eleocharis*), and patches of water lily (*Nymphaea*). This woodland, merging at higher elevations with the Pine-Oak, extends for about 48 km (30 mi) between elevations of about 2103 and 2255 m (6900 and 7400 ft), the most marked change seemingly about 9 or 10 km (6 mi) west of Mimbres.

Pine-Oak (Fig. 4)

On the plateau-like crest of the Sierra Madre is a forest of pines, principally Chihuahua pine (*Pinus leiophylla*), Durango pine (*P. durangensis*) and white pine (*P. strobiformis*), and several large oaks. The gently rolling terrain, often with rock outcroppings, has an open understory of grasses and herbs and scattered manzanita, junipers, and large madroños (*Arbutus*). On drier sites, generally at the lowest elevations or on south or east-facing slopes, oaks are more abundant than pines, whereas moist, deep, protected canyons often support fir (*Abies religiosa*) and Douglas fir (*Pseudotsuga mucronata*). Many swift, cold, clear-water streams (small trout and water ouzel observed) drain the plateau. Forested areas are interspersed with extensive meadowy areas. Herbs include various grasses, a yellow aster-like composite, buttercups, violets, geraniums, a white-flowered smartweed, and small euphorbs and mints. Rocky slopes moist from seepage support mosses, ferns, and in some places columbine (*Aquilegia*). Much of the area is grazed (cattle), lumbered, and cultivated (mostly corn and potatoes).

The Pine-Oak extends for about 116 km (72 mi) along the highway at a general elevation of 2438 m (8000 ft) where the maximum elevation is about 2804 m (9200 ft) between Las Adjuntas and La Ciudad; a few mountain peaks rise some

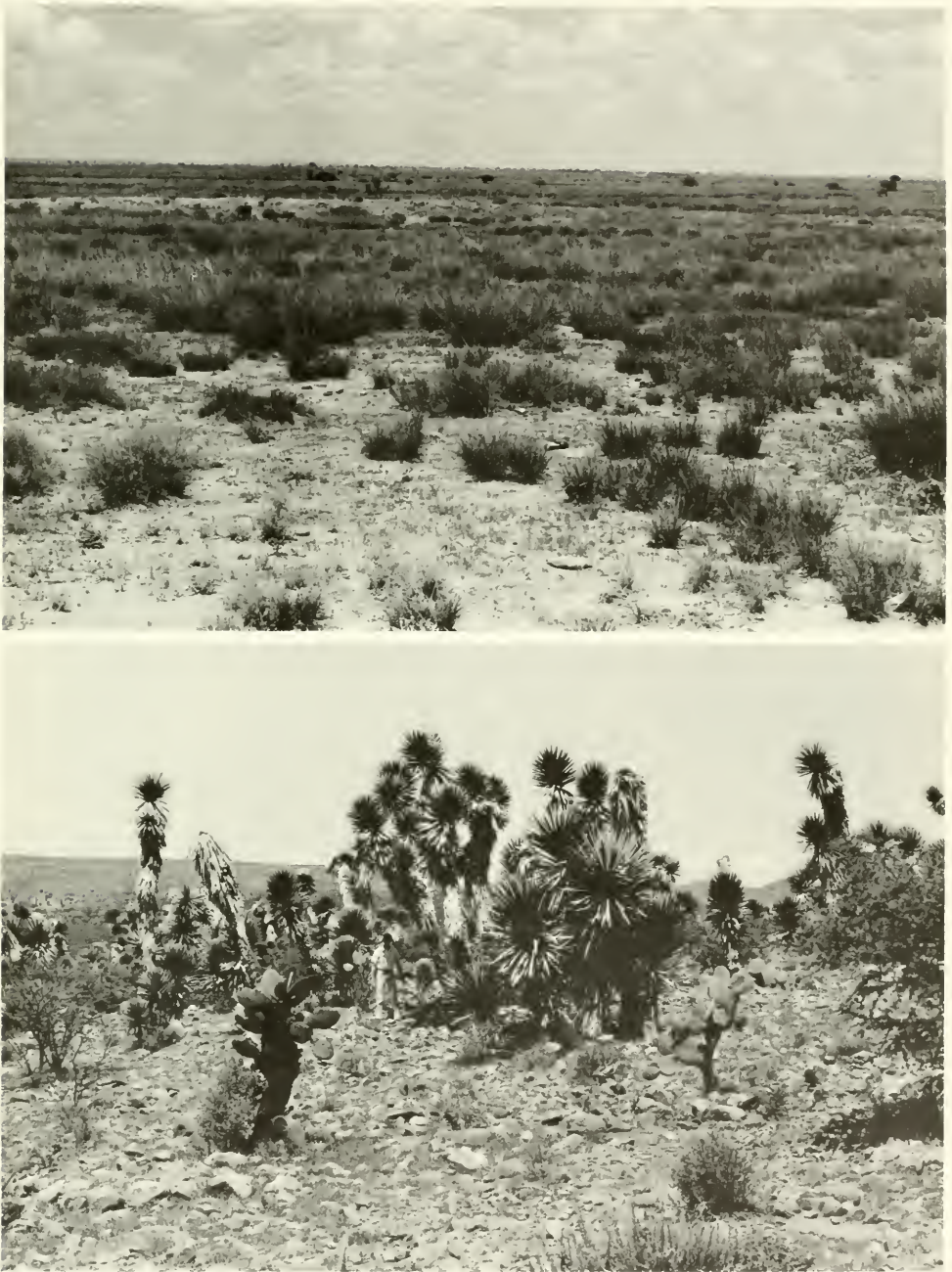


FIG. 3. Mesquite-Grassland. Top, ca. 182 airline km N Durango (3 km E La Zarca), Durango (24 July 1973). Bottom, foothill tree-yucca habitat, 4 km W Tapias, Durango (22 July 1973, both photographs by Richard C. Lovelace, Jr.).



FIG. 4. Pine-Oak, 10 road km SW El Salto, Durango (both photographs 11 July 1970 by author).

305 m (1000 ft) above this general level. A few kilometers west of Buenos Aires the Pine-Oak merges with the Mixed Boreal-Tropical region near 2408 m (7900 ft).

Mixed Boreal-Tropical (Fig. 5)

This habitat is unique, is relatively sharply delimited, and is somewhat transitional between the Pine-Oak and, at lower elevations, the Trop-

ical-Deciduous. The Mixed Boreal-Tropical covers rugged, mountainous terrain at the highest elevations in large barrancas and canyons, and is best developed on south-facing slopes. Steep boulder-strewn hillsides with rock outcrops, interrupted by small, relatively level areas, are covered in most places with a tall pine-oak woodland and often a dense understory of herbs, shrubs, and thick tangles of vines. Common pines are *Pinus oocarpa*, *P. teocote*, and *P. lunnholtzi* (the

“pino triste,” an indicator species for this region). Oaks include *Quercus macrophylla* (broadleaf), *Q. fulva*, and *Q. viminea*; other large trees are madroño (*Arbutus glandulosa*), and in some places magnolia (*Magnolia shiedeana*) and hop-hornbeam (*Ostrya virginiana*). The understory, dense in places, includes the large shrubs *Tithonia calva*, *Rhus terebinthifolia*, and *Cercocarpus macrophyllus*, tall herbs of the genus *Stevia* (spp.), the tree-like *Bocconia arborea*, thick brambles of *Rubus*, and some poison ivy (*Toxicodendron*). Open hillsides may have bracken fern (*Pteridium*) and scattered magueys and small prickly pears. Secluded moist areas may harbor begonias (*Begonia*) and a tropical bamboo palm (*Chamaedorea*). Orchids, ferns, lichens, and mosses are common, and many are epiphytic with bromeliads (most common are *Tillandsia exserta* and *T. benthamiana*) and mistletoe (*Psittacanthus*, usually on oaks). Along with mosquitoes, biting black flies (*Simulium*) are a nuisance in the rainy season. The Mixed Boreal-Tropical, recognized elsewhere in Durango (Webb and Baker 1962), has some resemblance to a cloud forest.

This region occurs for approximately 51 km (32 mi) along Highway 40 between elevations of 2408 (7900) and 1798 m (5900 ft). Some 8 or 9 km (5–6 mi) west of Buenos Aires the transition from the Pine-Oak is observed as the highway slowly descends on southerly facing slopes of large barrancas; about 13 or 14 km (8 mi) west of Buenos Aires, the vegetation has a tropical aspect with mosses, ferns, and dripping water on the sheer rock walls of the roadcuts. About 15 km (9 mi) west of El Palmito the highway crosses a saddle at Loberas onto the uppermost western slopes of the Sierra Madre and into a transitional zone with the Tropical-Deciduous.

Tropical-Deciduous (Fig. 6)

The Tropical-Deciduous covers most of the west-facing slopes of the Sierra Madre. At the highest elevations pines and oaks are common on the exposed tops of hills, but at lower elevations (ca. 1069 m or 3500 ft, and 4 km below Santa Lucía) pines are replaced by oaks, which in turn are mostly absent below 884 m (2900 ft). The oak woodland consists of both deciduous and evergreen species of *Quercus*. The probable climax vegetation, modified by clearing on many

hillsides, is most lush in the shaded and narrow mountainous ravines and arroyos and in the larger canyon bottoms. Trees and shrubs include morning-glory tree (*Ipomoea arborescens*), guavas (*Psidium*), sugar apple (*Annona squamosa*) pricklenut (*Guazuma ulmifolia*), coledo (*Oreopanax peltatum*), sandboxtree (*Hura polyandra*), the large eardrop tree (*Enterolobium cyclocarpum*), the *Acacia*-like *Lysiloma divaricata*, large figs (*Ficus*), as well as the genera *Brosimum*, *Ceiba*, *Haematoxylum*, *Bursera*, and *Acacia*. There is also some bamboo and, in broader valleys, bananas and papayas. Fresh-water crabs (*Pseudothelphusa*) occur in cascading rocky streams.

The Tropical-Deciduous occurs for about 77 km (48 mi) along the highway between elevations of about 1798 and 122 m (5900 and 400 ft). Thorny acacias become increasingly abundant at lower elevations and with the advent of organ-pipe cactus indicate the transition to the coastal lowland Thorn-Scrub; this rather broad transitional zone seems to extend from near Chupaderos to the vicinity of Concordia.

Thorn-Scrub (Fig. 7)

The vegetation of the Thorn-Scrub forms dense thickets, averaging about 7 to 9 m (25–30 ft) in height, and covers the coastal plain that is some 32 to 40 km (20–25 mi) wide. The relatively level terrain becomes increasingly more hilly inland with extensive rock outcrops in some places. The plant cover consists principally of species of *Acacia* (mostly *A. cymbispina*), *Mimosa*, *Cassia*, *Caesalpinia*, and *Bursera*, and the guamuchil (*Pithecolobium sonora*). The organ-pipe cactus (*Pachycereus pecten-aboriginum*) is scattered and characteristic. Terrestrial bromeliads and prickly pear, as well as some of the plants of the Tropical-Deciduous, are of occasional occurrence. Along the coast, water hyacinth mats are common in the rainy season in roadside sloughs. Large coconut palms (*Cocos nucifera*) occur near the beach and a mangrove (*Rhizophora mangle*) fringes coastal areas. Much of this habitat on either side of the coast highway between Villa Unión and Mazatlán is now being cleared for various purposes.

GAZETTEER

The place-names listed below, arranged alphabetically by states, are those mentioned in



the text. Each locality is followed by descriptive remarks, including approximate road distance from other localities, elevation, and faunal region. Most localities are indicated by signposts. All place-names along the transect route are not mentioned below. Elevations are approximate; they may vary many meters (depending on air pressure) when recorded at the same place at different times. Each entry terminates with a number in parentheses, which indicates its geographic position on the maps (Figs. 1 and 2).

Durango

Buenos Aires: Small settlement 4.8 km (3 mi) west La Ciudad and 3.2 km (2.2 mi) east Puerto Buenos Aires, 2591 m (8500 ft), Pine-Oak (15).

Coyotes, Estación: Lumber town about 2 km off highway, 4 km (2.5 mi) east Hacienda Coyotes and 12 km (7.3 mi) west Llano Grande, 2408 m (7900 ft), Pine-Oak (19).

Coyotes, Hacienda: Ranch 7 km (4 mi) east El Salto, 2454 m (8050 ft), Pine-Oak (19).

Durango (Ciudad): Capital of state and eastern terminus of transect, 320 km (198 mi) from Mazatlán and 92.5 km (57.5 mi) east El Salto; mileage from highway at Parque Guadiana on west side of city, 1905 m (6250 ft), Mesquite-Grassland (26).

El Espinazo (Espinazo del Diablo): Ridge (Devil's Backbone) connecting two ranges with drops of several hundred meters on either side; roadside stop and scenic view where monument commemorates dedication of completion of highway on 30 November 1960; 13 km (8 mi) west Puerto Buenos Aires and 20 km (12.3 mi) east Revolcaderos, 2377 m (7800 ft), Mixed Boreal-Tropical (13).

El Mil Diez: Small village, 2 km north highway at 1.2 km (0.8 mi) west El Salto, 2515 m (8250 ft), Pine-Oak (18).

El Salto: Large lumber town about 93 km (58 mi) west Durango and 95 km (59 mi) east El Palmito, Sinaloa, 2469 m (8100 ft), Pine-Oak (18).

La Ciudad (=Ciudad): Old lumber camp-town 26.3 km (16.4 mi) west Las Adjuntas and 4.8 km (3 mi) east Buenos Aires, 2484 m (8150 ft), Pine-Oak (16).

Las Adjuntas: Small village 17.7 km (11 mi) west El Salto, 2515 m (8250 ft), Pine-Oak (17).

Llano Grande: Large ejido 22.2 km (13.8 mi) east El Salto and 70.3 km (43.7 mi) west Durango, 2408 m (7900 ft), Pine-Oak (20).

Los Bancos: Small village observed about 1 km south of highway, 7 km (4.2 mi) west Puerto Buenos Aires and about 6 km (3.3 mi) east El Espinazo, 2286 m (7500 ft), Mixed Boreal-Tropical (14).

Metates: Small ejido on east brim of Arroyo Río Chico, 20.9 km (13 mi) west Durango and 4.0 km (2.5 mi) east Río Chico, 2195 m (7200 ft), Mesquite-Grassland/Pine-Oak transition (25).

Mimbres: Small village in Barranca de los Mimbres, 14.5 km (9 mi) west Río Chico and 30.9 km (19.2 mi) east Llano Grande, 2225 m (7300 ft), Mesquite-Grassland/Pine-Oak transition (23).

Navios: Small village about 11.3 km (7 mi) west Rancho Santa Barbara and 17.7 km (11 mi) east Llano Grande, 2438 m (8000 ft), Pine-Oak (21).

Puerto Buenos Aires: Roadside stop for scenic view, 3.2 km (2.2 mi) west Buenos Aires and 13 km (8 mi) east El Espinazo, 2560 m (8400 ft), Pine-Oak (15).

Rancho Santa Barbara (formerly Weicher Ranch): Cattle ranch 1.7 km (1.1 mi) west Mimbres and 29 km (18 mi) east Llano Grande, 2256 m (7400 ft), Mesquite-Grassland/Pine-Oak transition (22).

Revolcaderos: Small village 40.5 km (25.2 mi) west La Ciudad and 10.9 km (6.7 mi) east El Palmito, Sinaloa, 2042 m (6700 ft), Mixed Boreal-Tropical (12).

Río Chico: Small settlement in arroyo, 4.0 km (2.5 mi) west Metates and 14.5 km (9 mi) east Mimbres, 1981 m (6500 ft), Mesquite-Grassland/Pine-Oak transition (24).

Tapias: Small suburb of Durango, 3 km (1.9 mi) west Parque Guadiana, 1905 m (6250 ft), Mesquite-Grassland (26).

Weicher Ranch: See Rancho Santa Barbara.

Sinaloa

Chupaderos: Small village-truck stop at bridge across Río Chupaderos, 5.3 km (3.3 mi) west

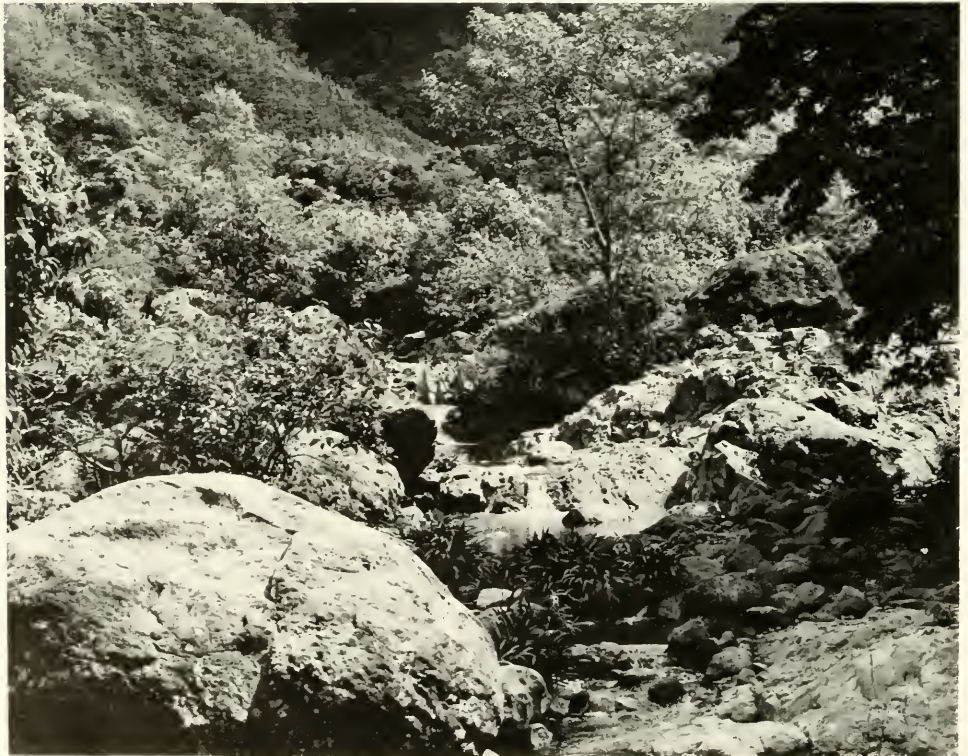




FIG. 7. Thorn-Scrubs. Top, leeward beachside thicket, 2 km N Mazatlán, Sinaloa (note startled ctenosaur atop organ-pipe cactus); habitat now destroyed (photograph 9 August 1957 by author). Bottom, 5 km E Villa Unión, Sinaloa (photograph 14 July 1973 by Richard C. Lovelace, Jr.).

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FIG. 6. Tropical-Deciduous. Top, panoramic view looking west showing Highway 40 and Santa Lucía, Sinaloa. Bottom, arroyo habitat with small creek, 2 km E Santa Lucía, Sinaloa (both photographs 13 July 1973 by Richard C. Lovelace, Jr.).

turnoff to Copala and 17.5 km (10.9 mi) east Concordia, 244 m (800 ft), Tropical-Deciduous/Thorn-Scrub transition (4).

Concordia: Large town 20.7 km (12.9 mi) east junction highways 40 and 15, 122 m (400 ft), Tropical-Deciduous/Thorn-Scrub transition (3).

Copala: Mining town (church observed in arroyo at Km signpost 70) reached by dirt road 2 km (1.2 mi) from turnoff at roadside truck stop (Copalita, mileages therefrom), 18 km (11.2 mi) west Santa Lucía and 5.3 km (3.3 mi) east Chupaderos, 579 m (1900 ft), Tropical-Deciduous (6).

El Batel: Small village 3.5 km (2.2 mi) east Potrerillos and 3.4 km (2.1 mi) west Loberas, 1646 m (5400 ft), Tropical-Deciduous (9).

El Palmito: Large village 1.2 km (0.8 mi) west Durango-Sinaloa state line and 14.1 km (8.8 mi) east Loberas, 1935 m (6350 ft), Mixed Boreal-Tropical (11).

Loberas: Roadside stop for scenic view westward (microondas station, and small group of casitas 0.8 mi to the east, erected in 1970's), 3.4 km (2.1 mi) east El Batel, 1922 m (6300 ft), Mixed Boreal-Tropical/Tropical-Deciduous transition (10).

Mazatlán: Seaport-tourist resort on small peninsula and western terminus of transect, about 22.5 km (14 mi) northwest Villa Unión, 15 m (50 ft), Thorn-Scrub (1).

Pánuco: Mining settlement 10 km (6 mi) by dirt road off highway at Km signpost 70, 1.1 km (0.7 mi) east Copala and 16.9 km (10.5 mi) west Santa Lucía, 640 m (2100 ft), Tropical-Deciduous (5).

Potrerillos: Highway construction village 8.5 km (5.3 mi) east Santa Lucía and 2.4 km (1.5 mi) west Santa Rita, 1615 m (5300 ft), Tropical-Deciduous (8).

Presidio (Presidio de Mazatlán): Same as Villa Unión (see Conant 1969:89, footnote); name retained for railroad stop, Estación Presidio, about 3 km south of Villa Unión, and for Río del Presidio (formerly Río Mazatlán).

Santa Lucía: Small village and truck stop, 18 km (11.2 mi) east Copala and 29.6 km (18.4 mi) west El Palmito, 1100 m (3600 ft), Tropical-Deciduous (7).

Santa Rita: Rancho and restaurant-bus stop, 1.1 km (0.7 mi) west El Batel and 2.4 km (1.5 mi) east Potrerillos, 1676 m (5500 ft), Tropical-Deciduous (9).

Villa Unión (formerly Presidio): Large town on south side of Río del Presidio, about 22.5 km (14 mi) southeast Mazatlán and 20.7 km (12.9 mi) from Concordia; mileage from junction of highways 40 and 15 about 1 km south of town, 30 m (100 ft), Thorn-Scrub (2).

COMPOSITION OF HERPETOFAUNA

This section documents the occurrence of the kinds of amphibians and reptiles in the five herpetofaunal regions along the transect. Introduced species (*Gehyra mutilata*, *Ramphotyphlops braminus*), the estuarine crocodile (*Crocodylus acutus*), sea turtles, and the sea snake (*Pelamis platurus*) are not included. Species will doubtless be added, especially in the Sinaloan tropical habitats. Known ranges probably will be extended northward (e.g., *Eumeces parvulus*) or southward (e.g., *Syrrhophus interorbitalis*, *Phyllorhynchus decurtatus*). The hiatus in geographic range of some excluded species will perhaps be rectified where records of occurrence to the north and south are not now available for the transect area (e.g., *Pseudoeurycea belli*, Lowe, Jones, and Wright 1968; *Terrapene nelsoni*, Smith and Smith 1980; *Tantilla bocourti*, McDiarmid, Copp, and Breedlove 1976; *Trimorphodon tau*, McDiarmid and Scott 1970, but see subsequent discussion of distribution patterns-barranca corridors).

Assignment of some species to faunal regions probably will be altered pending further data of collection (e.g., *Ctenosaura pectinata*, and several snakes, especially *Boa constrictor* and *Oxybelis aeneus*, which are here restricted to the Thorn-Scrub, probably occur in the adjacent Tropical-Deciduous). Taxa are assigned to a particular faunal region based on their overall distribution; several species (e.g., *Bufo kelloggi*, *B. marinus*, *B. marmoratus*, *Pachymedusa dactylos*, *Smilisca baudini*, *Coniophanes lateralis*) represented by many localities in, and assigned only to, the Thorn-Scrub penetrate eastward to the Chupaderos-Copala region, which is barely into but near the transition to the Tropical-Deciduous. No attempt is made to indicate relative abundance of species in particular faunal regions. Some species, however, are represented by only one locality in a region (e.g., *Hylactophryne tarahumaraensis*, *Sceloporus clarki*, *S. nelsoni*, *Eumeces brevisrostris*, *Pituophis deppei*, and *Crotalus molossus* in Mixed Boreal-Tropical;

Sceloporus jarrovi, *Gyalopion quadrangularis*, and *Crotalus lepidus* in Tropical-Deciduous) and seem to be of rare occurrence, not to mention the enigmatic *Anolis utowanae* in the Thorn-Scrub. Some species, excluded for various reasons, are discussed below.

Phrynohyas venulosa (Laurenti).—This large arboreal tree frog is reported from Presidio, Sinaloa by Boulenger (1882:327), Günther (1901[1885–1902]:272), and Gadow (1905:207). The record represents the northernmost on the west coast of México if the locality is correct. The vicinity of Villa Unión has been relatively well explored in recent years but no specimens have become available since.

Rana pipiens complex.—The taxonomic status and distribution of ranid frogs of the *R. pipiens* complex along the transect is unknown. In Sinaloa two species, *R. magnaocularis* and *R. forreri*, are sympatric at Concordia (Frost and Bagnara 1976:335). Frogs from the Pine-Oak region in Durango seem to represent the recently described *R. chiricahuensis* (Platz and Mecham 1979). Another taxon, presumably a subspecies of *R. berlandieri*, occurs in the Mesquite-Grassland of Durango.

Lepidochelys olivacea (Eschscholtz).—The ridley may be the most abundant species of sea turtle in the vicinity of Mazatlán. Carapaces and/or skulls were found on the beach north of Mazatlán on 12 August, 6 and 8 June, and 23 July (different years). Local fishermen say sea turtles (probably *Lepidochelys*) are caught in the vicinity of Mazatlán in July, August, and September; individuals float at the surface and are relatively easy to catch. Flesh and eggs are used locally for food. Some turtles nest near Mazatlán (North Beach and Isla de la Piedras) in May and early June, but adults are not captured then. The largest rookery in the general area is said to be south near Acaponeta, Nayarit.

Gehyra mutilata (Wiegmann).—This introduced lizard is abundant at night on the walls of beachfront establishments in Mazatlán. Increased urbanization along the beach north of Mazatlán as observed in the years since 1955 has favored the dispersal of this species. A hatchling (ca. 20 mm SVL, later destroyed) was active (night of 22 August) among window fixtures on the second floor of the Hotel Belmar. Both young and adults were captured on 7–8 June. Young geckos, about 25 mm SVL, have contrasting patterns of

dark brown and pale yellow spots on pale brown dorsal surfaces; these spots (brown and yellow alternating) are mostly in parallel rows on the back and tend to form bands on the tail. Yellow spots on the side of head tend to form pre- and postocular stripes. This juvenile pattern becomes obliterated with increase in size with the largest individuals mostly uniform pale brown or with evidence of indistinct yellow spots.

Urosaurus ornatus lateralis (Boulenger).—Hardy and McDiarmid (1969:141–142) discuss a questionable record for Presidio and mention the nearest locality as 36 miles north Mazatlán. These two localities are the southernmost for the species on the west coast of México. Occurrence of the species in the Mazatlán-Villa Unión area needs verification.

Coluber constrictor oaxaca Jan.—Wilson (1966) records one specimen of this snake from Coyotes, Durango. No other specimens are known from the state. The status of this species in Durango requires further study.

Geagras redimitus Cope.—Hardy and McDiarmid (1969:162) discuss the occurrence of this species of snake in Sinaloa based on the locality of “Mazatlán.” The only other few known records of occurrence in México are from the states of Michoacán and Oaxaca. Mazatlán may refer to another place of that name in Guerrero or Oaxaca (see comments concerning type-locality of *Sphaerodactylus torquatus* by Taylor 1947:304–305).

ACCOUNTS OF SPECIES

The amphibians and reptiles considered in the subsequent analysis of distributional patterns consist of 145 taxa. Discussion of them has been deferred for inclusion in the terminal APPENDIX.

DISTRIBUTION OF HERPETOFAUNA

The herpetofauna considered for distributional purposes consists of 145 taxa—2 salamanders (1.4%), 35 frogs (24.1%), 5 turtles (3.4%), 33 lizards (22.8%), and 70 kinds of snakes (48.3%). The assignment of these taxa to faunal regions allows for the discussion of the herpetofauna of each region and the distributional patterns along the transect. Representation of higher taxa in each of the five regions is shown in Table 1. The total number of taxa is greatest in the Thorn-Scrub

TABLE 1. Frequency (number and percentage) of higher taxa of amphibians and reptiles in the five herpetofaunal regions (MG, Mesquite-Grassland; PO, Pine-Oak; MBT, Mixed Boreal-Tropical; TD, Tropical-Deciduous; TS, Thorn-Scrub).

Taxa	MG (34)	PO (36)	MBT (32)	TD (45)	TS (72)
Caudata	1 (3%)	2 (6%)			
Anura	10 (29%)	7 (19%)	7 (22%)	13 (29%)	15 (21%)
Testudines	2 (6%)	2 (6%)		2 (4%)	3 (4%)
Sauria	7 (21%)	8 (22%)	10 (31%)	12 (27%)	16 (22%)
Serpentes	14 (41%)	17 (47%)	15 (47%)	18 (40%)	38 (53%)

(72). The kinds of frogs, lizards, and snakes decrease eastward in the tropical regions from Thorn-Scrub into the mountainous Tropical-Deciduous and Mixed Boreal-Tropical; however this trend does not correlate with the percentage of contained taxa, except for lizards (snakes relatively least and frogs most abundant in the Tropical-Deciduous). Snakes are the most abundant component in each region, especially in the Thorn-Scrub (53%). The Mesquite-Grassland, Pine-Oak, and Mixed Boreal-Tropical contain about the same number of taxa; no marked difference seems to exist in the relative percentages of higher taxa in the Mesquite-Grassland and Pine-Oak (slight decrease in frogs in Pine-Oak).

At least six species differentiate into subspecies along the transect. The two subspecies of *Hylactophryne augusti* in the Mesquite-Grassland and Tropical-Deciduous are doubtless interconnected through the inaccessible barranca habitats that provide for dispersal of tropical species eastward (see subsequent section, Barranca Corridors). Of interest is the occurrence of the two subspecies of *Arizona elegans* in the two geographically extreme faunal regions, the Mesquite-Grassland and Thorn-Scrub. Three subspecies of *Thamnophis cyrtopsis* form a continuum along the entire transect route, with *T. c. collaris* in the three tropical regions, *T. c. pulchrrilatus* in the Pine-Oak, and the nominate subspecies in the Mesquite-Grassland. *Thamnophis eques* is differentiated into two subspecies in the Pine-Oak and Mesquite-Grassland. One subspecies of *Crotalus lepidus* occurs in the Pine-Oak and another in the adjacent Mixed Boreal-Tropical and Tropical-Deciduous. Two subspecies of *Kinosternon integrum* (see account of species) occur on either side of the Sierra Madre with one subspecies in the Thorn-Scrub and Tropical-Deciduous and the other in Mesquite-Grassland and Pine-Oak.

Distributional Patterns

Endemism.—Each of the five recognized herpetofaunal regions contains endemic taxa—Mesquite-Grassland, 16 (47.1%, 3 frogs, 4 lizards, 9 snakes); Pine-Oak, 15 (41.7%, 1 salamander, 1 frog, 4 lizards, 9 snakes); Mixed Boreal-Tropical, 3 (9.4%, 1 frog, 1 lizard, 1 snake); Tropical-Deciduous, 8 (17.8%, 6 frogs, 1 lizard, 1 snake); Thorn-Scrub, 45 (62.5%, 11 frogs, 1 turtle, 9 lizards, 24 snakes). The degree of endemism (and total number of taxa) is about the same in the Mesquite-Grassland and Pine-Oak, but decreases in the tropical regions from the Thorn-Scrub eastward through the mountainous Tropical-Deciduous to the Mixed Boreal-Tropical. An endemism index (endemic taxa/non-endemic taxa) for each of the five regions marks the Thorn-Scrub (1.67) as most distinctive with a progressive decrease through the Mesquite-Grassland (0.89), Pine-Oak (0.71), Tropical-Deciduous (0.22) to the least distinctive Mixed Boreal-Tropical (0.10).

Variable Patterns.—Many kinds of amphibians and reptiles occur in two or more faunal regions. Ten taxa (1 salamander, 3 frogs, 2 turtles, 2 lizards, 2 snakes) occur only in the Mesquite-Grassland and Pine-Oak. Two of these (*Pituophis deppei* and *Crotalus molossus*) also occur in the adjacent Mixed Boreal-Tropical, whereas three (*Bufo occidentalis*, *Hyla arenicolor*, and *Sceloporus jarrovi*) that also occur in those three regions extend farther west into the Tropical-Deciduous. Six taxa (*Hylactophryne tarahumaraensis*, *Eumeces brevisrostris*, *Conopsis nasus*, *Diadophis punctatus*, *Storeria storerioides*, and *Crotalus pricei*) occur only in the Pine-Oak and Mixed Boreal-Tropical. Ten (3 frogs, 3 lizards, 4 snakes) occur only in the Mixed Boreal-Tropical and Tropical-Deciduous. Eight (4 lizards, 4 snakes) occur in all three tropical regions, Mixed

Boreal-Tropical, Tropical-Deciduous, and Thorn-Scrub; one of these (*Masticophis mentovarius*) that seems established in the Mesquite-Grassland is discussed below under Barranca Corridors. Sixteen taxa (2 frogs, 2 turtles, 3 lizards, 9 snakes) occur only in the Tropical-Deciduous and Thorn-Scrub. These variable distributional patterns are depicted in Fig. 2.

An unusual distributional pattern, not influenced by the east-west course of the transect, is the occurrence of four species in only the Mesquite-Grassland and Thorn-Scrub. This pattern, represented by *Scaphiopus couchi*, *Bufo punctatus*, *Hypsiglena torquata*, and *Arizona elegans* (two subspecies), is explained as southern attenuations of geographic ranges of Nearctic species on either side of the Sierra Madre.

Barranca Corridors.—The Sierra Madre Occidental is cut by many large barrancas and arroyos that provide corridors for the dispersal of tropical species eastward (all drainage westward to Pacific Ocean); the most notable involved drainage is that of the Río Mezquital with headwaters draining the vicinity of Ciudad Durango. Documentation of tropical species far to the east in these barrancas has been previously noted by Webb and Baker (1962) and by Crossin *et al.* (1973). Tropical species may extend into or very near non-tropical areas.

Dispersal of tropical species eastward in barranca corridors is exemplified by: 1) *Anolis nebulosus* and *Dryadophis cliftoni* near the brims, and *Geophis dugesi* in the more mesic bottoms, of large canyons near the Pine-Oak locality of Llano Grande, 2) a locality of 9.7 miles west Durango for *Trimorphodon tau* (Univ. New Mexico 22790) in Mesquite-Grassland, 3) the locality of "ca. 10 mi SW Durango" for *Elaphe triaspis* (Dowling 1960:76), 4) the occurrence of two specimens of *Masticophis mentovarius* from 6 miles southeast Durango and 7 miles northeast Durango (Johnson 1977:300), and 5) the doubtless continuity of populations of *Hylactophryne augusti* (disjunct along transect route, see species account) provided by rocky barranca habitats (an intervening locality for the species from such a habitat is 6 miles southeast Llano Grande, UTEP).

Faunal Assemblages

In an effort to determine the degree to which each of the four transition zones acts as a barrier

to east-west dispersal, I have compared only adjacent faunal regions along the transect. The numbers of taxa that bridge the four transitional zones between adjacent faunal regions are 15 (1 salamander, 5 frogs, 2 turtles, 3 lizards, 4 snakes), Mesquite-Grassland/Pine-Oak: 11 (3 frogs, 2 lizards, 6 snakes), Pine-Oak/Mixed Boreal-Tropical: 21 (5 frogs, 8 lizards, 8 snakes), Mixed Boreal-Tropical/Tropical-Deciduous; and 24 (2 frogs, 2 turtles, 8 lizards, 12 snakes), Tropical-Deciduous/Thorn-Scrub. The fewest number of shared taxa (11) suggests the most pronounced faunal break between the Pine-Oak and Mixed Boreal-Tropical. All 11 taxa that bridge the transition zone between those two regions extend their ranges west from the Pine-Oak (Fig. 2); this transition zone is thus most effective as a barrier to the eastern dispersal of tropical species. Ekman's (in Udvardy 1969:274) formula $A + B$ (total taxa of two compared regions)/ C (shared taxa), in which the highest numerical value indicates the greatest faunal change, also marks the most abrupt transition between the Pine-Oak and Mixed Boreal-Tropical with a value of 6.73 (Mesquite-Grassland/Pine-Oak, 4.67; Mixed Boreal-Tropical/Tropical-Deciduous, 3.67; Tropical-Deciduous/Thorn-Scrub, 4.87).

A slightly different manipulation of the numbers of total taxa in, and shared taxa between, each region marks the Mixed Boreal-Tropical as having the greatest discrepancy between percentages of shared taxa with adjacent regions (i.e., 65.6% of the taxa in this region is shared with the Tropical-Deciduous and only 34.4% is shared with the Pine-Oak, a difference of 31.2%). In the Tropical-Deciduous the discrepancy percentage of shared taxa with adjacent faunal regions is 6.7% (53.3% shared with Thorn-Scrub, 46.6% with Mixed Boreal-Tropical), and in the Pine-Oak is 10.2% (31.4% shared with Mixed Boreal-Tropical and 41.6% with Mesquite-Grassland). These data indicate the greatest east-west faunal break in the Mixed Boreal-Tropical, with the herpetofauna mostly aligned to the western tropical regions.

Although various formulas (primarily to adjust for the differences in magnitude of the two compared regions) have been proposed to indicate degree of faunal resemblance, all show the same general trend (as does Ekman's formula, see above). For example, the values based on the formulas of Jaccard, $C/N_1 + N_2 - C \times 100$, and Simpson, $C/N_1 \times 100$ (in Udvardy 1969:273),

and of Duellman (1965:677), $2C/N_1 + N_2 \times 100$ (here modified to avoid decimal fractions) when applied, respectively, to the four faunal transitions along the transect are: Mesquite-Grassland/Pine-Oak, 25.5, 44.1, and 40.6; Pine-Oak/Mixed Boreal-Tropical, 19.6, 34.4, and 32.8; Mixed Boreal-Tropical/Tropical-Deciduous, 37.5, 65.6, and 54.6; and Tropical-Deciduous/Thorn-Scrub, 25.8, 53.3, and 41.0. Lower values indicate fewer taxa in common to the two areas. These data indicate highest resemblance between the Tropical-Deciduous and Mixed Boreal-Tropical, about the same degree of resemblance between Mesquite-Grassland and Pine-Oak as between Thorn-Scrub and Tropical-Deciduous, and the least resemblance between Pine-Oak and Mixed Boreal-Tropical.

The distributional data, as well as the abrupt climatic change personally experienced in winter (see section on Physiography and Climate) emphasizes the distinction between the Pine-Oak and Mixed Boreal-Tropical. This transition corresponds to that between two major herpetofaunal assemblages, the classic Neotropical and Nearctic zoogeographical realms. Northern Nearctic and southern Neotropical species overlap on either side of the Sierra Madre along the east-west trending transect.

Nearctic Herpetofauna.—Aside from that of the Pine-Oak and most of the herpetofauna of the Mesquite-Grassland, some species of Nearctic affinities also have extended their ranges far to the south on the Pacific side of the Sierra Madre into tropical habitats.

Of the 93 taxa in the three tropical regions along the transect, 18 (19.4%) have Nearctic affinities, and all but one of them (*Gyalopion* recorded only once from the adjacent Tropical-Deciduous) are restricted to the coastal Thorn-Scrub. These 18 taxa, some of which seem to be near their southernmost extent of range (marked with asterisk), consist of four frogs (*Scaphiopus couchi*, *Bufo kelloggi*, **Bufo punctatus*, **Gastrophryne olivacea*), five lizards (**Coleonyx variegatus*, *Callisaurus draconoides*, *Holbrookia elegans*, *Sceloporus clarki*, *Eumeces callicephalus*), and nine snakes (**Arizona elegans*, *Gyalopion quadrangularis*, *Rhinocheilus lecontei*, *Phyllorhynchus browni*, *Pituophis melanoleucus*, *Salvadora deserticola*, *Sonora aemula*, *Tantilla yakuia*, **Micruroides euryxanthus*). Some of these species are represented by tropically adapted subspecies.

Neotropical Herpetofauna.—Taxa of tropical affinities occur not only in the Pacific coastal Thorn-Scrub, Tropical-Deciduous, and Mixed Boreal-Tropical, but also in the Mesquite-Grassland that is composed mostly of Nearctic species. The tropical species in these two regions of the transect represent two different tropical assemblages.

The Pacific coastal assemblage comprises about 75 (80.6%) of the total of 93 taxa in the three tropical regions. Fifteen of these that seem to reach their northernmost extent of range in the transect area include seven frogs (*Eleutherodactylus hobartsmithi*, *Tomodactylus nitidus*, *T. saxatilis*, *Syrrophophus teretistes*, *Hyla bistincta*, *H. smaragdina*, *Gastrophryne usta*), four lizards (*Sceloporus bulleri*, *S. heterolepis*, *S. utiformis*, *Eumeces colimensis*), and four snakes (*Dryadophis cliftoni*, *D. melanolomus*, *Rhadinaea hesperia*, *Leptodeira maculata*).

Of the 34 taxa in the Mesquite-Grassland, 4 (11.8%) are judged to have tropical affinities with the Mesa Central, the southern tropical highland of the Mexican Plateau. The four taxa include one frog (*Bufo occidentalis*), one turtle (*Kinosternon integrum* subsp.), one lizard (*Sceloporus spinosus*), and one snake (*Pituophis deppei*).

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SUMMARY

In studying the distribution of 145 kinds of amphibians and reptiles across the Sierra Madre Occidental from Cd. Durango, Durango to Ma-

zatlán. Sinaloa, five herpetofaunal regions are recognized (from east to west)—Mesquite-Grassland, Pine-Oak, Mixed Boreal-Tropical, Tropical-Deciduous, and Thorn-Scrub. An enumeration of localities places each of the 145 taxa in one or more region and provides for a distributional analysis of the herpetofauna along the transect route. The total number of taxa is highest in the coastal Sinaloan Thorn-Scrub, and snakes are the most abundant component in each region. Each region contains endemic taxa with the highest percentage in the Thorn-Scrub. The most abrupt faunal break is between the Pine-Oak and Mixed Boreal-Tropical, which also marks the transition between the Nearctic and Neotropical zoogeographical realms. New state records include *Diadophis punctatus* and *Pituophis deppei* for Sinaloa, and *Dryadophis cliffloni* and *Salvadora bairdi* for Durango.

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KU—Museum of Natural History, University of Kansas
 MCZ—Museum of Comparative Zoology, Harvard University
 MSU—The Museum, Michigan State University
 UIMNH—University of Illinois Museum of Natural History
 UMMZ—Museum of Zoology, University of Michigan
 USNM—National Museum of Natural History
 UTEP—Laboratory for Environmental Biology, University of Texas at El Paso

The reference Hardy and McDiarmid (1969), often cited for Sinaloa localities, is abbreviated to "H-M: [page number]"; some localities cited by them are modified for more precise orientation in faunal regions (stated mileage presumably by road). Supplementary data are provided for some Sinaloa species. Data for species in Durango are minimal (usually only localities) owing to contemplated publication of more detailed information elsewhere.

Class Amphibia

Order Caudata

Family Ambystomatidae

Ambystoma roseaceum Taylor. Durango: Vicinity El Salto to near La Ciudad (Anderson 1961); 1.6 km W Buenos Aires (Welbourn and Loomis 1970:69, 71). Pine-Oak.

Ambystoma tigrinum subsp. Durango: Navios, 1 mi S Navios (AMNH); 4 mi NE Navios (UTEP); 13 mi N Durango (MCZ). The taxonomic status of these salamanders in Durango is uncertain. Mesquite-Grassland and Pine-Oak.

Order Anura

Family Pelobatidae

Scaphiopus couchi Baird. Durango: Vicinity Durango (Chrapliwy, Williams, and Smith 1961:86). Sinaloa: Mazatlán-Villa Unión area east to 4.7 mi NE Concordia (H-M:71-72). Recently metamorphosed toadlets were active in daytime on 11 July about temporary rain pools 1 mi N Mazatlán: 26 (UTEP) ranged in length from 9 to 19, averaging 13.8 mm. Mesquite-Grassland and Thorn-Scrub.

Scaphiopus multiplicatus Cope. Durango: Several specimens within seven-mile radius Durango, 10 mi W Metates, 15 mi E Coyotes (MSU); 6 mi SE Llano Grande (UTEP). Mesquite-Grassland and Pine-Oak.

Family Leptodactylidae

Eleutherodactylus hobartsmithi (Taylor). Sinaloa: Vicinity Chupaderos [24.8 mi E jct hwy 40-15 = ca. 1 mi E Chupaderos], Santa Lucía (H-M:73). Tropical-Deciduous.

Eleutherodactylus occidentalis Taylor. Sinaloa: 7.1 mi E Concordia, 9.8 mi E Concordia, 15.7 mi E Concordia (H-M:74); 5 mi SW Copala, 2 mi SW Santa Lucía (MSU). The two MSU specimens were active at

APPENDIX

This appendix provides accounts of the 145 taxa that formed the data base for the analysis of distributional patterns. Accounts are brief, the primary intent being only to provide locality records that indicate occurrence in one or more of the faunal regions. Place-names are explained in the gazetteer and geographically oriented in Figs. 1 and 2. Localities are documented by either literature citations or by museum acronyms, the latter indicating one or more specimens in the following institutions:

- AMNH—American Museum of Natural History
- CSULB—California State University Long Beach (specimens now presumably in Los Angeles County Museum Natural History)

night on dirt roads in the rainy season (30 July and 1 August 1960). Food in the stomach of the Copala specimen (identified by Dr. George W. Byers, Department of Entomology, University of Kansas) consisted of: Neuroptera, Myrmeliontidae (1 larva); Diptera, Tipulidae, *Limonia*; Lepidoptera, Noctuidae (1 larva); Phalangida (2 specimens); and many earthworm fragments. Tropical-Deciduous.

Eleutherodactylus vocalis Taylor. Sinaloa: Vicinity Chupaderos [MCZ Concordia locality close to Chupaderos; 24.8 mi E jct hwy 40-15 = ca. 1 mi E Chupaderos] east to Santa Lucía and Potrerillos (H-M:75). Tropical-Deciduous.

Hylactophryne augusti cactorum (Taylor). Sinaloa: Vicinity Santa Lucía, 6-7 mi NE Concordia (H-M:72). Frogs of this species (KU), in company with individuals (KU) of the more frequently observed *Eleutherodactylus vocalis* (Webb 1960:289), were obtained at night as they perched on boulders wet from splashing water of a cascading stream near Santa Lucía. Tropical-Deciduous.

Hylactophryne augusti latrans (Cope). Durango: 2.5 mi W Tapias (AMNH). Durango specimens, tentatively assigned to *H. a. latrans*, may represent intergrades with *H. a. cactorum* (Zweifel 1967:41.3). Mesquite-Grassland.

Hylactophryne tarhumaraensis Taylor. Durango: 10 mi NW Las Adjuntas, 6 mi WSW Las Adjuntas (Zweifel 1956:29); 5.5 mi SW El Salto (KU); 6 mi SW El Salto (UTEP); 2 mi E El Espinazo (CSULB). Pine-Oak and Mixed Boreal-Tropical.

Leptodactylus melanonotus (Hallowell). Sinaloa: Mazatlán-Villa Unión area, 11 and 12 mi NE Concordia (H-M:78, as *L. occidentalis*). Thorn-Scrub.

Syrhophus teretistes Duellman. Sinaloa: Several localities extending from 3.4 mi NE Concordia to vicinity El Batel [47.2 mi NE Villa Unión = 1.4 mi NE El Batel] (H-M:78, as *S. modestus*). Tropical-Deciduous.

Tomodactylus nitidus petersi Duellman. Durango: 0.5 mi W Revolcaderos (MSU); 49 mi NE Concordia. Sinaloa [=ca. 1.5 mi SW Revolcaderos] (H-M:78). Sinaloa: Vicinity Santa Lucía east to Santa Rita and El Batel [47.2 mi NE Villa Unión = 1.4 mi NE El Batel] (H-M:78); 8 (road) mi W El Palmito (UTEP). Mixed Boreal-Tropical and Tropical-Deciduous.

Tomodactylus saxatilis Webb. Durango: 0.5 mi W Revolcaderos (MSU); 23.5 km SW Buenos Aires [=7.5 mi NE Revolcaderos] (Welbourn and Loomis 1970:71). Sinaloa: 8 (road) mi W El Palmito (H-M:79). Mixed Boreal-Tropical.

Family Bufonidae

Bufo cognatus Say. Durango: Several specimens within eight-mile radius Durango (AMNH, MSU, UTEP). Mesquite-Grassland.

Bufo compactilis Wiegmann. Durango: "near Durango, NE city" (UMMZ); 2 mi NE Coyotes, 9.7 mi NE El Salto, 10 mi W Metates (Webb 1972:1-2). Mesquite-Grassland and Pine-Oak.

Bufo debilis insidiar Girard. Durango: 5 mi S Durango (MSU). Mesquite-Grassland.

Bufo kelloggi Taylor. Sinaloa: Mazatlán-Villa Unión

area east to 4.7 mi NE Concordia and Copala (H-M:80). Thorn-Scrub.

Bufo marinus (Linnaeus). Sinaloa: Mazatlán-Villa Unión area east to 2 mi ENE Copala and 1 mi W Pánuco (H-M:81). Thorn-Scrub.

Bufo marmoratus Wiegmann. Sinaloa: Mazatlán and Villa Unión east to vicinity Chupaderos [26 mi NE Villa Unión = 2 mi NE Chupaderos] (H-M:82). Thorn-Scrub.

Bufo mazatlanensis Taylor. Sinaloa: Mazatlán-Villa Unión area east to 0.6 mi W Santa Lucía and 27.2 mi NE Concordia [=1.8 mi E Santa Lucía] (H-M:83-84). Tropical-Deciduous and Thorn-Scrub.

Bufo microscaphus mexicanus Brocchi. Durango: Several localities vicinity El Salto and Las Adjuntas (Webb 1972:5); 9 mi E El Espinazo [=1 mi E Puerto Buenos Aires] (CSULB). Pine-Oak.

Bufo occidentalis Camerano. Durango: 3 mi W Durango (UTEP), 10 mi SW El Salto (KU), 11 mi W La Ciudad (AMNH), 0.5 mi W Revolcaderos (MSU), 4 mi E El Palmito, Sinaloa (H-M:85). Sinaloa: Localities extending from 2.2 km NE Santa Lucía to 2.6 km SW El Palmito [47.2 mi NE Villa Unión = 1.4 mi NE El Batel] (H-M:85). Mesquite-Grassland, Pine-Oak, Mixed Boreal-Tropical, and Tropical-Deciduous.

Bufo punctatus Baird and Girard. Durango: Durango (AMNH); 2.5 mi W Tapias, Río Chico (UTEP). Sinaloa: 2 mi E Mazatlán, about 3 mi SE Mazatlán (H-M:86). Some literature records for Sinaloa attributed to Riemer by Hardy and McDiarmid (1969:86) seem to be in error. Riemer (1955:22) is only geographically orienting place-names in Sinaloa and other states. Mesquite-Grassland and Thorn-Scrub.

Family Hylidae

Hyla arenicolor Cope. Durango: Localities extending from Cerro de Mercado [=ca. 3 km N Durango] to 5 km W El Espinazo (Duellman 1970:698). Sinaloa: 44 mi NE Villa Unión, 47.2 mi NE Villa Unión [both localities near El Batel] (H-M:88); 6.4 km SE Santa Lucía (Welbourn and Loomis 1970:68); 8 (road) mi W El Palmito (UTEP). Mesquite-Grassland, Pine-Oak, Mixed Boreal-Tropical, and Tropical-Deciduous.

Hyla bistincta Cope. Durango: 5 km W El Espinazo (Duellman 1970:698). Sinaloa: 1.6 km E Santa Lucía (Duellman 1970:699). Mixed Boreal-Tropical and Tropical-Deciduous.

Hyla eximia Baird. Durango: Localities vicinity Durango west to 53 km SW El Salto and 14 km E El Espinazo [both localities near Puerto Buenos Aires] (Duellman 1970:702). Mesquite-Grassland and Pine-Oak.

Hyla smaragdina Taylor. Sinaloa: Localities extending from Copala east to Potrerillos [27.2 mi E Concordia = 1.8 mi E Santa Lucía] (H-M:89, Duellman 1970:712). Tropical-Deciduous.

Hyla smithi Boulenger. Sinaloa: Mazatlán-Villa Unión area east to 0.5 km S Santa Lucía and 11 mi NE Copala [=ca. 0.2 mi S Santa Lucía] (H-M:90). Tropical-Deciduous and Thorn-Scrub.

Pachymedusa dacnicolor (Cope). Sinaloa: Mazatlán-Villa Unión area east to 3.2 km SW Copala and 12 mi

NE Concordia [=ca. 2 mi SW Copala] (H-M:92-93). Thorn-Scrub.

Pterohyla fodiens Boulenger. Sinaloa: Mazatlán-Villa Unión area east to 4.7 mi NE Concordia (H-M:94). Thorn-Scrub.

Smilisca baudini (Duméril and Bibron). Sinaloa: Mazatlán-Villa Unión area east to 16.5 mi E Concordia [=2.3 mi NE Copala] (H-M:95-96). Thorn-Scrub.

Tripiron spatulatus spatulatus (Günther). Sinaloa: Localities in Mazatlán-Villa Unión area east to vicinity Concordia (H-M:88). Thorn-Scrub.

Family Microhylidae

Gastrophryne olivacea (Hallowell). Sinaloa: Mazatlán-Villa Unión area east to 5 km SW Concordia (H-M:98). Thorn-Scrub.

Gastrophryne usta (Cope). Sinaloa: Presidio and Venadillo [near Mazatlán], east to 4 km NE Concordia and 4.5 mi NE Concordia (H-M:99); 9 mi N Mazatlán, 11 mi SE Villa Unión (Nelson 1972:131). Thorn-Scrub.

Hypopachus variolosus (Cope). Sinaloa: Mazatlán-Villa Unión area east to 4.5 mi NE Concordia and 9 km NE Concordia (H-M:100, as *H. o. oxyrrhinus*). Thorn-Scrub.

Family Ranidae

Rana pustulosa Boulenger. Sinaloa: Several localities vicinity Santa Lucía (21 km in error for 2.1 km E Santa Lucía for KU 44631), 7.2 mi W Santa Rita (H-M:103); 14 mi SW El Batel, 10 mi NE El Batel [=ca. 1 mi W El Palmito] (Zweifel 1954a:131-132, H-M:103); cave below (west) Copalita [see Copala] (LACM). The above records of occurrence combine those listed by Hardy and McDiarmid (1969:103) for *R. pustulosa* and *R. sinaloae*. The two names are synonyms, the large holotype of *R. pustulosa* being indistinguishable from large females of *R. sinaloae*. However, some frogs from the Santa Lucía area (e.g., MCZ 32591-94) show features of *Rana tarahumarae*. For purposes of this report only one taxon is recognized. Mixed Boreal-Tropical and Tropical-Deciduous.

Class Reptilia

Order Testudines

Family Kinosternidae

Kinosternon hirtipes murrayi Glass and Hartweg. Durango: Several localities vicinity Durango extending west to 6 mi ENE El Salto (Smith and Smith 1980:146-147). Mesquite-Grassland and Pine-Oak.

Kinosternon integrum subsp. Durango: Localities vicinity Durango extending west to Hacienda Coyotes (Smith and Smith 1980:122). Sinaloa: Mazatlán-Villa Unión area east to vicinity Santa Lucía (H-M:104-105, Smith and Smith 1980:130). In this report two subspecies of *K. integrum* are recognized—Sinaloan specimens having coarse yellow-blotched head patterns in Thorn-Scrub and Tropical-Deciduous, and Durangan specimens that lack contrasting blotched head patterns

in Mesquite-Grassland and Pine-Oak. Fragmentary data on eggs deposited by a captive female (Río del Presidio, Sinaloa) are: 9 eggs (total), deposited 6 October (5), 8 October (2), and 11 October (2 eggs); weights (taken 6-13 October) ranged from 3.74 to 5.30, averaging 4.2 gm; measurements (taken 13 October) of length ranged from 25.0 to 27.1, averaging 25.6 mm, and of width from 15.4 to 16.8, averaging 16.3 mm.

Family Emydidae

Pseudemys scripta ornata (Gray). Sinaloa: Mazatlán-Villa Unión area (H-M:106, Smith and Smith 1980:518). Thorn-Scrub.

Rhinoclemmys pulcherrima rogerbarbouri (Ernst). Sinaloa: Mazatlán, Presidio de Mazatlán, 9 mi W Concordia, 7.5 mi E Concordia, Santa Lucía (H-M:107, Smith and Smith 1980:397). Thorn-Scrub and Tropical-Deciduous.

Order Squamata—Suborder Sauria

Family Gekkonidae

Coleonyx variegatus fasciatus (Boulenger). Sinaloa: 10 mi S Presidio, 7.4 mi S jct hwy 15 and 40 (H-M:110). Thorn-Scrub.

Phyllodactylus tuberculosus saxatilis Dixon. Sinaloa: Mazatlán-Villa Unión area east to near Santa Lucía (H-M:114). Over the relatively flat terrain in the immediate vicinity of Mazatlán and Villa Unión, these geckos occur under bridges and in road culverts. None could be found on likely rocky hillsides of oceanfront uplifts near Mazatlán. Tropical-Deciduous and Thorn-Scrub.

Family Iguanidae

Anolis nebulosus (Wiegmann). Durango: 0.5 mi W Revolcaderos (MSU, UTEP). Sinaloa: Mazatlán-Villa Unión area east to 5 km SW El Palmito (H-M:115-116). Gravid females were obtained on 22 and 29 June near Santa Lucía. Thorn-Scrub, Tropical-Deciduous, and Mixed Boreal-Tropical.

Anolis utowanae Barbour. Sinaloa: about 10 mi N Mazatlán (H-M:116). Thorn-Scrub.

Callisaurus draconoides bogerti Martín del Campo. Sinaloa: Several localities in immediate vicinity Mazatlán (H-M:119). Individuals seem mostly restricted to the leeward side of low sand dunes. Two gravid females were obtained on June 27; hatchlings and adult males and females were captured on 22 August (different years). Progressive urbanization along the beachfront north of Mazatlán, as witnessed in years since 1955, has eradicated suitable habitat for *Callisaurus*. Thorn-Scrub.

Ctenosaura pectinata (Wiegmann). Sinaloa: Mazatlán-Villa Unión area east to near Copala [1 mi S, 26 mi E Villa Unión] (H-M:124); 3 mi NE Copala (MSU). A low-flying hawk clutching a sizeable ctenosaur in its talons, alighted, and when startled, released the presumed prey unharmed (ca. 4 mi W Concordia, 30 June 1961). The record of *Ctenosaura* from La Ciudad, Durango is in error (see Conant 1969:86). Thorn-Scrub.

Holbrookia approximans subsp. Durango: Durango, Río Chico (AMNH); 4 mi E Durango (KU). The nomenclature is in accord with the as yet unpublished data of Ralph W. Axtell. Mesquite-Grassland.

Holbrookia elegans elegans Bocourt. Sinaloa: Mazatlán-Villa Unión area east to 10 km NE Villa Unión and 9.4 mi NE Villa Unión (H-M:126–127). North of Mazatlán, individuals do not occur in the sand-dune habitat with *Callisaurus draconoides*, but are found a few hundred meters inland in sparsely vegetated, open fields with a sandy substrate. The specific status of *H. elegans* anticipates ultimate documentation by Ralph W. Axtell. Thorn-Scrub.

Iguana iguana (Linnaeus). Sinaloa: Mazatlán-Villa Unión area (H-M:127–128). Just north of Mazatlán, a few hundred meters inland from the beach small iguanas rested at night on branches in a thorn-scrub thicket where the terrain was partly inundated by heavy rains (11 August 1957). Thorn-Scrub.

Phrynosoma douglasi brachycercum Smith. Durango: 5 mi N Durango (Reeve 1952:918, KU). Mesquite-Grassland.

Phrynosoma orbiculare bradti Horowitz. Durango: Coyotes (Smith 1939a:315). El Salto (Smith 1942:361), 10 mi E El Salto (Reeve 1952:940), La Ciudad (Boulenger 1885:242). Pine-Oak.

Sceloporus bulleri Boulenger. Durango: 0.5 mi W Revolcaderos (Webb 1967:206), 1.8 mi NE El Palmito, Sinaloa (AMNH). Sinaloa: Localities extending from vicinity Santa Lucía to near El Palmito [37 mi E Concordia = ca. 2 mi E Loberas] (Webb 1967:206; H-M:129); ca. 14 mi NNE Copala [ca. 2.5 mi SW Santa Lucía] (MCZ). Mixed Boreal-Tropical and Tropical-Deciduous.

Sceloporus clarki boulengeri Stejneger. Sinaloa: Mazatlán-Villa Unión area east to 5 km SW El Palmito (H-M:132–134). A gravid female (seven eggs) was obtained on 2 August 1960 (5 mi SW Copala). Mixed Boreal-Tropical, Tropical-Deciduous, and Thorn-Scrub.

Sceloporus grammicus microlepidotus Wiegmann. Durango: 7 mi SW Las Adjuntas, 2 mi E El Salto (Chrapliwy and Fugler 1955:124); La Ciudad (Boulenger 1885:233, Günther 1890[1885–1902]:72); Rancho Santa Barbara (MSU); Buenos Aires (AMNH). Pine-Oak.

Sceloporus heterolepis shannonorum Langebartel. Durango: 0.5 mi W Revolcaderos (Webb 1969:302, 307). Sinaloa: 5 km SW El Palmito, 8 mi (13 km) W El Palmito, 19.2 km NE Santa Lucía [=ca. 2.3 mi E Loberas] (H-M:139, Webb 1969:307); 37 miles by road from Concordia [=2 mi E Loberas or 6.8 mi W El Palmito, type-locality] (Langebartel 1959:25). Mixed Boreal-Tropical.

Sceloporus horridus albiventris Smith. Sinaloa: near Mazatlán (H-M:134). Thorn-Scrub.

Sceloporus jarrovi jarrovi Cope. Durango: 25 mi SE Durango (UTEP); 24 mi N Durango (UIMNH); 20 mi W Durango (AMNH); 10 mi W Metates (UTEP); El Salto (Dunn 1936:473); La Ciudad (Boulenger 1885:224, Günther 1890[1885–1902]:69); 16 mi SW La Ciudad, 17 mi NE El Batel, Sinaloa [=ca. 0.5 mi W Revolcaderos] (Zweifel 1954b:145). Sinaloa: 4.7 mi W El Palmito (UTEP), 10 mi NE El Batel (Zweifel 1954b:145), 1 km NE Santa Lucía (H-M:135). Mesquite-

Grassland, Pine-Oak, Mixed Boreal-Tropical, and Tropical-Deciduous.

Sceloporus nelsoni Cochran. Sinaloa: Mazatlán-Villa Unión area east to 5 km SW El Palmito (H-M:138). Mixed Boreal-Tropical, Tropical-Deciduous, and Thorn-Scrub.

Sceloporus poinsetti macrolepis Smith and Chrapliwy. Durango: Durango, Coyotes, La Ciudad (Smith 1938:614); El Salto, 10 mi W Durango (Smith and Chrapliwy 1958:268); 4 mi SW Coyotes (Chrapliwy and Fugler 1955:124); Buenos Aires (AMNH). Mesquite-Grassland and Pine-Oak.

Sceloporus scalaris Wiegmann. Durango: 9.9 mi W Durango (Ernest A. Linc. pers. comm.); localities extending from vicinity Neveria [=4 mi W La Ciudad] to 10 mi W Metates (Thomas and Dixon 1976:535). Mesquite-Grassland and Pine-Oak.

Sceloporus spinosus spinosus Wiegmann. Durango: Durango (Smith 1939b:93), 4 mi E Durango (KU), 2.5 mi W Tapias (UTEP). Mesquite-Grassland.

Sceloporus utiformis Cope. Sinaloa: Vicinity Villa Unión east to Santa Lucía area (H-M:140). Tropical-Deciduous and Thorn-Scrub.

Urosaurus bicarinatus tuberculatus (Schmidt). Sinaloa: Mazatlán-Villa Unión area east to Santa Lucía (H-M:141). The report of this species from La Ciudad, Durango is in error (see Conant 1969:86). Tropical-Deciduous and Thorn-Scrub.

Family Scincidae

Eumeces brevirostris bilineatus Tanner. Durango: Localities extending from 33 mi W El Salto [=near Los Bancos] east to Coyotes (Dixon 1969:14); localities extending from 24 km SW El Salto to 16 km E Llano Grande (Robinson 1979:11). Pine-Oak and Mixed Boreal-Tropical.

Eumeces callicephalus Bocourt. Sinaloa: 5 mi (8 km) N Mazatlán, Presidio (H-M:143, Robinson 1979:12); 1 mi N Mazatlán (MSU, UTEP). Four of these skinks (one adult, 12 July 1963, MSU; two adults and one hatchling, 23 July 1965, UTEP) were found in loose loamy soil among half-buried rocks, bricks, pieces of tile, and decaying palm fronds in a palm savanna. The three adults, 67, 72, and 73 mm SVL, have blue-brown tails and two have indistinct pale stripes on head and neck. The hatchling of 27 mm (colors in life) is black dorsally (head orange-brown) with dark blue tail, and pale orange head striping (ventrolateral stripe white on lip, yellow on neck). Midbody scale rows are 26, 26, 28, and 28. The record of *E. callicephalus* from La Ciudad, Durango (Boulenger 1887:378) is in error (see discussion by Conant 1969:86). Thorn-Scrub.

Eumeces colimensis Taylor. Sinaloa: 1.5–1.6 km E Santa Lucía (H-M:144, Robinson 1979:11). The only known Sinaloan specimen was foraging in early afternoon among rocks and dense broadleaf shrub-cover adjacent to a rocky, cascading stream. Another skink, believed to be this species, that later escaped was found in the morning of 5 August 1960 climbing up the side of our tent that was pitched in a level, dense herb-covered area, 5 mi SW Copala (just below Chupaderos). The small specimen was about 45 mm SVL, had a blue tail, whitish venter, broad white lateral stripes on anterior half of body, and a blackish head and back;

the pale head stripes were reddish. Tropical-Deciduous.

Eumeces lynxe belli (Gray). Durango: 30 mi E El Salto, Rancho Santa Barbara (Webb 1968:22). Pine-Oak.

Family Teiidae

Cnemidophorus costatus subsp. Sinaloa: Mazatlán-Villa Unión area east to 5 km SW El Palmito (H-M: 147, 148). Two subspecies, *C. c. huico* and *C. c. mazatlanensis*, intergrade in the transect area (not differentially influenced by faunal regions) and are not recognized in this study. Mixed Boreal-Tropical, Tropical-Deciduous, and Thorn-Scrub.

Cnemidophorus scalaris scalaris Cope. Durango: 5 mi S Durango (MSU); 2.5 mi W Tapias, Río Chico (UTEP). Mesquite-Grassland.

Family Anguillidae

Barisia imbricata ciliaris (Smith). Durango: Coyotes (Tihen 1949:245), 10 mi E El Salto (Tihen 1954:12), 15 km NE El Salto (MCZ), 10 mi SW El Salto (KU), 6 mi SE Llano Grande (UTEP). Pine-Oak.

Elgaria kingi ferruginea (Webb). Durango: 3.2 road mi NE El Palmito, Sinaloa (UTEP). Sinaloa: 1 km NE Santa Lucía (H-M:151). Mixed Boreal-Tropical and Tropical-Deciduous.

Gerrhonotus liocephalus liocephalus Wiegmann. Sinaloa: 7.2 mi E Santa Lucía, 19.2 km NE Santa Lucía, 5 mi SW El Palmito (H-M:151). Mixed Boreal-Tropical and Tropical-Deciduous.

Family Helodermatidae

Heloderma horridum horridum (Wiegmann). Sinaloa: Mazatlán area east to 2 mi ENE Copala (H-M: 153). Thorn-Scrub.

Order Squamata—Suborder Serpentes

Family Leptotyphlopidae

Leptotyphlops humilis dugesi (Bocourt). Sinaloa: Mazatlán, Presidio (H-M:156). Thorn-Scrub.

Family Boidae

Boa constrictor imperator Daudin. Sinaloa: Mazatlán-Villa Unión area east to 10 mi NE Concordia (H-M:156). Thorn-Scrub.

Family Colubridae

Adelophis foxi Rossman and Blaney. Durango: ¼ mi E El Mil Diez (Rossman and Blaney 1968). Pine-Oak. *Arizona elegans exposita* Klauber. Durango: 4.4 mi ESE Durango (UMMZ). Mesquite-Grassland.

Arizona elegans noctivaga Klauber. Sinaloa: 1.1 mi N Mazatlán (H-M:156). Thorn-Scrub.

Contiophanes lateritius lateritius Cope. Sinaloa: 8 km N Villa Unión and about 30 mi NE Villa Unión [=ca. 3 mi NE Copala] (H-M:157). Thorn-Scrub.

Conopsis nasus nasus Günther. Durango: 32.5 mi

W Durango City [=ca. 7 mi W Rancho Santa Barbara], 5 mi E El Salto (Tanner 1961:17); 0.5 mi W Revolcaderos (MSU, UTEP). Sinaloa: 19.2 km NE Santa Lucía [=ca. 2.3 mi E Loberas], 37 mi E Concordia [=ca. 2 mi E Loberas] (H-M:157). Pine-Oak and Mixed Boreal-Tropical.

Diadophis punctatus subsp. Durango: 32 mi W Durango [=ca. 6.5 mi W Rancho Santa Barbara] (McCoy 1964:47); 20 mi NW Los Coyotes (Gehlbach 1965: 307); 1.6 mi E El Palmito, Sinaloa (UTEP). Sinaloa: 1 mi W El Palmito (UTEP). The two UTEP specimens were found DOR. The Sinaloan specimen, the first recorded from that state, is badly mashed. Gehlbach (1965:305) regarded Durango ringneck snakes as intergrades (*D. p. dugesi* × *D. p. regalis*). Pine-Oak and Mixed Boreal-Tropical.

Dryadophis cliftoni Hardy. Durango: 0.5 mi W Revolcaderos (MSU), ca. 11 km W Los Bancos (AMNH). Sinaloa: 8 road mi SW El Palmito (UTEP); 19.2 km NE Santa Lucía, 1 km NE Santa Lucía, 1.1 mi W Santa Rita (H-M:158). The Durango specimens are the first recorded from that state. Mixed Boreal-Tropical and Tropical-Deciduous.

Dryadophis melanolomus stuarti Smith. Sinaloa: 8 km N Villa Unión (H-M:159). Thorn-Scrub.

Drymarchon corais rubidus Smith. Sinaloa: Mazatlán-Villa Unión area east to 2.2 km NE Santa Lucía (H-M:160). Tropical-Deciduous and Thorn-Scrub.

Drymobius margaritiferus fistulosus Smith. Sinaloa: Mazatlán, 5 mi N Mazatlán, Presidio (H-M:161). Thorn-Scrub.

Elaphe triaspis intermedia (Boettger). Sinaloa: Mazatlán-Villa Unión area east to Santa Lucía (H-M:162); 2.5 mi NE Santa Lucía (MSU). Tropical-Deciduous and Thorn-Scrub.

Geophis dugesi dugesi Bocourt. Durango: 1.8 mi NE El Palmito, Sinaloa (AMNH). Sinaloa: 19.5 mi SW Buenos Aires, Durango [=ca. 0.4 mi E El Palmito] (Fort Worth Museum of Science and History); Loberas at Km 1177 (AMNH); 5 km SW El Palmito, 19.2 km NE Santa Lucía [=ca. 2.3 mi E Loberas] (H-M:163, Webb 1977:551). Mixed Boreal-Tropical.

Gyalopion quadrangulare (Günther). Sinaloa: Mazatlán-Villa Unión area, and 3.2 km SW Santa Lucía (H-M:168–169, Hardy 1975:116). Tropical-Deciduous and Thorn-Scrub.

Heterodon nasicus kenerlyi Kennicott. Durango: 9 mi NE Durango (UIMNH), 29 km N Durango (Dunn 1936:476). Mesquite-Grassland.

Hypsigena torquata (Günther). Durango: Durango (AMNH), 16 mi N Durango (Zweifel 1954b:147), 2.5 mi W Tapias (UTEP). Sinaloa: Mazatlán-Villa Unión area east to 2.7 km NE Chupaderos (H-M:170–171). Nomenclature follows Hardy and McDiarmid (1969: 170). Mesquite-Grassland and Thorn-Scrub.

Imantodes gemmistratus latistratus (Cope). Sinaloa: Several localities vicinity Mazatlán, 2.2 km NE Santa Lucía (H-M:172–173). Tropical-Deciduous and Thorn-Scrub.

Lampropeltis getulus splendida (Baird and Girard). Durango: 5.1 mi ESE Durango (UMMZ). Mesquite-Grassland.

Lampropeltis mexicana (Garman). Durango: Mimbres (MCZ); Río Chico, Rancho Santa Barbara (Garstka 1982:31). Pine-Oak.

Lampropeltes triangulum sinaloae Williams. Sinaloa: Mazatlán-Villa Unión area east to 6 km SW Concordia (H-M:175, as *L. t. nelsoni*). Thorn-Scrub.

Leptodeira maculata Hallowell. Sinaloa: Mazatlán-Villa Unión area east to Santa Lucía (H-M:176). Tropical-Deciduous and Thorn-Scrub.

Leptodeira punctata (Peters). Sinaloa: Several records in Mazatlán-Villa Unión area (H-M:177–179). Thorn-Scrub.

Leptodeira septentrionalis polysticta Günther. Sinaloa: Three specimens from north of Mazatlán (the nearest, 29 km, H-M:179). Thorn-Scrub.

Leptodeira splendida ephippiata Smith and Tanner. Sinaloa: About 10 km SW Concordia, 12.3 km SW Santa Lucía, 2.4 km NE Santa Lucía, 14 mi SW El Batel, Presidio (H-M:180). Tropical-Deciduous and Thorn-Scrub.

Leptophis diplotropis (Günther). Sinaloa: Mazatlán-Villa Unión area east to 19.2 km NE Santa Lucía [=ca. 2.3 mi E Loberas] and 10.6 mi E Santa Lucía [=ca. 1 mi E Loberas] (H-M:182). Mixed Boreal-Tropical, Tropical-Deciduous, and Thorn-Scrub.

Masticophis bilineatus Jan. Sinaloa: Mazatlán-Villa Unión area east to 34 mi E Villa Unión [=ca. 4 mi SW Santa Lucía] (H-M:183). Tropical-Deciduous and Thorn-Scrub.

Masticophis flagellum lineatulus Smith. Durango: about 10 km SSE Durango (UTEP). Mesquite-Grassland.

Masticophis mentovarius striolatus (Mertens). Sinaloa: Mazatlán-Villa Unión area, 14 km E Concordia, Santa Lucía, 19.2 km NE Santa Lucía [=ca. 2.3 mi E Loberas] (H-M:186). Mixed Boreal-Tropical, Tropical-Deciduous, and Thorn-Scrub.

Masticophis taeniatus girardi Stejneger and Barbour. Durango: 8 mi W Durango (AMNH). Mesquite-Grassland.

Nerodia valida valida (Kennicott). Sinaloa: Mazatlán-Villa Unión area east to 24.8 mi E Villa Unión [=ca. 1 mi E Chupaderos] (H-M:187–188); Chupaderos on Río Chupaderos, 5 mi SW Copala (Conant 1969:88). Thorn-Scrub.

Oxybelis aeneus auratus (Bell). Sinaloa: Mazatlán-Villa Unión area, 4.4 mi SW Concordia, 20 mi E Villa Unión [=ca. 4 mi W Chupaderos] (H-M:189). Thorn-Scrub.

Phyllorhynchus browni Stejneger. Sinaloa: 10 km N Mazatlán (H-M:191). Thorn-Scrub.

Pituophis deppei deppei (Duméril). Durango: Coyotes, Llano Grande (Duellman 1960:605); 3 mi W Durango (UTEP). Sinaloa: 4 km E Loberas (12 km W El Palmito) (AMNH). The record for Sinaloa seems to be the first for that state. Mesquite-Grassland, Pine-Oak, and Mixed Boreal-Tropical.

Pituophis melanoleucus affinis Hallowell. Sinaloa: Mazatlán-Villa Unión area east to 5 mi SW Concordia (H-M:192). Thorn-Scrub.

Pseudoficimia frontalis (Cope). Sinaloa: Localities from 12.8 to 18.3 mi N Mazatlán, Presidio, 4 mi NE Concordia (H-M:194). Thorn-Scrub.

Rhadinaea hesperia Bailey. Sinaloa: Santa Lucía, 12.3 km SW Santa Lucía, 19.2 km NE Santa Lucía [=ca. 2.3 mi E Loberas] (H-M:194–195; Myers 1974:243); 2 km E Loberas, Km 1175 (Myers 1974:243). Mixed Boreal-Tropical and Tropical-Deciduous.

Rhadinaea laureata (Günther). Durango: Coyotes, 10 mi E El Salto, 10 mi SW El Salto (Myers 1974:244); 1 mi S Navios (AMNH); 6 mi SE Llano Grande (UTEP). Pine-Oak.

Rhinocheilus lecontei antonii Duges. Sinaloa: Mazatlán-Villa Unión area east to 1.4 mi E Concordia (H-M:195–196). Thorn-Scrub.

Salvadora bairdi Jan. Durango: 24 road mi W La Ciudad [=ca. 1 mi E Revolcaderos] (Univ. Arizona, Charles M. Bogert, pers. comm.). Sinaloa: 2.2 km NE Santa Lucía, 19.2 km NE Santa Lucía (H-M:198); 9 mi W El Palmito (MSU). The MSU specimen was found DOR, as well as another badly mashed specimen (from 4 mi SW El Palmito, Sinaloa) that was not saved. The Durango locality is the first in the state for this species. Mixed Boreal-Tropical and Tropical-Deciduous.

Salvadora deserticola Schmidt. Sinaloa: 9 mi N Mazatlán, 10 mi S Villa Unión (H-M:199). Thorn-Scrub.

Salvadora grahamiae grahamiae lineata Schmidt. Durango: 2.5 mi W. Tapias, 10 mi E El Salto (AMNH); 15 mi ENE El Salto (MCZ). Mesquite-Grassland and Pine-Oak.

Sonora aemula (Cope). Sinaloa: 40 mi S Mazatlán (McDiarmid, Copp, and Breedlove 1976:12). Thorn-Scrub.

Storeria storerioides (Cope). Durango: La Ciudad, El Salto (Anderson 1960:63). Sinaloa: 19.2 km NE Santa Lucía [=ca. 2.3 mi E Loberas], 9.6 mi SW El Palmito (H-M:201). Pine-Oak and Mixed Boreal-Tropical.

Sympholis lippiens Cope. Sinaloa: 9 mi N Mazatlán, 10.8 mi N Mazatlán, 13.3 mi SE Río Presidio (H-M:202). Thorn-Scrub.

Tantilla calamarina Cope. Sinaloa: Mazatlán, 29 km N Mazatlán (H-M:203). Thorn-Scrub.

Tantilla wilcoxi wilcoxi Stejneger. Durango: 15 km WSW Durango (MCZ), 2.5 mi W Tapias (MSU), Río Chico (UTEP). Mesquite-Grassland.

Tantilla yaquia Smith. Sinaloa: 5.8 mi N Mazatlán, 16 mi N Mazatlán (H-M:203, McDiarmid 1968:176). Thorn-Scrub.

Thamnophis cyrtopsis collaris (Jan). Durango: 1.6 km E Sinaloa-Durango state line (Webb 1966:62). Sinaloa: Mazatlán-Villa Unión area east to 5 km SW El Palmito (H-M:205–206). Mixed Boreal-Tropical, Tropical-Deciduous, and Thorn-Scrub.

Thamnophis cyrtopsis cyrtopsis (Kennicott). Durango: 12 mi N Durango, 10 mi W Metates. Río Chico (Webb 1966:59). Mesquite-Grassland.

Thamnophis cyrtopsis pulcherratus Cope. Durango: 2 mi NE El Salto, 3 mi E El Salto, Hacienda Coyotes (Webb 1966:66). Pine-Oak.

Thamnophis elegans errans Smith. Durango: Several localities extending from Hacienda Coyotes to 1 mi W Buenos Aires (Webb 1976:12). Pine-Oak.

Thamnophis eques megalops (Kennicott). Durango: Vicinity Durango west to 33 mi ENE El Salto [=Mimbres] and Rancho Santa Barbara (Conant 1963:487). Mesquite-Grassland.

Thamnophis eques virgatenuis Conant. Durango: Localities extending from near Coyotes west to 3 mi E Las Adjuntas (Conant 1963:490). Pine-Oak.

Thamnophis melanogaster canescens Smith. Durango: Durango, 6 mi E Durango, 10 mi N Durango, Río Chico, Mimbres, Coyotes, Hacienda Coyotes, 6 mi SW

El Salto, S side El Mil Diez (Conant 1963:481–482). Mesquite-Grassland and Pine-Oak.

Thamnophis nigronuchalis Thompson. Durango: 5.6 mi W El Salto (Thompson 1957:1), 6 mi SW El Salto (UTEP). Two snakes from Coyotes and from 33 mi ENE El Salto [=Mimbres], although referred to *Thamnophis rufipunctatus* (Thompson 1957:9; Conant 1963:480), were discussed by Conant (1963:481) as having features of *T. nigronuchalis*. Pending further study, *T. rufipunctatus* is excluded from consideration in this report. Pine-Oak.

Trimorphodon biscutatus biscutatus (Duméril, Bibron, and Duméril). Sinaloa: Mazatlán-Villa Unión area east to 4.8 km NE Santa Lucía (H-M:208, as *T. lambda paucimaculata*). Tropical-Deciduous and Thorn-Scrub.

Tropidodipsas annulifera Boulenger. Sinaloa: Mazatlán area east to Santa Lucía (H-M:209–210). Tropical-Deciduous and Thorn-Scrub.

Tropidodipsas philippi (Jan). Sinaloa: 31.6 mi N Mazatlán (H-M:210). Thorn-Scrub.

Family Elapidae

Micruroides euryxanthus neglectus Roze. Sinaloa: 16.3 mi NNW Mazatlán, 20 mi N Mazatlán (H-M:210–211). Thorn-Scrub.

Micrurus distans distans (Kennicott). Sinaloa: 9.9 mi N Mazatlán, 11.6 mi N Mazatlán, 9.1 mi NE Concordia, 6.5 km SW Concordia (H-M:211–212). Thorn-Scrub.

Family Viperidae

Agkistrodon bilineatus bilineatus (Günther). Sinaloa: 7.5 mi N Mazatlán, Mazatlán, Presidio (H-M:213); 4 mi SE Villa Unión (UTEP). Thorn-Scrub.

Crotalus basiliscus basiliscus (Cope). Sinaloa: Mazatlán-Villa Unión area east to 19.2 km NE Santa Lucía

(H-M:214–215); 4 km S Santa Lucía, 5 mi W Concordia (Armstrong and Murphy 1979:6); 5 mi W El Palmito, 8 road mi W El Palmito (UTEP). Mixed Boreal-Tropical, Tropical-Deciduous, and Thorn-Scrub.

Crotalus lepidus klauberi Gloyd. Durango: Rancho Santa Barbara (MSU), Coyotes (Gloyd 1940:112). Pine-Oak.

Crotalus lepidus maculosus Tanner, Dixon and Harris. Durango: 15 mi W La Ciudad and 16 mi SW La Ciudad [both ca. 2–3 mi W El Espinazo], 1 km W Los Bancos, 11 mi W La Ciudad [=ca. 2 mi E El Espinazo] (Tanner, Dixon, and Harris 1972:16–17). Sinaloa: 5 km SE El Palmito, 19.2 km NE Santa Lucía, 7 and 9 mi NE El Batel (H-M:216); 10 mi W Durango-Sinaloa state line, 4.8 mi E Santa Rita, 12.5 mi W El Palmito [=ca. 0.5 mi E Potrerillos] (Tanner, Dixon, and Harris 1972:16–17). Mixed Boreal-Tropical and Tropical-Deciduous.

Crotalus molossus nigrescens Gloyd. Durango: Coyotes, El Salto (Gloyd 1940:164); 16 km W Durango, 8.3 km E Coyotes, Los Bancos (Armstrong and Murphy 1979:33). Mesquite-Grassland, Pine-Oak, and Mixed Boreal-Tropical.

Crotalus pricei pricei Van Denburgh. Durango: Las Adjuntas, near Coyotes, 14 mi ENE El Salto, Llano Grande, Los Bancos (Armstrong and Murphy 1979:38). Pine-Oak and Mixed Boreal-Tropical.

Crotalus scutulatus scutulatus (Kennicott). Durango: 5 mi S Durango (MSU), 10 mi W Durango (AMNH), 2.5 mi W Tapias (UTEP). Mesquite-Grassland.

Crotalus stejnegeri Dunn. Sinaloa: 2.2 km NE Santa Lucía (H-M:217); between 10 and 15 mi NE Concordia, 10 mi E Concordia (McDiarmid, Copp, and Breedlove 1976:14). Tropical-Deciduous.

Crotalus willardi meridionalis Klauber. Durango: Coyotes and Weicher Ranch (Klauber 1949:133); near Llano Grande (Armstrong and Murphy 1979:65). Pine-Oak.

Systematic Review of the Percid Fish, *Etheostoma lepidum**

ALICE F. ECHELLE, ANTHONY A. ECHELLE, AND CLARK HUBBS

Until recently, the greenthroat darter, *Etheostoma lepidum* (Baird and Girard), was known only from south and central Texas in east-flowing drainages of the Edwards Plateau (Strawn 1955a, 1957). However, Hubbs and Echelle (1972) reported that Koster's (1957) "*Etheostoma* sp." in the Pecos River drainage of New Mexico is *E. lepidum*. This extended the known range of the species well to the north and west and to the opposite side of the High Plains Divide from the previously recognized distribution. Hubbs and Echelle (1972) noted that the New Mexico population had declined since the time of W. J. Koster's collections in the 1940's and 1950's. The disjunct occurrence and declining status of the New Mexico population prompted the present review of the species. Other studies of geographic variation in morphological characters of *E. lepidum* are Strawn's (1955a, 1961) descriptions of variation in dorsal fin color and five meristic characters of Texas populations. Hubbs (1967) described variation in survival of offspring from intra- and interspecific crosses involving several Texas populations, and Hubbs and Delco (1960) described some aspects of geographic variation in egg complements of Texas populations.

MATERIALS AND METHODS

Collections examined.—Museum abbreviations in the following list are: UNM = University of New Mexico Collection of Vertebrates; TNHC = Texas Natural History Collection of the Texas Memorial Museum, University of Texas at Austin; OSU = Museum Collection of Fishes, Oklahoma State University; TU = Tulane University. Collections used for counts and measurements are as follows (letters in parentheses refer to localities as given in Tables 1–5; complete locality data available from authors):

E. lepidum: Pecos River drainage: (A) OSU 11342, 11343, 11344; (B) UNM 50, 55; (C) UNM 52, 63; (D) UNM 51, 57, 59; (E) UNM 65, 66,

67, 3064; (F) UNM 53; (G) UNM 49. Colorado River drainage: (H) TNHC 2435, 3096; (I) TNHC 2071, 3121. Guadalupe River drainage: (J) TNHC 6116, 2977. Nueces River drainage: (K) TNHC 3225, 3057; (L) TNHC 5282, 3105, 5645.

E. grahami: Rio Grande drainage: (M) TU 27708; (N) TNHC 3264, 3615; (O) TNHC 3475, 3536.

Counts and Measurements.—Fin ray and scale counts and body measurements follow Hubbs and Lagler (1958) except as follows: number of transverse scale rows is counted from anal fin origin to base of first dorsal fin; two counts were made at minimum depth of caudal peduncle—scales above lateral line begins with the scale row above the lateral line and includes the median dorsal scale, scales below lateral line begins with the scale row below the lateral line and ends with the median ventral scale; caudal fin length is from caudal base to tip of middle ray; pectoral and pelvic fin lengths and heights of first and second dorsal fins are lengths of longest rays.

Scalation in various areas was coded as follows: 0 = no scales; 1 = one to several imbedded or exposed scales covering less than one-half the area; 2 = partially unscaled, but scales covering more than one-half the area; 3 = completely scaled. For the nape and belly, a score of 0 meant no scales on midline from, respectively, origin of dorsal fin to head and origin of anal fin to base of pelvics.

Etheostoma (Oligocephalus) lepidum

(Baird and Girard)

Figs. 1–2. Tables 1–5

Types and Nomenclature.—Baird's and Girard's (1853) original description of the species as *Boleosoma lepida*, was based on specimens collected from the Rio Leona, a tributary of the Nueces River, at Uvalde, Texas, by J. H. Clark during the first United States and Mexican Boundary Survey. Existing type specimens include one syntype at the University of Michigan Museum of Zoology (UMMZ 86335) and six syntypes at the U.S. National Museum of Natural History (USNM 744). Following article 74

* Dedicated to Henry S. Fitch and Virginia R. Fitch, esteemed parents and friends.

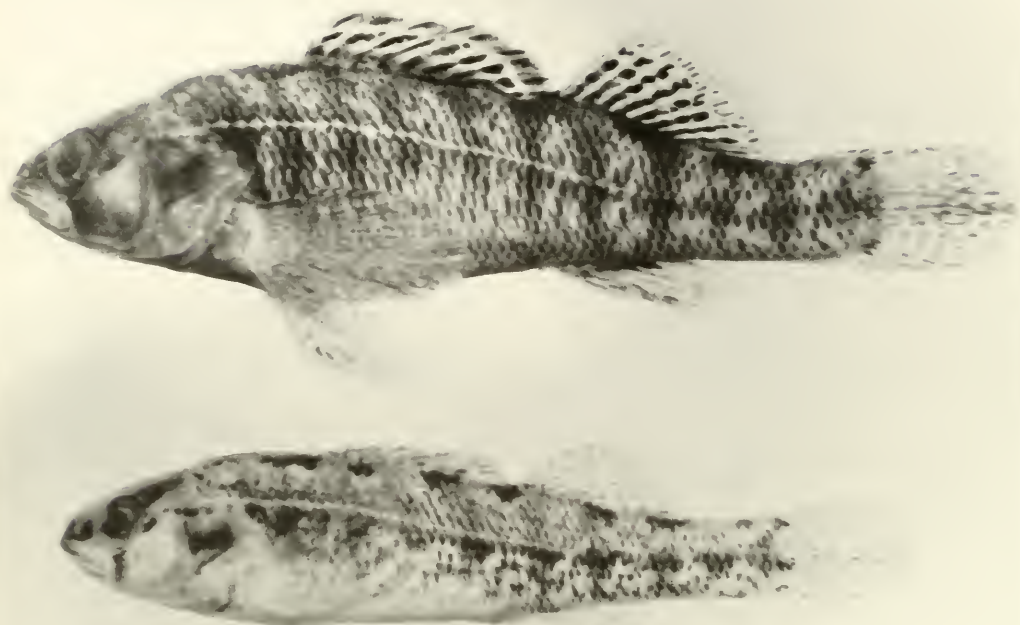


FIG. 1. Mature adults of *Etheostoma lepidum* from Sago Spring, upper end of Unit 4, Bitter Lake National Wildlife Refuge, Roswell, New Mexico. OSU 11342, 2 June 1971. Top, male, 45.1 mm SL. Bottom, female, 37.7 mm SL.

of the International Code of Zoological Nomenclature we designate as paralectotypes of *E. lepidum*, UMMZ 86335, and under a new catalog number (USNM 223024), five specimens of USNM 744. The sixth specimen of USNM 744 retains the original number as the lectotype. Girard (1859a) referred to *E. lepidum* from the upper Nueces (Leona River) as *Poeciliichthys lepidus* and, in a paper published in the same volume (Girard 1859b), described *Oligocephalus leonensis* as a new species, also from Leona River. Two syntypes bearing the latter name are at the Museum of Comparative Zoology (MCZ 24580) with the information that they were collected in the Nueces River by J. H. Clark and sent to MCZ from USNM in 1853. Evermann and Kendall (1894) regarded *O. leonensis* a junior synonym of *E. lepidum*. However, Collette and Knapp

(1966) noted that the syntypes have "well-developed ctenoid scales on the opercle, a character of *E. grahami* . . ." They note, however, that although badly dried, the body appears more elongate than in either *E. lepidum* or *E. grahami*. A junior synonym of *E. lepidum*, *Etheostoma lepidogenys*, was described by Evermann and Kendall (1894), from Comal Springs of the Guadalupe River drainage as a result of a mistaken comparison (Hubbs, Kuehne, and Ball 1953) with *E. spectabile* rather than *E. lepidum*. The two syntypes for the latter description are deposited at the National Museum of Natural History (USNM 44840). Hubbs, Kuehne, and Ball (1953) and Hubbs and Echelle (1972) used the trinomial, *E. lepidum lepidogenys* in reference to, respectively, Guadalupe River populations and "the Guadalupe-Colorado river stocks."

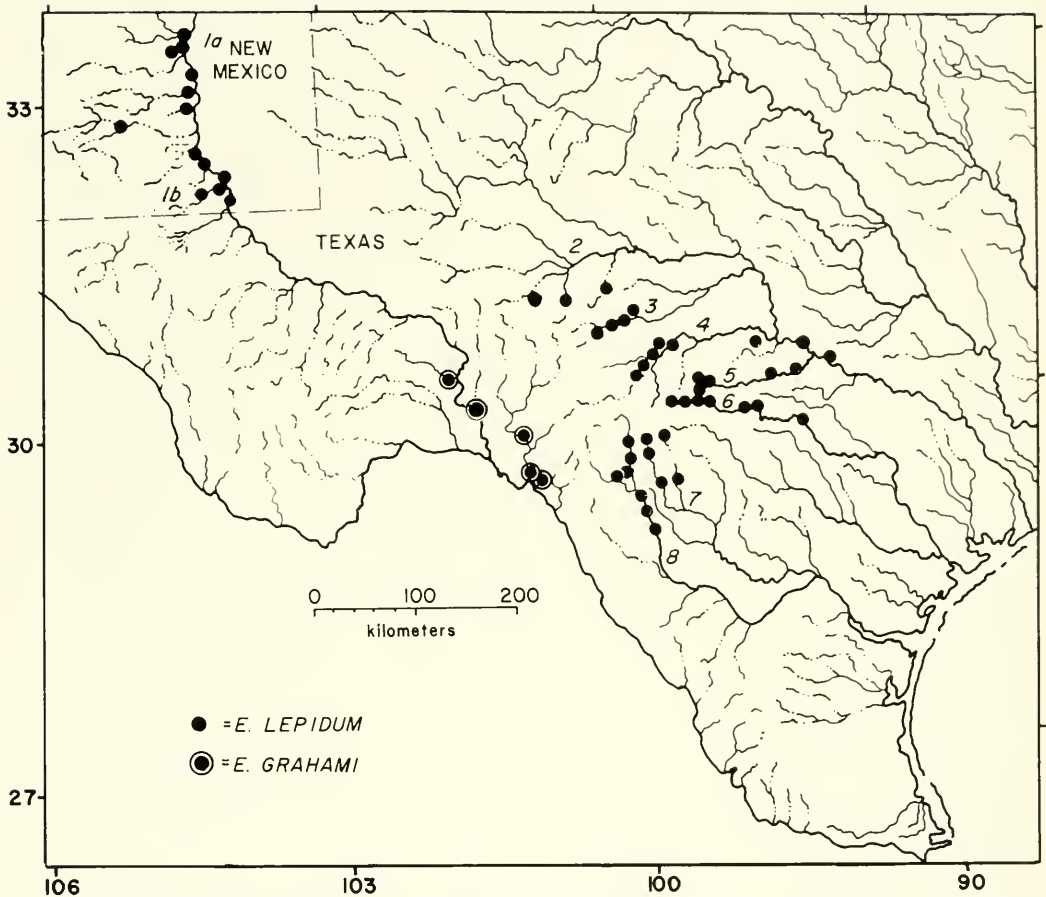


FIG. 2. Distributions of *Etheostoma lepidum* and *E. grahami*. Overlapping symbols and imprecise localities omitted. Based on records at UNM, TNHC, OSU, and TU, in addition to New Mexico records provided by J. E. Sublette from various institutions. Numbers for drainages are as follows: 1 = Pecos River drainage, 1a = Bitter Lake National Wildlife Refuge (nearest two dots), 1b = Blue Spring; 2–5 = Colorado River drainage, 2 = South Concho River, 3 = San Saba River, 4 = Llano River, 5 = Pedernales River; 6 = Guadalupe River drainage; 7–8 = Nueces River drainage, 7 = Frio River, 8 = East Nueces River. Southern tributaries of the Rio Grande in Mexico are not shown. One questionable locality record (see text) for *E. grahami* in the Pecos River near Dexter, New Mexico, is not shown.

In the 1800's and early 1900's, various workers (e.g., Evermann and Kendall 1894; Jordan, Evermann, and Clark 1930) considered *Etheostoma grahami* (Girard), a species of Rio Grande tributaries in Texas and Mexico, to be a junior synonym of *E. lepidum*, but beginning with Strawn (1957) most workers have considered them separate species. Most early literature records of *E. lepidum* (e.g., Jordan 1929; Jordan, Evermann, and Clark 1930) were based on misidentifications of *E. spectabile pulchellum* (see Distler 1968, for review) and the erroneous com-

ment by Eddy and Underhill (1978) that *E. lepidum* occurs from "Oklahoma south through central Texas" apparently resulted from this confusion. Bailey and Gosline (1955) placed *E. lepidum* in the subgenus *Oligocephalus* along with the wider ranging sympatric species *E. spectabile* and two allopatric species, *E. pottsi* of Mexico and *E. grahami* of the Rio Grande drainage of Texas and Mexico. Taxonomic relationships within the group are not well understood, but *E. grahami* and *E. pottsi* are included with *E. lepidum* in a subgroup of *Oligocephalus* which lacks

breeding tubercles (Collette 1965), a character which sets these three species apart from *E. spectabile*.

Diagnosis.—A member of the subgenus *Oligocephalus* characterized by the following combination of traits: no breeding tubercles in males; branchiostegal membranes, breast, and pelvic and anal fins blue green in breeding males; first dorsal fin in breeding males with two red bands and 1–2 blue to blue green bands (always one on distal margin); nape and breast largely naked; opercle naked; checks unscaled or partially so, rarely completely scaled; lateral line moderately arched, incomplete, total lateral line scales 44–60, pored scales, 19–42.

Description.—Counts are presented in Tables 1–4. Measurements are shown in Table 5. General aspects of body form and pigmentation are shown in Fig. 1. Strawn (1961) presented data on variation in five counts (lateral line scales, anal soft rays, and rays in first dorsal, second dorsal and pectoral fins). In the following account, ranges for Strawn's (1961) data are presented in brackets.

Fin rays of spinous dorsal 7–12 [4–11], modally 9 in all populations except two tributaries of Colorado River where mode = 10. Soft dorsal fin rays 9–13 [8–14], most frequent mode = 11. Anal soft rays 5–8 [4–9], rarely 5. Anal spines 1 or 2; in New Mexico populations, 2 more common than 1; in Texas, 2 is almost the exclusive count. Pectoral rays, 10–13 [9–14], usually 11 or 12. Pelvics have one spine and 5, rarely 4 or 6 (in New Mexico) soft rays. Lateral line scales 44–60 [45–67], usually 48–55; pored lateral line scales 19–42, usually 29–36. Transverse scale rows 12–19, modally 14–16. Caudal peduncle scales 4–6 (modally 5) above lateral line and 4–7 (mode = 6 in all populations except one with 5) below lateral line.

Belly usually completely scaled, but occasional specimens with small naked area anteriorly or on the midventral line and rarely $\frac{1}{3}$ to more than $\frac{1}{2}$ naked. Variation in codes for anterior squamation is given in Table 4. Opercles completely naked. (The comment by Moore 1968, that specimens from San Saba River have scaled opercles is incorrect.) Other areas of anterior squamation generally naked or lightly covered, but with specimens from Blue Spring, New Mexico, and San Saba and Guadalupe rivers, Texas, more heavily scaled. Cheeks completely naked in all specimens

from New Mexico except those from Blue Spring where 12 of 55 (22%) had 1–5 small, imbedded, nonoverlapping scales adjacent to the posterior and/or ventral border of eye; Texas samples generally as described for Blue Spring, but specimens from San Saba and Guadalupe rivers more fully scaled, occasional specimens with cheeks completely covered with large overlapping scales. Moore's (1968) comment that the cheeks are fully scaled in *E. lepidum* may have been based on such specimens, but this is uncommon for the species. Nape naked to lightly scaled (posterior region) except in Blue Spring and in Guadalupe River where occasionally more than half-covered with scales, rarely (two specimens from Blue Spring) completely covered. Breast completely naked in New Mexico samples except in Blue Spring where 47% (26 of 55) had light scalation near bases of pectoral fins; largely naked in Texas samples, but specimens often have scales similar to those described for Blue Spring.

Preopercular pores 5–7, modally 6. Mandibular pores 2–7, modally 4. Infraorbital pores 2–8, modally 6 with canal interrupted and 4 pores anteriorly, 2 posteriorly. Supratemporal pores generally 1–3, modally 2. Supratemporal canal usually interrupted middorsally, but occasionally uninterrupted; when uninterrupted, an extra pore occurs middorsally.

Coloration, Breeding Males.—Head dark brown dorsally followed posteriorly by 8–10 dark brown to olive brown blotches; 10 to 12 dark greenish brown lateral bars on body, darker and more complete on caudal peduncle; abdomen whitish gray ventrally with immaculate genital papilla; sides of abdomen dark red to reddish orange or rust colored; similar pigmentation extends dorsally between lateral bars and well above lateral line. Suborbital bar pronounced, extends downward from orbit to well below angle of jaw. Ventrolateral sides of head, branchiostegal membranes and breast blue green. Pectoral fins with 6–7 variably distinct vertical rows of dusky spots on rays, usually a reddish to rust-colored spot in axil. Pelvic fins dark blue green to blackish mesially with, in more brightly colored individuals, scattered red, orange, or rust-colored spots laterally. Anal fin blue green, darker at base, often with 2–3 horizontal rows composed of 2–3 small, red, orange or rust-colored interradiial spots. Caudal fin with 5–7 vertical rows composed of dusky to reddish brown spots on rays. First dor-

TABLE 1. Caudal peduncle scale counts in *E. lepidum* and *E. grahami*. Locality letters refer to museum collection numbers as listed in Materials and Methods.

Species and locality	Above lateral line				Below lateral line				
	4	5	6	\bar{x}	4	5	6	7	\bar{x}
<i>E. lepidum</i>									
New Mexico									
A. Bitter Lake Nat. Wildlife Refuge	3	10	2	4.9		9	6		5.4
B. Mouth of Rio Felix		29	9	5.2		8	29	1	5.8
C. Pecos R., S. of Lake McMillan		9	2	5.2		1	10		5.9
D. Pecos R. near Carlsbad		24	2	5.1		3	23		5.9
E. Blue Spring	9	44	2	4.9		25	29	1	5.6
F. Mouth of Black River		21	2	5.1		4	19		5.8
G. Pecos River near Red Bluff Lake		14	6	5.3			17	3	6.2
Texas									
H. South Concho River drainage	7	28		4.8	1	13	21		5.6
I. San Saba River drainage	2	25		4.9		1	26		6.0
J. Guadalupe River and tributary		29		5.0		2	27		5.9
K. Frio River and tributary	5	29	6	5.0		2	34	4	6.1
L. East Nueces and tributary		38	4	5.1		3	38	1	6.0
<i>E. grahami</i>									
M. Independence Creek	5	9		4.6		11	3		5.2
N. Devils River	13	9		4.4		13	9		5.4
O. San Felipe Creek	12	3		4.2		15			5.0

sal fin with reddish or rust-colored interradial spots at base followed distally by, in some populations, a blue green band, and then a whitish or clear, a red, a whitish or clear, and finally a blue green band; sub-basal blue band absent in most populations. Second dorsal fin with 4–6 variably distinct horizontal rows composed of red to orange, or rust-colored interradial spots which may appear as dots or dashes running parallel to rays.

Coloration, Females and Nonbreeding Males.—Olive green to brown dorsally and laterally, white ventrally; pattern of markings on fins and body generally same as described for breeding males, but without blues, greens and reds, and lateral bars less strongly developed, usually obscure to absent. First dorsal dusky, bordered on distal margin by variably distinct gray or bluish gray band.

Sexual Dimorphism.—Besides the above-mentioned sexual differences in color, *E. lepidum* exhibits sexual dimorphism in morphometric characters (Table 5). All fin measurements are larger in males than in females, and the head is slightly longer in males.

GEOGRAPHIC VARIATION

Strawn (1955a) described variation in color of the first dorsal fin in Texas populations as follows: "The uppermost band . . . is an intense blue green. Below, a narrow white band separates it from a broad bright rust-colored band. Ventral to this rust band, males from the South Concho River have a broad blue green band and those from the San Saba River have a more narrow blue green band that is usually lacking in males from Llano and Pedernales rivers of the Colo-

TABLE 2. Lateral line scale counts in *E. lepidum* and *E. grahami*. Locality letters as in Table 1.

Species and locality	Counts																			\bar{x}	
	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59		60
<i>E. lepidum</i>																					
New Mexico																					
A					1		1		2	4	3	2	1		1						50.3
B								2	2	4	6	10	5	1	3	4	1				51.2
C								1			2		1	2	4	1					52.4
D								1	3		2	5	3	7	2		1	1			51.8
E				2	3	3	8	11	8	10	5		1	3	1						48.8
F								1		5	4	2	3	4	1	1	2				51.4
G									1		1	1	5	2	3	3	3			1	53.5
Texas																					
H					1	1	3		1	3	6	6	4	3	4	1	2				50.9
I										1	1	7	6	3	3	1	3	2			52.8
J											2	4	4	2	4	4	3	2	4		54.1
K											1	2	3	3	6	10	2	7	5	1	55.0
L								1	3	2	3	5	8	9	1	5	3	1	1		52.4
<i>E. grahami</i>																					
M	1		1	3	2		1	4	1												45.7
N			1	1	2	4	3	2		3		4	1	1							48.9
O	1		1	2	4	2	3	2													46.3

rado River System and the Guadalupe and Nueces River Systems." Thus, in Texas populations, variation in development of the subbasal, or ventral, blue green band is clinal from north to south. Among New Mexico populations we have seen males in bright breeding colors from Blue Spring and from Bitter Lake National Wildlife Refuge and none had the ventral blue band in the first dorsal fin. Brightly colored males from the New Mexico populations differ from those in Texas populations in that the red on the body and especially on the dorsal fins is a dark "brick" red instead of the reddish orange to rust color that is typical of most Texas populations. Populations from South Concho River may have a bright red pigmentation, but it is of a lighter hue than that of New Mexico populations. Other possible differences in breeding colors seem relatively minor and inconsistent.

Strawn (1961) noted that in Texas populations, consistent intradrainage differences occurred between downstream and spring populations, with the latter having lower lateral line counts and pectoral ray counts. Our observations on New Mexico populations are similar. Only two of the New Mexico samples were from strictly springfed environments; these were Bitter Lake

National Wildlife Refuge (Dragonfly Spring and Sago Spring) and Blue Spring; correspondingly, those two samples had lower counts for lateral line scales, caudal peduncle scales, and pectoral fin rays than all other New Mexico samples (Tables 1–3). Thus, as in Texas populations (Strawn 1961), there seems to be a strong environmental component in accounting for local variation in such characters.

The Blue Spring population differs from all other New Mexico populations and more nearly resembles certain Texas populations in having more extensive cheek, nape, and breast scalation (Table 4). This difference may be maintained by restricted gene flow. The Blue Spring population is isolated from downstream areas by a 15 m waterfall at the confluence with Black River. However, Mike Hatch (pers. comm.) noted that this barrier was less pronounced prior to recent human activity.

Considerable variation in scale and fin ray counts exists among Texas populations (Tables 1–4; also see Strawn 1961), but geographic patterns are weakly developed. However, a number of notable differences exist between New Mexico and Texas populations. New Mexico populations have slightly greater numbers of pored lateral

TABLE 3. Fin ray counts in *E. lepidum* and *E. grahami*. Locality letters as in Table 1.

Species and locality	First dorsal spines							Anal spines			Pectoral rays				
	7	8	9	10	11	12	\bar{x}	1	2	\bar{x}	10	11	12	13	\bar{x}
<i>E. lepidum</i>															
New Mexico															
A		6	9				8.6	2	13	1.9	2	12	1		10.9
B		8	25	5			8.9	8	30	1.8		17	20	1	11.6
C		4	7				8.6	3	8	1.7		3	8		11.7
D		3	16	7			9.2	4	22	1.8		9	16	1	11.7
E	4	13	27	8	3		8.9	10	45	1.8	16	39			10.7
F			16	6		1	8.9	7	16	1.7		10	13		11.6
G	1	5	12	1	1		8.8	3	17	1.9		9	11		11.6
Texas															
H			14	21			9.6	4	31	1.9		11	22	2	11.7
I		1	16	10			9.3		27	2.0		6	20	1	11.8
J		1	17	10	1		9.4		29	2.0		6	20	3	11.9
K		4	26	10			9.2		40	2.0		1	34	5	12.1
L	1	3	25	13			9.2		42	2.0		3	32	7	12.1
<i>E. grahami</i>															
M			2	9	3		10.1		14	2.0		3	9	2	11.9
N				18	4		10.2	1	21	2.0		7	15		11.7
O			1	12	2		10.1		15	2.0		6	9		11.6

line scales than populations from all Texas drainages except the Guadalupe. Numbers of spines in the first dorsal fin generally average lower in New Mexico than in Texas, but the modes are the same, and the average difference is small. Percentages of New Mexico specimens with a single spine in the anal fin range from 13 to 30 ($\bar{x} = 18$), while in Texas single spines occur only in the South Concho drainage (11% of specimens). Numbers of pectoral rays average higher in Texas drainages than in New Mexico; in New Mexico percentages of specimens with 11 or fewer pectoral rays range from 27 to 100 ($\bar{x} = 55$) while in Texas the percentages range from 3 to 31 ($\bar{x} = 17$), with the smallest percentages in the Nueces drainage (E. Nueces and Frio rivers). The various headpore counts show little geographic variation; a notable exception, however, is the high frequency (51%) of specimens from Blue Spring, New Mexico, with seven or more infraorbital pores. Also, except in Blue Spring, New Mexico populations generally have higher frequencies than Texas populations of specimens with supratemporal canals uninterrupted mid-dorsally; percentage of specimens with uninterrupted canals is 2% (1 of 55) in Blue Spring and 25–36% in all other New Mexico populations.

Texas specimens with uninterrupted canals occurred only in the Guadalupe and East Nueces drainages (10 and 12% of specimens, respectively).

As with meristic characters, the major pattern of variation in morphometrics is between New Mexico and Texas populations. The males and, in general, the females of New Mexico populations are deeper bodied and have shorter caudal peduncles than do Texas populations (Table 5). In addition, the pectoral fin is markedly larger in the former.

While geographic variations are evident, the observed differences do not warrant recognition of subspecies in *E. lepidum*. Variation in the ventral blue band of the first dorsal fin in males shows marked differentiation. However, as noted above, development of the band shows a north-south cline in Texas. The observed meristic differences cannot be used in identifying populations because the differences are minor, and Strawn (1961) demonstrated the ontogeny of such counts in *E. lepidum* to be strongly controlled by environment rather than genetic differences. Texas populations vary in egg complement (Hubbs and Delco 1960), and New Mexico populations differ from Texas populations in three

TABLE 4. Codes for anterior squamation in *E. lepidum* and *E. grahami*. See Methods for description of codes. Locality letters as in Table 1.

Species and locality	Cheek					Opercle					Nape					Breast			
	0	1	2	3	\bar{x}	0	1	2	3	\bar{x}	0	1	2	3	\bar{x}	0	1	\bar{x}	
<i>E. lepidum</i>																			
New Mexico																			
A	15				0.0	15				0.0	11	4			0.3	15		0.0	
B	38				0.0	37	1			0.3	20	18			0.5	38		0.0	
C	11				0.0	11				0.0	8	3			0.3	11		0.0	
D	26				0.0	26				0.0	26				0.0	26		0.0	
E	43	12			0.2	55				0.0	7	34	12	2	1.2	29	26	0.5	
F	23				0.0	23				0.0	22	1			0.04	23		0.0	
G	20				0.0	20				0.0	12	8			0.4	20		0.0	
Texas																			
H	31	4			0.1	35				0.0	32	3			0.1	32	3	0.1	
I	4	16	5	2	1.2	27				0.0	22	5			0.2	13	14	0.5	
J		18	5	6	1.6	29				0.0	3	17	9		1.2	6	23	0.8	
K	13	27			0.7	40				0.0	24	16			0.4	30	10	0.3	
L	29	13			0.3	42				0.0	6	36			0.9	36	6	0.1	
<i>E. grahami</i>																			
M	10	3			0.2		2	11	2.8	12	1				0.1	13		0.0	
N	16	6			0.3		3	3	16	2.6	21	1			0.05	21	1	0.05	
O	2	8	5		1.2				15	3.0	10	4	1		0.4	4	11	0.7	

morphometric characters. However, sufficient overlap occurs that these characters do not allow reliable identification of individuals. The comment (Hubbs and Echelle 1972) that "... the Pecos darter seems more similar to Guadalupe-Colorado river stocks . . . than to the Nueces River population . . ." was based on a preliminary assessment and is not supported by the present analysis.

Interspecific Comparison.—Past taxonomic confusion of *E. lepidum* with the consubgeneric *E. grahami* has probably resulted from the superficial resemblance and geographic proximity of the two species. The most striking differences between them are in male breeding colors. Strawn (1955a) provided a brief description of coloration in the two species. The following is from his description, supplemented by our observations. *E. grahami* lacks bright blues and greens. Anal and pelvic fins are orange rather than primarily blue green as in *E. lepidum*. Strawn (1955a) described the dorsal fins of *E. grahami* as "whitish lavender with orange dots"; however, orange is the predominant color. The first dorsal fin has no strongly developed bands. Pattern of markings on head and body is similar in the two species.

As emphasized by Strawn (1961) for the five counts he examined, meristic characters of *E.*

lepidum and *E. grahami* overlap broadly. However, *E. grahami* tends to have larger scales; this is reflected by the smaller average number of lateral line scales and caudal peduncle scales above and below the lateral line (Table 1). In addition, *E. grahami* has a higher modal number of spines in the first dorsal fin (10 vs. 9, Table 3).

E. lepidum and *E. grahami* differ markedly in opercle scalation with the latter usually having completely scaled opercles while the former has scaleless opercles (Table 4).

A major morphometric difference between *E. grahami* and *E. lepidum* is in height of first dorsal fin in males. The erect first dorsal fin in *E. grahami* males is greater or almost equal in height to the erect second dorsal fin while in *E. lepidum* the first is much shorter than the second (Table 5). Other marked differences are the longer caudal, pectoral, and pelvic fins in *E. lepidum* (Table 5).

Ecology and Abundance.—Koster (1957) noted from his extensive experience with the "Pecos darter" in New Mexico that the species was most abundant among "rocks and weeds" and (pers. comm.) that they prefer the latter, even in the presence of riffles. Both presently large New Mexico populations (Blue Spring and Bitter Lake

National Wildlife Refuge—see Fig. 2) are closely associated with dense vegetation. In Texas the species occurs most abundantly in vegetated riffles when in sympatry with *E. spectabile*, but a shift toward gravel riffles occurs in the Nueces River drainage where *E. spectabile* is absent (Hubbs, Kuehne, and Ball 1953).

E. lepidum occurs abundantly in most springfed habitats of the Edwards Plateau, and also does well in certain reservoirs of the area. Distribution and abundance of Texas populations has not been substantially altered by human activities. However, pumping of water from underground aquifers will eventually have adverse effects as springs diminish in flow.

The abundance of *E. lepidum* has declined in New Mexico. The following account is based on W. J. Koster's early collections and a compilation of other records assembled by J. E. Sublette of Eastern New Mexico University. Although never abundant in the Pecos River proper (Koster, pers. comm.), several large collections (32–330 specimens) were made in the 1940's and early 1950's from the Pecos River and the mouths of large tributaries, Black River and Rio Felix; as late as 1961 a collection of 60 specimens (Arizona State University #0936) was taken from Cottonwood Creek, N of Artesia, Eddy County. Large populations are now known only from three localities: 1) Blue Spring, a 4 km spring and spring run of the Black River drainage, 8 km E of Whites City, Eddy County, 2) small springs and waterfowl management ponds on the Bitter Lake National Wildlife Refuge near Roswell, Chaves County, and 3) Pecos River (Mike Hatch, pers. comm.) at Boiling Springs (Major Johnson Spring), 9.6 km S of Lakewood, Eddy County. Since 1961, and excepting a small, uncatalogued collection by a party from New Mexico State University which was taken at Carlsbad in 1966 (D. Jester, pers. comm.), the species has been taken from only three additional locations, and each consisted of single specimens. However, one of the three collections (Eastern New Mexico University #015.02) was made from the Rio Penasco, 1.7 km S, 29.2 km E Mayhill, Chaves County, an area sufficiently isolated from presently known major populations that it is difficult to explain the single specimen as a stray individual from known areas of dense concentration. Thus, a permanent population may occur somewhere in the Rio Penasco drainage. The virtual elimination of *E. lepidum* from the Pecos River and

the mouths of its major tributaries has resulted from extensive habitat alterations which include channel straightening, brush removal, irrigation diversions, and pollution from oil fields, municipalities, and cattle feedlots. The populations at Blue Spring and Bitter Lake National Wildlife Refuge are well protected by the present ownerships and seem in no immediate danger of elimination.

Strawn (1955b) noted that greenthroat darters "will spawn repeatedly when kept at temperatures ranging from . . . [16] (and probably lower) to [23°C] . . ." Hubbs (1961, 1967) described developmental temperature tolerances (7–29°C) of the South Concho River and Nueces River populations. Hubbs and Strawn (1957) noted that, in the Guadalupe River, at a springfed locality with relatively uniform temperatures, the breeding season is 10 to 12 months long with depressed breeding in mid-summer, while at a locality with more variable water temperatures, breeding occurred from November through April. The New Mexico populations seem to respond similarly. Based on dissection of females larger than 35 mm SL, ripe eggs were present in all collections examined from Blue Spring (collections made in April, May, October, and November) and in a June collection from Sago Spring on the Bitter Lake National Wildlife Refuge, but in an August collection of 3 females from Dragonfly Spring on the Refuge none had ripe eggs. Koster's collections from the Pecos River and the mouths of larger tributaries include two February collections in which 7 of 8 females were ripe, one July collection in which only 1 of 22 females was ripe, and six August collections in which, excluding a collection from the mouth of Black River, only 1 of 24 was ripe; in the excluded collection, 6 of 14 females were ripe. Thus, New Mexico populations apparently experience depressed breeding activity in the summer.

Zoogeography.—The New Mexico population of *E. lepidum* represents a disjunct occurrence of the species (Fig. 1). Elsewhere, the species is restricted to limestone springs and associated waters of the Edwards Plateau where its range coincides well with the Balconian Province as defined by Blair (1950).

The similar *E. grahami* occurs in the lower Pecos and elsewhere in the Rio Grande drainage (Fig. 1). At present *E. grahami* is isolated from *E. lepidum* by a 300 km segment of the Pecos River (from Malaga, New Mexico to Sheffield,

TABLE 5. Means and, in parentheses, standard deviations of standard length (SL) and proportional measurements, as thousandths of SL, for *E. lepidum* and *E. grahami*.*

Sample size, character, and sex	<i>E. lepidum</i>						<i>E. grahami</i> Dolan Creek
	New Mexico			Texas			
	Blue Spring	Bitter Lake National Wildlife Ref.	South Concho River	San Saba River	Guadalupe River	East Nueces River	
Sample size							
Male	13	5	4	3	12	10	8
Female	13	3	5	4	10	10	6
Standard length (mm)							
Male	39.5 (5.2)	40.6 (2.8)	39.0 (4.9)	46.5 (1.9)	40.7 (2.4)	37.2 (1.9)	39.7 (4.0)
Female	39.4 (3.9)	37.6 (0.4)	46.6 (3.9)	47.0 (3.0)	39.7 (3.3)	37.1 (2.9)	35.6 (2.2)
Body depth							
Male	228 (11.5)	246 (13.5)	202 (13.2)	214 (3.6)	192 (7.7)	212 (4.2)	211 (6.1)
Female	224 (9.7)	230 (7.6)	220 (8.3)	210 (4.4)	196 (10.8)	220 (11.2)	211 (7.2)
Snout length							
Male	62 (4.8)	55 (3.1)	59 (3.0)	65 (0.6)	60 (3.2)	67 (4.5)	60 (2.7)
Female	59 (3.3)	52 (6.1)	60 (1.6)	59 (3.7)	60 (1.6)	67 (2.8)	64 (5.6)
Head length							
Male	300 (13.3)	273 (8.3)	281 (9.5)	280 (7.8)	278 (9.2)	295 (6.7)	288 (4.8)
Female	295 (8.3)	277 (5.1)	271 (6.4)	264 (9.2)	276 (5.9)	294 (9.3)	296 (10.2)
Orbit length							
Male	76 (5.5)	62 (3.2)	68 (5.4)	66 (2.1)	69 (2.1)	76 (3.7)	72 (2.4)
Female	75 (4.7)	62 (6.1)	63 (2.3)	65 (2.5)	68 (4.2)	72 (2.2)	78 (4.6)
Caudal peduncle length							
Male	241 (9.5)	252 (9.1)	284 (4.7)	263 (8.4)	283 (10.8)	262 (4.8)	254 (3.9)
Female	248 (12.2)	258 (5.3)	284 (11.8)	284 (10.2)	285 (11.0)	255 (19.3)	254 (8.0)
Caudal peduncle depth							
Male	130 (6.4)	119 (0.8)	116 (7.2)	127 (2.5)	118 (5.5)	119 (3.3)	117 (2.9)
Female	124 (5.8)	110 (4.0)	118 (6.2)	116 (3.8)	118 (9.2)	112 (4.0)	115 (4.4)
First dorsal fin height							
Male	113 (13.1)	103 (9.6)	109 (2.6)	104 (2.0)	100 (8.4)	100 (8.0)	146 (11.3)
Female	92 (6.7)	86 (12.5)	96 (5.6)	95 (7.3)	95 (7.7)	87 (10.8)	98 (8.3)
Second dorsal fin height							
Male	143 (14.9)	136 (9.8)	134 (7.1)	150 (3.5)	126 (9.1)	137 (10.2)	130 (7.5)
Female	131 (8.1)	128 (3.8)	121 (10.1)	135 (8.3)	119 (8.4)	126 (7.7)	119 (4.5)

TABLE 5. Continued.

Sample size, character, and sex	<i>E. lepidum</i>						
	New Mexico			Texas			
	Blue Spring	Bitter Lake National Wildlife Ref.	South Concho River	San Saba River	Guadalupe River	East Nueces River	<i>E. grahami</i> Dolan Creek
First anal spine length							
Male	73 (6.9)	71 (12.5)	72 (3.4)	71 (1.7)	79 (7.3)	77 (9.2)	76 (7.7)
Female	65 (6.3)	72 (6.1)	61 (4.0)	66 (4.2)	74 (7.2)	65 (8.0)	69 (4.6)
Pectoral fin length							
Male	250 (14.8)	256 (7.0)	231 (6.3)	232 (3.8)	219 (8.9)	230 (14.7)	209 (13.8)
Female	242 (16.4)	246 (15.2)	214 (13.5)	217 (9.1)	211 (9.8)	225 (11.7)	197 (20.0)
Pelvin fin length							
Male	202 (12.9)	195 (7.9)	196 (7.4)	197 (6.6)	192 (10.1)	201 (10.4)	180 (9.2)
Female	188 (10.3)	182 (10.2)	181 (6.7)	179 (10.1)	182 (11.1)	188 (11.2)	173 (12.2)
Caudal fin length							
Male	212 (13.6)	208 (9.4)	200 (13.6)	209 (13.9)	184 (5.8)	189 (10.3)	172 (11.8)
Female	208 (16.0)	209 (8.1)	187 (6.2)	189 (11.9)	183 (9.7)	182 (4.8)	173 (14.0)

* Museum collection numbers for the above specimens as follows: Blue Spring, UNM 65; Bitter Lake Nat. Wildlife Refuge, OSU 11342; South Concho River, UT 2435; San Saba River, UT 2071; Guadalupe River, UT 6116, 2977; East Nueces River, UT 5282; Dolan Creek, UT 3264.

Texas) which often has dissolved solids in excess of 10 ppt. The only exception to this distribution is a collection of three *E. grahami* (UMMZ 201701) which were collected by L. Q. Carmen of the U.S. Fish and Wildlife Service in 1939-1940; according to the locality data, this collection was taken from the Pecos River near Dexter, Chaves County, New Mexico. The locality data are questionable because, in the 1940's and 1950's, W. J. Koster collected extensively in the Dexter area, and we have found no *E. grahami* in his collections.

We hypothesize that, perhaps in Pliocene times, *E. grahami* and *E. lepidum* diverged in allopatry, the former in the ancestral Rio Grande, the latter in more northern drainages of the Gulf Coast. Thomas (1972), in a review of the history of the Pecos River, suggested that in late Pliocene and early Pleistocene the Pecos may have extended northward only to the Sacramento Mountains (roughly at the present southern boundary of New Mexico). During that time it began eroding headward at a rapid rate (Thomas 1972;

Leonard and Frye 1975), and may have eventually captured a portion of the upper Colorado River (Echelle and Echelle 1978) and a population of the then more wide-ranging *E. lepidum*. Subsequent extirpation of *E. lepidum* in the remaining upper Colorado River would have produced the present disjunct distribution.

SUMMARY

The greenthroat darter, *Etheostoma lepidum*, is redescribed. The species shows weakly developed geographic variation in scale and fin ray counts, degree of anterior scalation, breeding colors of males, and body proportions. No subspecies are recognized. The species differs markedly from the geographically associated species, *E. grahami*, in various scale and fin ray counts and body proportions, in opercular scalation, and in coloration.

E. lepidum occurs abundantly in springfed habitats and certain manmade reservoirs on the Edwards Plateau of south and central Texas. A

widely disjunct population in the middle Pecos River drainage of southeastern New Mexico has declined noticeably since the 1950's; at present, large populations occur only in Blue Spring, near Whites City, and at the Bitter Lake National Wildlife Refuge, near Roswell. The New Mexico population conforms with published reports on breeding season in Texas populations; ripe females occur during most months of the year, but breeding condition declines in summer.

It is hypothesized that, in Pliocene times, *E. lepidum* and *E. grahami* diverged in allopatry, the latter in the ancestral Rio Grande and the former in more northern drainages of the Gulf Coast. In late Pliocene or early Pleistocene the lower Pecos River (presently occupied by *E. grahami*) eroded headward and presumably captured the middle to upper Pecos from the Colorado River or another drainage of central Texas. The latter event brought *E. lepidum* into the Pecos River and created the present disjunct distribution of the species. At present *E. lepidum* and *E. grahami* are separated by a saline, 300 km segment of the Pecos River.

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Anolis fitchi, A New Species of the *Anolis aequatorialis* Group from Ecuador and Colombia

ERNEST E. WILLIAMS AND WILLIAM E. DUELLMAN

The *aequatorialis* group of the iguanid lizard genus *Anolis* is characteristic of cloud forests on the slopes of the Andes in northwestern South America. Vast areas of these forests still remain inaccessible, and the *Anolis aequatorialis* group, like many other elements of the cloud forest fauna, has remained poorly known. The only published field observations on any of these lizards are those of Henry S. Fitch. Therefore, it is particularly appropriate to associate his name with a handsome new species in the *eulaemus*¹ subsection of the group.

Anolis fitchi new species

Frontispiece

Holotype.—KU 142865, an adult male, from 16.5 km (by road) north-northeast of Santa Rosa, Provincia Napo, Ecuador, 1700 m elevation, obtained on 19 October 1971 by William E. Duellman.

Paratypes.—ECUADOR: Provincia Napo: KU 142864, 142866, same data as holotype; KU 142867–69, Río Azuela at Quito-Lago Agrio road, 1740 m, William E. Duellman and Joseph T. Collins, 20–21 October 1971; MCZ 158324, same locality, Kenneth Miyata, 24 February 1979; KU 164162, Río Salado, 1 km upstream from Río Coca, 1410 m, William E. Duellman, 7 October 1974; KU 164163–65, same locality, William E. Duellman and Alan H. Savitzky, 18 March 1975; KU 178960, same locality David C. Cannatella, 18 July 1977; KU 178961, same locality, Martha C. Lynch, 17 July 1977; MCZ 124350–51, “Loreto region,” collector and date

unknown; AMNH 28900, “Volcán Sumaco,” Carlos Olalla, January, 1924; USNM 214869, “upper Río Napo,” Jorge Olalla, date unknown; USNM 214870, La Alegría on Río Chingual, ±3 km N Sibundoy, ±20 km N La Bonita, 1930 m, James A. Peters, 24 June 1962. COLOMBIA: KU 169823–26, Departamento de Putumayo: 10.3 km W of El Pepino, 1440 m, William E. Duellman, 27–29 September 1974.

Diagnosis.—*Anolis fitchi* is a member of the *eulaemus* subgroup of the *Anolis aequatorialis* species group; i.e., it has the moderate size and narrow toe lamellae characteristic of all members of the group but has the subdigital pad under the phalanx projecting above the proximal end of phalanx I, rather than continuous with the latter (“*Norops* condition” as understood by Boulenger 1885). *Anolis fitchi* is similar to *A. eulaemus* Boulenger but differs in having the dewlap on the male with dark skin and large scales in single or double lines (rather than light skin and minute scales in multiple lines) and in the presence of a moderate-sized mottled or spotted dewlap in females (female dewlap rudimentary with dark skin in *eulaemus*). *Anolis fitchi* is similar also to *A. ventrimaculatus* Boulenger but differs by having the scales around the interparietal slightly larger than those on the nape (those scales smaller, hardly distinguishable from nape scales in *A. ventrimaculatus*) and in the presence of the moderate dewlap in females (no trace of a dewlap in female *A. ventrimaculatus*).

Description (Counts for Holotype in Parentheses).—Anterior head scales small, multicarinate, tuberculate, or wrinkled; 11–18 (16) scales across snout between second canthals; some scales within shallow frontal depression larger than those immediately anterior to depression; 6–9 (9) scales bordering rostral posteriorly; 10 or 11 scales between supranasals dorsally; anterior nasal above, or just behind, suture between rostral and first supralabial (Fig. 1). Supraorbital semi-circles separated by 1–3 (3) scales; no differentiated supraocular disc, but some scales slightly enlarged, keeled; one moderately elongate supraciliary followed by one or two shorter scales,

¹ By a lapsus, Williams (1976) used the name *aequatorialis* group in a table and *eulaemus* group in a key on the following page. The intention was to use the oldest name in each group as the nominate form. *Anolis aequatorialis* Werner 1894 antedates *A. eulaemus* Boulenger 1908, and hence is the appropriate name for the whole defined series. However, *A. eulaemus* is the earliest-named member of one of the two quite distinct subgroups, which therefore are called the *A. aequatorialis* subgroup and the *A. eulaemus* subgroup.

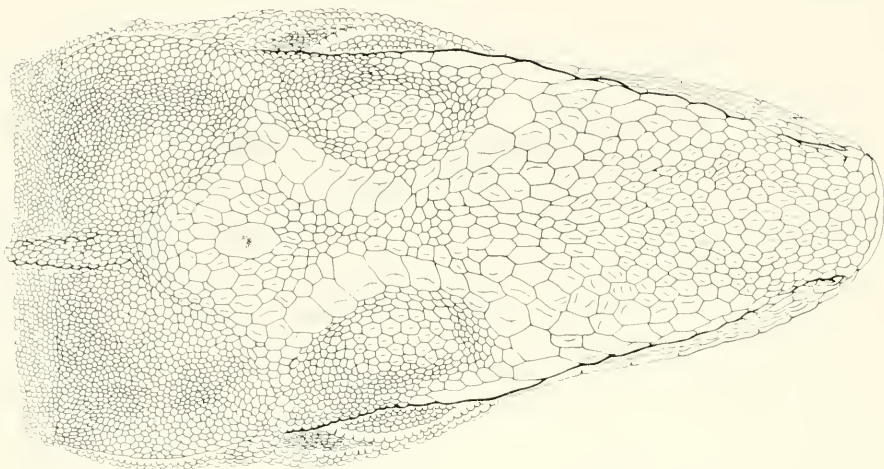


FIG. 1. Dorsal view of head of holotype of *Anolis fitchi*.

first and second largest; 7–10 (8) rows of loreals, uppermost longest. Temporal and supratemporal scales granular; no differentiated double intertemporal line of enlarged scales; scales in depression surrounding interparietal distinctly but variably enlarged, posterior and posterolateral ones grading abruptly into dorsals and supratemporals; interparietal smaller than ear, separated from supraorbital semicircles by 3–6 (4) scales. Suboculars separated from supralabials by one row of scales or narrowly in contact; 8–11 (11) supralabials from rostral to middle of eye (Fig. 2). Mental semidivided, wider than long, posteriorly in contact in an approximately transverse line with 5–8 (6) scales between infralabials; sublabials not clearly differentiated; median throat scales small, swollen, grading into much longer scales laterally.

Dewlap large in male, extending to middle of belly; scales in closely packed single rows, separated by naked skin; lateral scales larger than ventrals; dewlap in females extending just posterior to level of axilla.

Two to four middorsal rows of body scales slightly enlarged, keeled, swollen, subimbricate; lateral granules swollen, pointed, juxtaposed; ventrals larger than dorsals, imbricate or subimbricate, smooth, tending to be in transverse rows.

Some larger scales on limbs multicarinate; scales on dorsum of hand large, multicarinate; supradigital scales multicarinate; digital expan-

sions narrow; 21–24 (22) lamellae under phalanges II and III of fourth toe.

Tail compressed but without dorsal crest; verticils not distinct; two enlarged middorsal rows of scales; postanals weakly enlarged in males, sometimes not evident.

Color in Preservative.—Dorsum pale brown with broad dark brown middorsal blotches confluent with or narrowly separated from broad diagonal marks on flanks, or flanks dark brown with many round pale spots. Head pale brown above; limbs pale brown above with broad dark brown transverse bars. Tail pale brown with broad brown blotches becoming indistinct posteriorly. Venter dull tan, flecked or not with dark brown; throat dark with lighter spots or transverse streaks. Male dewlap dark brown with tan scales. Female dewlap blotched black on brown. In both sexes a more or less conspicuous complex light, often white, blotch containing black spots or oblique streaking just above dewlap.

Color in Life (See Frontispiece).—Dorsum olive-green to tan with dark brown markings, with or without yellowish tan flecks and/or round spots laterally; often a tan vertebral stripe in females; venter brown to yellowish green; male dewlap dark brown with yellowish tan to yellowish green scales; female dewlap mottled or spotted; iris dull bluish gray; tongue pinkish gray.

Males and females may differ sharply in color. This is emphasized by descriptions of a male and female paratype from the same Ecuadorian lo-

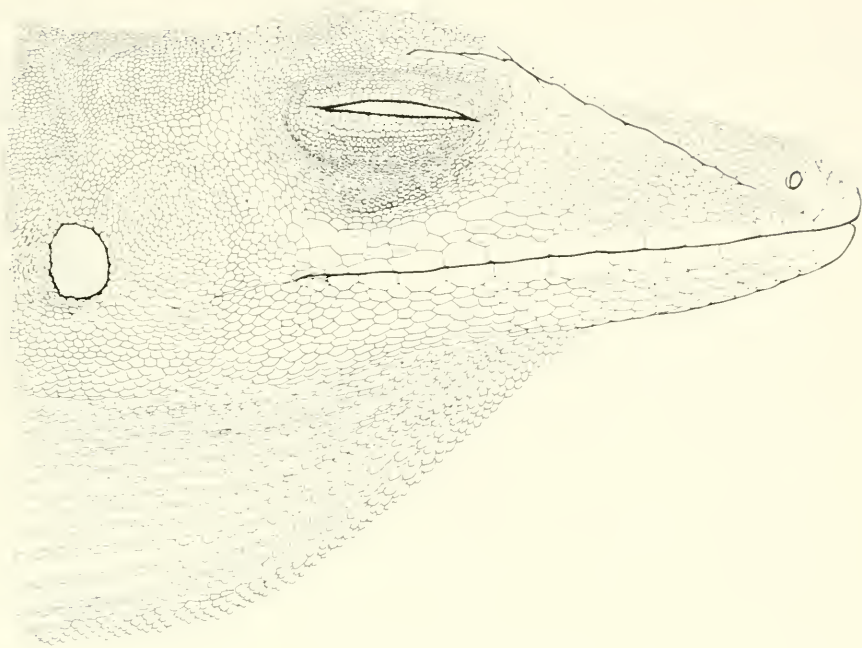


FIG. 2. Lateral view of head of holotype of *Anolis fitchi*.

cality: KU 178960, ♂: "Green with reddish-brown markings. Hint of yellow along lateral surfaces. Venter yellow. Dewlap brown with green scales at base, becoming yellow laterally. Tongue cream, iris gray." KU 178961, ♀: "Dorsal stripe cream with some reddish-brown infusion; laterally dark brown, then bright lime green. Dewlap scales dull orange at edge, yellow toward throat, marbled with black, belly dirty cream with gray-brown spots. Tongue dark gray. Iris blue-green." (Field notes, John D. Lynch). Colombian specimens may differ slightly; KU 169823, ♂: "Dorsum pale green with dark brown transverse markings. Venter pale brown with dark brown flecks. Dewlap brown with dull yellowish green stripes. Iris, tongue, and lining of mouth blue." KU 169826, ♀: "Dorsum green with brown flecks and dorsal blotches. Dewlap greenish white with brown flecks proximally and orange bars distally. Iris pale blue." (Field notes, W. E. Duellman).

Measurements of Holotype (mm).—Snout-vent length 88; tail length 221; head length 24; head width 12.5.

Distribution and Ecology.—Most specimens of *A. fitchi* have been collected in cloud forest at elevations of 1410–1930 m on the eastern slope

of the Andes (Fig. 3). Loreto is at 550 m. The specimen from "Volcán Sumaco" collected by Carlos Olalla most likely came from the vicinity of the village of San José Viejo (Peters 1955:345; Paynter and Traylor 1977:110). The imprecise locality, "upper Río Napo," presumably is less than 500 m. Extensive collections assembled by Duellman and field associates at several localities on the lower Andean slopes and in the upper Amazon Basin in northern Provincia Napo (Cordillera del Dué, 1150 m; Bermejo, 720 m; Puerto Libre, 570 m; Santa Cecilia, 340 m; Lago Agrio, 340 m) do not contain examples of *A. fitchi*.

We have adopted a restricted concept of *A. fitchi*; only specimens from Provincia Napo, Ecuador and adjacent Departamento de Putumayo, Colombia, are included in the type series. Specimens from farther south (Provincias Pastaza, Tungurahua, and Morona-Santiago, Ecuador, and Departamento Amazonas, Perú) obviously are close to *A. fitchi*. However, these specimens appear to differ in coloration and may represent more than one taxon. The present samples are inadequate to make a decision at this time.

The range of unequivocal *A. fitchi* extends into southern Colombia, at least into Putumayo. To

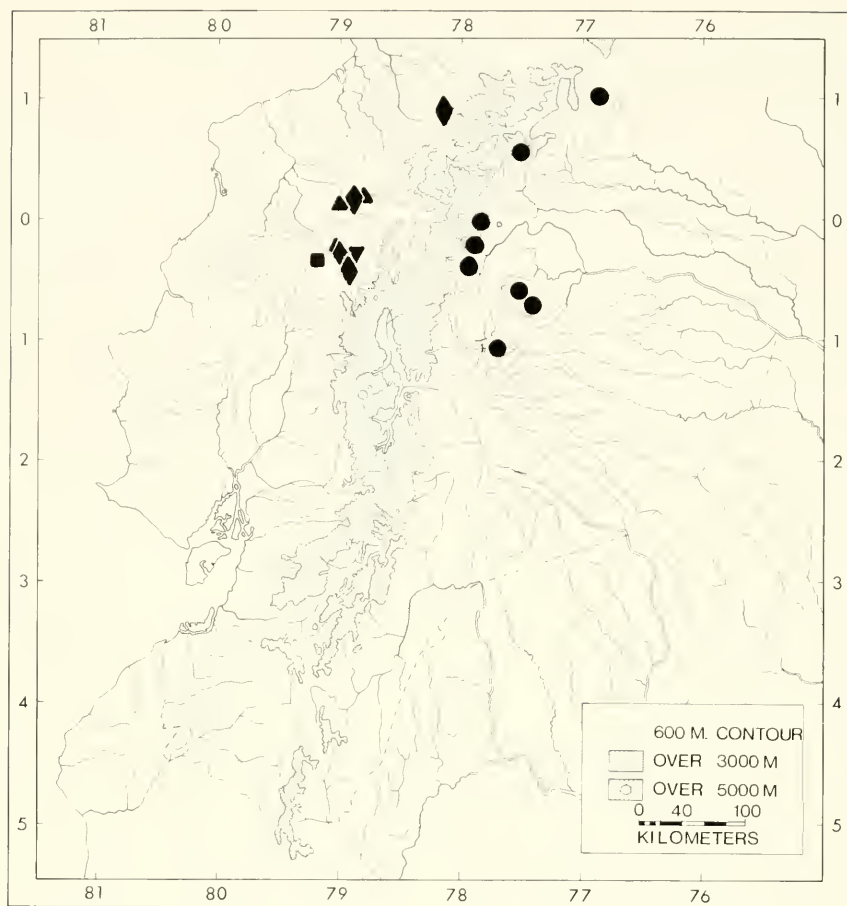


FIG. 3. Distribution of the *Anolis aequatorialis* group in Ecuador and adjacent Colombia: *A. aequatorialis* (triangles), *A. fitchi* (dots), *A. gemmosus* (inverted triangles), *A. aequatorialis* and *A. gemmosus* (diamonds), *A. parilis* (square).

the south the range may be limited by the Pastaza trench, which forms a barrier to many cloud forest inhabitants, such as frogs of the genus *Eleutherodactylus* (Lynch and Duellman 1980). *Anolis fitchi* occurs at moderate elevations on the Andean slopes to the north of the trench but at low elevations at the base of the trench. This pattern is like that of *Eleutherodactylus peruvianus* (Melin), which also extends southward and eastward into the Amazon Basin in Perú (Lynch 1980).

Like many other anoles inhabiting Andean cloud forests, specimens of *A. fitchi* were found only while they were sleeping at night. All were head up on leaves of large herbs, on bushes, palm fronds, or sticks. One was only 0.5 m above the

ground, and most others were at heights of 1.5–2.0 m.

The type locality is a small stream crossed by the road between Quito and Lago Agrio, 16.5 km north-northeast of the small village of Santa Rosa. The locality is on the upper, north-facing slope of a ridge immediately south of the Río Salado, which is a tributary of the Río Coca. In 1971 this locality was pristine cloud forest characterized by numerous large tree ferns. By 1974 much of the area was under cultivation, and remnants of cloud forest remained only in ravines and on steep slopes. Kenneth Miyata (pers. comm.) reported that in 1979 there was virtually no undisturbed forest along the road in the vicinity of the type locality.

TABLE 1. Scale characters in the *Anolis eulaemus* subgroup.

	<i>A. eulaemus</i>	<i>A. ventrimaculatus</i>	<i>A. fitchi</i>	<i>A. gemmosus</i>
Adult male size	to 100 mm	to 80 mm	to 91 mm	to 63 mm
Scales across snout				
between second canthals	14-19	11-19	11-17	10-17
Scales between semicircles	2-4	2-6	1-3	2-6
Loreals	8-10	7-11	7-10	5-10
Interparietal/ear	<	≤/x	<	≤/x
Scales between semicircles and interparietal	4-6	5-12/x	7-10	4-8/x
Scales between suboculars and supralabials	1-2	0-2	0-2	0-1
Enlarged middorsal rows	(2)	(2)	2-4	(1)
Lamellae under phalanges II and III of fourth toe	21-23	17-22	21-24	14-20

x = interparietal absent—a frequent anomaly in *A. ventrimaculatus*, less common in *A. gemmosus*.

Relationships.—*Anolis fitchi* belongs to the *aequatorialis* species group (Williams 1976). This group is poorly known but can be divided into two distinctive subgroups on the basis of digital structure. The *aequatorialis* subgroup has a *Norops*-type digit (*sensu* Boulenger 1885), in which the digital pad does not project above the proximal end of the first phalanx. In contrast, members of the *eulaemus* subgroup have a typical *Anolis* digit, in which the distal lamellae of phalanx II distinctly overlap the proximal scales of phalanx I.

Three moderate-sized species (± 80 –120 mm snout–vent length) are currently recognized in the *aequatorialis* subgroup, all on the Pacific side of the Andes: 1) *A. aequatorialis* Werner 1894, which reaches a maximum size of ± 120 mm, known from a number of localities at moderate elevations on the western slope of the Andes in Ecuador; 2) *A. mirus* Williams 1963, from the “Río San Juan” in Colombia, the unique type (105 mm snout–vent length) with imprecise locality; 3) *A. parilis* Williams 1975, with a unique type (81 mm snout–vent length) from the Río Baba, 2.4 km south of Santo Domingo de los Colorados, Provincia Pichincha, Ecuador.

Almost as little is known of the ecology of the *aequatorialis* subgroup as of its distribution; no notes are available for the two species known from unique types. Although *A. aequatorialis* is common in recent collections, most have been obtained at night when they were sleeping on ferns and bushes. The only diurnal observations are those by Fitch *et al.* (1976:120): “Five *Anolis aequatorialis* were captured at Tandapi, Pichin-

cha Province, Ecuador, on 18, 19 and 23 February, 1975. All were between 2 and 3 m above ground on the outer twigs or foliage of small trees or herbaceous plants. They were not wary or elusive but seemed to depend on concealment for escape and were well hidden by screening vegetation. They were found in the same sorts of situations as the smaller and much commoner *Anolis gemmosus*. Partitioning of resources was not evident.”

Until recently, the *eulaemus* subgroup was in as bad a state. More material, including specimens from both sides of the Andes, had been collected, but most specimens were incorrectly identified; AMNH 28900 from Volcán Sumaco in eastern Ecuador, here regarded as a paratype of *A. fitchi*, was reported by Burt and Burt (1931) as *A. fasciatus* Boulenger, an unrelated species restricted to the lowlands of western Ecuador.

However, even the new material does not permit complete elucidation of the *eulaemus* complex, which is now known to extend from Departamento Antioquia, Colombia, to at least the Río Cenepa, Perú. The peripheral specimens are all represented by one or two specimens poorly preserved and with no information on color in life. In this puzzling set of animals, scale counts broadly overlap, and scale characters (e.g., size of scales around the interparietal) are not always clearly diagnostic. Presence or absence of a dewlap in females, dewlap scale size, and coloration, at least in combination, set off *A. fitchi* and the three species with which it is here compared—*A. eulaemus*, *A. ventrimaculatus* and *A. gemmosus*: these four taxa can be defined adequately.

TABLE 2. Dewlap and body pattern differences in the *eulaemus* subgroup (pattern differences in preservative emphasized because color in life of *eulaemus* is unknown).

		Dewlap	
		♂♂	♀♀
<i>A. eulaemus</i>	Large, skin dull, scales lighter, minute, in multiple lines (5–6) separated by naked skin.	<i>Rudimentary</i> , represented by folds of skin that are emphasized by intervening dark pigment.	
<i>A. ventrimaculatus</i>	Large, skin dark or light, scales light, large, in single or double lines separated by naked skin.	<i>None</i> .	
<i>A. gemmosus</i>	Large, skin dark at base or all light, scales light, large, in multiple lines (3–4) separated by naked skin.	<i>None</i> .	
<i>A. fuchi</i>	Large, skin dark, scales light, large, in single or double rows separated by naked skin.	<i>Moderate</i> , skin mottled or spotted, scales light, large, in single or double rows separated by naked skin.	
BODY PATTERN			
Side of Neck			
<i>A. eulaemus</i>	Pattern dull, vague; a poorly bounded black blotch just above the dewlap.	A dark area above the rudimentary dewlap bounded dorsally by an arc of light pigment arising from the ear and then descending to the shoulder. ¹	
<i>A. ventrimaculatus</i>	A narrow light line from labials arching over the upper margin of the ear and continuing to the shoulder; above this a black blotch.	Uniform dark, rarely some vague light spots.	
<i>A. gemmosus</i>	A light line from labials not arching above ear, no black blotch above it.	Faint bluish tinge on side of neck, no well-defined pattern.	
<i>A. fuchi</i>	A light blotch containing black spots or oblique streaks contiguous with the base of the dewlap.	A black blotch in front of shoulder just behind a light blotch containing black spots.	
Throat			
<i>A. eulaemus</i>	Gray, lighter laterally.	Uniformly dark.	
<i>A. ventrimaculatus</i>	Uniform dark or very weakly vermiculate (juveniles may show bold vermiculation).	Boldly vermiculate, dark on light.	
<i>A. gemmosus</i>	Nearly uniform, at most shades of purple (juveniles may have dark spots on a light ground).	Weakly to strongly vermiculate, dark on light.	
<i>A. fuchi</i>	Some light streaks or spots on a light ground.	Light marks or spots on dark background.	
Dorsum			
<i>A. eulaemus</i>	"Purplish brown above with rather indistinct transverse bars on back and large round lighter spots on sides." Boulenger 1908.	Oblique narrow white bars with somewhat irregular margins meeting in forward pointing angles middorsally and separated by wide areas of uniform brown.	
<i>A. ventrimaculatus</i>	Middorsum uniform dark or crossed by narrow dark bars containing light spots. Flanks boldly spotted with lighter.	A longitudinal dorsal light zone bounded by dorsolateral lightbands or a narrow middorsal light line or a series of middorsal multiply-shaped figures. Flanks with strong to weak or absent spotting or vermiculation.	

TABLE 2. Continued.

		Dewlap
		♂
<i>A. gemmosus</i>	Dark transverse bands widest dorsally separated by areas with bold and irregular spotting. Transverse bands tapering on flanks which become entirely spotted or pale dorsum and flanks nearly uniform.	A middorsal light zone with dark margins or a narrow middorsal light line or short transverse bands not extending onto flanks. Flanks patternless or with some dark spotting.
<i>A. fitchi</i>	Broad dark transverse bands dorsally. Flanks more or less boldly spotted or vermiculate.	A middorsal light zone with dark margins or dark transverse bands narrowed in center (butterfly pattern). Flanks may be obscurely vermiculate or spotted with darker.
Venter		
<i>A. eulaemus</i>	Venter obscurely but densely vermiculate, dark on light.	Sides of venter pepper and salt becoming more uniform brown in center.
<i>A. ventrimaculatus</i>	Densely and finely spotted (juveniles also vermiculate).	Light with weak dark vermiculations or spotting.
<i>A. gemmosus</i>	Belly with spotting encroaching from flanks or nearly uniform bluish.	Venter immaculate or more or less densely but obscurely vermiculate and spotted.
<i>A. fitchi</i>	Belly darkish, edge invaded by dark spots.	Belly with dark spots or markings, most prominent laterally.

¹ All comments on the female of *eulaemus* are based only on AMNH 118980.

Anolis eulaemus was described from a unique male type (BMNH 1946.8.13.31) from Pavas (near San Antonio), Departamento Valle, Colombia, and *A. ventrimaculatus* from two syntypes—an adult female and a juvenile from the Río San Juan, Intendencia Chocó, Colombia. We here designate the adult female syntype (BMNH 1946.8.13.5) as the lectotype; it is uncertain that the faded juvenile is the same species.

Recently collected material from cloud forests in the Departamento Valle, Colombia, including material from the vicinity of San Antonio, provides an excellent match for the female syntype of *A. ventrimaculatus*, which lacks any trace of a dewlap. Males from the vicinity of Lago Calima, Departamento Valle, recently collected in numbers along with females of *A. ventrimaculatus*, agree with these females and not with the type of *A. eulaemus* in the small size of the scales surrounding the interparietal and differ sharply from *A. eulaemus* in the squamation of the dewlap. The type of *A. eulaemus* has minute lateral scales on the dewlap that are smaller than the ventrals and are crowded in multiple series of rows that are widely separated by naked skin. On the contrary, in males referred to *A. ventri-*

maculatus, the lateral scales are large, as in *A. fitchi*, larger than the ventrals, and in single series in rows that are closely packed.

The new series has permitted recognition as *A. ventrimaculatus* of a specimen (Instituto La Salle 109) collected by Niceforo María at Pueblo Rico, Risaralda (formerly Caldas). This specimen makes more plausible Boulenger's inexact locality "Río San Juan" for the syntypes of *A. ventrimaculatus*. Pueblo Rico is near the source of the Río San Juan, and M. G. Palmer, who collected both syntypes of *A. ventrimaculatus* and the type of *A. eulaemus*, is reported by Boulenger (1911) in the same paper in which he described *A. ventrimaculatus*, to have obtained *Leptognathus* (= *Dipsas*) *sancti-joannis* at "Pueblo Rico, slopes of San Juan River, Colombian Choco, 5200 feet." It is possible that Niceforo María's specimen is topotypic or near-topotypic, but Boulenger's careful avoidance of precision leaves the question open.

On the basis of the new collections, *A. ventrimaculatus* seems to be common, but *A. eulaemus* remains rare in collections. No material has been collected recently near the type locality. A single male (AMNH 110495) was collected at Lago Cal-

ima by Stephen C. Ayala in 1974. None has been obtained in more recent collections from that area. Four other males are known: two from Peñas Blancas (where *A. ventrimaculatus* also occurs), one from the "Farallones de Cali, Pichinde," and one from "región alta cerca al Lago Calima." The probable female of the species is represented by AMNH 118980 from "mountains above the north side of Lago Calima (1700 m)."² All of these localities are on the Pacific versant of the Cordillera Occidental in Departamento Valle, Colombia. The female has no well-developed dewlap, but the area is indicated by longitudinal throat folds. A specimen (BMNH 1910.7.11.4) from "Siató, near Pueblo Rico, Chocó," collected by Palmer, indicates that *A. eulaemus* occurs somewhere near the probable type locality of *A. ventrimaculatus*. Thus the two species appear to be broadly sympatric; whether they are ever syntopic, like *A. aequatorialis* and *A. gemmosus*, is unknown.

The dewlap of male *A. ventrimaculatus* has two color morphs—one with dark brown skin covered by yellow lines of scales and one with orange skin covered by lighter lines of scales and with a dark blotch at its base.

Anolis gemmosus from the western slope of the Andes in Ecuador, the third previously described member of the *eulaemus* subgroup of the *aequatorialis* species group has not previously been associated with this group. Williams (1976) placed it in the *punctatus* group in error. The digital dilations of *gemmosus* are narrow as in the *aequatorialis* group, not wide as in the *punctatus* series (cf. the key in Williams 1976). However, *A. gemmosus* (maximum δ size 66 mm) is smaller than any other member of the group, and this fact contributed to the failure of Williams to recognize its true relationships. It is interesting that the smallest member of the group co-occurs with the *A. aequatorialis*, some individuals of which reach the maximum size for the group. Size differences of this magnitude imply a par-

tioning of resources which Fitch *et al.* (1976) with their restricted sample (five) of *A. aequatorialis* could not demonstrate.

The second smallest member of the *aequatorialis* group (*A. ventrimaculatus*, 80 mm maximum snout-vent length) is a parallel case; its sympatry with *A. eulaemus* (100 mm snout-vent length) is again a case of co-existence of two related species that differ significantly in size.

Anolis gemmosus is morphologically somewhat intermediate between *A. eulaemus* and *A. ventrimaculatus*: it has the lateral scales of the male dewlap in multiple lines as in *A. eulaemus* but as large or larger than ventrals as in *A. ventrimaculatus*. *Anolis gemmosus* shares with *A. ventrimaculatus* a condition that has been considered very rare in *Anolis*—absence of the parietal eye. Frequently in *A. ventrimaculatus*, less commonly in *A. gemmosus*, there may be no scale recognizable as an interparietal by size, position, or the presence of a central spot or window.

Anolis gemmosus resembles *A. ventrimaculatus* in variable dewlap coloration, but as Fitch *et al.* (1976:121) reported, and K. Miyata (pers. comm.) confirms, there appear to be no discrete morphs, either within or between populations. Fitch *et al.* commented: "The highly variable dewlap did not seem to comprise well-defined classes but tended to form a continuum between extremes. At one extreme were dewlap with little contrast, dull yellowish-green on the basal area, shading to dull greenish-yellow on the outer part. The more contrasting and colorful type of dewlap was similar in having a dull greenish-yellow on the outer part, but the basal part was bluish-green with six narrow sharply defined white stripes diverging from a center on the anterior basal portion. The stripes had bright blue edges proximally at their origins, but distally the blue changed to green and the stripes themselves became suffused with the yellow background and finally blended into it and blended with their brighter colored edges."

Miyata (pers. comm.) mentioned some variations: "The dewlap skin is basically a pale yellowish-green. In many specimens there is a distinct orange or yellow wash along the edge as well, and in some specimens there is also a dark blue area anterobasally, and, in some, a white area posteriorly. The extent and intensity of these colors is quite variable and in some individuals

² That this is a female of *A. eulaemus* must remain somewhat doubtful, for it was not taken in association with any male. However, there is available something lacking for any of the males, color in life: "Green with broad blackish gray diagonal bars on sides. Throat and venter light brown. Small dewlap brown with black stripes. Iris brown. Tongue gray, throat lining unpigmented." (C. W. Myers, in litt.)

the colors grade into each other while in others they remain as discrete patches. The dewlap scales are arranged in distinct longitudinal rows; these scales are normally white, but in many specimens they are green and, in a few individuals, they are yellow. In some specimens the anterior scales are white and the posterior scales either green or yellow, or sometimes all three colors. These scales, if they are white or yellow, are bordered by either green or blue scales, the latter only if there is blue on the anterobasal dewlap skin."

Interpopulational variation in dewlap color is, as Fitch *et al.* stated, ordinarily rare or minor in anoles. It is presumably another indication of the affinity of *A. gemmosus* and *A. ventrimaculatus* that they show such variability. However, *A. fitchi* is not known to show comparable variation. Difference in *A. fitchi* is primarily sex dimorphism, although the extent of blotching is variable in the female dewlap.

Body color in *A. gemmosus* also is highly variable (Fitch *et al.* 1976; also see Table 2 for pattern repertoire). *Anolis andiamus* Boulenger (1885) from Milligalli, Provincia Pichincha, Ecuador, appears to be well within this variation, both in scales and color, and we here formally synonymize it with *A. gemmosus* O'Shaughnessy (1875).

Anolis gemmosus is known from Maldonado in Provincia Carchi, Ecuador, very close to the northern border of the country; the species very probably extends northward into at least the Departamento Nariño, Colombia.

Anolis fitchi in Provincia Napo, Ecuador, obviously is a close relative of the three species from the western slopes of the Andes. Scale counts for all four taxa overlap (Table 1). Differences in coloration are noted in Table 2; it is conspicuous there that males and females of these taxa show different interspecific differences and resemblances. Although the unity of the group is confirmed by the cross-affinities, it is not easy to say that any one species is most closely related to any other.

The presence of related species in cloud forests on the opposite sides of the Andes in Ecuador and southern Colombia is now known to be a rather common distribution pattern in lizards, snakes, and frogs (Duellman 1979). The differentiation of cloud forest inhabitants on either side of the Andes is most likely a late Cenozoic phenomenon. The final elevation of the northern Andes occurred in the late Pliocene and up to

the Recent (Simpson 1979). Application of the albumin clock hypothesis (Wilson *et al.* 1977) to immunological data on frogs of the genus *Gastrotheca* inhabiting cloud forests on opposite sides of the Andes shows a divergence time of 2–3 million years (Scanlan *et al.* 1980). If the time of speciation events in *Gastrotheca* are indicative of that for other groups, such as anoles, it might be assumed that populations of cloud forest inhabitants were continuous across the Andes in the late Pliocene, and subsequently were fragmented by the orogenies and climatic and vegetational shifts in the Pleistocene documented in the palynological record (van der Hammen 1974).

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