CONSEQUENCES OF LARVAL ECOLOGY FOR TERRITORIALITY AND REPRODUCTIVE SUCCESS OF A NEOTROPICAL DAMSELFLY

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Abstract. Male territorial behavior and female oviposition behavior of Megaloprepus coerulatus, a damselfly that develops in water-filled tree holes, is interpreted in light of its larval ecology. Sexual selection favors large males because they win more territorial contests than do smaller males, and females mate only in the vicinity of defended tree holes (i.e., passive female choice). Small males behave as territory holders until displaced, and/or act as subordinate satellites at large territories. Females are more predictably found in forest light gaps, even though they oviposit in both gap and understory tree holes. Males defended only 14% of the sites used by ovipositing females.

Large tree holes are relatively rare, but support a greater number of emerging adults per season and produce larger adults than tree holes containing ≤1 L of water, which rarely produce more than one individual per season. By defending only large tree holes in gap areas, a male increases his chances of mating, and of producing multiple offspring and reproducitively successful sons. Results from a field experiment suggest that both mate acquisition and procurement of superior larval habitats have been selective pressures in the evolution of male territory choice. Because even large holes are inadequate to support a female's entire clutch, and the presence of conspecific and heterospecific odonate larvae makes offspring survival uncertain, selection favors a female that partitions her clutch among multiple tree holes.

Key words: larvae; Neotropical; odonate; oviposition; Pseudostigmatidae; reproductive success; territoriality; tree hole.

INTRODUCTION

By definition, sexual selection occurs during mate acquisition via competition among males for mates or female choice of potential partners (Darwin 1871). In species that lack parental care but whose males defend reproductive resources, territoriality is considered to result from sexual selection (Emlen and Oring 1977, Thornhill and Alcock 1983) because territorial males obtain a disproportional share of mates (e.g., Waage 1973, Wells 1977). This scenario assumes that natural selection has favored females that oviposit at sites where offspring survivorship and/or quality will be optimal. Males then simply defend areas where encounter rates with potential mates are high.

Of course, defense of reproductive resources such as oviposition sites can enhance a male’s fitness if it promotes both his mating opportunities and the survivorship (or quality) of his offspring (e.g., Howard 1978). Hence, in addition to acting as selective pressures on a female’s choice of oviposition sites, larval survivorship, growth rates, or phenotypic quality of offspring may ultimately influence male choice of territories. If fitness is measured only in terms of mating (or fertilization) success, however, a male phenotype that enhanced territory-holding ability might be misinterpreted as wholly a product of sexual selection. On the other hand, if relative fitness under field conditions is assessed in terms of the number and quality of offspring surviving to adulthood, the potential consequences of larval ecology for adult behavior of both sexes can be determined, in which case the dichotomy between sexual and natural selection becomes less distinct.

Megaloprepus coerulatus (Drury) is a neotropical damselfly (Odonata: Pseudostigmatidae) whose females oviposit in water-filled tree holes that are defended by males (Fincke 1984a). Because its larval habitat is defendable, discrete, and variable in quality, this is an ideal species with which to examine how adult use of oviposition and territorial sites affects the fate of developing offspring, and in turn, how larval ecology ultimately affects adult mating behavior. For example, males may defend certain tree holes because that is where they are most likely to encounter females (mate acquisition hypothesis) and/or they may defend tree holes that are good larval habitats (larval habitat hypothesis). Likewise, females may mate at defended sites because by so doing they gain superior mates and/or gain access to superior larval habitats.

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2 Address for reprint requests.
Here, I show that the territorial sites defended by males cannot be predicted adequately from the spatial or temporal distribution of either females or oviposition sites. I show that a male’s size affects his ability to defend territories, and consequently, influences both his mating success and his use of an alternative mate acquisition tactic. I link adult behavior to larval ecology by showing that number and size of emerging adult offspring are correlated with the size of the larval habitat. By experimentally separating two proximate criteria that males could use to choose territories, I demonstrate that the ultimate function of male territoriality in *M. coerulatus* is both mate acquisition and the procurement of superior larval habitats.

**Study Animal and Habitat**

The study was done in the lowland moist forest of Barro Colorado Island (BCI) in the Republic of Panama. The 1600-ha island experiences a dry season from late December to April and a wet season from May to December. *M. coerulatus* males are easily distinguished from females, even in flight, by the presence of white wing bands that females lack. Adults are visual predators of web-building spiders (Calvert 1923, Young 1980, Fincke 1992a), which they capture in light gaps in the forest canopy. Males defend tree holes by chasing and sometimes hitting intruder males. Multiple matings by females, guarding (noncontact) of ovipositing mates (Fincke 1984a), and a bifurcated penis structure (O. M. Fincke, personal observation) suggest that mating males displace sperm of previous mates, an ability that is widespread among the Odonata (Fincke 1984b, McVey and Smittle 1984, Siva-Jothy 1984, Waage 1986). A territorial male does not allow detected females to oviposit in a defended tree hole without first mating with him. Nor does he pursue unwilling females beyond the defended area. Mating and defense behaviors have been described elsewhere (Fincke 1984a, 1992a, Rüppell and Fincke 1989) and have been filmed by Rüppell (1987).

In addition to *M. coerulatus*, two smaller pseudostigmatids (*Mecistogaster linearis* and *Mecistogaster ornata*) and a larger aeshnid dragonfly (*Gynacantha membranalis*) overlap in their use of tree holes. None of these other guild members defend tree holes, which are a limiting resource (Fincke 1992b). Odonate larvae are the top predators within tree holes, and even with unlimited prey, larger larvae readily kill smaller ones (O. M. Fincke, unpublished manuscript). Competitive ability among the larval odonates increases with mean final instar body lengths, which are 22, 28, and 37 mm for the two *Mecistogaster* species, *Megaloprepus coe-
rulatus, and G. membranalis, respectively (Fincke 1992a).

**METHODS**

*Temporal and spatial distribution of adults*

The study area comprised mature forest adjacent to the trails leading from the laboratory clearing up to and including the island’s central plateau (Fig. 1). Between October 1983 and December 1984 I noted the location of all adult *M. coerulatus* I saw, and marked as many of them as possible (*N* = 236, 73% of males seen; *N* = 90, 63% of females seen) by writing a number on the forewing with an indelible “Pilot” pen. I measured forewing length and abdomen length, and noted relative age by the degree of wing opaqueness and damage, body pruinosity, and the presence of algae growing on the thorax (see Fincke 1984a). Relative life-span was measured as the duration between the first and last sighting of an individual.

I measured the abundance of adults in gaps and understory by recording adults seen opportunistically (i.e., 0.5–5 min at any given location) while walking 1–4 h/d over 2–6 km of trails to and from the laboratory clearing to sites in the study area. On BCI, light gaps comprise roughly 2.8% of the forest (Brokaw 1982); thus most of my travel time was spent in forest understory. To determine which tree hole sites were defended, during the wet season of 1983–1984 I made a total of 869 checks (minimum of 3 checks per site) at 54 small and 28 large tree hole sites in gaps and understory. “Site” hereafter refers to the immediate vicinity of a tree containing either a single or multiple tree holes. The attractiveness of the above sites to males and females was determined by comparing the number of each sex sighted within the first 5 min of observation at a given site. So measured, the frequency of females was not significantly correlated with the number of checks at a site (*r* = 0.15, *N* = 82, *P* < .2), whereas the frequency of males was slightly correlated with the number of checks made (*r* = 0.24, *P* < .04).

To determine if the lack of adults that I observed in the late dry season resulted from adults abandoning drying tree holes, or might have been caused by some other factor (e.g., physiological intolerance of late dry season conditions: see Windsor 1990), I conducted two watering experiments. In mid-March 1983, when all of the tree holes were dry, I watered 8 tree holes known to have been defended in December 1982. For 10 d I checked them for the presence of adult *M. coerulatus*. During the dry season of 1984, I kept 14 defended artificial holes full, and, at least once a week for the remainder of the study, checked them for the presence of adults.

*Territorial behavior and mating success of males*

Territorial and mating behavior was studied at natural and artificial tree holes by making relatively short (5–20 min) daily observations at 30 hole sites known to be defended by at least one male during the study (*X* = 1 ± 1 se = 33.0 ± 4.1 checks per site), and at 84 undefended tree hole sites (8.2 ± 0.6 checks per site). In addition, 49 longer observations of 60–180 min (*X* = 120 min) were made at 18 defended sites (*X* = 1 ± 1 se = 2.7 ± 0.4 checks per site). I classified a male as territorial if he successfully defended a site or was the sole male present for at least three consecutive days. Sex ratios and male behavior at these territories were compared with observations made on 29 consecutive days at a single large territory in February 1986, when adults were observed between 0900 and 1500 (*X* ± 1 se = 3.1 ± 1.2 h/d). One very overcast day was excluded from the analysis of that site because under such conditions, both males and females are inactive. That intensive study confirmed that territorial males spend most of their daily active period (1000–1430) near the defended site. Thus, in calculating the duration over which a given male was the territory holder at a site (hereafter “territory-holding duration”), I credited a male with being present between days on which he was known to defend the territory successfully.

I determined the effect of body size on success of territorial defense by noting the outcome of natural territorial fights and, in addition, by staging seven encounters between males of different sizes. In the latter cases, I first removed the territorial male and then introduced a marked male that was allowed to establish residency. The original male was then released at the site 45–150 min later, and the outcome of the ensuing fight recorded. Males that failed to return to the territory within 5 min after the encounter were scored as losers.

To control for any effects that the addition of artificial holes may have had on the frequency of territoriality or mating within the population, I present data on male mating success in 1983–1984 and 1986 with data taken in the same study area in 1982 (October–December), when no artificial holes were present and 7 tree hole sites were known to be defended. Throughout, means are reported with ±1 se, *t* values refer to Student’s *t* tests, and comparative tests are two-tailed unless otherwise noted.

*Quality of tree holes as larval habitats*

In 1983–1984, to determine which tree holes were the best larval habitats, I censused 212 water-filled tree holes within 2 m of ground level and over 0.04-L volume (the minimum in which larvae were found). Tree holes were classified as being in either understory (<10% open canopy, as measured by a densiometer) or in gap areas (≥10% open canopy). All observations of ovi-positing females were noted; I also used the presence of *M. coerulatus* larvae as evidence that at least 1 female had laid eggs in a given hole. “Large” holes or sites refers to those containing >1 L of water; “small” holes or sites contained 1 L or less.
TABLE 1. Frequency of *Megaloprepus coerulatus* damselsfly adults observed during the first 5 min of checks at natural tree holes. Data are means ± 1 se.*

<table>
<thead>
<tr>
<th></th>
<th>Tree hole site volume†</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Large (≥1 L)</td>
<td>Small (≤1 L)</td>
<td></td>
</tr>
<tr>
<td>Gaps</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of tree holes</td>
<td>11</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>No. checks/hole</td>
<td>23.6 ± 6.3</td>
<td>7.0 ± 1.6</td>
<td></td>
</tr>
<tr>
<td>No. females/check</td>
<td>0.12 ± 0.05</td>
<td>0.13 ± 0.12</td>
<td></td>
</tr>
<tr>
<td>No. males/check</td>
<td>0.28 ± 0.10</td>
<td>0.08 ± 0.04</td>
<td></td>
</tr>
<tr>
<td>Understory</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of tree holes</td>
<td>17</td>
<td>46</td>
<td></td>
</tr>
<tr>
<td>No. checks/hole</td>
<td>10.7 ± 2.0</td>
<td>8.1 ± 0.8</td>
<td></td>
</tr>
<tr>
<td>No. females/check</td>
<td>0.03 ± 0.02</td>
<td>0.00</td>
<td></td>
</tr>
<tr>
<td>No. males/check</td>
<td>0.07 ± 0.03</td>
<td>0.00</td>
<td></td>
</tr>
</tbody>
</table>

* For females, canopy cover had a significant effect on frequency (two-way ANOVA, $F_{1,80} = 10.7, P < .002$) whereas site volume did not ($F_{1,80} = 0.01, P < .8$). Interaction effect, $F_{1,80} = 0.40, P < .6$. Both canopy cover ($F_{1,80} = 14.3, P < .0003$) and site volume ($F_{1,80} = 12.2, P < .0002$) had effects on male frequency at a site (interaction effect, $F_{1,80} = 2.8, P < .1$).

† Combined volume of all tree holes at a given site.

I estimated the minimum time span required for a *M. coerulatus* larva to emerge from a given hole as the time between the filling of the hole (i.e., onset of wet season rains) and the date the first larvae emerged. The size and number of adults emerging from tree holes between May and December 1984 was determined by removing all final instar larvae (i.e., those with well-developed wing pads) in a subset of holes that were checked at least once a month until the tree holes dried up (for details see Fincke 1992b). These larvae were held individually in jars (with ad libitum food: newly hatched *Physalaemus pustulosus* tadpoles) until they emerged (9.7 ± 1.0 d, $N = 65$) in an outdoor insectary. Because larvae typically stopped feeding ≈7-10 d before they emerged, any increase in their size after they were removed from tree holes was minimal. Teneral adults were marked 24 h after emergence and released at various sites in the study area. Time required for sexual maturation was measured as the minimum time after emergence that a marked female was seen mating or ovipositing, or that a marked male was seen defending a territory.

**Site selection by males**

Both females and large tree holes were disproportionately located in gaps, which were also the sites favored by territorial males. Thus, to determine the relative importance of mate acquisition vs. control of favorable larval habitats as possible functions of male territoriality, I experimentally tested the relative importance of canopy openness vs. tree hole volume as criteria for male site selection. Male choice of potential territories was monitored at artificial tree holes placed singly in open gaps and in shaded understory. None of the artificial holes were in the vicinity of any known tree holes, and all were at least 0.1 km from each other. Artificial holes were small (0.2 L), medium (2-3 L), or large (9-16 L) plastic tubs, lined with black plastic, and positioned so as to collect rainwater. Such holes were readily colonized by odonates, other aquatic invertebrates, and tadpoles. The sites were checked for the presence of adults at least once per week over a 3-mo period during the rainy season. In this paper, “tree holes” refers to natural holes only, whereas “holes” may refer to samples comprising both artificial and natural tree holes.

**RESULTS**

**Spatial and temporal distribution of adults in the forest**

Because their foraging is limited to sunlit areas (Fincke 1992a), both females and males frequented gap areas and were less often found in the understory, even though flying damselsfly were easily visible there. Most (70%) sightings of nontenereal females ($N = 145$) were at territory sites (Fig. 1). These results, however, were biased by the presence of resident males that displayed conspicuously (see Rüppell 1987, Rüppell and Fincke 1989), probably cueing odonate females (as they did me) to the presence of a nearby tree hole. Of the 93 nontenereal females sighted within the first 5 min at a site where no males were present, 88% were in gap areas (59/82 at sites with tree holes, 23/82 at sites without tree holes). In contrast, only 12% were sighted in the understory (4/11 at sites near holes, 7/11 at sites where holes were absent). Using the conservative estimate that only 20% of my observation time was spent in forest understory, this distribution of females was nonrandom with respect to canopy cover ($\chi^2 = 3.9, 1 \text{ df}, P < .05$). Furthermore, females visited tree holes in gaps, independent of their volume, more frequently than either large or small tree holes in the understory (Table 1).

Of the total sightings of nontenereal males ($N = 687$, excluding multiple sightings per male per day), 94% were at territories (all of which were in gaps or adjacent to a gap). Of the 38 males seen at sites other than territories, 73% were in light gaps (21/28 without holes). Only one was near an understory hole, and none were in the presence of a female. Like females, males visited tree holes in gaps more often than those in the understory, but unlike females, they frequented large holes in gaps more often than small ones (Table 1).

Although emergence of adults was staggered throughout the year, during late dry season (April) few adults were found (see “young” individuals, Fig. 2). The scarcity of adults at this time was at least partly due to inactivity (rather than death). In early wet season (May-July) most of the individuals sighted were sexually mature. Because the minimum developmental time to emergence in the field was 130 d, mature adults
seen in May–June must have emerged before tree holes dried out in March. Most of the young adults in early wet season were likely those emerging from holes artificially watered in the dry season, whereas some might have survived naturally in drying tree holes.

Only 8.6% of the 116 tenereal males and 5.8% of the 137 tenereal females marked and released were resighted in the study area within 12 mo. The minimum time to sexual maturation was 39.2 ± 1.0 d for females (range 37–42 d, N = 4) and 24.7 ± 1.0 d for males (range = 20–25 d, N = 6). Sexually mature individuals released as tenerals were resighted within 0.3–1.7 km of their release site. Even though males acquired adult coloration within a day of emergence, three teneral males marked near tree holes were never sighted there after a week, consistent with the hypothesis that males do not “inherit” territory sites from their fathers.

Spatial use of tree holes by males and females

Of 85 natural sites whose tree hole contents were checked at least three times during 1983–1984, 22 contained more than one hole. Fallen trees had significantly more holes (1.7 ± 0.3 holes, N = 51 trees, range 1–11 holes) than did upright living trees (1.1 ± 0.03 holes, N = 155 trees, range 1–4 holes) or dead trees (1.2 ± 0.1 holes, N = 21 trees, range 1–2 holes, ANOVA, F_{2, 224} = 6.6, P < .002). Most (62%) of the tree holes were <1 L in volume, and most of these small holes (85%) were in forest understory. Tree holes located in gaps were larger (volume = 2.9 ± 0.7 L, N = 69) than those in the understory (1.4 ± 0.3 L, N = 159, t = −1.86, P < .05).

Over 15 mo, only 11 (13%) of the 85 natural sites, or 31% of the 119 tree holes checked, were defended by an adult male *M. coeruleus* (Fig. 3). Males defended a subset of tree holes that were larger (volume = 6.2 ± 1.4 L, N = 37) and in more open areas (openness = 28.4 ± 2.8%) than those used by females (volume = 2.4 ± 0.5 L, N = 114, t = −2.4, P < .01; openness = 16.0 ± 1.5%, t = −3.9, P < .01). Eight (73%) defended sites were in fallen trees that created the gaps and the remaining 3 understory sites were adjacent to gaps. At these latter sites, females were usually initially encountered in the gap, after which the territorial male “chased” a potential mate toward the understory hole. Because at least one female oviposited in at least one tree hole at 80 (94%) of the 85 sites, the spatial overlap in site use by males and females was only 14% (11/80 sites, Fig. 3). Even if males eventually found all the sampled sites that contained medium to large tree holes in gap areas, the degree of overlap at best would be only 17.5%.

There was high year-to-year consistency in sites defended by males, as long as the tree holes held water. All of the territorial sites defended in 1983 were again defended in 1984. Because most defended tree holes were in fallen trees that eventually rot, only 4 of the 6 tree holes defended in 1982 were still in use in 1984. The only one still used in 1990 (latest check) was in a live *Ceiba pentandra* tree. In contrast, of the 25 oviposition sites in live trees used by females in 1982 that were again checked in 1990, all were still larval odonate habitats.
Table 2. Size of sexually mature *Megaloprepus coerulatus* males. For small sample sizes, *U* refers to Mann-Whitney *U* test. Tests are one-tailed for mated vs. unmated males.

<table>
<thead>
<tr>
<th>Year</th>
<th>Type of male</th>
<th>N</th>
<th>Wing</th>
<th>Abdomen</th>
</tr>
</thead>
<tbody>
<tr>
<td>1986</td>
<td>Territorial</td>
<td>6</td>
<td>73.4 ± 1.8</td>
<td>86.9 ± 2.4</td>
</tr>
<tr>
<td></td>
<td>Satellite</td>
<td>6</td>
<td>58.6 ± 1.2</td>
<td>71.3 ± 1.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>U</em> = 0**</td>
<td><em>U</em> = 0**</td>
</tr>
<tr>
<td>1982</td>
<td>Mated</td>
<td>6</td>
<td>71.8 ± 2.1</td>
<td>84.5 ± 2.6</td>
</tr>
<tr>
<td></td>
<td>Unmated</td>
<td>27</td>
<td>67.0 ± 1.3</td>
<td>79.1 ± 1.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>t</em> = 1.6</td>
<td><em>t</em> = 1.7*</td>
</tr>
<tr>
<td>1983–1984</td>
<td>Mated</td>
<td>28</td>
<td>68.8 ± 1.0</td>
<td>82.8 ± 1.2</td>
</tr>
<tr>
<td></td>
<td>Unmated</td>
<td>178</td>
<td>67.0 ± 0.4</td>
<td>80.3 ± 0.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>t</em> = −1.6*</td>
<td><em>t</em> = −1.9*</td>
</tr>
<tr>
<td>1982</td>
<td>Territorial</td>
<td>10</td>
<td>73.2 ± 1.8</td>
<td>86.0 ± 1.9</td>
</tr>
<tr>
<td></td>
<td>Nonterritorial</td>
<td>23</td>
<td>65.6 ± 1.2</td>
<td>77.5 ± 1.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>t</em> = −3.5**</td>
<td><em>t</em> = −3.6**</td>
</tr>
<tr>
<td>1983–1984</td>
<td>Territorial</td>
<td>78</td>
<td>68.3 ± 0.6</td>
<td>82.0 ± 0.7</td>
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<tr>
<td></td>
<td>Nonterritorial</td>
<td>128</td>
<td>66.5 ± 0.5</td>
<td>79.7 ± 0.6</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td><em>t</em> = −2.2**</td>
<td><em>t</em> = −2.6**</td>
</tr>
</tbody>
</table>

* *P* < .05, **P* < .01.

Male territorial behavior

Based on their behavior at a defended area, males were classified as territory holders, intruders, or satellites. Satellites were present on only 2 (18%) of the natural territories monitored in 1983–1984, both of which were large-volumed sites (57 and 8.7 L). Whereas contesting intruder males flew conspicuously in the center of the territory, satellites spent most of their time perched in the shadows near the defended tree hole. Contests between a territorial male and satellites did not escalate into the full-blown fights (3–5 min) that characterized take-over attempts by intruder males. Satellites frequented a defended site repeatedly (6.2 ± 2.1 d, *N* = 6) whereas intruders seldom returned on subsequent days to sites where they had been defeated. Satellites were characteristically much smaller than territorial or intruder males (Table 2), but individuals were plastic in using alternative mating tactics. Upon discovering an undefended hole, a male acted as a territory holder until displaced by a larger male. In one case, a male performed as a satellite at a defended hole, but after being chased away, appeared at an artificial hole ≈100 m away where he displayed as a territorial male.

In all study years, about one-third of the sexually mature males marked were known to be territorial at some time during the study (Table 2). On average, a territorial male held a given site 20.2 ± 2.0 d (1983–1984 data, range = 3–83 d). Twenty-two males (28%) sequentially defended more than one territory, and 5 were territory holders at three sites over the course of the study. There was no correlation between the total volume at a defended natural site and the proportion of wet-season days checked that a site was defended (*r* = 0.15, *N* = 11, *P* > .4), suggesting that once a large-volumed site was abandoned, subsequent males had as much difficulty in finding it as they did sites with fewer or smaller holes.

Territorial males were significantly larger than males not known to defend territories (Table 2). Larger males were more likely to win a territorial fight than were males smaller than their opponent (Fig. 4). More natural fights (85%) were won by territory holders than by intruder males, but the latter were usually smaller than the former (83% of the encounters). Nevertheless, prior ownership per se conferred little advantage in winning territorial disputes. Territory holders that won fights were not more likely to be smaller than their opponents than were intruders that won fights (*χ*² = 0.029, 1 df, *P* < .5). In all seven trials with introduced males, the original territory holder quickly tried to defend his territory, even after being held for 2.5 h. Original territory holders defeated two of the three smaller introduced males (the exception was only slightly smaller than the territory holder it defeated) but lost to all four of the larger introduced males. Moreover, for males seen more than once, there was a slight but significant positive correlation between a male's wing length and the number of days a male spent at a given territory (*r* = 0.20, *N* = 96, *P* < .05). The number of females encountered by a territorial male was positively correlated with his territory-holding duration (*r* = 0.39, *N* = 96, *P* < .0001).

Results from the watering experiments revealed that territories were abandoned in late dry season for reasons other than tree hole drying. Males and females abandoned tree holes as early as a month before the standing water had evaporated. In 1984, all but 2 of the 14 holes kept continuously filled during the dry season were abandoned 3 wk or more (37.6 ± 4.3 d) before the first rain of the wet season on 18 April. On average, territories were abandoned for 52.5 ± 3.4 d (*N* = 11) between late dry and early wet season. None
of the tree holes watered in the dry season of 1982 attracted males or females (only one individual, a male, was sighted during the entire 10-d study in mid-March).

The average time elapsing between the first rain and renewed defense of a previously defended territory was 27.2 ± 4.1 d (range, 1–80 d, N = 25), which corresponded roughly with when females began ovipositing again (Fincke 1992b). Two males that had defended artificially watered holes were the only males resuming defense of the same site in the wet season; these males returned to their territories 1 and 3 d after the first rains. The wing length of the 20 males (69.6 ± 1.3 mm) that were the first ones seen in early wet season at a previously defended territory did not differ significantly from that of the other 216 marked males in the population (67.2 ± 0.3 mm, t = −1.6, P < .1).

**Frequency of adults at territories**

Females were more likely found at defended holes in gaps (0.17 ± 0.05 females per check, N = 8 sites) than at undefended holes in gaps (0.09 ± 0.09 females per check, N = 11 sites, Mann-Whitney U = 8, P < .002). Moreover, as many as 6 females oviposited in the same defended tree hole within a 4-wk span, whereas no multiple ovipositions were ever observed at undefended holes. Even so, the frequency of adults at territories was low. At the 18 defended sites observed for an average of 2 h per check, the number of males seen was 1.4 ± 0.13 individuals per check. Female visits were even rarer (0.5 ± 0.15 individuals per check, N = 18), resulting in a sex ratio of 0.51 ± 0.15 (females : males, N = 49 checks). Territorial males were present at a site on 0.59 ± 0.05 of the shorter checks (N = 27 sites), whereas the known territory holder was sighted during all but 1 of the 49 longer checks. The number of tree holes at a territory (2.4 ± 0.7, N = 18), was not significantly correlated with the mean frequency of visits by males (r = −0.45, P < .07) or females (r = 0.21, P < .5).

The greatest number of adults were recorded at the large territory monitored in 1986, yet even here, no females visited on nearly half of the days (13/28), even though 1–6 males were always present. Here, the mean of the daily sex ratio was 0.23 ± 0.05 (females : males, range = 0.6–3.4). The average encounter rate of a territory holder with females was 0.66/d (0–3 females/d). An average of 2.8 ± 0.2 males (satellites included) were present per day (range = 1–6 males/d).

**Factors affecting male mating success**

All 59 observed matings were within ≈5 m of defended holes, despite the fact that 40% of the checks were at undefended holes. Conservatively estimating that defended holes were observed as much as four times longer than undefended holes, the lack of matings at undefended holes was highly significant (χ² = 9.8, 1 df, P < .0001). Neither the distribution of males at tree holes nor observations of ovipositing females suggested that males mated at other than defended sites. The mean number of males seen in the first 5 min at defended sites was 0.29 ± 0.04 individuals (N = 30), and only 0.01 ± 0.005 individuals at undefended sites (N = 84). Moreover, of the 45 observed ovipositions in defended holes, 78% occurred in the presence of a guarding male, whereas none of the 9 females seen to oviposit in undefended tree holes in the understory were accompanied by a male (χ² = 19.6, 1 df, P < .001).

Males were larger than females (wing length of males = 67.2 ± 0.3 mm, range 45.0–85.2 mm; N = 236 males; wing length of females = 61.4 ± 0.6 mm, range 49.2–70.1 mm; N = 90 females, t = 8.8, P < .001). Although females could avoid being taken in tandem by not perching, and unwilling tandem females could resist copulation (see Fincke 1984a), once at a territory, females did not actively discriminate among males on the basis of size or territorial status. For example, two females mated with a territorial male and then readily remated when taken in tandem by small satellites (wing lengths = 61.7 mm and 59.9 mm). Nor was there evidence of assortative mating by size (i.e., wing length) (r = 0.36, N = 13, P > .2). Only three of the six satellites at the site monitored in 1986 mated. Copulations by satellites were significantly longer in duration (129.0 ± 16.8 min, N = 3) than those by residents (67.1 ± 7.0 min, N = 18, U = 4, Mann-Whitney U test, P < .02).

Large males had an advantage in obtaining mates.
Males that obtained at least one mating were generally larger than males not known to have mated (Table 2). Total size (wing plus abdomen) of mated males was significantly greater than that of unmated males in both 1982 ($t = 1.68, P < .05$) and 1983–1984 ($t = 1.79, P < .04$, one-tailed $t$ tests). Because females mated only at territories, and territory holders were significantly larger than nonterritorial males, my a priori hypothesis was that mated males were larger than unmated males; hence I used one-tailed tests for these comparisons. Moreover, although only $\frac{1}{3}$ of the males were territorial, they obtained $\approx \frac{1}{3}$ of the observed matings (Table 3). The size of sexually mature males seen more than once did not correlate with longevity ($r = 0.07, N = 96, P > .5$), indicating that the mating advantage of large males stemmed from greater mating efficiency rather than from increased survivorship. The mean life-span of males seen more than once was 33.9 ± 3.6 d (range = 2–165 d).

**Female oviposition behavior**

After 10 (91%) of the 11 copulations that terminated naturally at the 1986 site, females oviposited in at least one tree hole before leaving their mate's territory or remating with a second male. The exception was the mate of a satellite male, which remated with the territorial male before she began ovipositing. Females oviposited for longer periods in larger tree holes (regardless of whether they were defended) than in smaller ones (Fig. 5). In small cages under ambient conditions, females oviposited 10–270 eggs within 2 h (66.8 ± 19.9 eggs, $N = 13$). Based on this maximum oviposition rate ($270/120 = 2.3$ eggs/min), a female may have laid as many as 124 eggs in a typical large tree hole, and up to 38 eggs in a small one.

Before mating again, at least some females oviposited at holes other than defended ones. One marked female that was first sighted ovipositing alone at an undefended understory hole was found 7 d later mating at a territory. Another female that was marked while mating at a territory was resighted 37 d later ovipositing alone at an undefended understory tree hole. Five days thereafter, she was seen ovipositing yet again in a defended tree hole from which the territorial male was temporarily absent.

**Effects of the larval habitat on the number and quality of offspring**

Based on the number and quality of larvae surviving to emergence, large holes were superior to small ones as larval habitats. Large holes supported up to 13 times as many emerging adults as did smaller tree holes (Fig. 6A). Large tree holes persisted nearly a month longer and supported faster larval growth than did smaller holes (Table 4), thereby permitting at least two generations to emerge before they dried up. In contrast, small holes did not produce more than a single adult at a time, and only rarely supported more than one adult per season.

In addition to their shorter developmental period, adults emerging from large tree holes were significantly larger than those emerging from smaller tree holes ($t = 2.171, P < .02, N = 64$). Moreover, for males, but not for females, there was a positive correlation between adult wing length and the volume of the larval habitat (Fig. 6B). This effect was likely due to the relatively greater availability of food in large holes. The largest available prey items (i.e., tadpoles of Physalae-
mus pustulosus, Agalychnis callidryas, and Dendrobates auratus) were found in 21 tree holes, all but 2 of which were >1 L (\(\bar{X} \pm 1 \text{ SE} = 5.9 \pm 1.7 \text{ L}\)).

**Sources of larval mortality and consequences to reproductive success**

One predictable cause of larval mortality was the seasonal drying of tree holes. All tree holes were dry by 30 March 1984, remained dry for at least 26 d, and were not consistently full until 14 May. Despite the abnormally wet dry season in this year (see Windsor 1990), only 5 (5%) of the 93 tree holes containing small to medium-sized larvae (7–15 mm) in late January 1984 (i.e., those that could not have emerged before the tree hole dried up) contained medium to large-sized larvae (i.e., those too big to have hatched after the first wet season rains) in June 1984.

A second cause of larval mortality was cannibalism. Despite lengthy, multiple ovipositions into some large tree holes, no more than 15 *M. coerulatus* larvae >7 mm were ever found in any hole at any given check, even in the absence of other guild species. Evidence of cannibalism (e.g., dead larvae missing legs, caudal lamellae, or part of the abdomen and/or with holes in the thorax) was occasionally found even in large holes.

A third threat to *M. coerulatus* larvae was intraguild predation. By the time *M. coerulatus* started ovipositing in the wet season, half of the tree holes were already occupied by other odonate species (Fincke 1992b). In small tree holes, the first individual to hatch was usually the only one to emerge. In large holes, later arriving (i.e., initially smaller) *M. coerulatus* are able to kill an incumbent (i.e., initially larger) Mecistogaster, but not a larger dragonfly (*G. membranalis*) occupant (Fincke 1992b). Neither male nor female *M. coerulatus* gave any indication they could detect the presence of either con- or heterospecífic larvae (which usually hide under leaves), and neither sex discriminated against tree holes that I knew contained larvae. Furthermore, territorial males apparently could not prevent colonization by the dragonfly; the proportion of large tree holes that contained *G. membranalis* larvae was exactly half for tree holes that were defended (22/44) and undefended (10/20) by *M. coerulatus*.

**Table 4.** Differences between large and small natural tree holes as larval habitats. Data are means ± 1 se.

<table>
<thead>
<tr>
<th></th>
<th>Minimum no. days required for larval development</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>No. days dry</strong></td>
<td></td>
</tr>
<tr>
<td>Small tree holes</td>
<td>83.6 ± 5.2 (N = 32) 185.3 ± 7.2 (N = 8)</td>
</tr>
<tr>
<td>Large tree holes</td>
<td>53.5 ± 3.6 (N = 31) 167.5 ± 11.5 (N = 6)</td>
</tr>
</tbody>
</table>

\[ t = -4.8^* \quad t = -2.3^{**} \]

* \(P < .05\), ** \(P < .001\), Wilcoxon rank sum tests.

**Fig. 6.** (A) Number of final instar *Megaloprepus coerulatus* collected over 8 mo, as a function of hole volume. The five sizes of circles represent 1–5 holes. (B) Size of adult *M. coerulatus* as a function of the volume of the hole in which they developed.

Of the 67 artificial and natural holes defended in 1983–1984 (checked bi-monthly), 42 contained only larvae of *M. coerulatus* (all of these holes produced adults), and 25 contained larvae of *G. membranalis* in addition to those of *M. coerulatus*. In 7 of these latter holes, no *M. coerulatus* survived to emergence, whereas both species emerged from 13 holes. Two defended tree holes, one of which had been held by the same male for nearly 3 mo, contained only larvae of *G. membranalis* Thus, 13% (9/67) of the defended tree holes produced no *M. coerulatus* offspring. There was no correlation between the day of tree hole filling and duration of oviposition in large holes \((r = -0.23, N = 21, P < .34)\), indicating that large holes did not lose their value to ovipositing females as occupancy by con- or heterospecific guild members became more certain.

**The function of territories for males**

If territoriality functions solely in mate acquisition, then, because females spend more time in gaps than
TABLE 5. Proportion of artificial holes defended by male *Megaloprepus coerulatus* within 3 mo. (Number of replicates is in parentheses.) Holes that were overtaken by animals or branch falls are excluded. $G = 34.4, 4$ df, $P < .005$.

<table>
<thead>
<tr>
<th>Canopy openness</th>
<th>Hole size</th>
<th>Large (9–16 L)</th>
<th>Medium (2–3 L)</th>
<th>Small (0.2 L)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gaps</td>
<td>1.0</td>
<td>1.0</td>
<td>0.13</td>
<td>(10)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(7)</td>
<td>(8)</td>
<td>(9)</td>
</tr>
<tr>
<td>Understory</td>
<td>0.22</td>
<td>0</td>
<td>0</td>
<td>(6)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(6)</td>
<td>(8)</td>
<td>(9)</td>
</tr>
</tbody>
</table>

in forest understory, all of the experimental holes placed in gaps should have been defended, regardless of volume. On the other hand, if territoriality functions mainly to procure high-quality larval habitats, then, because tree holes >1 L produced multiple, relatively large adults, all large and medium holes should have been defended, regardless of their location in gaps or understory. Results of the site choice experiment indicated that males chose sites that fulfilled both of these functions.

During the 3-mo experiment, 20 holes were defended within 33.1 ± 7.5 d after they were put in the field. Males defended all of the large and medium holes placed in gaps but failed to defend all but one of the small holes in gaps (Table 5). Thus, of the holes predicted by the mate acquisition hypothesis to be defended, 72% (18/25) were chosen by territorial males. In contrast, no medium holes and only two large holes in the understory were defended. Both of these latter holes were adjacent to gaps where males patrolled, thus confounding the two possible criteria used by males in selecting these sites. Excluding these two cases, 57% (17/30) of the holes predicted by the larval habitat quality hypothesis to be defended were chosen by territorial males.

**Discussion**

**Territoriality and the evolution of sexual size dimorphism**

In species whose males control resources necessary to female reproduction, variation in male mating success may result (even if all males are phenotypically identical), simply because territories differ in their attractiveness to females (e.g., Ubukata 1984, Waage 1987, Warner 1987). In *M. coerulatus*, by contrast, differential male mating success stems from phenotypic variation among males in their ability to defend resources. Larger males won more territorial contests, resulting in their higher mating efficiency relative to smaller males. Because larger males did not live longer than smaller males, my results lend support to the hypothesis that the male-biased size dimorphism of *M. coerulatus* has resulted primarily from sexual, rather than from natural, selection on male size (see also Gilbert and Williamson 1983, Woolbright 1983, Shine 1989). Higher mating efficiency of large males relative to small ones has been demonstrated in only two other odonates, where, as in *M. coerulatus*, males are larger than females (Miller 1983, Moore 1990).

In contrast to *M. coerulatus*, most odonate males are smaller than conspecific females (d’Aguilar et al. 1985), including libellulids and calopterygids whose males defend oviposition sites (e.g., Heymer 1972, Waage 1973, McVey 1988). All relevant studies to date support my hypothesis that, in odonates with such female-biased size dimorphism, large male size confers no advantage in mating efficiency (e.g., Fincke 1982, 1988, Banks and Thompson 1985, Koenig and Albano 1987, Tsukaki and Ono 1987, McVey 1988). In a study that seemingly contradicts the above trend, Harvey and Corbet (1985) reported that mated males were larger than unmated males in the coenagrionid, *Pyrrophosoma nympha*. However, because they compared the size of mature, mated males with that of unmated, sexually immature males, their results confound natural and sexual selection on male size (i.e., very small males are probably less likely than larger ones to survive to sexual maturity; see also Gribbin and Thompson 1991). Moreover, although *P. nympha* males were described as territorial, they only defend perches on the bank rather than oviposition sites (I. F. Harvey, personal communication).

Adult body size of *M. coerulatus* was considerably affected by variation in volume of the larval habitat, which explained 23% ($r^2$) of the observed variation in male size. Large males controlled access to larval habitats that produced the largest males. Thus, even in the absence of additive genetic variance for body size, phenotypic selection resulting from this paternal effect (see Kirkpatrick and Lande 1989) favors large males and discriminating females that mate with territory holders (Fig. 7). However, I also found small but significant family differences in adult body size of individuals reared under identical conditions (O. M. Fincke, unpublished manuscript). This heritable component of size potentially could allow the current population to respond to sexual selection for large males. Any genetic propensity for large size would be maximally expressed in large tree holes.

Two factors countered directional selection for large size on *M. coerulatus* males, and may maintain additive genetic variation for body size at some equilibrium level. First, very small males occasionally obtained fertilizations. Second, females oviposited in small tree holes as well as large ones, thereby increasing the environmental component of phenotypic variation among sibs, which would decrease the ability of natural selection to "detect" underlying genetic differences among individuals (see also Price et al. 1988, Alatalo et al. 1990).
Megaloprepus coerulatus

Fig. 7. Schema by which variation in the larval habitat generates variation in male size on which phenotypic selection could act in the absence of additive genetic variation for size.

Consequences of larval ecology for adult reproductive behavior

Three features of the larval habitat favored females using a wider range of tree holes than were defended by males: (1) holes that produced the largest and greatest number of offspring were relatively rare, (2) even large holes were too small to support an entire clutch to emergence, and (3) prior occupancy of holes by potential predators was unpredictable. By partitioning a clutch among holes and placing a few eggs in small holes whenever she encountered them, a female hedged her bets against ovipositing in a previously occupied tree hole. Females put more eggs in larger holes and visited large-volumed sites in gaps more frequently than small-volumed sites, further suggesting that site selection by females optimizes the number and quality of surviving offspring. By mating only at defended sites (i.e., passive mate choice), females gained access to superior larval habitats that males controlled, and in addition may have acquired genetically superior mates. The latter advantage is suggested by the observation that females sometimes failed to oviposit at defended sites when the territory holder was absent (Fincke 1984a), but current results do not permit me to assess the relative value of these two advantages.

By using a single proximate “rule of thumb,” namely by defending only medium- to large-volume sites in gap areas, a territorial male M. coerulatus simultaneously gained access to a disproportionate share of potential mates as well as to larval habitats that increased his chances of producing reproductively successful sons. Nevertheless, several lines of evidence support the hypothesis that larval survivorship and/or quality functions as an ultimate criterion for male site selection, independent of female encounter rate. Even though small-volume sites in gaps were relatively rare (9.4% of total), failure of males to defend small holes in light gaps could not be explained by the lack of females in gaps. Indeed, in the absence of males, six times as many females were found in gaps without tree holes than at understory tree holes. Moreover, the few understory tree holes that were defended were adjacent to gaps that territorial males patrolled for incoming females. Thus, gaps per se were sufficiently attractive to females to make defense of small holes in gaps worth the time investment to males if the sole function of territoriality was to gain access to females, rather than also to secure a high-quality larval habitat.

Further evidence that male territorial site selection was in part ultimately influenced by larval habitat quality is that, unlike many territorial animals whose males use the presence of females as the major criterion for site selection (e.g., Warner 1987), male M. coerulatus used cues other than conspecifics. The defense of some holes in as few as 1–2 d after their placement in the field, before males would have had time to assess female encounter rates at those sites, was evidence that a male’s initial choice of a territory was independent of female presence. Furthermore, naive males predictably selected the same sites that were defended in previous years.

Failure of odonate larvae to survive the dry season in tree holes and the colonizing advantage of predatory heterospecifics that ensues when habitats are seasonally cleared of larvae (Fincke 1992b) countered any benefit M. coerulatus males might otherwise have gained by defending small tree holes in gaps. Despite the greater risk of Gynacantha occupants in large holes, the maximum fitness payoff for a satellite frequenting a single
territory was 2.0 offspring (0.15 \times 13\) offspring per large hole per season). This calculation assumes a fertilization success of 0.15 (0.23 mating success \times 0.66 fertilization success per mating) and equal likelihood of ovipositing females producing offspring from a given tree hole. In contrast, the first *M. coeruleatus* male to discover and defend a small hole in a gap could at best produce a single offspring per season (two offspring per small hole per season \times 0.5 probability of previous occupancy by *Mecistogaster*). Moreover, females that mated at small holes would mate again at large-holed territories. The longer copulation duration of a satellite relative to a territorial male may increase the satellite’s chances of fertilizing eggs laid by a female that leaves the territory and oviposits in undefended holes before mating again at a defended site (see also Miller 1983, Siva-Jothy 1987).

Plasticity in the use of the two alternative mating tactics was advantageous because males had to reestablish residency each wet season, when small and large males had equal chances of discovering large tree holes. Even after all suitable territories had been found, holes in newly fallen trees provided small males with additional opportunities to be residents.

*Implications for studies of adult reproductive behavior*

Because I assessed relative fitness in terms of offspring surviving to adulthood, my results hold several implications for studies of reproductive success. First, reproductive success measured as the number of eggs fertilized (e.g., Fincke 1986, Koenig and Albano 1987, McVey 1988) may be a poor indicator of fitness because there may be little relationship between the number of eggs laid and the number of offspring that survive (see also Clutton-Brock 1988). Some males in this study that were highly successful in terms of territory tenure and mating success leading to ovipositions had low fitness in terms of offspring produced per territory. Second, in this study, the quality of surviving offspring was variable. Males (and possibly females if fecundity is related to body size) emerging from large tree holes had a higher chance for reproductive success than those emerging from small tree holes, making larger tree holes a more valuable resource for parents.

Third, this study illustrates the confusion that may result if variation in reproductive success is partitioned into artificially discrete selective episodes of natural and sexual selection (see Arnold and Wade 1984, Clutton-Brock 1988). Territorial defense held three advantages for *M. coeruleatus* males. It increased a male’s chances of mating and of producing multiple offspring and reproductivey successful sons. If one views the latter two advantages as resulting from paternal investment by males via territorial defense (as did Howard 1978), then the opportunity for sexual selection on male mating success relative to the total opportunity for selection on male reproductive success should decrease to the extent that offspring survivorship varies as a function of territory quality. Alternatively, one might argue that all advantages of territoruality are components of sexual selection because territorial defense increased the number of matings that led to the production of viable offspring. In this case, variance among mated males in the number of offspring produced would increase the relative opportunity for sexual selection on males. Thus, opposing conclusions about the potential strength of sexual selection could be drawn from the same data.

Finally, this study demonstrated how larval ecology can ultimately affect oviposition and territorial site selection of adults. Female oviposition behavior is thought to have evolved to maximize survivorship or quality of offspring, yet only a few previous studies (e.g., Via 1986, Singer et al. 1988, Craig et al. 1989) have demonstrated that it does so. The effect of larval survivorship as a selective pressure on male behavior is even less well documented. Howard (1978) found that male bullfrogs significantly increased egg survivorship by defending certain areas of the pond, and Greenfield et al. (1989) reported that male grasshoppers defended bushes that permitted superior growth rates of juveniles and females. To my knowledge, my study is the first that documents that the behavior of adult males affects the potential mating efficiency of their sons.

The consequences of larval ecology for adult behavior should be greatest where, as in *M. coeruleatus*, (1) neither the vagility of larvae nor interspecific larval competition unduly limits adults’ influence over the fate of offspring (e.g., Fincke 1992b), and (2) male or female fitness traits are environmentally modifiable (e.g., Sigurjonsdottir 1984, Pickup and Thompson 1990; O. M. Fincke, unpublished manuscript), and/or (3) abiotic and biotic factors affecting the developmental habitat affect the spatial distribution and/or temporal patterns of emerging adults (e.g., Banks and Thompson 1987, Crowley et al. 1987). The above conditions are likely to be widespread in animals with complex life histories, and especially in insects, whose adult size is fixed at emergence. Future studies that address the interplay of selective pressures at the larval and adult stages of the life history should go far in explaining patterns of adult reproductive behavior (see also Buskirk and Sherman 1985).

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