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GORDON PRITCHARD
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GIANT DAMSELFIES IN A TROPICAL FOREST:
REPRODUCTIVE BIOLOGY OF MEGALOPREPSUS
COERULATUS WITH NOTES ON MECISTOGASTER
(ZYGOPTERA: PSEUDOSTIGMATIDAE)

OLA M. FINCKE
Department of Zoology, University of Iowa
Iowa City, Iowa, 52242, U.S.A.

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 Megaloprepsus coerulatus occupied larger treeholes than those of Mecistogaster
linearis or M. ornatus. Males of the sexually dimorphic Megaloprepsus 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
Megaloprepsus 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 Megaloprepsus. Matings in Mecistogaster appear to result from random encoun-
ters in light gaps where both sexes forage on spiders.

1. Present address: c/o Dr. Peter Miller, Department of Zoology, South Parks Road, Oxford University,
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 skewed towards males, and consequently competition for mates is intense (e.g. CAM-PANELLA & 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 defendable 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 coeruleus* 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 coeruleus*. I present observations of repro-

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Barro Colorado, a 1600 ha Panama Canal, is composed BUDOWSKI, 1956). It r than 8.6 cm of rainfall/mo area (roughly 250 ha trans yrs) on the central plateau (less than 150 yrs) on the from January-June during in and 1983, and at the end of 1981.

Adult *Megaloprepus coe known, are found year-round except at the end of the dry 1.4 S.E.) after oviposition adults, depending upon CALVERT (1908) reports 65-88 mm wing length; for and 54-75 mm wing length.

In contrast with *Megaloprepus* and *Pseudostigma accedens*, population numbers peak in the dry season when none are found, sighted only rarely, it was mentions size ranges from A 44-57 mm wing length and 44-59 mm wing length. Of 109-118 mm and 50-60 mm from 66-97 mm and 42-62 mm.

Ranging patterns were *Mecistogaster linearis* and individuals as possible by felt-tip pen. I noted activity usual with reference to trail in next 50 ha plot in the center.

Reproductive states of each of the three species collected mature eggs was noted. Roughly once every 3 days a
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 ($\bar{x} = 30.2$ days $\pm 1.4$ 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 109-118 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.

Rearing 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 the location 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
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**Upper figure:**
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.

**Lower figure:**
Fig. 1. Size of male and female *Megalopeplus coeruleus*. Correlations
of wing length and abdomen length are 0.96 for females and 0.95 for all
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 coerulatus* 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. coerulatus* 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 ovipositions in defended holes in the absence of the resident male), I do not know if *M. coerulatus* males defend holes against other pseudogastromatids. 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 could usually bring the around the hole (I suspe Males apparently use conspecifics. A male would face off, lowering his a spiral around the intrusk would fly out of the ga resident male) would be twice seen to orient to t white banded wings w *Megaloprepus.*

A male’s reaction to mates when females entered in search of water-filled movement as she change a female, a male *M. cc around the treehole (as if hovering about her until male was ever seen to see one spot, a male could so ground and taking her i flying out of the area. A but if unsuccessful in se perch by the hole. Of 30 resident male was pre detected by the resident respond to the male’s ma detected, a female was unless she mated with the

Copulation in *Megaloprepus* little as 52 min or as long to 7 times ($\bar{x} = 5.3$, $n = 3$) a female in tandem, and a to his penis vesicle (mea. He then “jerked” the fem the female to copulate abdomen to the male’s geni from the female before sp occur for many zygopt era tion of copulation was duration between sperm the first 10 min or so of each movements with his abd his abdomen remained mo
small fluttering spots completely black for all when the insect perches. Females retained the dry season, the wings yellow tips. Female M. m, n = 19) than did lengths did not differ mm for females and

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one time during the 3 one treehole for up to 2 s found perching by the defended the hole from specific males out of the (characteristic of rapid t always, made contact. s Mecistogaster linearis am. As I never saw a territorial Megaloprepus absence of the resident id holes against other fly at and hit a female tempting to oviposit in n above their defended in the same treefall area, ay from each other. A ill area to feed on spiders 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 chionaeus, 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 (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 rotted 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
n (4-7 copulation “bouts”), and fluttered around it until typically clung to the side of the single hole was highly = 8), and was usually, but sometimes chased away any intruder. Male was ovipositing, and entered the area. Males did so on one occasion, a male had managed to enter the site beside the mated female. The male to be at a given position to one hole — rather than the same treefall, as well as to the forest.

Territorial males (Fig. 1). Clearings that did not harbor the same site for longer (wing length) that had been territory for 2 days before the male (64.7 mm wing length) entered a small clearing. All but one of the males was a male *Entandra* tree next to a trail of undefended holes that also contained females (Fig. 3).

 Resident males than for males for territorial males was 1.6 to each territory during the 3 months was seen to resident was in *copula* with another she had first detected a territory when the resident male or a minimum of 10 min, but nales left while in the second hour without ovipositing. 30.5 ± 6.7 days (n = 10, 2 to defend 2 different sites months early, in November. Dried out. On several occasions filled by rain. Larvae could 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 *Mectistogaster linearis* and *M. ornatus* adults were sighted frequently during this period.

![Available Holes Diagram](image)

**Available Holes**

- **Volume (l):**
  - < 1
  - 1-2.9
  - 3-8.9
  - 9-14
  - > 14

**Defended Holes**

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 Mectistogaster**

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 leaftips 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; clearly distinguishing tip of each caudal *linearis* larvae in insectary, 7 were similar to those of instar larvae of the body length = 9 mm, n = 7, *Megaloprepus* ave.

Eight of the hol larvae, but neither except in one case. No hole under one. Because both Mec. 2 litres, there was Mecistogaster lar *Megaloprepus* in e Megaloprepus lar and from Pseudost containing odonate Gynacantha. 9.0 litres (n = 8) for M.

In *Megaloprepus* pseudostigmatid species, males were better at attracting females and these matings result in the formation of a defended hole, and fended treeholes. This suggests that if males sequester sperm into the female, several zygopterans non-territorial males: the male size was found but they were usually direct male-male competition and resulted in much mortality between the sexes on males, although
Original one (maximum up to mid to late dry season), a large treefall during rains (see below). The eneral area is 3.

Pairs of *M. linearis* and *M. ornatus*, perched in the same vicinity as the *Gynacantha* species (made by branches), I saw was 4.5 min. A large pair of *M. ornatus* that mated from 4-24 min were the pairs was seen. *Megaloprepus* was of all the species associated again. In three, the area for 2-10 min, *linearis* males that was the spot where he was gain.

*M. linearis* probe about a the area, detected the er, she eluded him and crossed the area. The first of the area. One of the ever indicated he had *M. linearis* was seen at dry and May contained mast, none of the 8 *M. linearis* eggs or carried sperm in the abdominal cavity, *ornatus* females collected the 6 carriied sperm. In water-filled treeholes, *Megaloprepus* was occupied by at least one and in 27 (38%) of the 8 (25%). *Pseudostigma* and the larvae of the *M. linearis* were found in the of the insectary, I cons represented all four pseudostigmatic 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 pseudostigmatic 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 zygopterns; 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; GWINNE, 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 exhibited 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. coerulatus 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 treecfalls 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 (libelluli small treeholes us defending such a extremely cryptic of

Without more why male M. line CALVERT (1919) females to lay eggs true, but the arguments those of females. T in this study were different in such holes, p mens relative to the beings able to enter longer abdomens fo that of Megaloprepus conspecific male.

All three species and yet potentially d limiting resource for the sample were occ hole is limited by can larvae (pers. obs.). S some larvae probably larvae could have been deeper and hiding in that territoriality sh male could defend ble competition for ncess among males. Th —treeholes used by b but only M. coerulatus. defend only a small at attract enough female treecfall areas because trees acts as a pan fo which are more likely canopy than are small in treefall areas or othe a female who is se he increases the numb retain water longer in small holes (pers. obs. male is also more like advantage over smallle
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ls) 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
ture, 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 perpendicularly when they face off with a
conspecific male.

All three species studied were found to use oviposition sites that were dispersed,
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. coerulatus 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. 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 short-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 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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