

Use of Forest and Tree Species, and Dispersal by Giant Damselflies (Pseudostigmatidae): Their Prospects in Fragmented Forests

Ola M. Fincke

Department of Zoology, University of Oklahoma, Norman, OK 73019 USA
fincke@ou.edu

ABSTRACT

Phytotelmata, or water-filled plant containers, provide an important aquatic habitat in tropical forests typically depauperate of permanent ponds and lakes. As top predators in these microhabitats, species of Pseudostigmatidae offer a rare opportunity to measure the effects of forest plant species on the abundance and distribution of their aquatic occupants. Like the specialists of bromeliads, which depend on the presence of a small group of epiphytic plants, odonates ovipositing in water-filled tree holes and fruit husks require a non-random assortment of tree sizes and species. The size and density of microhabitats ultimately affect larval abundance, although, for most species, it remains unclear how closely adult recruitment tracks larval survivorship. Within its geographic range, *Megaloprepus* relies more heavily on primary forests than do species of *Mecistogaster* that are adapted to dryer conditions and hence are more tolerant of secondary and highly disturbed forests. An experiment with *Megaloprepus* revealed that it exhibited relatively low flight endurance, particularly in females, which rarely dispersed across open areas.

Recent comparative work challenges the status of *Megaloprepus* as a monospecific genus, and suggests that many pseudostigmatid populations may be highly structured genetically. The larval ecology and adult behavior of *Megaloprepus* suggest that its populations should be more highly structured than those of the more vagile tree-hole aeshnids. Collectively, the data reviewed here suggest that forest fragmentation, exacerbated by less predictable threats from global warming, may pose a greater threat to *Mega-*

loprepus and similar species such as *Microstigma rotundatum*, than to species of *Mecistogaster*. The fate of all pseudostigmatids is intimately tied to that of the plant species harboring them. As predators of phytotelm mosquito larvae, some of which are disease vectors, the demise of pseudostigmatids may affect not only forest food chains, but also human health.

HABITATS AND HABITS OF PSEUDOSTIGMATIDS

Phytotelmata, or water-filled plant containers, provide an important microhabitat in tropical forests (Lounibos 1980; Frank & Lounibos 1983; Kitching 2000; Greeney 2001), areas depauperate of permanent ponds and lakes, which in temperate regions were often formed during past glaciation events. The odonate species that depend on phytotelmata are limited to tropical forests of Central and South America, Africa, Asia, and Australia (reviewed by Corbet 1983). Their dependence on a relatively small group of plant species for larval survivorship makes these odonate predators well-suited for measuring the variables limiting the local abundance and geographic distribution of closely related species. Because, as both adults and larvae, the species are differentially adapted to drying conditions, changes in their abundance and distribution could serve as indicators of forest conversion and/or climate change. Although this review focuses primarily on the Pseudostigmatidae, because phytotelmata generally, and tree holes in particular, impose similar selective pressures regardless of the continent on which they occur (e.g. Orr 1994), general trends found in pseudostigmatids are likely to be relevant for the phytotelmata niche throughout the tropics.

Of the 20 species attributed to the family Pseudostigmatidae by Davies & Tobin (1984), three, *Mecistogaster amazonica*, *M. garleppi* and *Microstigma calcipennis* are considered synonyms of *Mecistogaster buckleyi* and *Microstigma anomalum*, respectively (Lencioni 2005; D. Paulson, pers. comm.). Because of similarities in its morphology, feeding habits, and larval habitat, the monospecific *Coryphagrion grandis* of east Africa has long been suspected to be a closely related taxon, but recent genetic work places the African species squarely within the Pseudostigmatidae, close to *Mecistogaster* (Groeneveld et al. 2006). The latter finding changes the way we view the evolutionary history of the family, as it suggests that the last common ancestor of *Coryphagrion* and the New World clades is quite ancient (see Clausnitzer and Lindeboom 2002). To date, the genus *Megaloprepus* is considered monospecific; *M. caerulatus* is here referred to by its genus name only. Other odonates that regularly co-exist in tree holes with pseudostigmatids are the aeshnid dragonflies, *Gynacantha membranalis* and *Triacanthagyna dentata* (DeMarmels, 1992; Fincke 1992a, Fincke 1998). Epiphytic

bromeliads harbor an even greater array of small coenagrionid species (reviewed in Corbet 1983), although little is known about odonate interactions within bromeliads.

Of the phytotelmata available to odonates, bromeliads and tree holes provide the two most distinctive, persistent, and widespread larval niches. Despite our ignorance about 6 species (i.e. *Anomisma abnorme*, *Mecistogaster asticta*, *M. buckleyi*, *M. lucretia*, *M. martinezi* and *M. pronoti*), the majority of pseudostigmatids depend on tree holes rather than bromeliads (Table 1), contrary to Calvert's (1911) prediction that most members of the family probably depend on bromeliads. Calvert speculated that the phytotelm habit originated in flooded forests of the Amazon, where, at high water, low hanging bromeliads might have been mistaken for aquatic vegetation by ovipositing females. Similarly, the origin of tree hole use might have arisen from oviposition 'mistakes' in holes of trees that fall over or along streams or other water bodies, not an uncommon occurrence

Table 1. Larval habitats of pseudostigmatids.

Larval habitat: T= treehole, B = bamboo, F = fruit husk, BR = bromeliad. ? = larvae has yet to be found. *Mecistogaster n sp.* is very similar to *M. jocaste* (J. Louton, pers. comm.)

Genus	species	Habitat:				Reference
		T	B	F	BR	
<i>Anomisma</i>	<i>abnorme</i>	?				
<i>Coryphagrion</i>	<i>grandis</i>	x	.	x	.	Clausnitzer and Lindeboom (2002)
<i>Mecistogaster</i>	<i>amalia</i>	x	.	.	.	F.A.A. Lencioni (pers. comm.)
	<i>asticta</i>	.	?	.	.	F.A.A. Lencioni (pers. comm.)
	<i>buckleyi</i>	?				
	<i>jocaste</i>	x	.	.	.	Machado and Martinez 1982
	<i>linearis</i>	x	.	.	.	Fincke 1984, 1992a, 1998;
	<i>lucretia</i>	?				
	<i>martinezi</i>	.	?	.	.	F.A.A. Lencioni (pers. comm.)
	<i>modesta</i>	.	.	.	x	Calvert 1911; Melnychuk and Srivastava 2002
	<i>n sp.</i>	.	x	.	.	Louton et al. 1996
	<i>ornata</i>	x	.	.	.	Fincke 1984, 1992a
	<i>pronoti</i>	?				
<i>Megaloprepus</i>	<i>caerulatus</i>	x	.	.	.	Young 1980; Fincke 1984, 1992a;
<i>Microstigma</i>	<i>anomalum</i>	.	.	x	.	Caldwell, 1993
	<i>maculatum</i>	x	.	.	.	A.A. Lencioni (pers. comm.)
	<i>rotundatum</i>	x	.	x	.	De Marmels 1989, Santos 1981, S. Yanoviak (pers. comm.)
<i>Pseudostigma</i>	<i>aberrans</i>	x	.	.	.	Fincke 1998
	<i>accedans</i>	x	.	.	.	Fincke 1992a

in Panama. Evidence in support of this hypothesis comes from northern Venezuela, where *Libellula herculea* breeds in quiet pools of mountain streams, but, when there is a flood, holes and crevices in boulder stones in or at the margin of streams fill up and later contain *L. herculea* larvae (J. De Marmels, pers. comm.).

Whereas tree-hole species may also be found in fruit husks, and possibly bamboo internodes, they have seldom been found in bromeliads. One exception is *Gynacantha membranalis*, found in Peru with unidentified *Mecistogaster* larvae in an *Aechmea* sp. of bromeliad that held over 100 liters of water (J. Hoffmann, pers. comm.). Similarly, bromeliad species have not been reported in tree holes or other microhabitats. This is probably due to larval adaptations to dissolved oxygen, which is much higher in bromeliads (Laessle 1961) than in the more anoxic tree holes, where pH also varies across forests (Fincke 1998, 1999; Clausnitzer and Lindeboom 2002). Behavioral differences among larvae offer further evidence that odonates have specialized on tree holes or bromeliads, but not both. For example, larvae of the tree hole species *Megaloprepus*, *Mecistogaster linearis*, and *M. ornata* seldom if ever climb out of rearing jars. In contrast, larvae of *M. modesta*, a bromeliad species, typically crawl out of the same jars (Fincke 1998). The latter behavior would be adaptive in their native bromeliads, as growing larvae move from smaller to larger leaf axils. Similar behavior was described by Machado for the protoneurid, *Roppaneura beckeri*, which lives in leaf axils of *Eryngium floribundum* (see Corbet 1983). Of note is the habit of *Coryphagrion grandis* larvae, which float upside down in a conspicuous manner (Clausnitzer and Lindeboom 2002). To my knowledge, that behavior distinguishes them from any neotropical phytotelm species.

In forests where tree holes are rare, some pseudostigmatids may oviposit in fallen fruit husks that fill with water. In the Brazilian forest where *Microstigma anomalum* occupied the fruit husks of Brazil nut trees, *Bertholletia excelsa* (Caldwell 1993), tree holes were uncommon (J. Caldwell pers. comm.). In Kenya, larvae of *Coryphagrion grandis* were found both in tree holes and water-filled coconut husks (Clausnitzer and Lindeboom 2002). In Panama, on Barro Colorado Island (BCI), where tree holes are common, I have seen only one pseudostigmatid, *Mecistogaster ornata*, oviposit in a fruit husk (*Tonelea ovalifolia*), but I have never found any larvae in husks. In the lowland Atlantic forest of La Selva field station in Costa Rica, odonate larvae were never found in husks of *Lecythis costaricensis*, despite repeated checks. There, fruit husks dry out more readily than tree holes and risk being overturned by animals (Fincke 1998). Fallen palm bracts are the least stable of the phytotelmata available in the tropics; to date, sampling of this microhabitat has not revealed any odonate larvae (e.g. Fincke 1998; Greeney 2001).

One as yet unidentified pseudostigmatid is known to use bamboo internodes (Louton et al. 1996a), and two other small species, *Mecistogaster asticta* and *M. martinezi* are also suspected to do so (F.F. Lencioni, pers. comm.). The unidentified larvae found in Peruvian bamboo were never found in exposed internodes that tended to quickly dry out. Rather, females used only internodes that were accessed via small perforations created by beetles (Louton et al. 1996a), suggesting that this species might be a true bamboo specialist, unlike the asian non-pseudstigmatids known to use both tree holes and bamboo (reviewed by Corbet 1983). Females were similar to *M. jocaste* but smaller, and laid their eggs endophytically (J. Louton, pers. comm.). *M. jocaste* females have been described as 'shooting' into a tree hole eggs subsequently found floating on the water surface (Machado & Martinez 1982). Note that Machado, in an unpublished record, later described the species as *M. martinezi* (J. Louton, pers. comm.). However, I suspect that the female was merely hitting the water surface with her abdomen to make sure that the hole held water, similar to the behavior of female *M. linearis* before they perch to lay their eggs endophytically (Fincke 1992b). When reared, eggs floating on the water surface of Peruvian tree holes were always those of *Toxorhynchites* mosquitos (J. Louton, pers. comm). To my knowledge, all other observations of pseudostigmatid egg-laying, as well as the structure of the ovipositor, suggest endophytic oviposition. Work on a molecular phylogeny of the Pseudostigmatidae is underway, and should help resolve the above discrepancies and permit us to determine whether bamboo use has evolved multiple times, independently (Hadrys, Fincke, Lencioni, unpublished data).

Within phytotelmata, odonates are top predators whose prey include the larvae of mosquitos, ceratopogonids, chironomids, tipulids, other odonates, and the tadpoles of several anuran genera (Fincke 1992a, 1998, 1999; Caldwell 1993; Yanoviak 2001; Haugen 2002; Melnychuck and Srivastava 2002). Kitching (2000) offers a general summary of phytotelm food webs. However, the effects of specific odonates on the dynamics of prey species probably varies. *Megaloprepus*, for example, is a more voracious predator than co-occurring *Mecistogaster* larvae, and seems to have a disproportionately great impact on its prey (Fincke 1998). Although both pseudostigmatids and tree hole aeshnids can greatly reduce the percent of mosquitos that successfully emerge from tree holes, the smaller *Mecistogaster* larvae appear to be the least effective in doing so (Fincke et al. 1997, Fincke, unpublished data).

Some phytotelm prey have evolved responses to their odonate predators. In Jamaica, female crabs kill any odonate larvae in epiphytic bromeliads before laying their own eggs there (Diesel 1992). With over a hundred species of frogs also breeding in tree holes, bamboo, fruit husks, and brome-

liads (Lehtinen 2004), one expects similar adaptations among phytotelm anurans, but few have been documented. Female *Dendrobates pumilio* search the tree hole or bromeliad before laying their eggs there (Summers 1989), a tactic that apparently reduces the risk of odonate predation on tadpoles (Fincke 1998). In Amazonian Peru, a female laughing frog, *Osterocephalus planiceps* lays hundreds of eggs into a single bromeliad leaf axil (Haugen 2002), and the resulting viscosity of the egg mass suffocates any odonate larva present (L. Haugen pers. comm.).

As adults, *Coryphagrion*, *Mecistogaster*, *Megaloprepus*, *Microstigma*, and *Pseudostigma* have all been observed to prey on small orb-weaving spiders, which are plucked from their webs (Calvert 1911, 1923; Young 1980; Fincke 1992b; Clausnitzer & Lindeboom 2002; F.A.A Lencioni, pers. comm.). Although they specialize on taking spiders, pseudostigmatids are known occasionally to take the wrapped prey in spider webs (Stout 1983; Young 1980). In my experience, typical spider prey are ≤ 6 mm in total length. Within the forest, the damselflies forage on spiders in sun flecks and sunny gaps created by large branch or tree falls. These high-light environments enable the damselflies to detect spider webs; in low light they risk becoming entangled in the webs, which is one reason why it is difficult to keep pseudostigmatids alive for very long in small, outdoor insectaries (Fincke unpublished data). The UV-reflectant wing and abdominal signals of *Megaloprepus* and *M. linearis*, respectively, are also adapted to high-light conditions (Schultz and Fincke, unpublished data). Although there may be some habitat partitioning with respect to foraging height among co-existing adults (Fincke 1992b), the abundance of their spider prey is unlikely a factor limiting the number of adult pseudostigmatids. More significant limiting factors are the seasonal duration of tree holes and the abundance of that larval resource, coupled with the dynamics of cannibalism and intraguild predation in the larval stage (Fincke 1992a,c, 1994).

SIZE AND DENSITY OF MICROHABITATS

All the original data presented herein were collected from the lowland, seasonally moist forest of Barro Colorado Island (BCI), Panama (for its general ecology, see Leigh et al. 1982; Leigh 1999). Over the past two decades, I have tagged and censused several hundred individual tree holes used as habitats (i.e. containing ≥ 100 ml water) by treehole odonates to quantify the distribution and species interactions of 5 species of odonates, 3 species of tadpoles, and the predatory mosquito larva, *Toxorhynchites* (Fincke 1984, 1992a, 1994, 1998). Occupancy by odonates never exceeded 70% of tree holes sampled frequently.

Tree holes, particularly those formed when a tree falls and indentations in the trunk fill with water, harbor as much as 50 l of water (Fig. 1a, b). However, the majority of tree holes hold less than one liter (Fig. 1c, d). Persistence of a hole from one year to the next depends primarily on whether it is in a live or dead tree. Due to the rapid rate of decomposition on BCI, only 42% of the holes in fallen trees and 56% of those in dead, upright trees held water for more than two years. In contrast, only about 3% of the holes in live, upright trees failed to hold water from one year to the next (Yanoviak and Fincke 2005).

Although the limiting nature of such larval habitats predisposes them to be defended by adults, variation in the mating system of pseudostigmatids indicates that their value to adults varies across species. Whereas some species defend large microhabitats (e.g. *Megaloprepus* Fincke 1992c, *Microstigma rotundatum*, De Marmels 1989, *Mecistogaster modesta*, Srivastava et al. 2005), others briefly defend light gap areas where matings occur (*M. linearis*, Fincke 1984) or merely mate in sun flecks and gaps where feeding occurs (*M. ornata*, Fincke 1984). Such differences in mating tactics reflect differences among species in the competitive ability of their larvae; there is minimal niche partitioning based on the characteristics of tree holes used by each species (Fincke 1992a).

Within occupied phytotelmata, larval density depends on priority effects and the species' propensity for cannibalism and intraguild predation (Fincke 1992a, 1999). In *Megaloprepus*, females oviposit in a wider assortment of tree hole volumes and shapes than are defended by males. Females lay more eggs in large tree holes than small ones. But regardless of the size, females typically lay many more eggs than could ever survive in any given hole. For example, clutch size of *Megaloprepus* ranges from about 50 to 500, but larval density is reduced via cannibalism and obligate siblicide (Fincke 1994, Fincke & Hadrys 2001, Fincke unpublished data) to about one larva /l (Fincke 1992a). Most *Megaloprepus* recruited to the next generation are produced in the largest holes, which can produce three cohorts per season, or an estimated few dozen individuals surviving to emergence (Fincke 1992b, 1998). Tree holes under one liter rarely produce more than one adult at a time, and rarely more than two adults per wet season on BCI. Similarly, the density of *Microstigma* in fruit husks is usually one per husk, the volume of which, in one study, never exceeded 245 ml. (Caldwell 1993).

Preliminary results from a census of water-filled tree holes under 2 m in height, in a tract of primary forest in Panama indicated an estimated density of 13.87 usable holes per hectare (Fincke unpublished data). Similarly, in a west African forest on the Ivory Coast, tree hole habitats occurred at a mean density of 8.3 tree holes/ha, the highest density being 23/ha (Rödel et al. 2004). Such measures underestimate the true density of available larval microhabitats be-

cause tree holes occur from the ground level to the forest canopy (Yanoviak 1999), above the level at which holes can be monitored easily. But even if we assume the density to be twice the above estimates, they would still be an order of magnitude less than the density of bromeliad microhabitats.

The largest epiphytic bromeliads typically hold at most a few liters of water in a central tank-like container with surrounding leaves (Laessle 1961; Richardson 1999). Because they are divided into multiple leaf axil compart-



Fig. 1. Variation in trees and their tree holes a) large pan hole in a fallen *Platypodium elegans*, BCI that was a habitat for two years before rotting through b) large hole (30-50 l) in *Ceiba pentandra* tree, known to be consistently defended by *Megaloprepus* from 1982 until the tree fell in 1990 c) bowl-shaped hole (< 1 l) in live tree d) tiny hole in a root buttress, too small to support an odonate to emergence e) *Bursera semiruba* at Los Tuxtlas, Mexico, a species in which I have never found tree holes.

ments, bromeliads support a higher density of odonates per ml of water than do tree holes and fruit husks. In the wet forest at Pitilla Biological Station in Guanacaste, Costa Rica, where *Mecistogaster modesta* was the only odonate occupant, larval density in occupied bromeliads ranged from 1-2 per plant in the primary forest canopy, where most plants contained less than one liter of water (Melnychuk and Srivastava 2002), and 1-26 larvae/plant in the secondary forest at the same site (Srivastava et al. 2005). Although they are typically smaller in volume than the largest tree holes, epiphytic bromeliads can occur at much higher density of microhabitats per hectare. In the above secondary forest, the density of bromeliads above 40 cm diameter, roughly the minimum size for odonate development, was about 680 per hectare (Melnychuk and Srivastava 2002). Here, in early May, adults were commonly seen at bromeliads and 73% of those inspected contained larvae in Oct-Nov. (Srivastava et al. 2005). This compared with about 420 suitable bromeliads/hectare in primary forest, where only 23% had larvae (Srivastava et al. 2005). In the lowland, aseasonally wet forest at the La Selva station in Costa Rica, only about a third of bromeliads sampled in June and July held larvae (Fincke 1998). The inability of females to find all of the oviposition sites scattered about a forest may explain these intermediate levels of microhabitat occupancy.

A critical question for species conservation is how larval abundance translates into adult abundance. Based on an apparently high density of bromeliads relative to tree holes in wet forests such as La Selva, one might predict that the smaller *Mecistogaster modesta* should outnumber the larger *Megaloprepus*, but this does not seem to be the case. In a pooled sample of 64 pseudostigmatid adults caught over 18 days between Sept. 1966 and Aug. 1967, 56% were *Megaloprepus*, 39% were *Mecistogaster modesta*, and 4% were *M. linearis* (D. Paulson, pers. comm.). At the same site, another sample of 93 marked adults (i.e. to avoid recounts of the same individual) between June and July, 1991 gave: 70% *Megaloprepus*, 18% *Mecistogaster modesta*, 2% each of *M. linearis* and *Pseudostigma aberrans* (Fincke 1998). The sample differences may reflect seasonal trends in the abundance of *M. modesta* (see Hedström and Sahlén 2001), but they don't explain the dominance of *Megaloprepus*.

EFFECTS OF TREE SIZE AND SPECIES

The abundance and geographic distribution of pseudostigmatids depends not only on their adaptation to abiotic conditions of tropical forests and the suite of odonates present, but on a non-random array of plant species. Among bromeliads, only a subset of species such as those in the genera *Aechmea*, *Guzmania*, and *Vriesia* retain sufficient water to provide suitable habitats for

odonates (Corbet 1983; Melnychuk and Srivastava 2002). Even fewer species (e.g. *Bertholletia excelsa*, *Lecythis costaricensis*, *Tonelea ovalifolia*) produce fruits whose fallen husks collect water. In addition to particular species of bamboo, the use of that microhabitat may also require the presence of a katydid to create the initial hole (Louton et al. 1996a).

Among tropical forests, the presence of tree holes is expected to vary as a function of tree-species composition, which can vary considerably among geographic areas (e.g. Gentry 1990). Because the formation of holes depends on upon features such as indentations in the tree bole or in buttresses, and the propensity for burls or holes to form, species with very smooth boles, such as *Bursera simarouba*, are unlikely ever to have tree holes (Fig. 1e). In my experience, the density of pseudostigmatids is relatively high on BCI, where tree-hole species such as *Platypodium elegans* and *Ficus* spp. are common (Fincke 1992a, herein). The abundance of *Megaloprepus* is also relatively high at La Selva, where an estimated 1/3 of all stems are the woody tree, *Pentaclethra macroloba* (Hartshorn and Hammel, 1994), the trunk morphology of which provides multiple holes in a single tree (Fincke 1998). In contrast, at Aceer station in northern Peru, the forest is depauperate of tree holes, and *Microstigma rotundatum* is relatively scarce (personal observation). We have only begun to quantify the tree species that provide tree hole habitats.

Here I report on a subset of 110 tree holes on BCI for which the tree species were known. The forest there comprises 409 woody tree species, providing a canopy height of 25-35 m featuring a few emergents over 40 m (Foster and Brokaw 1982). Some of the trees holes sampled were located in 90-yr-old secondary forest, but most were coincidentally located in the Hubbell-Foster 50-hectare plot. This is an intensively studied plot of primary forest on the central plateau of the island, where every stem over 2 cm diameter at breast height (dbh) has been tagged and identified to species as part of an ongoing study of forest dynamics (Hubbell and Foster 1983). The plot contains 75% of the island's woody tree species > 1 cm dbh, and 317 woody species > 100 mm dbh. Treeholes in this study were located primarily along trails or in treefall gaps, and my sample was not designed to be representative of the plot itself. All tree holes in my sample were below 2 m. in height, above which it was impractical to monitor tree holes (see Yanoviak and Fincke 2005 for sampling methods). Data from an ongoing census of the 50-hectare plot, once completed, will be reported elsewhere. All variables were log transformed for statistical analysis.

For the 52 trees in my sample for which tree dbh, species identity and tree hole volume were known, dbh was positively correlated with tree hole volume (Fig. 2) and the total water held in holes ($r = 0.94$, $P < 0.0001$), but not with the number of holes per tree ($r = 0.08$, $P = 0.52$). The three largest trees were all *Ceiba pentandra*, which collectively accounted for 47.5 litres of water, 36% of the total 132 liters held by the 52 trees in the sample. The

smallest tree with a tree hole over 0.1 l was a *Eugenia oerstediana* whose dbh was only 45 mm. My results suggest that tree hole volume increases with the age of a tree species, at least up to a certain age, after which the number of holes may not increase with dbh.

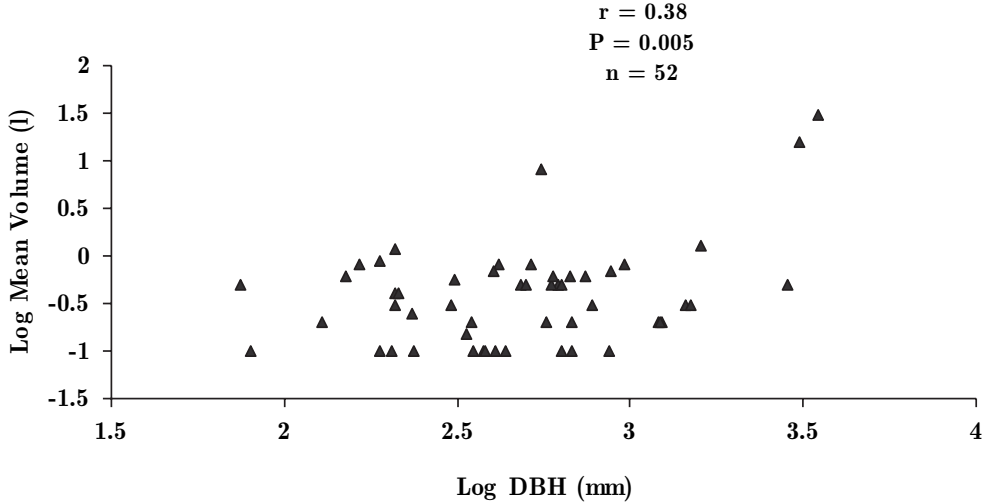


Fig. 2. Tree-hole volume as a function of host tree dbh on BCI, Panama.

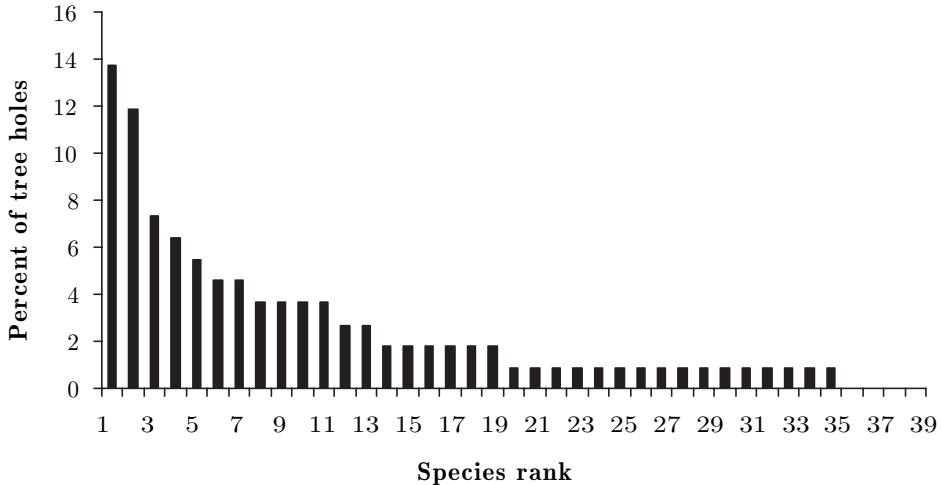


Fig. 3. Species rank, by percentage contribution to the total holes sampled (n= 110) on BCI, Panama. The top 11 species are *Platypodium elegans*, *Quararibea asterolepis*, *Ficus trigonata*, *Trichilia tuberculata*, *Ceiba pentandra*, *Alseis blackiana*, *Gustavia superba*, *Randia armata*, *Eugenia oerstediana*, *Hirtella triandra*, *Brosimum alicastrum*.

The 110 tree holes in my sample were found in a total of 35 tree species in 32 genera (Table 2). Of these, only 23% are known to be colonizing species (see

Table 2. Family, genus and species, mean holes per tree (range), and volume per hole. N = 110 tree holes known to be larval habitats. * indicates colonizing species (see Condit et al. 1996); † includes 1 fallen tree.

Family	Genus	Species	Mean \pm s.e. holes/tree	Mean \pm s.e. liters/hole
Annonaceae	<i>Guatteria</i>	<i>dumetorum</i>	1	0.6
Apocynaceae	<i>Aspidosperma</i>	<i>cruenta</i>	1	0.5
Bignoniaceae	<i>Jacaranda</i>	<i>copaia</i> *	1	0.6
Bombacaceae	<i>Ceiba</i>	<i>pentandra</i>	1.7 (1-3)	9.5 \pm 5.9
	<i>Quararibea</i>	<i>asterolepis</i>	1.6 (1-3)	0.66 \pm 0.6
	<i>Dipteryx</i>	<i>panamensis</i>	2.5 (2-3)	1.15 \pm 1.6
Boraginaceae	<i>Cordia</i>	<i>bicolor</i> *	1	0.3
Chrysobalanaceae	<i>Hirtella</i>	<i>americana</i>	1	0.8
		<i>triandra</i>	1	0.47 \pm 0.08
Elaeocarpaceae	<i>Sloanea</i>	<i>terniflora</i>	2	0.9
Euphorbiaceae	<i>Adelia</i>	<i>triloba</i> *	1	.
	<i>Sapium</i>	<i>acuparium</i>	1	.
Fabaceae: Caesal.	<i>Tachigali</i>	<i>versicolor</i>	1	0.35 \pm 0.15
Fabaceae: Papil.	<i>Andira</i>	<i>inermis</i>	1	0.5
	<i>Dipteryx</i>	<i>oleifera</i>	1	0.7
	<i>Platypodium</i>	<i>elegans</i> *	3.7 (1-10) †	2.0 \pm 2.5
	<i>Pterocarpus</i>	<i>rohrii</i>	1	0.1
Flacourtiaceae	<i>Casearia</i>	<i>arborea</i> *	1	0.1
Lauraceae	<i>Ocotea</i>	<i>whitei</i>	1	0.8
Lecythidaceae	<i>Gustavia</i>	<i>superba</i> *	1	0.17 \pm 0.06
Meliaceae	<i>Trichilia</i>	<i>pallida</i>	1	0.8 \pm 0.40
		<i>tuberculata</i>	1	0.42 \pm 0.11
Moraceae	<i>Brosimum</i>	<i>alicastrum</i>	1	0.3
	<i>Ficus</i>	<i>costaricana</i>	1	.
		<i>trigonata</i>	2.67 (1-6)	1.0 \pm 0.40
Myristicaceae	<i>Virola</i>	<i>sebifera</i>	1	0.1
Myrtaceae	<i>Eugenia</i>	<i>oerstedeana</i>	1	0.13 \pm 0.04
Nyctaginaceae	<i>Guapira</i>	<i>standleyanum</i>	1	0.1
Rubiaceae	<i>Alseis</i>	<i>blackiana</i>	1.3 (1-3)	9.2 \pm 12.6
	<i>Guettarda</i>	<i>foliacea</i>	2	0.1
	<i>Macrocnemum</i>	<i>glabrescens</i> *	1	0.35 \pm 0.17
	<i>Randia</i>	<i>armata</i>	1.3 (1-2)	0.62 \pm 0.6
Sapotaceae	<i>Pouteria</i>	<i>stipitata</i>	2	0.25 \pm 0.18
Tiliaceae	<i>Apeiba</i>	<i>membranacea</i>	1	0.3
	<i>Luehea</i>	<i>seemannii</i> *	1	0.2

Condit et al. 1996), and hence, common in secondary forests (R. Condit pers. comm.). Over half the holes were accounted for by eight species (Fig. 3). For trees with holes, there was no relationship between tree species abundance rank and its rank by tree hole number ($r = -0.04$, $P = 0.83$). However, of the species that represented half the individuals in the respective growth forms of canopy (6 species) or midstorey (9 species) trees on BCI (Hubbell & Foster 1992), three mid-storey (*Eugenia oerstedeana*, *Hirtella triandra*, *Virola sebifera*) and three canopy trees (*Alseis blackiana*, *Tachigali versicolor*, and *Trichilia tuberculata*) provided water-filled tree holes in my sample. And of these, *A. blackiana* and *T. tuberculata* are the two most common canopy species on BCI. Nevertheless, most species were represented by only one individual, and hence my analysis of species nested within genus indicated no effect of species identity on hole volume or total water volume; even the effect of genus on volume was insignificant ($F_{1,30} = 2.06$, $P = 0.16$). Preliminary results from censusing all tree holes under 2 m in 13 of the 50 hectares indicated that several tree species provided more tree holes than expected from their abundance (*Ceiba pentandra*, *Dipteryx oleifera*, *Platygodium elegans*, Fincke unpublished data). Of these, *P. elegans* is a colonizing species, and where present, offers considerable potential for providing larval habitats in secondary forests.

USE OF PRIMARY VERSUS SECONDARY FORESTS

Given the increasing rate of tropical deforestation, the survival of primary forest odonates will depend on their ability to survive in conditions less than pristine. Pseudostigmatids are differentially susceptible to dry conditions, and may thus differ in their ability to avoid local extinction after forest clearing and succession. Within its geographic range, *Megaloprepus* is notably absent from tropical dry forests, where *Mecistogaster ornata* are common (Hedström and Sahlén 2001). Several lines of evidence suggest generic differences in physiological tolerance to drying. Whereas both *M. linearis* and *M. ornata* can be found flying throughout the dry season on BCI, *Megaloprepus* siccitates during that time (Fincke 1992b). And even in the wet season, adults avoid flying across the large laboratory clearing, and do not frequent extremely large natural gaps that offer no shaded perches (O.M. Fincke personal observation). Yanoviak (1999) found larvae of *M. linearis* and *M. ornata*, but not *Megaloprepus*, in canopy tree holes on BCI. In the high-light environment of open canopy, water temperature was higher and pots (i.e. plastic surrogate tree holes) were more likely to dry out than those in understory. As adults, pseudostigmatid genera also use the forest differently. On BCI, where the primary forest (> 400 yrs) is contiguous with 90-yr-old secondary forest, adult *Megaloprepus* colonized tree holes in both forest types. Nevertheless, despite continuous canopy over both

forest types, *Megaloprepus* were more abundant in primary forest, whereas two co-occurring *Mecistogaster* (*linearis* and *ornata*) were more common in the secondary forest. Similarly, in a forest of the Nairi reserve in Limón province on the Caribbean slope of Costa Rica, *Megaloprepus* failed to colonize pots adjacent to recently logged forests. In contrast, co-existing *Mecistogaster linearis* colonized pots in both forest types (Fincke and Hedström, in review). These results were similar to data from Amazonian Peru, where *Microstigma rotundatum* colonized bamboo pots in successional and primary forests, but not in small-scale subsistence clearings (Yanoviak et al. 2006).

Although *Mecistogaster modesta* and the bromeliads on which they depend rely on relatively wet forests, they are found in both primary and secondary forests. In Costa Rica where the high-light environment of a secondary forest favored a great abundance of bromeliads, Srivastava et al. (2005) predicted abundance of *M. modesta* to be a remarkable 36x higher than in a nearby primary forest. It is not known whether differences in adult abundance were of similar magnitude. No adults were found in the primary forest during the surveys, and were rarely seen at that site, suggesting that this species has a preference for secondary forest.

DISPERSAL ABILITY OF *MEGALOPREPUS*

In contrast with tree-hole aeshnids, pseudostigmatids are not strong flyers. From the canopy tower on BCI, I have often watched dragonflies foraging in the canopy, but these never included pseudostigmatids, probably because the high wind velocity of the canopy is not conducive to the hovering flight needed to forage on web-building spiders there (see Ruppell and Fincke 1989). However, pseudostigmatids can and do disperse considerable distances in forest understorey. Studies of marked individuals within forests indicate that *Mecistogaster linearis* and *M. ornata* can travel several km. in a few weeks, and *Megaloprepus* can travel 3.5 km in less than a week (Fincke 1984, unpublished data). A factor critical to their conservation is the extent to which tree-hole species disperse across an unforested landscape.

As a first step towards answering this question, in January 1997, I measured the maximum flight duration of individual *Megaloprepus* released over Gatun Lake, Panama (see map in Leigh et al., 1982). Flight was measured in early morning, starting shortly after sunrise on clear, sunny, days with little or no wind. Individuals were collected from the field during the previous afternoon and held individually in small cages overnight. The next morning, each individual was marked if it wasn't already, weighed, and scored for age, based on wing wear, from 1-3, 3 being old and 1 being young. The damselflies were put in a small cage and transported by motor boat north of the island to a marker buoy

in Lake Gatun. Upon release, an individual was followed by boat until it fell into the water, at which time it was retrieved. The compass direction of its initial flight and any change in direction was recorded. Total flight time was recorded, and the individual's final position was estimated relative to marker buoys in the lake. The distance flown was then estimated using nautical maps showing the position of canal buoys. This method ignores actual distance flown if the individual circled. Except for one male (of unknown territorial status) that died after falling into the water after 212 sec. of flight, all individuals were released in the BCI forest less than 2 hrs after the start of the experiment. Variables were log transformed for analysis. Means are reported \pm s.e.

In total, 8 males and 3 females were tested. Of the males, five were age 1 and three were age 2; three were current territory residents at defended sites, two were satellite males, and the remainder were not collected at a territory. Despite a general trend for males of this species to be larger than females (Fincke 1992c), the males used for testing did not differ significantly from the 3 females in abdomen ($t = -1.9$, $P = 0.09$) or wing length ($t = -1.06$, $P = 0.32$); nor were they significantly heavier ($t = -1.56$, $P = 0.17$). Consequently, there was no difference in wing loading between the sexes in this sample ($t = -1.3$, $P = 0.23$).

There was no trend in the direction the damselflies took upon release over water. Three headed east, two south, two west, two north, and two circled. As shown in Fig. 4, males flew significantly longer ($\bar{x} = 554.8$ sec, range = 114-968 sec) than did females ($\bar{x} = 65.0 \pm 27.5$ sec, range 10-94 sec, $t = -4.0$, $P = 0.004$). There was no difference between satellite and non-territorial males in flight duration or distance flown, so the two groups were pooled for analysis. Relative to males not known to be territorial, territorial

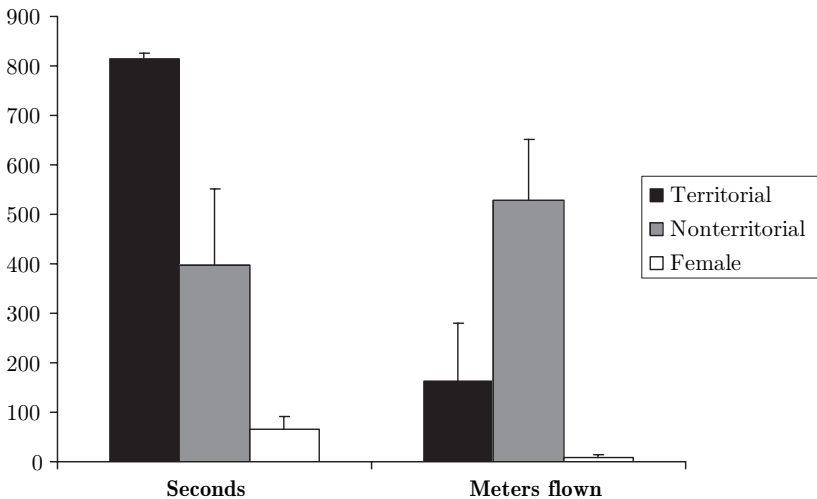


Fig. 4. Flight duration and distance traveled by 8 male and 3 female *Megaloprepes* over Gatun Lake, Panama.

males flew for a longer time ($t = -2.70$, $P = 0.05$), but they frequently circled. Consequently, they covered less distance than did the non-territorial males ($t = 2.68$, $P = 0.04$). The longest distance traversed was an estimated 969 m by a non-resident male that flew for 968 sec, equivalent to a speed of 1 m/sec. The fastest rate was 4.9 m/sec, by a non-resident male that flew for 114 sec. There was no effect of male age on flight duration ($r_s = -0.11$, $P = 0.79$) or distance flown ($r_s = -0.23$, $P = 0.59$). Males flew farther ($\bar{x} = 391.2 \pm 106.4$ m) than females ($\bar{x} = 8.3 \pm 6.0$ m, $P < 0.01$). The female flying the longest (94 sec) circled frequently, and traversed only 20 m. All 3 females and the 7 remaining males flew off with no apparent difficulty when later released into the forest.

Although none of the *Megaloprepus* flew from BCI across the canal to the mainland on the north, the flight time of males would have been sufficient for males to cross the relatively more narrow stretch of water separating BCI from Gigante Peninsula on the mainland on the south side of the island. Because I found *Megaloprepus* larvae in tree holes on small Pepper Island in the canal, this species may also reach the mainland by island hopping. The most difficult result to explain is the behavior of the females. Despite the small sample size, females were strikingly different from the males in their reluctance to fly over open water. This suggests that the sexes may differ in their effective dispersal among forest patches. That the test females had the ability to disperse is evident from their immediate flight upon being released in the forest.

GEOGRAPHIC VARIATION IN *MEGALOPREPUS* POPULATIONS

Dispersal ability directly affects gene flow among populations. I expect, based on differences in flight endurance, that gene flow would be greater among the faster-flying treehole aeshnids (see Wikelski et al. 2006) than among pseudostigmatids. Species differences in mating systems, patterns of female oviposition, and degree of cannibalism and intraguild predation among larvae all have consequences for the effective population size N_e , the number of adults that contribute genes to the next generation (for the formula, see Futuyma 1998). Using microsatellite genetic markers (Hadryś et al. 2005) to quantify parentage of larvae successfully emerging from holes, Fincke and Hadryś (2001) demonstrated that its resource-defense mating system, coupled with high larval cannibalism, reduced N_e of *Megaloprepus* well below the number of sexually mature adults. For non-territorial species or those whose larvae cannibalize only when hungry, N_e should more closely approach the number of mature individuals. Because genetic variation should decrease as N_e and dispersal decrease (see Futuyma 1998), I expect populations of *Megaloprepus* to be more highly structured genetically than those of *Mecistogaster ornata* or the more vagile tree-hole aeshnids.

Initial comparative work on *Megaloprepus* offers some support for the prediction that its populations are highly structured genetically (i.e. among population genetic variance \gg than the genetic variation within populations). First, populations differ in body size. At La Selva in Costa Rica and at Los Tuxtlas field station in Veracruz, Mexico, males and females were larger than on BCI in Panama (Fincke 1998, unpublished data). Secondly, at Los Tuxtlas, as on the Osa Peninsula on Costa Rica's Pacific coast (D. Paulson, pers. comm.), males lack the broad white wing band that characterizes the sexually dimorphic species in Panama and throughout most of its range (Hadrys and Fincke unpublished ms.). On BCI, it is the female's white wing tip that reveals her sex to males. A male will take in tandem a male whose wing tips have been painted white, whereas he will try to fight with a female whose white wing tips have been artificially darkened (Fincke, unpublished ms.). Cues to sexual recognition in the more sexually monomorphic populations remain unknown.

Preliminary analysis of the Los Tuxtlas and BCI populations indicated that their genetic divergence is nearly as great as it is between some other odonate species (Hadrys and Fincke unpublished ms.). Such strong population divergence may reflect past or current geological barriers. However, current populations are becoming increasingly isolated due to the rapid deforestation that has occurred throughout Central America (Brown and Hutchings 1997). Los Tuxtlas has become an island of tropical forest in a sea of cow pastures and agricultural lands. Based on the station's collection of *Megaloprepus* and my own experience with this population since 1994, it appears to be in decline (also, E. González Soriano, pers. comm.). Preliminary results from a dispersal experiment suggested that *M. caerulatus* does not readily colonize secondary forest patches one km away from primary forest (Fincke and Haalboom, unpublished data). Subspecies status of populations within *M. jocaste*, *M. linearis*, *M. lucretia*, *M. modesta*, and *M. ornata* (R. Garrison 2004) are also indicative of genetically structured populations.

FUTURE PROSPECTS FOR PSEUDOSTIGMATIDS

Much of the work on the effects of forest fragmentation on the fauna of primary tropical forests has focused on birds or mammals, there being relatively little work on insects (e.g., Pimm and Raven 2000; Frankie and Matta 2004). Because of their visually conspicuous adults and discrete larval habitats in a small subset of plant species, phytotelm odonates are well suited for documenting the effects of forest conversion across species that differ in vagility and habitat requirements. Collectively, the data reviewed here suggest that *Megaloprepus*, and by analogy, *Microstigma rotundatum*, are reliable

indicators of primary forest, and consequently more vulnerable to forest fragmentation than some species of *Mecistogaster*, a genus which also occurs in tropical dry forests. In a survey of Peruvian odonates, Louton et al. (1996b) found that of five tree-hole odonates, only *Gynacantha membranalis* and *Mecistogaster linearis* were present at all three of their collecting sites, which spanned a distance of about 1,000 km. Those data support my conclusion that the ability of a phytotelm odonate to persist in secondary forests will depend both on its tolerance of such sites, and its ability to disperse across open areas. Hence, one might expect the distributions of species such as *Microstigma rotundatum* and *Megaloprepus* to become increasingly disjunct, unless dispersal routes via riparian or forested corridors are maintained to connect primary forest habitats. Ongoing work focuses on quantifying the genetic structure of pseudostigmatid populations in comparison with tree-hole aeshnids to test such predictions (Hadrys and Fincke, unpublished data).

Global warming is also likely to affect the future of the guild of phytotelm odonates, but in less predictable ways. El Niño effects may provide some clues (see Curtis and Adler 2003). In one experiment I conducted on BCI during 1997-1998, when, due to El Niño effects, the dry season was greatly extended, tree holes dried a full month earlier than usual, and larvae took nearly twice as long to emerge from experimental pots that were kept filled with water (Fincke, unpublished). This was a curious result because there was no lack of mosquito prey. Elevated water temperature might have played a role. Deforestation is already reducing rainfall in some tropical areas (e.g. Rand & Rand, 1982). Global warming may exacerbate the trend, threatening tree hole aeshnids, which require a minimum of 4-5 months to develop (Fincke 1992a), or species in forests where the wet season is already relatively short (e.g. Los Tuxtlas, González Soriano 1997).

As important natural predators of larval mosquitos (Fincke et al. 1997), the fate of pseudostigmatids in tropical forests will have consequences reaching beyond their effects on species assemblages of phytotelm habitats. Several tree-hole mosquitoes are important disease vectors (e.g. Galindo et al. 1955; Theiler and Downs 1973; Pecor et al. 2000; Jones et al. 2004). Given that larvae of *Megaloprepus* and the tree hole aeshnids are more voracious predators than are those of *Mecistogaster* (Fincke unpublished ms.), the elimination of the former may have a greater impact on mosquito populations than the disappearance of the latter. Documenting the effects of forest clearing on the abundance of phytotelm species requires long-term data. Unfortunately, given the unrestrained growth of the human species, increasing stress will be imposed on many pseudostigmatid species, whose future, like so much of the world's biodiversity, remains uncertain.

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