

**GIANT DAMSELFLIES IN A TROPICAL FOREST:
REPRODUCTIVE BIOLOGY OF *MEGALOPREPUS
COERULATUS* WITH NOTES ON *MECISTOGASTER*
(ZYGOPTERA: PSEUDOSTIGMATIDAE)**

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The tropical forest of Barro Colorado Island, Panama, harbors three common species of giant damselflies which are atypical odonates in several respects. Adult pseudostigmatids can detect non-moving prey and feed on small web-building spiders, occasionally taking wrapped prey from webs. On BCI, females of all three species oviposit in randomly distributed, water-filled treeholes. Larvae of the large *Megaloprepus coerulatus* occupied larger treeholes than those of *Mecistogaster linearis* or *M. ornatus*. Males of the sexually dimorphic *Megaloprepus* held mating territories around water-filled treeholes for up to two months, defending them from conspecific males and permitting only females with whom they had mated to oviposit in the holes. Territorial males were significantly larger than non-territorial males and all but one of the 16 observed matings involved resident males. In addition, defended treeholes were larger than undefended holes that also contained *Megaloprepus* larvae. However, because larval habitats vary greatly in quality, environmental influences on body size may greatly reduce the opportunity for the population to respond directly to selection on body size. Neither *Mecistogaster linearis* nor *M. ornatus* held territories nor remained localized in an area. Both species of *Mecistogaster* were less sexually dimorphic in size and coloration than was *Megaloprepus*. Matings in *Mecistogaster* appear to result from random encounters in light gaps where both sexes forage on spiders.

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INTRODUCTION

The Pseudostigmatidae is a small family of neotropical damselflies which inhabit mature forests from Mexico to Brazil (CALVERT, 1908). The large size (wing spans up to 170 mm) and unusual feeding habits of these magnificent insects caught the attention of nineteenth century naturalists (see CALVERT, 1911, 1923), yet our knowledge of their reproductive biology and ecology remains anecdotal (e.g. YOUNG, 1980, 1981). Unlike most odonates which catch flying insect prey, the pseudostigmatids can orient to non-moving prey (FINCKE, unpub. ms.), feeding on small web-building spiders (2-5 mm body length) and occasionally taking wrapped prey from the webs. Most temperate zone odonates breed in dense aggregations around predictable oviposition sites concentrated on streams or quiet bodies of water. At these sites operational sex ratios are usually highly skewed towards males, and consequently competition for mates is intense (e.g. CAMPANELLA & WOLF, 1974; WAAGE, 1979a; FINCKE, 1982). In contrast, the long-lived pseudostigmatid damselflies remain dispersed as mature adults (rarely more than 1-2 in the same area) and mate as isolated pairs, after which females oviposit in water-filled plant containers (CORBET, 1983). Females of *Mecistogaster* are known to oviposit in tank bromeliads (CALVERT, 1911) or water-filled treeholes (MACHADO & MARTINEZ, 1982). Larval habitats of other genera have not previously been determined for certain.

On Barro Colorado Island in Panama, where tank bromeliads are rare, I have found the larvae of three genera of pseudostigmatids (*Mecistogaster*, *Megaloprepus*, and *Pseudostigma*) developing in water-filled treeholes. The treeholes, which are more or less randomly scattered throughout the mature forest, occur in burls, crotches of trees, in decaying branch stumps or in the decaying trunks of fallen trees. Such holes are somewhat unpredictable as suitable larval habitats because persistence of water in them (once the dry season begins) varies greatly as a function of hole volume (0.1-36 litres), size and morphology of the hole opening, and location in either sun or shade. New sites may be created suddenly when a large tree falls and the flutings of the trunk subsequently collect water. In addition, the quality of the holes as larval habitats varies considerably with respect to food availability and the presence and number of predatory dragonfly larvae.

The dispersed distribution of both adults and oviposition sites suggested that competition among males for females may be low among the pseudostigmatids. And yet, if oviposition sites were limiting, a treehole might represent a defensible resource over which males could compete, and with which a single male could attract many mates. Differences in the degree of sexual dimorphism among the three common species suggested that sexual selection (either as competition among males or female choice) may have been more important in the evolution of the largest species, *Megaloprepus coerulatus* Drury than in the smaller *Mecistogaster linearis* Fabricius or *Mecistogaster ornatus* Rambur. In this paper, I document differences in sexual dimorphism among the three species and then describe the reproductive biology of *Megaloprepus coerulatus*. I present observations of repro-

ductive behavior in *Mecistogaster* and suggest why the two genera differ in their mating systems. This work represents the initial results from an on-going study of the ecology and reproductive biology of pseudostigmatids on BCI.

MATERIALS AND METHODS

Barro Colorado, a 1600 ha island located in Gatun Lake in the middle of the Panama Canal, is composed of tropical lowland moist forest (HOLDRIDGE & BUDOWSKI, 1956). It receives an average annual rainfall of 270 cm, with less than 8.6 cm of rainfall/month during the dry season from January-April. The study area (roughly 250 ha transected by 8 km of trails) included old forest (over 150 yrs) on the central plateau and southwest portion of the island, and younger forest (less than 150 yrs) on the eastern portion of the island. Observations were made from January-June during the dry season and beginning of the wet season in 1981 and 1983, and at the end of the wet season, October-December, 1982.

Adult *Megaloprepus coerulatus* (a monotypic genus), the largest zygopteran known, are found year-round on the island. Matings occur throughout the year, except at the end of the dry season. Eggs hatch from 3-7 weeks ($\bar{x} = 30.2 \text{ days} \pm 1.4 \text{ S.E.}$) after oviposition, and the larvae take from 3-7 months to emerge as adults, depending upon food quality in the treehole (FINCKE, unpubl. ms.). CALVERT (1908) reports size ranges for males of 73-100 mm abdomen length, 65-88 mm wing length; for females, size ranges from 64-85 mm abdomen length and 54-75 mm wing length.

In contrast with *Megaloprepus*, the smaller *Mecistogaster linearis*, *M. ornatus* and *Pseudostigma accedens* Selys emerge from early to mid dry season, with population numbers peaking from January-March and declining until the late wet season when none are found (e.g. October-November). Because *P. accedens* was sighted only rarely, it was excluded from the present study. CALVERT (1908) mentions size ranges for *M. ornatus* males of 67.5-88 mm abdomen length and 44-57 mm wing length and for females from 62.5-86.5 mm abdomen length and 44-59 mm wing length. On BCI, I have found that *M. linearis* size ranges from 107-118 mm and 50-60 mm male abdomen and wing lengths respectively, and from 66-97 mm and 42-62 mm abdomen and wing ranges for females.

Ranging patterns were determined by counting all adults of *Megaloprepus*, *Mecistogaster linearis* and *M. ornatus* that I encountered, and marking as many individuals as possible by writing a number on the hindwing with an indelible felt-tip pen. I noted activity at the time of sighting and the location of the individual with reference to trail markers or 20 m quadrants of the Hubbell-Foster permanent 50 ha plot on the central plateau.

Reproductive states of females were determined by dissection of mature females of the three species collected between January and April; presence of sperm and/or mature eggs was noted. Reproductive activity of *Megaloprepus* was monitored roughly once every 3 days at 9 different sites, all but one of which was located in

relatively open (30-80%) canopy in treefall gaps. Between 10:00 and 14:00 hr when individuals were the most active, I recorded the behavior of males and females present during 15-45 min visits to the sites. Reproductive activity of *Mecistogaster* species was observed opportunistically because mating pairs could not be found in predictable sites.

To determine use of possible oviposition sites, I sampled a total of 71 water-filled treeholes for larvae by shining a light into the hole, while gently lifting up the leaves and detritus with a wooden ruler. This method proved better than siphoning, which excluded and/or damaged many of the larger larvae. I searched all the holes for larvae at least once a week and measured the depth of standing water over a three-month period from October-December. Hole volumes were calculated by multiplying average width and length by average depth of water. Means are reported with their standard errors. In order to correctly identify larvae to species, I collected last instar larvae from a subsample of holes and allowed them to emerge in an outdoor insectary (3x3x7 m), holding the adults for up to 10 days to note the developmental color changes in the wings.

RESULTS

Sexual Dimorphism

Of the three species studied, *Megaloprepus coerulatus* was the most strikingly sexually dimorphic in both wing coloration and body size. Within a day of emergence, males developed a conspicuous white band just proximal to a large dark blue band on the distal portion of the wing. The extreme tip of the wing was clear. In contrast, females lacked the white band but had two small white patches on the tips of the wings, distal to the blue band. These differences in wing color produced two distinct visual patterns when the insects flew or hovered over treeholes. The white tips of the female appeared to an observer as four fluttering spots while the wings of a male produced a broad blue and white stripe in flight. Males of this species were conspicuously larger than females, having significantly longer wings and abdomens than females (t-test, $p < 0.001$) (Fig. 1).

The two species of *Mecistogaster* were far less sexually dimorphic. The wings of *M. linearis* and *M. ornatus* changed color with age. The wing tips of *M. linearis* were milky white in individuals less than a week old. Males and females collected in mid dry season (*i.e.* after January) had a black pseudostigma along the dorsal edge of the wing. Mature males had clear wing tips (the wings had a brownish tinge) while the wing tips of mature females were a faint opaque white. In addition to this slight but consistent difference in wing appearance, males had significantly longer abdomens than did females, but did not show a corresponding difference in wing length (Fig. 2).

The least sexually dimorphic species was *M. ornatus*, in which the development of sexual dimorphism in wing coloration coincided with the breaking of reproductive diapause in the late dry to early wet season. Until May, both males and

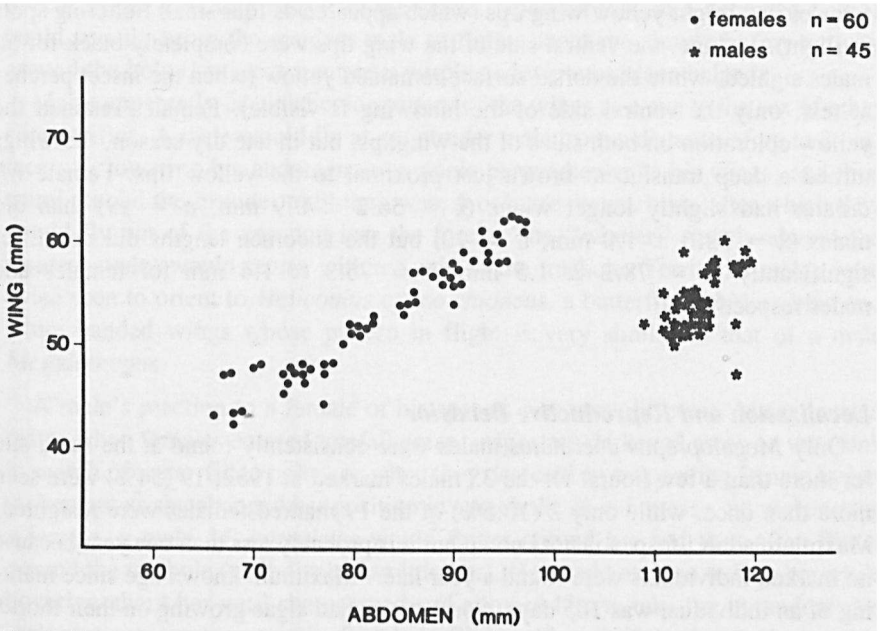


Fig. 1. Size of male and female *Megaloprepus coerulatus*. Correlations of wing length and abdomen length are 0.96 for females and 0.95 for all males.

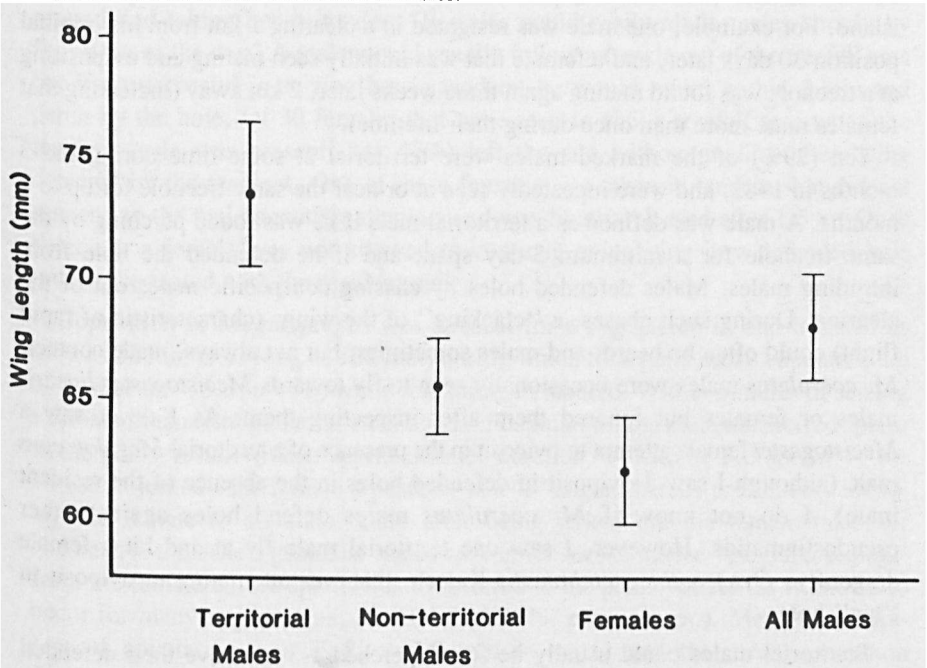


Fig. 2. Size of female and male *Mecistogaster linearis*. Correlations of wing length and abdomen length are 0.97 for females and 0.56 for males. Sample sizes are: $n = 10$ for territorial males, $n = 25$ for non-territorial males, and $n = 19$ for females. Mean sizes are shown with 95% confidence intervals.

females had bright yellow wing tips (which appeared as four small fluttering spots in flight). In June, the ventral side of the wing tips were completely black for all males sighted, while the dorsal surface remained yellow (when the insect perches at rest, only the ventral side of the hindwing is visible). Females retained the yellow coloration on both sides of the wingtips, but in late dry season, the wings turned a deep translucent brown just proximal to the yellow tips. Female *M. ornatus* had slightly longer wings ($\bar{x} = 56.2 \pm 0.9$ mm, $n = 19$) than did males ($\bar{x} = 52.6 \pm 1.0$ mm, $n = 10$) but the abdomen lengths did not differ significantly ($\bar{x} = 78.2 \pm 1.5$ mm, $\bar{x} = 76.3 \pm 1.4$ mm for females and males respectively).

Localization and Reproductive Behavior

Only *Megaloprepus coeruleus* males were consistently found at the same site for more than a few hours. Of the 35 males marked in 1982, 19 (54%) were seen more than once, while only 2 (10.5%) of the 19 marked females were resighted. Maximum adult lifespan is not known but it is probably less than one year because no marked individuals were found a year later. Maximum known age since marking of an individual was 165 days. Some males had algae growing on their thorax and wings; the time necessary for such growth to occur is estimated to be at least several months (D. WUJEK, pers. comm.). Adults wandered widely over the island. For example, one male was resighted in a clearing 1 km from his original position 30 days later, and a female that was initially seen mating and ovipositing at a treehole was found mating again three weeks later, 2 km away (indicating that females mate more than once during their lifetime).

Ten (29%) of the marked males were territorial at some time during the 3 months in 1982, and were repeatedly seen at or near the same treehole for up to 2 months. A male was defined as a territorial male if he was found perching by the same treehole for a minimum 3-day span, and if he defended the hole from intruding males. Males defended holes by chasing conspecific males out of the clearing. During such chases, a "clacking" of the wings (characteristic of rapid flight) could often be heard, and males sometimes, but not always, made contact. *M. coeruleus* males were occasionally seen to fly towards *Mecistogaster linearis* males or females but ignored them after inspecting them. As I never saw a *Mecistogaster* female attempt to oviposit in the presence of a territorial *Megaloprepus* male (although I saw 3 oviposit in defended holes in the absence of the resident male), I do not know if *M. coeruleus* males defend holes against other pseudostigmatids. However, I saw one territorial male fly at and hit a female dragonfly, *Gynacantha membranalis* Karsch, that was attempting to oviposit in "his" hole.

Territorial males could usually be found perched 1-3 m above their defended hole by 10:30 hr. Two males never defended two holes in the same treefall area, and the closest neighboring territories were 0.3 km away from each other. A resident male would periodically wander around the treefall area to feed on spiders in sunny spots, but would usually return to the treehole within 15 min, fluttering

over it before perching near it in the shade. Upon arriving at a defended hole, I could usually bring the resident male to flutter about me simply by my activity around the hole (I suspect wearing a purple and white bandana helped).

Males apparently used the color pattern of the wings as a cue to the sex of other conspecifics. A male would fly at an intruder male from a distance of up to 20 m, face off, lowering his abdomen at an angle perpendicular to his wings, and then spiral around the intruder until they were 5 or more metres high, after which they would fly out of the gap and into the forest. The "winner" (nearly always the resident male) would return within 5 min to the treehole. Territorial males were twice seen to orient to *Heliconius cydno chioneus*, a butterfly with dark blue and white banded wings whose pattern in flight is very similar to that of a male *Megaloprepus*.

A male's reaction to a female of his species was very different. Males located mates when females entered treefall areas, inspecting darkened areas on the trunk in search of water-filled-holes, or when they detected an ovipositing female by her movement as she changed her position in a treehole. In either case, upon detecting a female, a male *M. coerulatus* would flutter around her and then often flutter around the treehole (as if displaying it to her). He would attempt to face her while hovering about her until she perched and allowed him to take her in tandem. No male was ever seen to seize a female in flight, although if the female hovered in one spot, a male could sometimes pounce on her from above, knocking her to the ground and taking her in tandem. Females could easily elude males simply by flying out of the area. A male would usually follow a female out of the treefall area but if unsuccessful in seizing her in tandem, he would return within 5 min and perch by the hole. Of 30 females that were seen to visit a treefall area when the resident male was present, 14 (47%) left the site without mating after being detected by the resident. One of these females was taken in tandem, but did not respond to the male's mating attempts and was finally released after 1.5 hr. Once detected, a female was not allowed to continue ovipositing in a defended hole unless she mated with the resident male.

Copulation in *Megaloprepus* was unusual for a zygopteran in that it lasted as little as 52 min or as long as 108 min, during which time pairs broke copulation up to 7 times ($\bar{x} = 5.3$, $n = 6$) while remaining in tandem. Within minutes of seizing a female in tandem, and after each break of copulation, the male transferred sperm to his penis vesicle (mean sperm transfer duration = 15.6 ± 2.0 sec, $n = 8$). He then "jerked" the female repeatedly at a 45° angle, thereby presumably inducing the female to copulate. Only after being jerked did the female raise her abdomen to the male's genitalia. Males were never seen to induce "genital touching" from the female before sperm was transferred to the penis vesicle (as is known to occur for many zygopterans, H. ROBERTSON, pers. comm.). Mean total duration of copulation was 79.8 ± 8.9 min ($n = 6$) and the mean copulation duration between sperm transfers was 14.5 ± 0.8 min ($n = 35$). During the first 10 min or so of each copulation "bout", the male performed undulating movements with his abdomen. During the last several minutes of each copulation, his abdomen remained motionless.

A pair broke tandem only at completion of copulation (4-7 copulation "bouts"). The male then "chased" the female back to the hole and fluttered around it until she began to oviposit. During oviposition, the female typically clung to the side of the treehole, moistened her abdomen with water, and then laid eggs either directly on the moist bark just above the water line, or inserted the eggs into floating leaves or softer pieces of rotting bark. Oviposition duration at a single hole was highly variable, from 4-45 min ($\bar{x} = 27.7 \pm 7.0$ min, $n = 8$), and was usually, but not always, of longer duration at larger treeholes. Males chased away any intruder male conspecifics that entered the area while the female was ovipositing, and would attempt to mate with any additional females that entered the area. Males did not seem to be able to "count" mates and consequently, on one occasion, a resident remained perched while a second female who had managed to enter the hole without being detected by the male, oviposited beside the mated female. However, it was uncommon for more than one female or male to be at a given treefall on any one day. Females did not limit their oviposition to one hole — rather they were seen to switch between holes within the same treefall, as well as to oviposit alone at small, unguarded treeholes in shaded forest.

Territorial males were significantly larger than non-territorial males (Fig. 1). Non-territorial males were often found in treefall areas or clearings that did not contain water-filled holes, but they were never found at the same site for longer than a day. In one instance, a small male (66.6 mm wing length) that had been continually chased by a resident male, occupied a territory for 2 days before he was displaced by a second larger male. Another small male (64.7 mm wing length) sporadically perched around a small (< 1 litre) hole in a small clearing. All but one of the resident males held territories in treefall gaps. The one exception was a male that defended a large burl hole in a huge *Ceiba pentandra* tree next to a trail clearing. Defended holes held more water than those undefended holes that also contained *Megaloprepus* larvae (and were thus used by females) (Fig. 3).

Mating success appeared to be much higher for resident males than for males without territories. The mean number of matings seen for territorial males was 1.6 ± 0.6 (range 0-5) during an average of 11 visits to each territory during which the resident male was present. In contrast, only one of the 29 males that were not seen to defend a territory at any time during the 3 months was seen to mate. This male mated at a defended hole whose resident was *in copula* with another female. No female was seen to mate unless she had first detected a water-filled hole. In 2 cases, a female entered a territory when the resident male was absent, detected the treehole, perched above it for a minimum of 10 min, but never oviposited in it. After perching, one of the females left while in the second case the female foraged in the treefall area for over an hour without ovipositing.

The mean duration of territory residency was 30.5 ± 6.7 days ($n = 10$, range = 7-59 days). One of the males was seen to defend 2 different sites sequentially. In 1982, the dry season came nearly 2 months early, in November. No male maintained a territory after his treehole had dried out. On several occasions holes would dry out and later be temporarily filled by rain. Larvae could withstand temporary drying in moist holes for up to a week, but would die if the

hole dried out completely. Ants were found to occupy moist and drying treeholes, and probably carried off larvae that were forced to the surface of the mud as the water evaporated. Upon returning to the study site for one week in March, 1982, I found all of the 71 holes were completely dry, and neither male nor female *Megaloprepus* were found around treefalls. In fact, adults appeared to be either very inactive and/or few in number at this time because I found only one male during an entire week's search. However, both *Mecistogaster linearis* and *M. ornatus* adults were sighted frequently during this period.

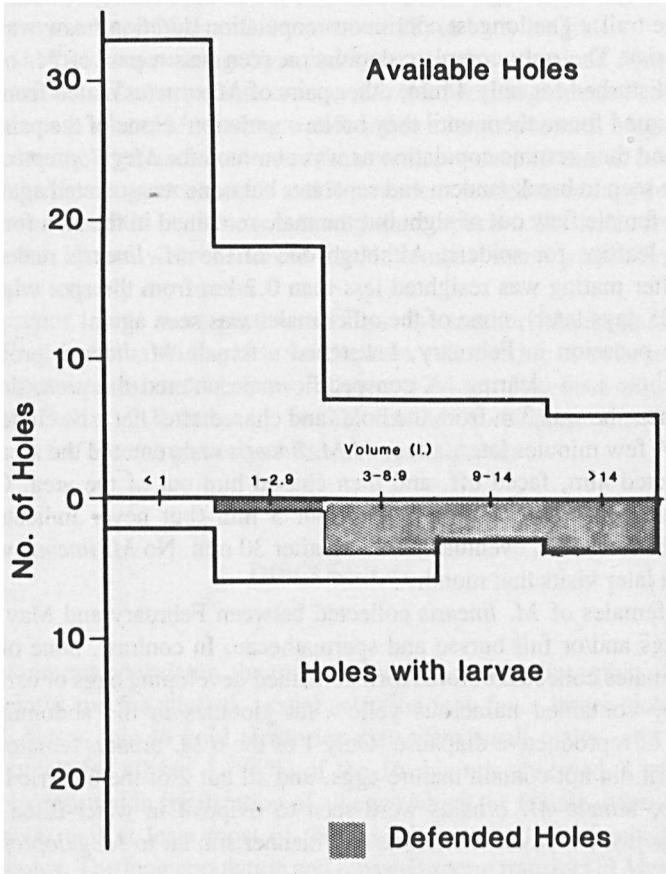


Fig. 3. Volumes of treeholes containing *Megaloprepus* larvae relative to the 71 treeholes sampled. Mean volume of defended holes was 13.6 ± 3.3 litres ($n=9$) while mean volume of undefended holes containing larvae was 4.7 ± 2.0 litres ($n=12$) (t-test, $p < 0.05$).

Localization and Reproductive Behavior of *Mecistogaster*

Of the 112 marked *M. linearis* (54 males, 58 females), only 6 were resighted again and only 2 of these were in the same location (maximum interval of 29 days and 3 km from site of marking). One female remained in a treefall area for 5 days and a teneral male was repeatedly found in a clearing with a treehole for a 17-day span. Of the 34 marked *M. ornatus* (12 males, 22 females), 4 were resighted a

second time, but all 4 were in locations different from the original one (maximum interval was 85 days and 0.5 km between sightings). Although in mid to late dry season it was not uncommon to find two individuals visiting a large treefall during an hour interval, I saw few interactions between individuals (see below). The greatest number of *Mecistogaster* I have seen in the same general area is 3.

In late dry and early wet season (April-June), I found 4 pairs of *M. linearis* and 5 pairs of *M. ornatus* mating in late morning or early afternoon, perched in the forest understory. Only 1 of the pairs (*M. ornatus*) was in the vicinity of a water-filled hole, although all were in or near small clearings (made by branch falls or the trail). The longest continuous copulation duration I saw was 40.5 min (*M. linearis*). The only complete copulation seen was a pair of *M. ornatus* that mated undisturbed for only 4 min; other pairs of *M. ornatus* mated from 4-24 min from the time I found them until they broke copulation. None of the pairs was seen to break and then resume copulation as was common for *Megaloprepus*. All of the pairs were seen to break tandem and separate, but none reassociated again. In three cases, the female flew out of sight but the male remained in the area for 2-10 min, searching leaf tips for spiders. Although one of the *M. linearis* males that was marked after mating was resighted less than 0.2 km from the spot where he was marked (85 days later), none of the other males was seen again.

On one occasion in February, I watched a female *M. linearis* probe about a small treehole in a clearing. A conspecific male entered the area, detected the female when she was 3 m from the hole, and chased after her; she eluded him and perched. A few minutes later, a second *M. linearis* male entered the area. The first male detected him, faced off, and then chased him out of the area. One of the males returned to the clearing after about 5 min (but never indicated he had detected the treehole), eventually leaving after 30 min. No *M. linearis* was seen at the site on later visits that month.

All 13 females of *M. linearis* collected between February and May contained mature eggs and/or full bursae and spermathecae. In contrast, none of the 8 *M. ornatus* females collected before April contained developing eggs or carried sperm loads; they contained numerous yellow fat globules in the abdominal cavity, indicative of reproductive diapause. Only 1 of the 6 *M. ornatus* females collected in late April did not contain mature eggs, and all but 2 of the 6 carried sperm. In early June, female *M. ornatus* were seen to oviposit in water-filled treeholes, laying eggs just above the water line in a manner similar to *Megaloprepus*.

Distribution of Larvae in Treeholes

Of a sample of 71 water-filled treeholes, 54 (76%) were occupied by at least one odonate larva. *Megaloprepus coerulatus* larvae were found in 27 (38%) of the holes sampled, while *Mecistogaster* larvae were found in 18 (25%). *Pseudostigma accedens* larvae were found in 3 (4%) of the treeholes and the larvae of the dragonfly *Gynacantha* occupied 13 (18%) of the holes. Exuviae were found in the vicinity of several treeholes, indicating that the larvae were able to undergo complete development there. By allowing larvae to emerge in the insectary, I confirmed that the larvae found in a subsample of holes represented all four

pseudostigmatid species found on BCI. Larvae of *Megaloprepus coerulatus* were clearly distinguishable from those of other pseudostigmatids by the white dot at the tip of each caudal lamella. I could not distinguish between *M. ornatus* and *M. linearis* larvae in the field. Of the 10 *Mecistogaster* larvae that emerged in the insectary, 7 were *linearis* and 3 were *ornatus*. *Pseudostigma accedens* larvae were similar to those of *Mecistogaster* in being completely brown in color, but, the last instar larvae of the former were much larger than those of *Mecistogaster* (mean body length = 30.1 ± 1.0 mm, $n = 3$; *M. linearis*, $\bar{x} = 21.5 \pm 0.8$ mm, $n = 7$, *M. ornatus*, $\bar{x} = 22.8 \pm 1.1$, $n = 3$). Last instar larvae of *Megaloprepus* averaged 28.1 ± 0.4 mm ($n = 28$) in body length.

Eight of the holes containing *Gynacantha* larvae also contained *Megaloprepus* larvae, but neither of these species co-occurred with *Mecistogaster* or *Pseudostigma* except in one case where *M. ornatus* was found in a large hole with *Megaloprepus*. No hole under one litre contained more than one larva over 10 mm in body length. Because both *Mecistogaster* species and *P. accedens* tended to occupy holes under 2 litres, there was little coexistence among these species. Six holes from which *Mecistogaster* larvae were removed in November were later colonized by *Megaloprepus* in early dry season.

Megaloprepus larvae were partitioned from the smaller *Mecistogaster* species and from *Pseudostigma* on the basis of the hole volume. Mean volumes of holes containing odonate larvae were as follows: 17.4 ± 3.9 litres ($n = 8$) for *Gynacantha*, 9.0 ± 2.0 litres ($n = 21$) for *M. coerulatus*, and 1.3 ± 0.4 litres ($n = 8$) for *Mecistogaster* and *Pseudostigma* larvae.

DISCUSSION

In *Megaloprepus coerulatus*, the most strikingly sexually dimorphic of the three pseudostigmatid species studied, sexual selection may favor larger males. Larger males were better able to hold territories than were small males, and territorial males accounted for all but 1 (94%) of the 16 matings observed. I assume that these matings resulted in fertilization of all eggs which the female oviposited in the defended hole, and at least most of the eggs subsequently oviposited in undefended treeholes. The long copulation and repeated sperm transfers in *Megaloprepus* suggest that if males can displace sperm of previous matings they do it by packing sperm into the female's storage organs rather than by removing it (as is known for several zygopterans; e.g. WAAGE, 1979b; FINCKE, 1984). It is unlikely that non-territorial males represent a successful alternative mating tactic. Variation in male size was found to be continuous. Small males attempted to hold territories but they were usually replaced by larger males within a short time. I assume that the direct male-male interactions which I saw between residents and intruders resulted in much of the displacement, although I cannot rule out differential mortality between large and small males on territories (I saw no cases of predation on males, although I often found evidence of wing damage). Because females

frequently eluded even territorial males' mating attempts, it seems improbable that a male could attract a female in the absence of a water-filled hole.

While body size has been shown to be important to mating success in several insects (e.g. ALCOCK *et al.*, 1977; BORGIA, 1980; GWYNNE, 1980; JOHNSON, 1982), this is one of the first reports of a male size advantage in an odonate (see also MILLER, 1983). In contrast, evidence for stabilizing selection on body size was found for a non-territorial damselfly, *Enallagma hageni* (Walsh), which exhibits scramble competition for mates and in which females are slightly larger than males (FINCKE, 1982). The advantage of large size for *Megaloprepus* males may be that large individuals are stronger flyers, and may be better able to chase off intruders as well as fly the long distances necessary to find treeholes randomly distributed in the forest. While selection for large body size appeared to be strong on *Megaloprepus*, I have found that larvae occupying large treeholes emerged as larger adults than those in very small holes (FINCKE, unpub. ms.). Until it can be shown that size differences among males are in part due to differences in genotypes, it remains uncertain if the population of *Megaloprepus* can respond directly to selection for body size.

Because intruder males were always chased off when detected by a resident male, the mating system of *M. coeruleus* is best described as resource-defense polygyny rather than a lek (*i.e.* aggregations of males to attract females) as was suggested by YOUNG (1980) who found up to 5 males in a clearing in Costa Rica. It is not clear whether he observed five different *Megaloprepus* visiting the clearing at the same time, or whether the same or different unmarked individuals visited the clearing sequentially. The photo published by YOUNG (1981) described as a *Megaloprepus* female that had just finished ovipositing is in fact a male *Megaloprepus* (as indicated by the broad white band) guarding an oviposition site. While I found that females "exchanged" fertilizations for the opportunity to oviposit in a large defended treehole, the relative importance of the territory for mating versus oviposition remains unclear. The high rate of rejection of resident males' mating attempts suggests that females were originally attracted to clearings in search of oviposition sites rather than in search of a male with which to mate. However, virgin females or females that have run out of sperm may visit territories in order to mate (which may explain the 2 cases where females detected but did not oviposit in treeholes in the absence of the resident male).

Mecistogaster ornatus was in reproductive diapause during the dry season and was seen to oviposit only after treeholes filled with water. *M. linearis* females matured eggs throughout the dry season, even when treeholes were drying up; it is possible that females of this species can lay diapause eggs. However, as I was unable to induce gravid *M. linearis* females to oviposit in the laboratory (as *Megaloprepus* routinely did), I could not test this prediction. The lack of localization of *M. linearis* coupled with the paucity of matings observed, despite the fact that females carried sperm, suggest that individuals encounter mates at random, most likely meeting in sun-flecked areas in the forest or light-gaps at treefalls where adults were found to forage on spiders. Large light-gaps are frequented by many insect species (e.g. asilids, lepidopterans, weevils) and particularly other

odonates (libellulids) which also use them as mating sites (pers. obs.). Because small treeholes used by *Mecistogaster* are usually under closed canopy, a male defending such a spot may have difficulty detecting females. I found *M. linearis* extremely cryptic even in flight, unless they were in sunlight.

Without more observations of reproductive behavior, it is difficult to explain why male *M. linearis* have longer abdomens than do females of this species. CALVERT (1911) suggested that long abdomens of pseudostigmatids enabled females to lay eggs through narrow openings of tank bromeliads. In general this is true, but the argument does not explain why male abdomens should be longer than those of females. The only odonate larvae found in treeholes with narrow openings in this study were those of pseudostigmatids. *Gynacantha* larvae were never present in such holes, probably because adult females of that genus have short abdomens relative to their wings which they hold horizontally, preventing them from being able to enter holes with narrow openings. Male *M. linearis* may use their longer abdomens for sexual recognition, displaying them in a manner similar to that of *Megaloprepus*, which hold them perpendicular when they face off with a conspecific male.

All three species studied were found to use oviposition sites that were dispersed, and yet potentially defendable. It is reasonable to assume that treeholes represent a limiting resource for pseudostigmatids on BCI because 76% of available holes in the sample were occupied by at least one larva. The number of larvae in any one hole is limited by cannibalism and/or killing (but not eating) among pseudostigmatid larvae (pers. obs.). Seventy-six percent is a minimal estimate of occupancy because some larvae probably emerged from the holes before I sampled them, and some larvae could have been overlooked because of their habit of swimming to the bottom and hiding in the muck if disturbed. EMLEN & ORING (1977) predicted that territoriality should evolve where resources are clumped such that an individual male could defend them, but that where resources are widely dispersed, scramble competition for mates should evolve, resulting in more equitable mating success among males. This prediction does not strictly hold true for all pseudostigmatids—treeholes used by females of the 3 species were defendable, limiting resources, but only *M. coeruleatus* males were territorial. I propose that *Megaloprepus* males defend only a small subset of available holes because only large water-filled holes attract enough females over time to be worth defending. Large holes are often in treefall areas because when prone, the entire length of the trunk of many tropical trees acts as a pan for catching water. Treefalls result in large canopy openings which are more likely to be detected by the pseudostigmatids as they fly high in the canopy than are small treeholes in the understory. Thus, by defending only holes in treefall areas or other large clearings, a male increases his chances of encountering a female who is searching for either a mate or an oviposition site. In addition, he increases the number of offspring that emerge as adults, because larger holes retain water longer in the dry season and contain more last instar larvae than do small holes (pers. obs.). Perhaps most importantly, by defending large holes, a male is also more likely to produce a large male offspring that will have a mating advantage over smaller males. Because *Megaloprepus* live for such a long time,

sexual competition among males over their lifetime may be as intense as competition among territorial males of shorter-lived temperate species.

It remains unclear why *Mecistogaster* is not also territorial. A single small treehole may not attract a sufficient number of females to be worth defending, but if so, why do *Mecistogaster* males not defend large holes? The current evidence suggests that *M. linearis* is not excluded from using large holes by territorial male *Megaloprepus*. Even if interspecific defense does exist, *M. linearis* could maintain territories at large, drying holes after they are left by *Megaloprepus*, since *M. linearis* females seem to oviposit in dry holes. The niche partitioning among larval *Megaloprepus* and *Mecistogaster* may be the result of differences in female oviposition site preference between the two genera, resulting from past but not current competition between the species. *Mecistogaster* larvae may be better adapted to survive in the more depauperate, small water-filled containers. Because *Mecistogaster* larvae are smaller, in large holes they would be more likely to be eaten by *Gynacantha* than would *Megaloprepus*, whose larvae can escape predation after growing to a size of about 20 mm. It may be that where large tank bromeliads are more abundant, *Mecistogaster* females use them to the exclusion of treeholes.

The discrete larval habitats of pseudostigmatids offer a unique opportunity to study environmental effects of larval habitats on adult reproductive success, effects of adult behavior on larval survivorship within a species, competition among species for limiting resources, and effects of larval niche partitioning on seasonality of adults. In addition, by being top predators of tropical treeholes, odonate larvae are probably important in controlling the populations of smaller aquatic hole dwellers (notably mosquitoes). I am currently investigating these topics using laboratory and field experiments in Panama.

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REFERENCES

- ALCOCK, J., G.C. EICKWORT, & K.R. EICKWORT. 1977. The reproductive behavior of *Anthidium maculosum* (Hymenoptera: Megachilidae) and the evolutionary significance of multiple copulations by females. *Behav. Ecol. Sociobiol.* 2:385-396.
- BORGIA, G. 1980. Sexual competition in *Scatophaga stercoraria*: Size- and density-related changes in male ability to capture females. *Behavior* 75:185-206.
- CALVERT, P.P. 1908. Odonata. In: F.D. Godman, [Ed.], *Biologia Centrali-Americana. Vol 50. Insecta, Neuroptera.* 51-57.

- CALVERT, P.P. 1911. Studies on Costa Rican Odonata II. The habits of the plant dwelling larva of *Mecistogaster modestus*. *Ent. News* 221:402-411.
- CALVERT, P.P. 1923. Studies on Costa Rican Odonata X. *Megaloprepus*, its distribution, variation, habits and food. *Ent. News* 34:168-174.
- CAMPANELLA, P.J., & L.L. WOLF. 1974. Temporal leks as a mating system in a temperate zone dragonfly (Odonata: Anisoptera) I. *Plathemis lydia* (Drury). *Behavior* 51:49-87.
- CORBET, P.S. 1983. Odonata in phytotelmata. In: J.H. Frank & L.P. Lounibos, [Eds.], *Phytotelmata: Terrestrial plants as hosts for aquatic insect communities*. 29-54. Plexus Pub. Inc., Medford, N.J.
- EMLEN, S.T., & L.W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215-223.
- FINCKE, O.M. 1982. Lifetime mating success in a natural population of the damselfly *Enallagma hageni* (Walsh) (Odonata: Coenagrionidae). *Behav. Ecol. Sociobiol.* 10:293-302.
- FINCKE, O.M. 1984. Sperm competition in the damselfly *Enallagma hageni* (Walsh) (Odonata: Coenagrionidae): Benefits of multiple matings for males and females. *Behav. Ecol. Sociobiol.* 14:235-240.
- GWYNNE, D.T. 1980. Female defense polygyny in the bumblebee wolf *Philanthus bicinctus* (Hymenoptera: Sphecidae). *Behav. Ecol. Sociobiol.* 7:213-225.
- HOLDRIDGE, L.R., & S.G. BUDOWSKI. 1956. Report on an ecological survey of the Republic of Panama. *Caribb. For.* 17:92-110.
- JOHNSON, L.K. 1982. Sexual selection in a tropical brentid weevil. *Evolution* 36:251-262.
- MACHADO, A.B.M., & A. MARTINEZ. 1982. Oviposition by egg-throwing in a zygopteran *Mecistogaster jocaste* (Pseudostigmatidae). *Odonatologica* 11:15-22.
- MILLER, P.L. 1983. The duration of copulation correlates with other aspects of mating behavior in *Orthetrum chrysostigma* (Burmeister) (Anisoptera: Libellulidae). *Odonatologica* 12:227-238.
- WAAGE, J.K. 1979a. Adaptive significance of postcopulatory guarding of mates and nonmates by male *Calopteryx maculata* (Odonata). *Behav. Ecol. Sociobiol.* 6:147-154.
- WAAGE, J.K. 1979b. Dual function of the damselfly penis: Sperm removal and transfer. *Science* 203:916-918.
- YOUNG, A.M. 1980. Feeding and oviposition in the giant tropical damselfly *Megaloprepus coerulatus* (Drury) in Costa Rica. *Biotropica* 12:237-239.
- YOUNG, A.M. 1981. Notes on the oviposition microhabitat of the giant tropical damselfly *Megaloprepus coerulatus* (Drury) (Zygoptera: Pseudostigmatidae). *Tombo* 23:17-21.