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Behavioural ecology of the Giant Damselflies of Barro Colorado Island, Panama

(*Odonata: Zygoptera: Pseudostigmatidae*)

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INTRODUCTION

The Pseudostigmatidae is a small family of giant damselflies whose distribution is limited to New World lowland or montane forests (below 1200 m) from Mexico to Bolivia (Table 7.1, see also Calvert 1908). The family is so named because the pterostigma (a thickened opaque spot along the costal margin of the wing) is either absent or is replaced by a pseudostigma, which is traversed by cross-veins and differs between fore- and hindwings (Davies and Tobin 1984). Their large size and graceful flight make these damselflies a notable attraction to both visitors (e.g. Calvert 1908, 1911, 1923) and natives (e.g. Geijskes 1975) of neotropical forests. The unusual biology of this family illustrates the potential of odonates to adapt to life in neotropical forests, where the standing water required by their aquatic larvae is often scarce (Note 1). Unlike their temperate counterparts, which are typically found in great numbers at breeding sites along streams or lakes, sexually mature pseudostigmatids range widely and lay their eggs in water-filled plant containers such as treeholes and bromeliads randomly scattered throughout the forest. Adult pseudostigmatids feed on web-building spiders. Because one rarely encounters more than a dozen of them during a day's search, studying these elusive insects presents a challenge to the field ecologist.

Table 7.1. Known species of Pseudostigmatidae (modified from Davies and Tobin 1985), and their geographic distribution.

Name		Distribution
Anomisma	*abnorme* (McLachlan 1877)	S. America
Mecistogaster	*amalia* Burmeister, 1939	S. America
	amazonica Sjoestedt, 1918	Brazil
	asticta Selys, 1860	Brazil
	buckleyi McLachlan, 1881	Ecuador
	garleppi Foerster, 1903	Peru
	jocaste Hagen, 1869	Amazonia
	linearis (Fabricius, 1777)	Central and S. America
	lucretia Drury, 1773	S. America
	martinezi Machado, 1985	Bolivia
	modesta Selys, 1860	Central America
	ornata Rambur, 1842	Trinidad, Central and S. America
	pronoti Sjoestedt, 1918	Brazil
Megaloprepus	*coerulatus* (Drury 1782)	Central and S. America
Microstigma	*anomalum* Rambur, 1842	Amazonia
	calcipennis Fraser, 1946	Bolivia
	maculatum Selys, 1860	Amazonia
	rotundatum Selys, 1860	S. America
Pseudostigma	*aberrans* Selys, 1868	Central America
	accedens Selys, 1868	Central America

Here I summarize the behavioural ecology of four species of pseudostigmatids that occur on Barro Colorado Island (BCI), Panama, where I have studied them intermittently from 1981–90 (Fincke 1984*a*, 1992*a*, 1992*b*, unpublished mss. *a*, *b*;

Table 7.2. Patterns of larval ecology and adult behaviour among odonates developing in water-filled treeholes on Barro Colorado Island.

Species	Final instar size (mm)	Size of treehole larval habitat	Dry season adaptation	Duration of female receptivity (months)	Male mating strategy
Gynacantha membranalis	36.8	medium–large	aestivation?	?	?
Megaloprepus coerulatus	28.1	small–large	aestivation	7–8	defence of medium–large treeholes
Mecistogaster linearis	22.3	small	egg diapause?	5–6	defence of gaps
Mecistogaster ornata	22.4	small	reproductive diapause	3–4	no defence

Rüppell and Fincke 1989*a, b*). *Megaloprepus coerulatus* (Drury, 1782), *Mecistogaster linearis* (Fabricius, 1777), and *Mecistogaster ornata* Rambur, 1842, are common on BCI, and also occur on the Atlantic mainland of Panama (Calvert 1908; personal observation). A fourth species, *Pseudostigma accedens* Selys, 1868, was seen less than a dozen times on the island during a 14-month study in 1983–4, and is mentioned only briefly.

A major goal of this paper is to offer possible explanations for species differences in larval ecology and adult reproductive behaviour (Table 7.2). To this end I summarize the results of field and laboratory experiments that demonstrate an interplay of selective pressures acting on adults and larvae and suggest that interspecific competition has been important in shaping pseudostigmatid behaviour. Where possible, the biology of these Panamanian pseudostigmatids is related to the biology of other members of this little known family.

SPECIES IDENTIFICATION AND SEXUAL DIMORPHISM

Although the pseudostigmatids can be distinguished on the basis of differences in wing venation (Fig. 7.1; see also May 1979), the species on BCI can easily be identified in flight by differences in wing coloration and/or the proportions of the characteristically slender bodies. As with most odonates, the sexes are distinguished by the presence of an ovipositor on the final abdominal segment of females, whereas in males, this segment carries a pair of claspers used to hold a female by her pronotum prior to and during copulation. Females typically have broader wings than males, probably to reduce wing loading of gravid individuals. Species differences in the degree of sexual dimorphism correspond to differences in the ability of males to monopolize receptive females and/or oviposition sites, and are thought to reflect differences in the opportunity for sexual selection on males (Fincke 1984*a*, 1988).

Megaloprepus coerulatus, the largest (but not the heaviest) extant odonate known, has a wing length of up to 88 mm and an abdomen as long as 100 mm. This species is easily recognized by the wide, dark blue (sometimes appearing black) band that covers the lower one-third of the wings of males and females (Fig. 7.1(a)). It is the most sexually dimorphic pseudostigmatid with respect to body size and wing coloration. Although highly variable in size, males are on average larger than females (Fincke 1984*a*), and have a large white patch (which disappears in dried specimens) on the wing, anterior to the blue band. The extreme portion of a male's wing tip is hyaline, whereas that of a female is milky white, where the veins remain indistinct.

At emergence, *Mecistogaster linearis* has milky white wing tips which become clear in older males and remain slightly whitish in older females. The pseudostigma on the dorsal edge of the wing of both sexes becomes black with age (Fig. 7.1(b)). In addition to the slight differences in wing coloration, sexual dimorphism is evident in the male's disproportionately long abdomen, which probably functions in sexual displays with competitors (see Fincke 1984*a*).

Mecistogaster ornata, a relatively small pseudostigmatid, is characterized by opaque, yellow-tipped wings throughout the dry season (Fig. 7.1(c)). However, when the adults break reproductive diapause in late April or early May, the ventral sides of the male's wing tips turn deep brown and eventually black, whereas those of the female become edged in brown with the yellow colour predominating. Thus, when a male holds his wings together, as he does when perching, the wing tips appear black, whereas in flight they still appear yellow-tipped. Males and females do not differ significantly in the length of the wings or abdomen.

With its yellow-tipped wings, *Pseudostigma accedens* appears similar to *M. ornata* in flight (Fig. 7.1(d)), but the large size and robust body are more reminiscent of *M. coerulatus*. I have seen too few *P. accedens* males to know if their wings change colour when they are reproductively active. However, none of the males or females observed between late dry and mid wet seasons had white or clear wing tips, as is implied for this species in May's (1979) key. Male *P. accedens* have longer abdomens than do the females, suggesting that competition for mates in this species may involve male–male displays as in *M. linearis*.

The four species are more difficult to distinguish as larvae. The exception is *M. coerulatus*, whose larvae are characterized by a conspicuous white dot on each of the three caudal lamellae (leaf-shaped structures at the base of the abdomen which function in respiration). The larvae of *M. linearis*, *M. ornata*, and *P. accedens* are uniformly brown, although *M. linearis* often appear nearly black. The *Pseudostigma* larva can be distinguished from *Mecistogaster* larvae because it grows to a final instar length (excluding caudal lamellae) of 30 mm, whereas the final instar of both *Mecistogaster* species is only about 22 mm in length. In older *Mecistogaster* larvae, the wing pads of *M. ornata* appear yellowish whereas those of *M. linearis* appear clear or whitish. For these four pseudostigmatid species, the length of the final instar larva is positively correlated with the length of the adult's wings and abdomen (Fincke unpubl. ms. *a*).

LARVAL HABITAT AND HABITS

Unlike most odonates, which develop in streams, lakes, or ponds, pseudostigmatid larvae have been found only in water-filled plant containers (phytotelmata; see Corbet 1983). In one of the earliest reports on a pseudostigmatid, Calvert (1910) described a *Mecistogaster modesta* larva from a bromeliad in Costa Rica. Santos (1981) found the larva of *Microstigma* in water-filled Brazil nut pods and De Marmels (1989) has found larvae of *Microstigma rotundatum* in water-filled crevices of fallen trees in Venezuela.

On BCI, the four pseudostigmatids and a dragonfly *Gynacantha membranalis* (Aeshnidae) comprise a guild of odonates

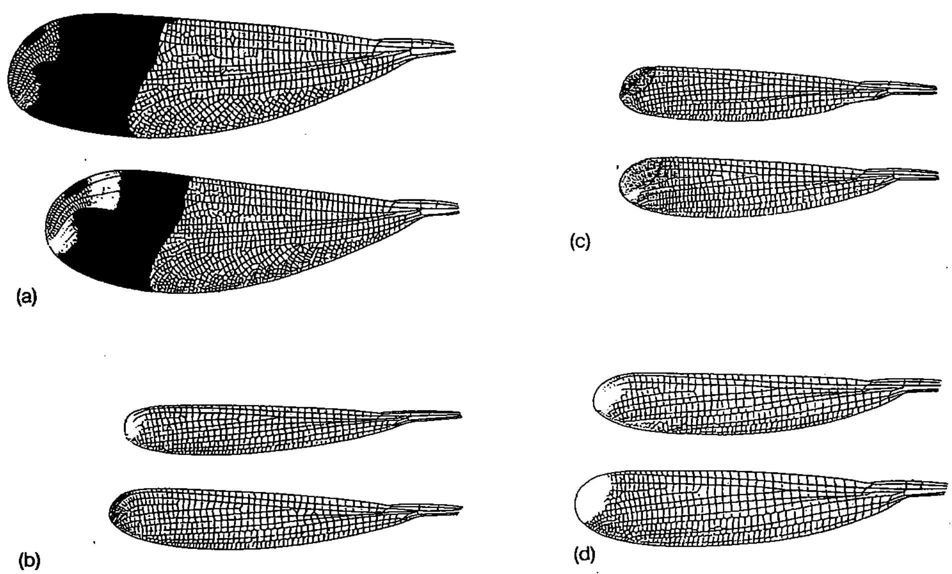

Fig. 7.1 Forewing of male (above) and female (below) pseudostigmatids. The wings were xerocopied, and are presented here at a scale of 0.65 of actual size. (a) *Megaloprepus coerulatus*, (b) *Mecistogaster linearis*. The top wing is that of a teneral male whose pterostigma is still indistinct. (c) *Mecistogaster ornata*, (d) *Pseudostigma accedens*.

whose larvae develop in water-filled treeholes. I have never found their larvae in the seasonal streams, in the one natural pond (Kingfisher Pond), or in two artificial ponds on the island. Selection of oviposition site by females appears to be fairly specific, and these pseudostigmatids probably do not colonize bromeliads, even where tank bromeliads such as *Aechmea tillandsioides* are more common than they are on BCI (see Croat 1978; Young 1981). Although female guild members oviposited readily in artificial holes (plastic tubs lined with black plastic) secured to living or fallen trees (between ground level and a height of 2 m), I never found their larvae in a stone 'metate' (an Indian grinding basin) on the forest floor in the same study area. Nor did ovipositing *Mecistogaster* and *Megaloprepus* females show interest in the tank bromeliads that were placed in gap areas close to artificial holes where they did oviposit. Although I once saw *M. ornata* oviposit briefly in a water-filled fruit husk of *Tontelea richardii*, I never found odonate larvae in that microhabitat on BCI. Finally, I never found odonate larvae in the large, water-filled palm fronds that fell to the forest floor, and were readily colonized by mosquitos.

Odonate larvae are opportunistic predators, and represent the highest trophic level of the water-filled treehole communities on BCI. Newly hatched pseudostigmatids are about 2 mm in length, and feed on micro-crustaceans. Mosquito larvae (e.g. *Toxorhynchites*, *Haemagogus*, *Aedes*, *Culex*, *Anopheles*) are the most common and abundant food source for older larvae, particularly in small treeholes (see also Corbet and McCrae 1981). Larger treeholes (i.e. > one litre) sometimes harbour tadpoles and syrphid fly larvae, and such prey are preferred by intermediate to large odonate larvae. Predation by larger individuals on smaller ones (within and between species) is a major source of larval mortality. Evidence of cannibalism (e.g. larvae missing caudal lamellae, dead larvae with holes chewed in the thorax or abdomen, partially consumed larvae) is common even in large treeholes. The spacing of odonate larvae within a treehole probably reduces the risks of intra- and interspecific predation. Larvae under 7 mm in length are often found resting on leaves and detritus near the surface of the water, or in shallow areas of long basin-like holes. In contrast, medium to large pseudostigmatid larve are usually found under leaves or detritus in deeper water along the side of the treehole, with their caudal lamellae held near the water surface. Large *G. membranalis* larvae usually rest on the bottom of treeholes.

The behaviour of *M. coerulatus* larvae suggests that food limitation has been a selective agent in their evolution. These larvae display to each other by raising their caudal lamellae and sparring with their mandibles. In lab experiments using small artificial holes provided with food *ad libitum*, *M. coerulatus* killed but did not necessarily eat other individuals of similar size (Fincke, unpubl. ms. *a*), suggesting that in nature, food routinely becomes limiting (see also Corbet and Griffiths 1963). The killing of smaller larvae thus functions as an extreme form of interference competition rather than simple predation. In large artificial holes containing a grid of regularly spaced leaves, individuals did not defend any particular area or leaf, but when short of food, they killed and often ate the smaller conspecifics encountered. Smaller conspecifics were tolerated (i.e. several different instars were often found under the same leaf with no evidence of aggressive interactions) only with tadpole prey *ad libitum* (Fincke, unpub. ms. *a*). Thus, *M. coerulatus* larvae can only be considered to be territorial if the territory is defined as an entire small treehole. In large treeholes, larger individuals apparently exert dominance over smaller individuals, which either move out of the way or risk being attacked.

With food available *ad libitum* in the lab, ranges of post-hatching developmental times were 4.5–5.5 months for *G. membranalis*, 3.5–4.5 months for *M. coerulatus*, and 4.3–4.7 months for *Mecistogaster*. Under field conditions, developmental times ranged from the above minimum durations to 8 months or even longer depending on the quality of the treehole habitat.

Pseudostigmatid larvae that do not emerge before the treeholes dry up, as they normally do by March, usually die in most years. A drying experiment with *M. coerulatus* larvae revealed that this species could not withstand more than three weeks of drying (Fincke, unpubl. ms. *a*). Even if some treeholes remained moist during exceptionally wet years, such as 1984, coatimundis routinely searched for food by digging through the detritus of treeholes in fallen trees, and ants often invaded drying holes in upright trees, making larval survivorship low. In May, 1984, shortly after the treeholes refilled with the first wet season rains, I found larvae (over 10 mm) in only 5 of the 93 treeholes known to harbour odonates in January. Because most treeholes are spatially isolated, moving in response to drying is unlikely to be adaptive (but see Machado 1981*a*).

Water-filled treeholes vary considerably in their temporal and spatial predictability, accessibility to ovipositing females, and in their quality as habitats for odonate larvae. In living trees, holes that form in a branch crotch or break-off point, or in a partially rotted burl may persist for decades. Treeholes that form suddenly when a tree falls and its crevices or trunk flutings fill with rain, usually hold water for less than two seasons before completely rotting out. Treehole openings vary in shape from a narrow slit to an open bowl. Pseudostigmatid females can insert their characteristically long abdomens into treeholes whose openings are only a few centimetres wide. Because the dragonfly *G. membranalis* holds its wings out horizontally when perched, it is prevented from ovipositing in narrow-mouthed treeholes. In one study (Fincke 1992*a*) treeholes that contained odonate larvae varied in volume from 0.1 to roughly 50 litres. Large treeholes contained more prey and a greater variety of prey than did small ones, and generally dried up later in the dry season. Consequently, for a given odonate species, there was a positive correlation between treehole volume and the number of larvae surviving to emergence per season (maximum = at least 15). Treeholes of under one litre in volume rarely produced more than one adult per season. Although adult *M. coerulatus* emerging from large artificial holes in the field were more variable in size than those emerging from small holes, large holes produced the largest individuals.

Treeholes appear to be a limiting resource for guild members (Fincke 1992*a*). Most of the sampled treeholes contained less than one litre of water (Fig. 7.2). Three-quarters of the treeholes contained at least one odonate larva, and 99 per cent of the treeholes over one litre did so. Moreover, nearly all of the 48 artificial holes placed in gaps and in the understorey were colonized by at least one guild member within three months (Fincke 1992*a*). Because adult guild members dispersed widely over the island, it was impossible to determine if adult population size increased as the result of this increase in the number of larval habitats.

The distribution of larvae among treeholes suggested that the larval habitat was partitioned by the guild members. As shown in Fig. 7.2, treeholes of under one litre were disproportionately occupied by the two *Mecistogaster* species, whereas treeholes of over one litre were more likely to be occupied by either *M. coerulatus*, *G. membranalis*, or both. Two observations suggested that larval distribution in treeholes was the result of differential larval survivorship rather than differences in preference of adult females for oviposition sites. First, I saw females of *M. linearis*, *M. ornata*, and *M. coerulatus* oviposit in both large and small treeholes and artificial holes. Second, in treeholes where two or more species were present early in the wet season, usually only a single species survived to emergence. Differential larval survivorship could result from either:

(1) differences among species in their tolerance to some abiotic factor (e.g. pH, oxygen content, temperature), which may differ consistently between large and small treeholes; or
(2) interspecific differences in competitive ability of the larvae.

Although abiotic factors other than water volume and temperature have yet to be measured, year-to-year overlap in the species that successfully emerges from a given treehole argues against the first hypothesis. My experimental and field data currently support the second hypothesis.

The guild members exhibit a hierarchy of intrinsic growth

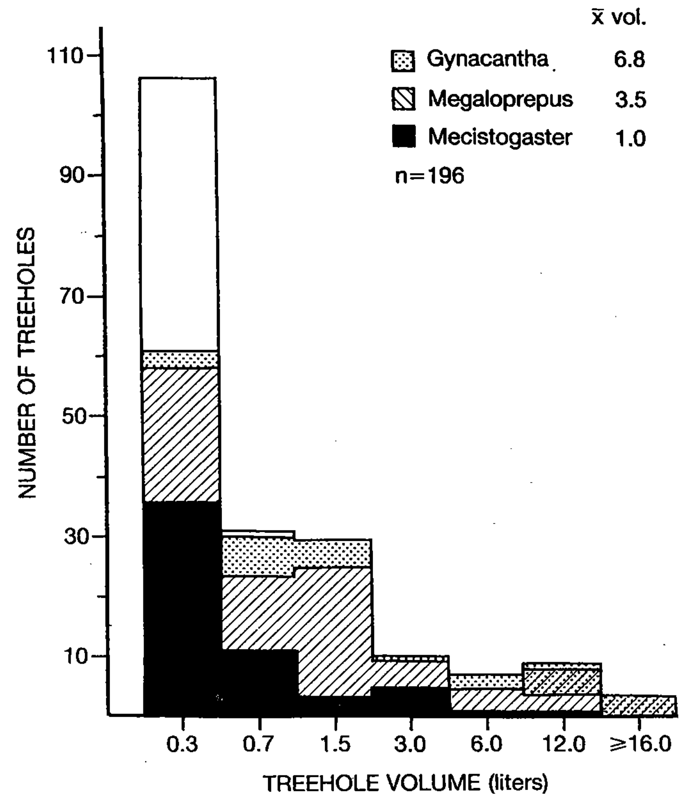

Fig. 7.2 The distribution of sampled treeholes of over 0.1 litre in volume. Each size class (shown by mid-point values) has been subdivided to show the number of treeholes containing at least one larva of the common guild members. Small to medium larvae of *M. linearis* could not be distinguished from those of *M. ornata*, hence the two species are pooled. Overlap of *Gynacantha* and *Megaloprepus* occurred in the two largest size classes of treeholes.

rates which corresponds to the ranking of final instar size. However, contrary to what might be expected, the minimum time required to emerge did not correspond inversely to size of the final instar. In an outdoor insectary, in which 7-mm individuals were reared separately under ambient temperature and with food provided *ad libitum*, the dragonfly *G. membranalis* (the heaviest guild member), overtook *Megaloprepus coerulatus* in size within 10 days. *M. coerulatus* in turn outgrew either *Mecistogaster* species within 7 days. The two *Mecistogaster* species, whose final instars are nearly identical in size, had similar intrinsic growth rates (Fincke 1992*a*). Although the size of the final instar of *M. coerulatus* was intermediate to that of the other guild members, *M. coerulatus* could emerge faster than any of the other species, in as little as 95 days post-hatching. The other guild members could not be reared from eggs, but a 4 mm *Mecistogaster ornata* fed *ad libitum* took 106 days to emerge, whereas a 5.8 mm *G. membranalis* required 131 days to emerge under the same conditions. Thus, even though *Mecistogaster* final instars are only about two-thirds the size of those of *Megaloprepus*, their developmental time is longer, increasing their risk of predation by *Megaloprepus* in treeholes where they co-occur.

In treeholes under 1 litre, which can be patrolled effectively by a single larva, the species that is the first to hatch is the one most likely to emerge successfully. In larger treeholes, however, the fate of a newly hatched pseudostigmatid depends on the presence and size range of other odonate occupants. For newly hatched *M. coerulatus* and *Mecistogaster* larvae, 'windows' of opportunity may exist, during which survival is possible because:

(1) the treehole was not previously occupied, and remains undiscovered by other ovipositing females until the larvae reach considerable size; or

(2) other occupant guild members are very large (preferring prey larger than newly hatched odonate larvae), and soon emerge. Because of its inferior competitive ability as larvae, such windows of opportunity for *Mecistogaster* primarily exist immediately following the first filling rains of the wet season, whereas for *M. coerulatus*, such opportunities would occur at unpredictable intervals. Its disproportionately greater growth rate, relative to the final instar size, probably accounts for the ability of *M. coerulatus* to emerge occasionally from treeholes that are simultaneously occupied by larvae of *G. membranalis*.

An experiment with paired larvae of *Mecistogaster* and *M. coerulatus* (Fincke 1992*a*) demonstrated that *M. linearis* and *M. ornata*, although the smallest of the treehole odonates, survived in small artificial holes with low prey numbers if they were given an initial size advantage of 5–7 mm over larvae of *M. coerulatus*. In small holes *Mecistogaster* detected and eventually killed (or ate) smaller *M. coerulatus* larvae, thereby maintaining their initial size advantage. In large holes provided with a greater number of hiding places and prey, *M. coerulatus* was able to escape predation long enough to overtake *Mecistogaster* larvae in size and eventually to kill them. In nature, *Mecistogaster* larvae would have an initial size advantage if they were the first to hatch subsequent to treeholes filling in the wet season (see page 108, Female Reproductive Behaviour).

DIURNAL AND SEASONAL ACTIVITY

Emergence of pseudostigmatid adults occurs in early morning (whereas *G. membranalis* emerges at night). The larvae climb out of the treeholes and may move as far as several metres before emerging, usually on the tree trunk. Newly emerged giant damselflies can fly within 1–2 h after emergence and disperse widely from the larval treehole habitat. Males require about 3 weeks to sexually mature, whereas females require about 5 weeks (Fincke 1992*b*). Pseudostigmatid adults are active from about 10 a.m. to 2–3 p.m. Like most odonates, their foraging and reproductive activity is curtailed by rain, but normally they forage and mate under light to moderate overcast conditions. Roosting sites for pseudostigmatids on BCI are unknown, although I once found a male *M. coerulatus* at 4.30 p.m., apparently roosting alone under a palm frond at a height of 1.8 m. I never found natural roosting aggregations of 2–6 individuals of *M. ornata* as was observed in Mexico (Beatty and Beatty 1963), but in an insectary with 5–10 individuals, *M. ornata* regularly roosted two to three per branch at 1.5–2 m above the floor. Pseudostigmatids appear to be susceptible to predation even when roosting, as evidenced by the wings of *M. linearis* and *P. accedens* found at the roosts of nocturnal, insect-gleaning bats (J. J. Bellwood, personal communication).

Adult pseudostigmatids are relatively long-lived, and on BCI must persist through the dry season to propagate the subsequent generation. Maximum spans over which individuals marked as mature adults were seen are 165 days for *M. coerulatus*, 84 days for *M. linearis*, and 85 days for *M. ornata*. The shorter flight season of *Mecistogaster* relative to that of *M. coerulatus* (Fig. 7.3) may be a consequence of the effective limitation of *Mecistogaster* larvae to small treeholes. Because development time is faster in larger than in smaller treeholes, at least two generations of *M. coerulatus* emerge per season, whereas only one generation of *M. linearis* and *M. ornata* emerges over the same time span.

On BCI, *M. coerulatus* adults emerge throughout the wet and early dry seasons, and fly throughout the year, except for the late dry season (mid-March to April). I suspect that the adults aestivate at this time, probably retiring to the cooler areas of the forest such as along stream beds or ravines. About a month after the first rains of the wet season, old adults can be seen mating and ovipositing. Old age is signalled by an increasing opaqueness of the wings, wing damage, and the presence of algae growing on the thorax of some individuals (Fincke 1984*a*). *Megaloprepus coerulatus* is notably absent in the dry forest of Santa Rosa National Park, Costa Rica, where *M. ornata* does occur (D. Janzen, personal communication), supporting the hypothesis that *M. coerulatus* has a lower physiological

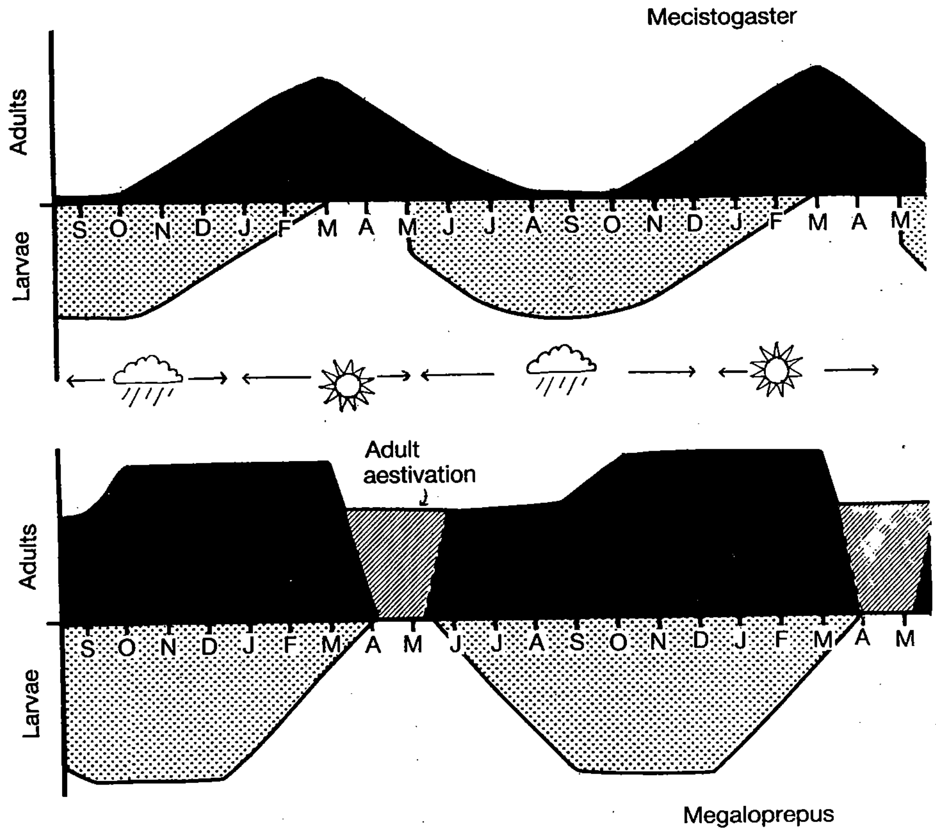

Fig. 7.3 The seasonal distribution of adult and larval *Mecistogaster* and *M. coerulatus*. Letters indicate months of the year. Figures in the centre show the general duration of the wet and dry seasons on Barro Colorado Island.

tolerance to low humidity than the other three pseudostigmatids. *Mecistogaster linearis*, *M. ornata*, and *P. accedens* begin to emerge in the late wet season (October and November) and peak in number in January–February. These three species forage throughout the dry season and are rarely seen after the middle of the wet season.

ADULT FEEDING BEHAVIOUR

Pseudostigmatids are perhaps best known for the unusual feeding habits of the adults (e.g. Calvert 1923; Young 1981). Rather than feeding on flying insect prey, they specialize in catching web-building spiders. In this habit they are not alone, because some small coenagrionid damselflies (e.g. *Neoerythromma cultellatum* (Hagen) and an *Argia* species) on BCI also take spiders. However, unlike pseudostigmatids, they also feed on flying and perched insects (Fincke, unpubl. ms. *b*; see also Jones 1986). During a 3-month study of foraging behaviour in 1981, I observed all four species of giant damselflies on BCI feeding nearly exclusively on web-building spiders, the exception being one case of feeding on wrapped prey in the web. The spiders caught by pseudostigmatids varied between approximately 3 and 6 mm in cephalothorax-abdomen length (see also Young 1980). Spiders much larger than this were actively avoided. Young (1981) reported that in Costa Rica male *M. coerulatus* frequented the webs of the large orb-weaver, *Nephila clavipes*, to forage on kleptoparasitic spiders. However, I never saw any of the BCI giant damselflies forage at *Nephila* webs, despite regular visits to *N. clavipes* webs. Nor have I seen pseudostigmatids trying to catch ground spiders or jumping spiders as Williams (1936) observed for a Hawaiian damselfly, *Megalagrion*.

Although there was considerable overlap in foraging heights among the BCI pseudostigmatids, I found some evidence of partitioning of the feeding niche with respect to height and exposure (Fincke, unpubl. *ms. b*). *Mecistogaster ornata* commonly foraged in full sun in gap areas, usually from ground level to about three metres up, whereas *M. linearis* foraged slightly higher, and was often found foraging in semi-shade. *Megaloprepus coerulatus* overlapped both *Mecistogaster* in foraging heights, and appeared to forage higher (i.e. above 6 m) than either, though data on foraging above 4 m were limited. I often found large dragonflies foraging above the canopy adjacent to the top of the 42-m meteorological tower on BCI, but I never found pseudostigmatids flying there. I suspect their flight is not strong enough to enable them to forage in such windy places. In Costa Rica, *Mecistogaster modesta* generally forages at heights under 2 m, primarily on theridiid spiders (L. Rayor, personal communication).

The giant damselflies are visual predators, and are susceptible to getting caught in spider webs when flying through shaded understorey. They search for webs in treefall gaps, branch falls, or leaf tips that are bathed in sunlight. Typically the damselflies move upwards on a tree, methodically searching leaf tips for webs, and then move downwards on the opposite side of the tree. When a web is located, the damselfly hovers in front of it (thus earning the name 'helicopter' damselfly), looking for the spider. After detecting a spider the damselfly typically backs up and, during a quick forward flight, catches the prey with its forelegs. The damselfly may hang on the web for several seconds before backing up and then perching to eat the prey. After each of the two dozen prey captures for which I have complete records, the damselfly consumed all of the spider save the legs, which were snipped off (as opposed to the head, see Stout 1983). After eating, they often preened themselves of gossamer threads by swinging their long abdomen up and forewards between their wings, and by rubbing their head and eyes with their forelegs.

Pseudostigmatids are highly skilled at locating and catching their spider prey. I have seen them pluck spiders out of rolled leaf retreats. On two occasions I watched as *M. linearis* darted into the leaf litter and came up with an unlucky spider that had tried to avoid capture by dropping from its web. In a large outdoor insectary, a *M. linearis* once hovered in front of a sheet of webbing, backed up, and then darted through the sheet, catching the spider on the other side. These anecdotes do not imply that such attempts are always successful. Prey were captured during only 7–16 per cent of sightings of foraging pseudostigmatids. More often the damselflies darted at a web and came away without prey, or sometimes grabbed small flowers or other detritus in the web. However, they quickly recognized unsuitable prey, and dropped such 'mistakes'. Rüppell has filmed foraging behaviour in *M. ornata* and analysed its flight manoeuvres at webs (Rüppell 1987*a*; Rüppell and Fincke, 1989*a*).

Spiders have undoubtedly evolved both behavioural and morphological traits in response to predation by giant damselflies. To drop from the web is a typical anti-predator behaviour of spiders, which is often used effectively against pseudostigmatids. Indeed, most of the successful prey captures observed were of spiders that remained on the web during the attack. Spiders sometimes avoided attacks by remaining in retreats located to the side of the webs. *Cyclosa* spiders, which typically rest on the web and camouflage themselves in a vertical line of debris strung across the web centre, could avoid being caught if they remained motionless while the pseudostigmatid hovered in front of the web. Large barrier webs such as those built by *N. clavipes* were also an effective deterrent. Spiders with hard carapaces such as *Micrathena* and *Gasteracantha* were more difficult for the damselflies to eat. When given an abundance of spider prey in an insectary, *M. linearis* ate these hard carapaced spiders last. One *M. linearis* required 45 min to consume a small *Micrathena*, whereas the same damsefly ate a similar sized soft-bodied *Philoponella republicana* in less than 3 min.

FEMALE REPRODUCTIVE BEHAVIOUR

Pseudostigmatid females search for treeholes by orienting to dark, moist places on tree trunks. The presence of water or, at least, moisture appears to be necessary to induce oviposition. At a small treehole in the understorey, I once saw a female *Mecistogaster linearis* repeatedly hit the water surface. To my surprise, she then flew up and perched with a water droplet between her forelegs. This female began ovipositing in the hole minutes later. Females typically dip their lower abdomen into the water before laying their eggs just above the water line. Although *M. linearis* oviposited in holes that were known to dry up completely a week later, I have never seen this species oviposit in a completely dry hole. Female *M. coerulatus* (but rarely *M. linearis* or *M. ornata*) when placed in a small cage will lay eggs into moistened filter paper. By ovipositing only into wet or moist treeholes, pseudostigmatids would reduce their chances of placing offspring into rotted holes that could never fill with water.

The pseudostigmatids on BCI (perhaps with the exception of *P. accedens*, which I have not seen ovipositing) perch at treeholes and lay eggs endophytically into rotted bark, leaf detritus, or into moss or algae on the side of the holes. Females are skittish when they first perch at a treehole. Large ctenid spiders were regularly found at certain holes, and I suspect these spiders prey on ovipositing females because twice I found the wings of female *M. coerulatus* floating in the water. Ovipositing *M. martinezi* (reported as *M. jocaste*) in Bolivia may avoid such predators by their habit of flicking eggs on to the water while hovering in front of a treehole (Machado and Martinez 1982).

Megaloprepus coerulatus females placed singly in small cages inserted 10–270 eggs ($\bar{x} \pm$s.e.$=66.8 \pm 19.9$, $n=13$) into moistened artificial substrates within 1–2 h. Under ambient temperatures, the eggs took 19–40 days to hatch, with a within-clutch hatching span of as long as 20 days. *Mecistogaster* females rarely laid eggs in captivity. Four *M. ornata* females laid from 4 to 61 eggs, which hatched as early as 12 days later. One *P. accedens* female laid 17 eggs, which hatched within 23 days, whereas eggs oviposited by another *P. accedens* in early February did not hatch until mid-April. It is possible that these latter eggs were in diapause.

For *Megaloprepus coerulatus*, duration of oviposition was positively correlated with treehole volume (Fincke 1992*b*). Uninterrupted ovipositions by *M. coerulatus* in the field varied from 4 to 65 min ($\bar{x}=24.6 \pm 4.2$, $n=17$), with a median of 16 min, whereas the few observations I have of oviposition for *M. linearis* and *M. ornata* were all under 15 min even in large treeholes. These results tentatively suggest that both *Megaloprepus* and *Mecistogaster* females divide their clutches among a number of treeholes. Females appear unable to determine whether treeholes are occupied by odonate larvae, which are usually not visible unless one lifts up leaves or detritus. After mating with a territorial male, female *M. coerulatus* routinely oviposited in defended treeholes, which usually contained several cohorts of larvae of various sizes. An extreme case was an artificial hole that had been colonized by *G. membranalis* larvae and was subsequenty defended by an adult male *M. coerulatus* for 39 days. At least 4 *M. coerulatus* females laid eggs in the hole, but at the end of the male's residency three months later, the only occupant that I could detect (i.e. larvae under 7 mm may have been missed) was a large *G. membranalis* larva. More commonly, a few small larvae are able to escape predation until larger larvae leave to emerge as adults, allowing for a staggered emergence of adults from large treeholes (Fincke 1992*b*).

Duration of sexual receptivity (indicated by presence of sperm and mature eggs in dissected females) among the BCI pseudostigmatids varied from three months in *M. ornata* to roughly 9 months in *M. coerulatus* (Fincke 1984*a*). Because emergence of *M. coerulatus* adults is staggered over a seven-month period, receptive females are available to males all year round, except for 2–3 months in the late dry and early wet season, when adults are rarely active. In contrast, *M. linearis* females are receptive for about six months or less, from the early dry season until the adult population declines in the middle of the wet season. Because females often oviposit in treeholes that dry up before the larvae can emerge, I suspect that this species lays eggs that remain in diapause until the holes refill in the wet season. Adult female *M. ornata* remain in reproductive diapause until the late dry or early wet season, when they then quickly mature a mass of eggs. This species is reproductively active for only 3–4 months.

Differences among guild members in the timing of egg-laying have important consequences for coexistence of the guild species. Small (< 7 mm) *Mecistogaster* larvae were found in 50 per cent of large and small treeholes sampled within a month of the first wet season rains, whereas by this time, only 13 and 6 per cent of the holes had been colonized by *M. coerulatus* and *G. membranalis* respectively (Fincke 1992*a*). *Mecistogaster*'s superior colonizing ability provided their larvae with the 'head start' in growth necessary for their survival in small holes. I found females of both *Mecistogaster* species ovipositing before or just after the first rains of the wet season, whereas *M. coerulatus* females were first seen to oviposit about 1 month after the treeholes filled with water.

MALE REPRODUCTIVE STRATEGIES

Pseudostigmatid females are more predictably found in open gap areas within the forest than in the shaded understorey, regardless of the presence or absence of water-filled treeholes in these places (Fincke 1992*a*, 1992*b*). Sunny gaps are a good place to forage on spiders and, because gaps are usually made by fallen trees or large branches, are a likely source of water-filled treeholes for gravid females. It is thus not surprising that mating pseudostigmatids were usually sighted in or near gaps or small clearings. However, despite similar 'rendez-vous' sites, male pseudostigmatids exhibit a range of mating strategies; these vary long-term defence of oviposition sites by territorial *M. coerulatus* to temporary defence of mating areas in treefall gaps by *M. linearis*, to a low degree of localization and lack of defence by *M. ornata* males, which mate opportunistically. The lower degree of localization and resource defence of *Mecistogaster* males is best understood in view of the shorter time spans over which their females are receptive and the inferior competitive ability of their larvae relative to those of *M. coerulatus* and *G. membranalis*.

Megaloprepus coerulatus

Individual *M. coerulatus* males defend water-filled treeholes in or adjacent to open gap areas for as long as three months. It is probably not a coincidence that the most highly territorial pseudostigmatid is also one whose mode of flight endows it with superior signalling ability relative to other members of the family, which employ a more efficient but less spectacular flight mode (see Rüppell and Fincke 1989*b*). Using a low number of synchronized wing beats/second, a territorial *M. coerulatus* male appears as a pulsating, blue and white beacon, signalling his presence (perhaps both to competing males and potential mates as well as to human observers). Males also make themselves conspicuous by perching in the centre of a gap and holding their broad wings horizontally, or by flying high into the clearing and then gliding down into it. The differences in wing coloration between males and females function in sexual recognition. Males will try to fight with a tethered female whose wings have been coloured like those of a male, whereas they try to clasp males whose white patches have been blocked out (personal observation). Although the flight of other pseudostigmatid species often attracts the attention of a resident male, he does not actively chase them away from the territory after inspecting them. Such visual discrimination of species and sex may be limited to sexually dimorphic odonates with distinct wing patterns Paulson (1974), for example, found that males of clear-winged coenagrionid damselflies with little differences in body coloration readily took heterospecific females in tandem. In these species, reproductive isolation was apparently maintained by differences in the male genitalia.

Before establishing residency at a treehole, males confirm the presence of water by fluttering close to and sometimes touching the water surface. A resident male regularly inspects the defended treehole(s) for ovipositing females by hovering briefly over the hole and then perching above, or adjacent to it. If he detects a female, he chases her away from the treehole, and if she cooperates by perching, he takes her in tandem. Copulation duration varied from 27 to 151 min ($\bar{x} = 71.2 \pm 8.4$, $n = 21$), with the longest matings being those by satellite males (see also Miller 1983). The male's behaviour suggests that he can displace sperm that may be initially present in his mate (see Fincke 1984*a*, *b*). After mating, the pair breaks tandem and the male follows the female back to the hole and guards her (non-contact guarding) while she oviposits. Females that try to leave the site are sometimes induced to return when the male flutters around the treehole and then around the female. Females that do not lay a complete clutch later oviposit alone in undefended holes in the forest understorey. Although females sometimes oviposit in defended holes without being detected by a male, once detected by a resident, females are not allowed to continue to lay eggs without first mating with the resident male.

Conspecific intruder males are chased away from the gap, usually after a series of face-offs as the contestants spiral higher and higher in the gap, before one is chased out. Fights between males of similar size are often intense and may continue intermittently over several days. Occasionally, tandem or copulating males continue to chase an intruder, despite the increased load of their passive mate. Sometimes the wings of two fighting males touch, and may be the source of the 'rustling' sound that can be heard during fights. Larger males are more successful in winning fights, independent of former ownership, and consequently, territorial males are, on average, larger than males never seen to hold a territory (Fincke 1984*a*, 1992*b*). Very old males tend to be displaced more readily from a territory than younger males. I have seen females mate only in the vicinity of a defended treehole. Because 82 per cent of 23 observed matings were with territorial residents, and mated males were significantly larger than unmated mates (Fincke 1992*b*), I conclude that sexual selection favours large male size in this species. Rüppell (1987*b*) has filmed fighting and reproductive behaviour in *M. coerulatus*.

Small males may act as territorial residents, defending a treehole until they are displaced by a larger male, or they may act as 'satellites', usually at large treefalls with several treeholes. Although the reisdent will chase a satellite if he detects him, the chases are usually less than a minute in duration, and do not escalate into the spiralling fights common in territorial disputes. Unlike intruder males that conspicuously challenge residents, satellite males routinely remain unnoticed by perching in the shadows near a treehole. Satellites occasionally mate with a female before she is detected by the resident, or while the resident male is mating, or chasing other males. However, such females are likely to remate with the resident if, while laying eggs, they are later detected by him. Males sometimes play both resident and satellite roles simultaneously at two different treeholes, changing their behaviour appropriately (Fincke 1992*b*). I found some males defending treeholes several kilometres from the treeholes at which they were marked several months previously, but there are too few such observations to determine whether there was a consistent pattern in territory changes, aside from those due to territory take-overs. Tenerals typically disperse from the treehole in which they developed within a period of days, making it highly improbable that male offspring 'inherit' treeholes from their father.

Territoriality requires males to be conspicuous and localized, predictably, possibly making them susceptible to predators that could learn their habits. Although I twice found all four wings of a male *M. coerulatus* on the forest floor, as if they had been left by a bird, I never saw attacks on any *M. coerulatus*, despite the hours spent watching them at territorial sites. However, skinks and other lizards commonly visit treefall gaps, and may be the cause of the rounded, bite-like holes found in the wings of several male *M. coerulatus*.

Territoriality in odonates is thought to evolve because by controlling access to oviposition sites used by females, males can sequester a disproportionate number of fertilizations (see e.g. Waage 1973; Robertson 1982). The discrete nature of the treehole larval habitat offers an additional advantage to territoriality for pseudostigmatid males, namely control over the habitat in which their offspring develop. Because as many as 13 *M. coerulatus* larvae can emerge from a large treehole per reproductive season, by controlling access to large treeholes a territorial male can influence the number of emerging offspring produced per mate that oviposits there. Because sexual selection in this species favours large males, territorial *M. coerulatus* might also increase their fitness by choosing larval habitats where offspring have the best chance to realize their maximum potential size. A male's ultimate 'decision' to defend a particular type of treehole may thus depend on either:

(1) the relative importance of the attractiveness of the treehole to receptive females; or
(2) the quality of the treehole as a larval habitat; or
(3) both 1 and 2.

Males and females differed in their use of treeholes. Of 68 treeholes that contained *M. coerulatus* larvae in 1983 (i.e. were used as oviposition sites by females), only 37 per cent were defended by males in that year. Whereas treeholes that contained *M. coerulatus* larvae were located both in gaps (40 per cent) and in the understorey (60 per cent), defended sites were limited to treeholes in open gap areas, or occasionally to those adjacent to a gap area where a male displayed (Fincke 1992*b*). Both receptive females and large treeholes are found disproportionately in gap areas, and consequently males may gain a dual fitness advantage (i.e. 3 above) by using the presence of a treehole in a gap as the criterion for estabishing residency.

A field experiment in which small, medium, and large artificial holes were placed in gaps and understorey, demonstrated the relative importance that mate attraction and quality of larval habitat may have played in the evolution of treehole selection by territorial males (Fincke 1992*b*). Males defended only 2 of the 23 artificial holes placed in the understorey, whereas they defended 18 of the 25 holes placed in gaps, suggesting that a site's ability to attract potential mates is an important criterion. However, only one of the 8 small holes placed in gaps were defended, despite the fact that the female encounter rates at gap areas was high, irrespective of the presence or absence of a treehole. None of the small holes placed in the understorey were defended. Thus, for males, territory site selection represents a trade-off between male investment in matings and male investment in producing high quality offspring that survive to emergence. The fitness of a female does not depend on her number of mates, but simply on the number of viable offspring she produces. By dividing their egg clutches among a wider range of treeholes than that defended by males, females can hedge their bets against ovipositing in treeholes that are already occupied.

Mecistogaster

Unlike *M. coerulatus* males, which have an opportunity to influence the number and quality of offspring produced from a mating by controlling access to high quality larval habitats, *Mecistogaster* males have little control over the fate of their larval offspring. Even if they defend large treeholes, the inferior competitiveness of their larvae greatly reduces the chance of survival in such treeholes (see above). *Mecistogaster* larvae survive best in small, previously uncolonized treeholes. Small treeholes (which at best could produce only two larvae/season) are found disproportionately in the understorey, where encounters with females are low. This might be the reason that *Mecistogaster* males invest maximally in acquiring mates rather than investing directly in offspring survivorship. Because mating *Mecistogaster* were observed only rarely, the conclusions below remain essentially tentative.

If male *Mecistogaster* mating strategies have indeed evolved to maximize the number of matings, then the difference in the degree of male localization between *M. linearis* and *M. ornata* is best explained by the difference in the availability of receptive females. *Mecistogaster linearis* males, whose females are receptive over a relatively long span, defended gap areas (usually without treeholes) for up to 16 days. When another male was encountered, a resident oriented face-to-face with him before one chased the other off. I once saw this behaviour in a gap with an artificial hole, but I assumed the treehole was not the defended resource, because the male did not orient to the hole regularly, as did *M. coerulatus*, nor did he return to it on subsequent days. Males did not guard or associate with females after mating, suggesting that females probably remate rarely, or that males are incapable of sperm displacement (see Fincke 1987).

Adult *M. ornata* are sexually active for a relatively short period, and males apparently compete for females by a diffused, 'scramble competition', mating opportunistically. Marked males were rarely found in the same vicinity a day later, the exception being a teneral male that was resighted in the same vicinity for nearly a week. The majority of the matings observed occurred in April or May. Mated pairs were usually found in or near sun-flecked or relativey open areas. Only one pair was in the vicinity of a water-filled treehole. Males did not associate with females after copulation, and neither sex remained long in the area after mating. Similar types of 'scramble competition' albeit at a much higher density of individuals, is characteristic of shorter-lived odonates whose ecology makes it inefficient to defend resources needed by females (e.g. Fincke 1982, 1988; Banks and Thompson 1985).

CONCLUSIONS

Among the Odonata, the habit of laying eggs in phytotelmata is, with one exception, limited to tropical or sub-tropical species (Corbet 1983), with over half of the 39 species known to develop in these microhabitats occurring in the neotropics. The moderate temperatures and high rainfall of the tropics make treeholes there a predictable and fairly persistent source of fresh water in moist forests where ponds and lakes are less common than they are in temperate regions, and where streams are often seasonal. On BCI, treeholes regularly hold water for as long as a month after the streams on the island have dried. Another important advantage of treeholes as larval habitats is their lack of fish and large invertebrates (e.g. belostomatid bugs, water scorpions) which are common predators of temperate odonate larvae. Such advantages are counter-balanced by the obvious constraint of space and low prey availability (for a discussion of constraints see Corbet 1983). Among the types of phytotelmata capable of supporting larval odonates, treeholes provide the largest areas and greatest volume of water (compare Picado 1913, Laessle 1961, Machado 1981*a* with Fincke 1992*a*) and can thus harbour a more complex aquatic community and larger odonates than do water-filled leaf axils or bromeliads (e.g. Calvert 1910; Machado 1981*a* with Fincke 1992*a*).

Treehole oviposition sites have played an inordinate role in shaping the behaviour and ecology of pseudostigmatids on BCI. Whereas effects of intra- and interspecific odonate predation in lake and pond species have been documented for field enclosure studies (e.g. Johnson *et al.* 1985; Crowley *et al.* 1987; Van Buskirk 1987; Wissinger 1989), the impact of cannibalism on natural populations remains controversial (e.g. Baker 1987, 1989). In treehole microhabitats, on the other hand, both cannibalism and intraguild predation unambiguously restrict the number of emerging pseudostigmatids on BCI. The scarcity of treeholes that can support multiple larvae per season makes this larval habitat a limiting reproductive resource, and has probably led to convergence in larval behaviour between pseudostigmatids and a smaller protoneurid damselfly that inhabits leaf axils (Machado 1981*a*, *b*).

On BCI, treehole odonates compete for larval habitats directly, as larvae, and indirectly, as ovipositing females. Adult reproductive behaviour of pseudostigmatids is best understood as resulting from an interplay of selective pressures on both life history stages. Interspecific larval interactions apparently restrict the smaller *Mecistogaster* species to small treeholes that support only a single generation per year, whereas the larger *M. coerulatus* can dominate large treeholes capable of supporting multiple generations per wet season. Differences in adult seasonality affect both the mode of female reproductive strategies as well as the availability of receptive females. Consequently, male reproductive strategies vary according to the duration over which receptive females are available, and to a lesser extent, the degree of control males have over the fate of their larval offspring.

Both the seasonal drying of the larval habitat as well as the unpredictability with which they may form, probably prevents the largest guild members from monopolizing this resource. Coexistence among treehole-breeding odonates on BCI appears to be possible because:

(1) the windows of opportunity for a given species to emerge from a treehole are somewhat unpredictable; and

(2) the two smaller *Mecistogaster* species, which are inferior competitors as larvae, are superior as adults in distributing their eggs in treeholes when they refill with wet season rains.

This adaptive scenario is currently being tested by comparative studies of *Mecistogaster* in areas where *M. coerulatus* and *G. membranalis* are absent. If the explanations given above are correct, then in such places (all else being equal!), we should find overlapping generations of *Mecistogaster* emerging routinely from large treeholes, and a greater degree of localization of males at oviposition sites than occurs on BCI. On the other hand, in wetter forests where treeholes do not dry out seasonally, *M. coerulatus* and *G. membranalis* should be able to exclude *Mecistogaster* from all treehole habitats. De Marmels (1989) described a male *Microstigma rotundatum*, at a site in Venezuela, that defended a treehole in a fallen tree in a manner nearly identical to my description of *M. coerulatus* males. Given the higher diversity of pseudostigmatids in Venezuela than on BCI, it is likely other pseudostigmatids at the site also lay eggs in treeholes. If so, it would be fascinating to know if they differ in reproductive strategies in a manner similar to the BCI guild.

The large size and long abdomens of pseudostigmatids are undoubtedly advantageous for exploiting treeholes as a larval habitat, regardless of whether these characteristics have been specifically adapted for that purpose. For example, their unusual proportions may have originally improved the ability to capture web-building spiders, and in any case, both male size and relative abdomen length probably have been further modified by sexual selection on male *M. coerulatus* and *M. linearis* males, respectively. Because the relatively small size of most zygopteran larvae would make them easy prey for large Anisoptera such as *Gynacantha membranalis*, it is not surprising that no small zygopterans colonize treeholes on BCI. The large size of pseudostigmatid larvae enable them to compete successfully with larvae of *G. membranalis* under certain conditions. In small treeholes, early arriving *Mecistogaster* are able to eat or kill any later arriving *G. membranalis*. The large size and disproportionately fast development time of *M. coerulatus* enables this species to compete successfully with *G. membranalis* even in large treeholes, provided that they hatch several weeks before the hole is colonized by *G. membranalis*. Although the extremely long, flexible abdomens of pseudostigmatids are not a prerequisite for laying eggs in treeholes, they are certainly advantageous in providing females with access to narrow-mouthed holes, thereby allowing some pseudostigmatid offspring to avoid *G. membranalis* larvae altogether. Interestingly, long abdomens are also characteristic of the megapodagrionid, *Coryphagrion grandis*, the largest known African zygopteran, which also oviposits in treeholes (Pinhey 1961, 1962). Is the uncanny resemblance of this unrelated damselfly, in both appearance and behaviour to *M. linearis* merely a coincidence or is it evidence of a remarkable convergence in their evolutionary history? Clearly, comparative studies that focus both on larval and adult pseudostigmatids, and other Odonata developing in phytotelmata are needed before we can fully understand the selective pressures that gave rise to these magnificant insects.

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Note 1. Members of the Societas Internationalis Odonatologica (S.I.O.) have agreed that, in the interest of uniformity of usage, the term 'larva' should replace the terms 'naiad' and 'nymph' to indicate pre-emergent forms of odonates.

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