

Aspects of the Reproductive Ecology and Behavior of the Tepui Toads, Genus *Oreophrynella* (Anura, Bufonidae)

ROY W. MCDIARMID AND STEFAN GORZULA

We report direct development for toads of the bufonid genus *Oreophrynella*, endemic to the tepuis of the Guayanan Highlands. Tepui toads place few (9-13), large (~3 mm diameter) eggs in a single or communal terrestrial nest. One communal nest found on Kukenan-tepui contained 102 toads (70 males, 30 females, 2 hatchlings) and 321 eggs in clumps of 8-35. All viable clutches from Kukenan were attended by an adult. One clutch of 13 eggs from Ilu-tepui was without an attendant adult. Calls of Kukenan males consist of 9-16 partially pulsed notes given at a rate of 5-7 notes per second. Calls and notes were modulated and increased or decreased in frequency; dominant frequencies of the calls ranged between 2650-3650 Hz. Tepui toads are diurnal, rock dwellers with a slow, deliberate walking gait. An unusual balling and tumbling behavior and bright colored venter may be associated with predator avoidance in some populations. Remarkable parallels in reproductive ecology and behavior between *Oreophrynella* and montane populations of the African bufonid *Nectophrynoides* are noted.

THE bufonid genus *Oreophrynella* is restricted to the unique montane environments characteristic of the tepuis of the Guayanan Highlands of southern Venezuela and adjacent Guayana and Brazil. The genus currently consists of two described species, *Oreophrynella quelchii* (Boulenger) known only from the summit of Mount Roraima and *O. macconnelli* Boulenger from two localities in the forest at the base of Mount Roraima (McDiarmid, 1971) and three undescribed ones (McDiarmid, unpubl.). The new species include one from Kukenan and Yuruani, one from Ilu-tepui, and a third from Auyan-tepui. Recent helicopter explorations and reconnaissance of the eastern tepuis of the Roraima group gave each of us independently the opportunity to study these poorly known toads in their natural environment. We report the first observations of the reproductive ecology and behavior of toads of the genus *Oreophrynella*.

METHODS

In January 1977, McDiarmid, Charles Brewer-Carias, and several other Venezuelan scientists visited four (Roraima, Kukenan, Yuruani and Ilu) of the seven tepuis making up the Roraima group and collected and observed the herpetofauna. Mount Roraima was revisited on 18-22 Feb. 1978 (Brewer-Carias, 1978). In late

April 1984 and June 1985, as part of an inventory of ecosystems of the Rio Caroni catchment area, Gorzula accompanied a joint mission of the hydroelectric company CVG Electrificación del Caroni C.A. (EDELCA), the New York Botanical Garden (NYBG), and the Universidad Central de Venezuela (UCV) and made brief helicopter landings on three of these tepuis (Kukenan, Yuruani, and Ilu). Their objectives were to gather information on the flora, herpetofauna, limnology, and geology from these remote and poorly known areas. The tepuis visited during these explorations are part of the Roraima chain in Estado Bolívar of southeastern Venezuela. From north to south the tepuis visited during our study, including camp and/or collecting sites, general elevations, and coordinates, are: Ilu-tepui, 2450-2650 m (05°25'N, 60°59'W); Yuruani-tepui, 2300 m (05°19'N, 60°51'W); Kukenan-tepui, 2500-2700 m (05°16'N, 60°48'W); Mount Roraima, 2600 m (05°12'N, 60°44'W). Toads of the genus *Oreophrynella* were found on all four tepuis.

RESULTS

Reproductive ecology.—One of our primary objectives was to increase our knowledge of the reproductive ecology and behavior of *Oreophrynella*. Egg size and number, reported from two preserved specimens of *O. quelchii*

(McDiarmid, 1971), suggested the possibility of direct development. Extensive searching in available aquatic sites on Mount Roraima in 1977 failed to reveal any anuran larvae, even though adults were active and males were heard calling. After extensive searches on Kukenan-tepui, a single clutch of eggs and attendant female were found beneath a small rock (Fig. 2A). The rock, $12 \times 8 \times 3$ cm, lay about 1 m above the ground on the side of a large sandstone boulder. The weathered boulder was in a sheltered area near the base of a cliff, and supported a sparse growth of bryophytes, ferns, bromeliads, and species of Xyridaceae. The clutch of eggs occupied a hollow beneath the central part of the rock; a short tunnel about 30 mm long connected the hollow to the outside of the boulder. The female, located next to the eggs and facing the tunnel entrance, was 23 mm SVL; the tunnel was about 20 mm wide. Nine white eggs in the nest adhered together. The clump was preserved in 10% buffered formalin and returned to the laboratory. Additional thorough searching was unsuccessful.

Diameter of each egg was about 3 mm. Developmental stages equivalent to stages 2, 3, and 4 in *Eleutherodactylus coqui* (Townsend and Stewart, 1985) were represented in the clutch. Dissection of the female revealed an enlarged oviduct on the right side and an ovarian complement of three yellowish ova (~ 0.6 mm diameter) and about 14 whitish ova (< 0.3 mm diameter). The oviduct on the left side was about half the size of that on the right; four yolked ova were about 0.7 mm and about 10 others were white and less than 0.4 mm diameter. Assuming that the female found in the nest laid the clutch, her enlarged right oviduct suggests that the nine eggs moved through a single oviduct. While ovulation from both ovaries cannot be ruled out, these observations support McDiarmid's (1971) suggestion that a female is capable of producing more than one clutch in a reproductive season.

On 15 June 1985, Gorzula found two other clutches of 10 eggs each beneath a stone on Kukenan-tepui. No adults were in attendance, and the eggs were decomposing. A single clutch of 13 eggs was found beneath a stone by Gorzula at 2450 m on Ilu-tepui on 18 June 1985. No adult toad was in attendance but the eggs were viable.

On 28 April 1984, Gorzula made a remarkable discovery in an isolated patch of vegetation on the bare sandstone surface of the summit of

Kukenan-tepui. Sharp, "peeet" calls heard from a distance of 10 m attracted his attention to this "island" of vegetation. On closer inspection he saw several toads walking toward the noise. The predominant plants forming these islands were *Connellia* sp. (Bromeliaceae), *Everardia* sp. (Cyperaceae), *Cyrilla racemiflora* (Cyrillaceae), and various species of Eriocaulaceae and Xyridaceae (Otto Huber, NYBG, pers. comm.). The island was approx. 1×0.5 m and contained many *Oreophrynella*. Because the helicopter would arrive within the hour, the vegetation was searched quickly. About 12 entrances connected an intricate network of tunnels that ran through the root mat and mossy base of the vegetative island. The tunnels were 20 mm in diameter and from them were extracted 102 toads and 321 eggs. The eggs were in clumps of 8–35 and always were attended by one or more toads. The eggs were white with a gelatinous adhesive outer envelope. All stages of development were found from clutches of recently deposited eggs to those containing embryos with four visible limbs. Hatchlings from the eggs were 4 mm SVL (Delia Rada de Martinez, UCV, pers. comm.).

Of the 102 toads taken from the tunnels, two were recently hatched, 70 were adult males with well developed testes, and 30 were females. These data suggest that males may remain at the deposition site for a longer period than do females. Male SVL ranged from 18.0–23.5 mm ($\bar{x} = 20.7$ mm, $SD = 1.03$), and of the females from 21.5–30.0 mm ($\bar{x} = 24.4$ mm, $SD = 1.62$). Only three females had spent ovaries; the others contained from 5–14 ($\bar{x} = 9.6$, $SD = 2.31$) large ovarian eggs. Two females collected outside the tunnel system contained 9 and 10 eggs. Random samples of mature males and females collected elsewhere on Kukenan did not differ in size from those of each sex found within the nest.

Sexual dimorphism in size was evident also in toads from Yuruani. A series of 13 males collected at the same time were 18.0–22.5 mm SVL ($\bar{x} = 20.4$, $SD = 1.50$), while 18 females measured 23.0–25.5 mm ($\bar{x} = 24.3$, $SD = 0.77$). Eight of the 18 females contained 11–15 eggs ($\bar{x} = 13.4$, $SD = 1.30$).

McDiarmid (1971) noted that eggs in one ovary of *O. quelchii* were larger than those in the other and suggested that this species may lay two clutches or more or possibly alternate ovaries. For verification, we examined several large females collected from Mount Roraima in Jan. and Feb. In three specimens (23.0–24.5

mm SVL) with mature eggs, two obvious size classes of eggs were present: eight (3 in left ovary and 5 in right) large (>2.0 mm diameter), yolked (yellow orange) eggs surrounded by 10–20 (each side) smaller (<0.5 mm), whitish eggs. While these data neither support nor refute McDiarmid's (1971) speculation, they do imply that a typical (single) clutch from *O. quelchii* probably is composed of eggs derived from both ovaries. Although the actual clutch size of *O. quelchii* from Roraima is unknown, we assume that it is similar to those of the other species and closer to eight than three or five. The fact that a few females from the communal nest of the Kukenan species had only five or six ovarian eggs does not preclude the possibility that the complement from a single ovary may be deposited in a communal nest. Between species differences in clutch size and reproductive behavior are possible.

Vocalization.—Calls thought to be from male *O. quelchii* were heard sporadically, usually in the early morning or late afternoon, from scattered localities on Mount Roraima in Jan. 1977. A few calls were recorded from a distance but no vouchers were collected. A single male was observed calling in a rock crevice near the western edge of the plateau at 1130 h on a sunny day. The male was in the shade of the rock facing head downward and moved deeper into the crevice when disturbed. In 1977, the only anuran known from the summit of Mount Roraima was *O. quelchii* and all calls heard were assumed to be of that species. However, in Nov. 1979, Brewer-Carias collected two specimens of an undescribed *Eleutherodactylus* from the summit. Therefore, some of the calls heard on Roraima could have been those of *Eleutherodactylus* and not *Oreophrynella*.

On Kukenan-tepui McDiarmid heard male *Oreophrynella* sp. calling at dawn on an overcast morning after a light rain in Jan. from open areas on the summit. Efforts to record the calls in the field were unsuccessful. Field notes (McDiarmid) state that calls from Kukenan males differ from those heard on Roraima and consist of several notes (about 10 per call) repeated in quick succession. He also heard calls thought to be from *Oreophrynella* on Ilu-tepui in Jan. and noted that they sounded intermediate between those from Roraima and Kukenan. In April, Gorzula heard calling males from the communal nest on Kukenan and scattered calling males on Ilu-tepui.

Some toads collected by McDiarmid in Jan. from Kukenan-tepui were taken to Caracas alive and recorded 4 d later as they called from plastic bags in the laboratory. Eight calls consisted of 6–16 partially pulsed notes (some calls were truncated at the beginning and probably contained a few more notes). Notes varied from 0.05–0.11 sec duration and were given at a rate of 4.3–6.5 per sec (Fig. 1). Calls were variable and had modulations in frequency and amplitude that increased slightly, stayed the same, or decreased slightly throughout the call. Notes within a call also were modulated and variable, with the frequency sweeping up 200–400 Hz or going up 300–350 Hz and then down 200–350 Hz within a note. This variation occurred between calls as well as within a single call. Dominant frequencies of the calls varied from a low of 2650 to a high of 3650 Hz. Low frequencies at the initiation of a note varied from 2650–3200 Hz; highest frequencies in a note varied from 3000–3650 Hz. A weak second harmonic between 6600 and 6900 Hz was present in the loudest notes of most calls.

Activity and behavior.—Our observations indicate that these toads are diurnal. Individuals have been seen and collected during most daylight hours on four tepuis. Toads were more active in earlier morning hours, especially on overcast days, than during mid-day. In Jan., pairs or small groups of 4–6 toads were observed in open areas on Kukenan-tepui shortly after dawn. When approached, some moved quickly towards islands of vegetation while others remained motionless but alert. Based on the vocal activity that morning, these pairs and groups may have been involved in courtship behavior. By mid-morning activity had decreased markedly. On Yuruani-tepui toads were active 27 April between 1445 and 1800 h and between 0600 and 1100 hr the following day. None was observed after sunset between 1945 and 2010 h.

Most active toads were found on bare sandstone in open areas on the tepuis. Some were collected beneath rocks resting on bare sandstone and a few were sitting <1 m above ground on leaves of *Stegolepis guianensis* (Rapateaceae), *Lomaria* sp. (Pteridophyta), and *Brocchinia hechtiioides* (Bromeliaceae). Inactive individuals occasionally were seen sitting on bare rock in the open during the day on Roraima and Kukenan.

Observed densities varied considerably among localities on tepuis and between tepuis. Toads on Yuruani-tepui were relatively abundant in

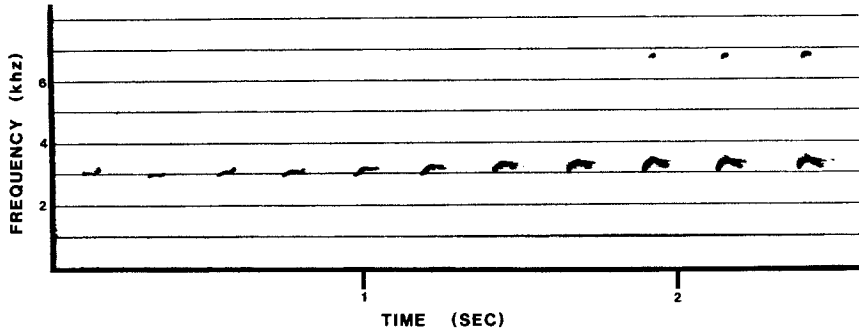


Fig. 1. Audiospectrogram of advertisement call of *Oreophrynella* sp. collected from Kukenan-tepui, Bolivar, Venezuela, on 9 Jan. 1977. Recording made with Uher 4000 Report L on 14 Jan. 1977 in laboratory in Caracas, Venezuela, from unspecified male calling in collecting bag with six other toads. Sonagram was made with high-pass filter at 1.5 kHz.

open sandstone areas in April; 23 were counted along a 60 m line transect. O. Huber (pers. comm.) visited the Yuruani site for a day in Feb. and saw no *Oreophrynella* in areas where they were common 2 mo later. All 17 specimens that McDiarmid collected on Yuruani-tepui on 11 Jan. 1977 were from beneath rocks. Likewise, 24 toads collected on Ilu-tepui in 3 h in Jan. were found beneath rocks even though the area was wet and some scattered calls, assumed to be from *Oreophrynella*, were heard. During 5 d on Roraima in Jan. 1977, toads were relatively abundant near our camp for the first 2 d but became very difficult to locate during the last 2 d when specimens were found only by rolling back clumps of *Stegolepis guianensis*. An extensive rainstorm had preceded our visit to Roraima and the area changed from wet to dry during our short stay. We suspect that temporal and seasonal differences accounted for much of the observed variation in densities and activity.

Contrary to McDiarmid's (1971) prediction that the opposable toes of *Oreophrynella* may reflect an arboreal existence, it is now clear that the species inhabiting the sandstone summits of the tepuis are rock dwellers. The toads apparently are unable to hop or jump effectively and rely on walking as their main locomotor mode. Their unusual walking gait, slow movements, and diurnal habits should expose tepui toads to intense predation. Individuals often exhibited a curious "balling" behavior by folding their arms and legs under their body and tucking their head when captured. When a toad is on an inclined surface, which is often, and assumes the balling position, it literally rolls downhill like a dislodged pebble. This behavior, com-

bined with their cryptic dorsal color and rugose skin, increases their resemblance to the dark gray-black, eroded, and encrusted sandstone surfaces of their habitat. This balling and rolling behavior often results in a toad's tumbling some distance into a crack or crevice where it is out of sight or difficult to reach. This combination of behavior and color may protect them from some predators. No snakes are known from the summits of the Roraima tepuis and the common birds are not known to eat vertebrates. Potential predators include large, terrestrial spiders (Theraphosidae) that are relatively abundant on the tops of the tepuis. Because spiders normally don't chase prey (J. Coddington, pers. comm.), the balling and tumbling behavior might be very effective in escaping from a large theraphosid. In one instance on Mount Roraima an individual tumbled down a nearly vertical face of a narrow rock passage for a distance of nearly 3 m. After a few minutes it unrolled and walked away. Balling may characterize the group as this behavior has been observed in species of *Oreophrynella* from Kukenan-tepui, from Ilu-tepui, and in *O. quelchii* on Mount Roraima. This behavior is not without its costs; one toad that tumbled from a rock face fell into a deep pool of water and apparently drowned. Although several were seen in shallow water following a recent rain on Kukenan-tepui, they apparently were unable to swim effectively.

Roraima toads have bright yellow-orange and black mottled bellies. Such coloration, suggestive of an aposematic function in toxic species, is not uncommon among some bufonids, such as some species of *Atelopus* and *Melanophryniscus* (McDiarmid, 1971). Many of the toads that tum-

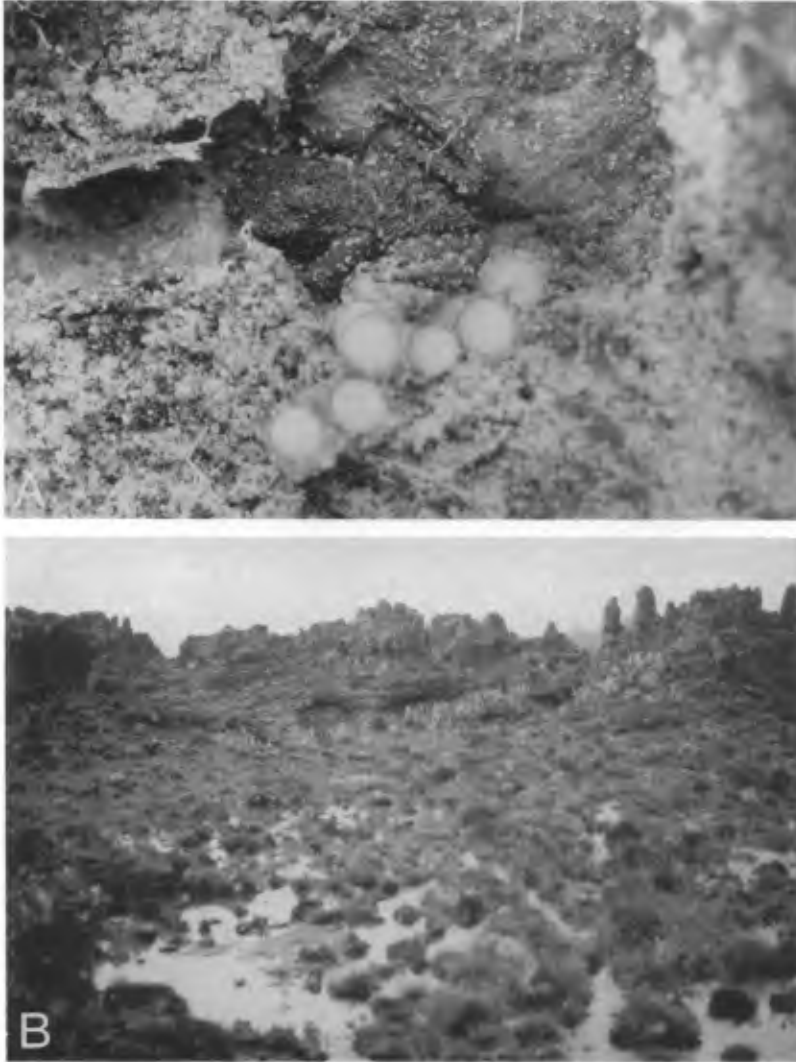


Fig. 2. A) Female *Oreophrynella* sp. with nine eggs found beneath a rock on the summit of Kukenan-tepui in Jan. 1977. B) Typical habitat of *Oreophrynella* sp. on Kukenan-tepui, 15 June 1985. Photos by the authors.

bled off a rock ended in the balled position, belly up, exposing the bright contrasting ventral coloration.

DISCUSSION

Most species of bufonid toads have the primitive reproductive mode characteristic of Anura, that is, aquatic eggs that hatch into mobile, feeding larvae that undergo metamorphosis and grow to a more terrestrial adult stage. A few forms have nonaquatic modes of reproduction

and include species of *Pelophryne* from the tropical forests of southeast Asia (Inger, 1960) and toads of the African genus *Nectophrynoides*. The latter includes some species with free-living larvae and some with modified direct development with terrestrial larvae or with young retained in the female in either an ovoviviparous or viviparous mode (Wake, 1980). Interestingly, species of *Nectophrynoides* with direct development live at high elevations where aquatic breeding sites are rare and long periods of cold common. Similar environments occur in South

America and are occupied by species of the family Bufonidae. While bufonid species normally don't make up more than about 10% of the anuran fauna at any given site, in montane areas of South America, bufonids are abundant and in some situations (e.g., *Atelopus ignescens* in some paramos of Colombia and Ecuador) may be the dominant anuran.

Our direct observations on the breeding ecology of the species on Kukenan and Ilu-tepui, and indirect evidence from the Roraima species, convince us that direct development is characteristic of *Oreophrynella*. The similarities in egg deposition sites between the single clutches and the communal nest indicate that use of a sheltered nest site with access tunnels, probably constructed by the male, is typical. Our impression is that suitable nest sites (areas beneath rocks and in vegetation not subject to flooding) are limited on some tepui summits. Whether the occurrence of communal nesting is an artifact of aggregative behavior at a particularly good breeding site (as in a chorus of male frogs at a pond) or involves other social interaction, warrants further research.

Parental attendance of the clutch by the female is known for a single clutch on Kukenan and possibly also characterizes the communal nest in spite of the ratio of 70 males to 30 females there. Whether these differences result from recent laying of the clutch by the single female (eggs in early stages of development) without adequate time for her departure from the site, or represent a real difference between nesting behavior in communal versus single sites is unknown. Perhaps males remain at the nesting site when the nature of the site (large vs small) allows for attraction of more than one female and room for more than one clutch. If this is true, then the 30 females collected in the communal nest could easily have accounted for the 302 eggs found there and the sex ratio would be appropriate for female attendance.

The tepui summits of the Roraima chain are extremely inhospitable environments for most amphibians (Fig. 2B). Bare rock accounts for 50–90% of the surface areas on their summits. Available water is derived entirely from rain or mist and the summits fluctuate from being waterlogged to extreme aridity in a matter of hours. Water level in a small stream draining the valley in which we were camped on Mount Roraima dropped more than 40 cm in 3 d. Standing water is temporary and may be absent for long and irregular periods in many areas. Fluctuations in

ambient temperature also are extreme and changes of 20 C in a short period are not uncommon. On Roraima we recorded nightly lows of 4–5 C and daily highs above 24 C. On Chimantá-tepui, 140 km to the west of the Roraima chain, temperatures rose from 3.8–24.8 C in 6 h (EDELCA, unpubl. data). The aquatic environment is extremely oligotrophic (J. Paolini, pers. comm.) and the water acidic (pH 5.3–5.9). The water is always clear and cold with few algae and other aquatic plants. Such conditions apparently favored amphibian species with direct development.

Similar patterns of communal nesting and a form of direct development have been reported for the African bufonid *Nectophrynoides malcolmi* (Wake, 1980). The genus *Nectophrynoides* includes eight species of African toads distributed at intermediate to high elevations from Liberia to Ethiopia. As a group it has a broad range of reproductive modes from species with free-living larvae and nonfeeding, terrestrial larvae to ovoviviparous and viviparous ones. The direct development mode described for *N. malcolmi* differs from that described for *Oreophrynella*. In *N. malcolmi* the eggs are placed in a terrestrial nest and the larvae hatch but are terrestrial. In *Oreophrynella* the entire developmental sequence occurs within the egg. In this respect *Oreophrynella* resembles frogs of the genus *Eleutherodactylus* (Leptodactylidae) more than other bufonids. Thus, the bufonids join the Leptodactylidae in having the greatest variety of reproductive modes within the Anura.

The similarity of reproductive patterns in bufonids from high elevation habitats in tropical Africa and South America raises several intriguing questions. Do the similarities reflect close phylogenetic relationship or result from convergence under similar selective regimes? Do species of *Oreophrynella* have a modified amplexus or internal fertilization as has been described for species of *Nectophrynoides*? Other patterns may remain to be discovered in the bufonid radiation in the Pantepui of southern Venezuela.

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Locomotor Performance of Hydrated and Dehydrated Frogs: Recovery Following Exhaustive Exercise

ROBERT E. GATTEN, JR. AND REBECCA MAHALEY CLARK

We induced frogs to jump to exhaustion, allowed them to rest for 15, 30, or 60 min, and then forced them to jump to exhaustion again. Each animal was tested at full hydration (100% of standard body mass) and after dehydration (to 80% of standard body mass). Two measures of locomotor performance were used during each test: distance to exhaustion and time to exhaustion. The frogs recovered their stamina (ability to perform for the initial duration of jumping) faster than they did their ability to jump for the initial distance. Both hydrated and dehydrated frogs recovered their jumping ability at the same rate; thus dehydration to 80% of standard mass does not impede the return of locomotor capacity following exhaustive exercise.

MOST terrestrial amphibians lose water rapidly when faced with even moderately arid conditions because their skin lacks an effective barrier to water movement (Schmid, 1965; Shoemaker and Nagy, 1977; Wygoda, 1984). In anurans, dehydration is accompanied by both behavioral and physiological changes. For example, loss of body water elicits a decrement in the locomotor ability of frogs and toads (Moore and Gatten, 1989) and a decline in the ability of toads to capture prey (Pough, pers. comm.). Such behavioral changes may be linked to the dehydration-induced decline in

the ability of frogs and toads to power locomotion by aerobic metabolism (Pough et al., 1983; Gatten, 1987). Although desiccation reduces the use of oxygen during a bout of exercise, it does not alter the return of oxygen consumption to resting level during the recovery period that follows exercise (Gatten, 1987). Thus, both locomotor performance and aerobic metabolism during muscular activity by anurans are reduced by dehydration, but the return of oxygen consumption to resting level following exercise is not impeded by water loss. During such a rest period at the end of exercise, when

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