Studies on Neotropical Fauna and Environment

Differences in forest use and colonization by Neotropical tree-hole damselflies (Odonata: Pseudostigmatidae): Implications for forest conversion

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ORIGINAL ARTICLE

Differences in forest use and colonization by Neotropical tree-hole damselflies (Odonata: Pseudostigmatidae): Implications for forest conversion

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Differential habitat use in primary and secondary forests was documented for two genera of giant damselflies (Pseudostigmatidae), important predators of tree-hole breeding mosquitoes in tropical forests. In a lowland moist forest of Panama, adults moved between old primary (>400 years old) and contiguous secondary forest (>60 years old) and reproduced seasonally in both types. However, the two *Mecistogaster* species were more common in secondary forest, whereas *Megaloprepus caerulatus* was most common in primary forest. These differences in landscape use were reflected in differential colonization of tree-hole analogs (plastic pots) in primary forest and highly altered secondary growth (<20 years old) in a lowland wet forest in Costa Rica where reproduction of both species was aseasonal. Larvae of *Mecistogaster linearis* were commonly found in pots at both habitat types, whereas *Megaloprepus*, the majority species, rarely colonized pots in altered sites. Our results suggest that *Megaloprepus* is particularly susceptible to forest conversion, and call for increased focus on the dispersal ability of all pseudostigmatids. In tropical moist and wet forests that harbor water-filled tree holes, the presence of the conspicuous *Megaloprepus* and similar species may serve as bio-indicators of a healthy predator guild, the loss of which may adversely impact human health.

Keywords: Adult recruitment; bioindicators; landscape ecology; *Mecistogaster*; *Megaloprepus*; mosquito predators

Introduction

In tropical America, as the result of logging operations, primary forests are rapidly being converted into human settlements and cattle ranches, without much concern for the needs of wildlife. Such activities severely reduce habitats for Neotropical migrant birds (e.g. Martin & Finch, 1995) as well as a great number of resident species that depend on undisturbed tropical forest habitats for their survival (Wilson, 1985; Pimm & Raven, 2000). Because changing patterns of land use have a direct impact on biodiversity (Brown & Hutchings, 1997; Frankie & Mata, 2004), a better understanding of how biodiversity is maintained at the landscape level is critical to managing natural resources in a sustainable fashion. Sustainable land management depends on the conservation of biodiversity in sufficient density and in spatial patterns to provide optimal values and services to human populations while maintaining viable ecological systems. But the level of biodiversity required for baseline ecosystem services remains unclear (reviewed by Srivastava & Velland, 2005).

One service provided by tropical forests is the maintenance of natural predators of disease vectors. Water-filled tree holes are a major habitat for many mosquito species (Jones et al., 2000; Kitching, 2000; Pecor et al., 2000), several of which transmit important human diseases (e.g. yellow fever, Gallindo et al., 1955; encephalitis, Jonkers et al., 1968; dengue fever, Monath, 1994). Much research has focused on the tree-hole mosquito, *Toxorhynchites*, whose predatory larvae are a potential bio-control agent (e.g. Steffan & Evenhuis, 1981; Bradshaw & Holzapfel, 1983; Lounibos et al., 1987). The effects of odonate predators on the population dynamics of disease vectors has been largely ignored, even though, as top predators in tree holes, their larvae can decrease the rate of recruitment of adult mosquitoes (Fincke et al., 1997). Forest conversion has been implicated in the rise of infectious diseases around the globe, particularly in tropical countries (e.g. Walsh et al., 1993; Patz et al., 2004). The reasons for the increase are complex, but changes in vector and non-human reservoir populations appear key (Real, 1996). If, for example, natural predators such

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as forest odonates prove to be more susceptible to deforestation than their mosquito prey, then in addition to decreasing biodiversity, forest conversion may affect human health directly.

As a first step in assessing the impact of forest conversion on tree-hole odonate populations, we here ask if landscape use by two genera of giant damselflies (Odonata: Pseudostigmatidae) in relatively old forests in Panama reflects their colonization success in more recently altered forest patches in Costa Rica. The three study species are all forest dwellers that breed exclusively in water-filled tree holes (reviewed by Fincke, 2006). The largest and most conspicuous of the three is *Megaloprepus caerulatus* Drury (hereafter ''*Megaloprepus*'', a monospecific genus). This species is common in primary as well as old secondary forests in Costa Rica (Fincke, 1998; Hedström & Sahlén, 2001, 2003; Hedström, 2006) and Panama (Fincke, 1992a), and occurs from southern Mexico to Bolivia, including Venezuela, Guyana, Colombia, Ecuador and Peru (Davies & Tobin, 1984; D. Paulson, personal communication). In Brazil and much of Peru, *Megaloprepus* is replaced by *Microstigma rotundatum* (D. Paulson, personal communication; see also Lencioni, 2005), whose males similarly defend tree-hole oviposition sites (de Marmels, 1989). *Mecistogaster linearis* Fabricius, with its more slender, white-tipped wings, occurs in moist and wet forests. It is primarily a South American species, observed from northern Costa Rica to Ecuador, Peru, Venezuela, Brazil and Argentina (Davies & Tobin, 1984; Fincke, 1998; Hedström & Sahlén, 2001; Sahlén & Hedström, 2005). The smaller *Mecistogaster ornata* Rambur occurs in tropical dry and moist forests from Mexico to Argentina (Fincke, 1984; D. Paulson, personal communication).

As adults, *Megaloprepus* can live as long as 8 months (Fincke, 1998), although the average lifespan of all three species is unlikely more than several months (Fincke, 1984). Like all pseudostigmatids, adults of the three study species forage in sun-lit areas on small web-building spiders (Fincke, 1992b), but differ in their mating systems (Fincke, 1984). In a moist forest in Panama, male *Mecistogaster ornata* do not defend territories, but during the early wet season, mate opportunistically at small light gaps where they forage. Male *M. linearis* briefly defend light gaps with or without tree holes; females lay eggs over many months. In contrast, over the 7–8-month wet season, individual male *Megaloprepus* may defend tree holes in large gaps over a span of a few days to up to 3 months. Female *Megaloprepus* mate only at sites defended by males, which are typically created when a tree falls and water collects in

indentations in the trunk (Fincke, 1992a). Newly created gaps also offer a high light environment, which enhances the UV reflectance of the sexually dimorphic wings of *Megaloprepus* (see Rüppell & Fincke, 1989) and the abdominal tip of male *Mecistogaster linearis* (T. D. Schultz & O. M. Fincke, unpublished data). High decomposition rates of fallen trees result in few *Megaloprepus* territories persisting for more than a season (Yanoviak & Fincke, 2005).

As larvae, the study species comprise a guild of top predators that opportunistically feed on an array of aquatic invertebrates including mosquito larvae (Fincke et al., 1997; Yanoviak, 2001a) and anuran tadpoles (e.g. *Agalychnis*, *Dendrobates*, *Physalaemus*; Fincke, 1992c, 1999). Cannibalism and intra-guild predation are common, reducing odonate larval density to about one per liter (Fincke, 1992a, 1994). Artificial tree holes are readily used by ovipositing females, and are colonized by a similar array of prey species as occurs in natural tree holes (Fincke et al., 1997; Yanoviak, 2001a, 2001b). Ovipositing females of the three species overlap in their use of tree holes with respect to water volume and the characteristics of the hole opening. Occupancy of a hole by a given odonate genus is random from one year to the next (Fincke, 1992a). In seasonal habitats, asymmetrical competition results in *Megaloprepus* eliminating *Mecistogaster* from large, but not small holes. Hence, both species of the latter typically emerge from holes $\leqslant 1$ liter, explaining why the two *Mecistogaster* species would not benefit by defending the limiting tree-hole resource (Fincke, 1992c).

Several lines of evidence suggest that among the three study species, as both adults and larvae, *Megaloprepus* is the most susceptible to dry conditions. First, based on collection records, *Megaloprepus* is absent in tropical dry forest but present in cooler montane forest (Hedström & Sahlén, 2001). In the moist forests of Panama, adults of both *Mecistogaster ornata* and *M. linearis* are active throughout the 3-month dry season, whereas adult *Megaloprepus* become inactive in late March and April (Fincke, 1992c), when humidity is at its nadir and temperatures peak (Rand & Rand, 1982). Finally, although larvae of both *Mecistogaster* species are found in tree holes from ground level to the canopy, *Megaloprepus* larvae have yet to be found in canopy holes, which experience higher water temperatures and more frequent drying than holes at lower levels (Yanoviak, 1999). Hence, we expected that relative to *Mecistogaster*, *Megaloprepus* would prefer older forests to younger ones, and hence be less likely to colonize recently deforested habitats. Because of differences in the seasonality and abundance of

rainfall between our study sites in wet and moist forests, we also assessed whether the species differed in their temporal use of forest across forest types.

Material and methods

Study sites and field methods in Panama

In Panama, data were collected from the lowland moist forest of Barro Colorado Island (BCI, 90°09′N, 79°51′W), located in Gatun Lake (see Leigh et al., 1982 for general ecology). About half of its 1500 ha is covered by primary forest estimated to be over 400 years old, whereas the northeastern portion harbors secondary forest estimated to be 60–100 years old at the time of our study (Piperno, 1990). The secondary forest is characterized by a variable canopy, which in patches is "scrubby" (Foster & Brokaw, 1982). The mean 2600 mm yearly rainfall is seasonally distributed (Rand & Rand, 1982). Typically, by the end of dry season in late March, water-filled tree holes have dried out completely, and any odonate larvae that have not emerged die before tree holes refill with the wet season rains in early May (Fincke, 1992c).

The BCI data were collected originally to address questions about the mating systems of adults (Fincke, 1984), effects of tree hole size and morphology on use by ovipositing females, and larval competition within holes (Fincke, 1992a, 1992c). Data on adult recruitment and reproductive activity across primary and secondary forest sites, and seasonal differences across moist and wet forests have not been analysed previously. Between January 1981 and July 1990, natural tree holes were tagged and repeatedly checked for odonate larvae, which were returned to holes after counting (for details see Fincke, 1992c). Adult recruitment was calculated from the number of final instar larvae removed from holes checked five or more times during the wet seasons of 1982 and 1983. Water volume, which was measured as the maximum held by a tree hole in wet season, was log transformed for analyses. Mean values are reported for untransformed data.

Both upright and fallen trees sometimes had multiple, water-filled holes. "Site" here refers to a single upright tree or a single tree-fall gap that may harbor multiple tree holes. Because of difficulty in distinguishing between the larvae of the two species of *Mecistogaster*, these species were pooled in the analysis of larval distributions. To determine whether there was a difference in their distribution by forest type, final instar larvae were collected from 34 tree holes and permitted to emerge in an outdoor insectary. The two other tree-hole specialists also present at BCI, the dragonflies *Triacanthagyna*

dentata and *Gynacantha membranalis* (Anisoptera: Aeshnidae), were not always distinguished as larvae (see Fincke, 1998) and are here pooled for analysis. As adults, these species are very inconspicuous and were not focal species in this study.

From January to April 1981, from October to December 1982, and from October 1983 to December 1984, the location and behavior of all pseudostigmatids encountered (by O.M.F.) were recorded on 254 days while walking an estimated 2–10 km/day along an extensive trail system that traverses primary and secondary forest. The total area surveyed was circa 250 ha, roughly half of which was in secondary forest as determined from its location adjacent to the lab clearing or the following trails: Synder-Moleno, Wheeler (<9), Barbor-Lathrop, Balboa (0–8), Fairchild, Thomas Barbor, Van Tyne, Chapman, Conrad, Hood. "Primary forest" was bisected by the following trails: Armour, Wheeler (>10), Drayton, Zetek, Stanley (see map in Foster & Brokaw, 1982). Numbers in parentheses above refer to trail markers that were posted at 100 m intervals. When walking off the trails, the estimated distance (i.e. up to 200 m) and direction from the trail was used to fix the location of sightings. Most sighting of damselflies occurred between 09:00 and 15:00 h when they were most active. A subset of adults was marked by writing an indelible number on the wing. For marked individuals, only the first activity observed was used in the analysis of habitat use. For pairs in copula, the observation was counted only for a female but not her male mate, to insure each observation was independent.

Of the 214 marked *Megaloprepus* males, 42% were resighted. Thus, sightings of unmarked male *Megaloprepus* were conservatively excluded from all analyses to insure independence of observations. Of the 91 marked female *Megaloprepus*, only two (2.1%) were resighted. For *Mecistogaster linearis*, resightings accounted for 11.7% of the 51 marked males and 1.8% for the 56 marked females. Three of the marked male *Mecistogaster linearis* were seen defending a gap, accounting for about half of the resightings in that species. One marked *M. linearis* male was seen repeatedly at a clearing that he defended for 14 days in September. Hence, the observation of a sole unmarked male *M. linearis* at defended sites on a given day within a week's span was counted as only one observation. Of the 14 marked male and 25 marked female *M. ornata*, only one individual of each sex was seen again. Save for the above exceptions, for analysis, each sighting was assumed to represent a unique individual. Sightings within forest types were assumed to be independent except for those at defended sites. Then, the number of site checks (ca.

5–15 min) offered a control for any unequal sampling by forest type.

To provide a more accurate picture of the time span over which *Mecistogaster* species are reproductively active, additional observations of the reproductive behavior of these two species were also noted opportunistically in 1996. Then, unlike years 1981–1984, when observer effort was roughly equal between primary and secondary forests, most of the observation time was in primary forest. Hence the latter data were not used in the analyses on spatial habitat use. For analysis of seasonal trends, a year was divided into four 3-month quartiles (i.e. January to March, April to June, July to September, October to December). All Fisher exact tests are two-tailed.

Study sites and field methods in Costa Rica

The Costa Rican study sites were adjacent to Barbilla National Park, on steep Caribbean slopes, approximately 0.5–1.0 h hike from the Nairi Field Lodge (NFL; 10°00′N, 83°26′W), Las Brisas de Pacuarito, Cantón de Siquirres, Limón Province. This area contained primary and altered forest habitats in the transition zone between tropical lowland wet forest (≤ 500 m) and tropical premontane wet forest with no effective dry season (Holdridge, 1947). Annual mean precipitation is 4130 mm (Institute of Costa Rican Electricity, 1992–2003 data). Four sites were located within and near the private Rio Dantas Wildlife Refuge (220–520 m a.s.l) in primary forest and the four "altered" sites were in 6–20-year-old secondary growth that remained after logging operations in the early 1980s and in 1997. The distance between primary and altered habitats ranged from 0.5 to 2.5 km. Within the two habitat types, the distance between sites varied from 0.6 to 3 km for the altered sites, and between 0.6 and 1.5 km for the primary forest sites. No major landscape changes have occurred in the area since February 1999.

Tree-hole analogs ("pots") used to sample odonate larvae were modified plastic soda bottles (volume 1–1.5 liters) that were painted black on the outside. A 20–25 cm stick with its bark intact was placed in each pot as an oviposition substrate. The pots were filled with water and hung on nails on 37 large standing trees (25–30 m tall) at a height between 1 and 2 m from the ground. One to three pots were attached to a given tree; a total of 15 pots were attached to three fallen trees. Within the eight sites, pots were within 5–60 m of each other. Between January 2000 and January 2004, pots were emptied, any larvae collected and the water replaced every 3–6 months (usually in January/February, April/May and

September/October). Vegetation around the pots was kept open by cutting down new saplings.

Fifty pots were distributed among four natural light gaps located in primary forest. The four numbered sites consisted of: (1) 10 pots near a 3–4 m waterfall (230 m a.s.l., 10°00′N, 83°26′W); (2) 10 pots in a 4–5-year-old light gap over a small creek, near the small lake, La Laguna (450 m a.s.l., 09°59′N, 83°26′W), 1 km east of the NFL; (3) 20 pots in a gap located near a small creek (240 m a.s.l., 09°59′N, 83°26′W); and (4) 10 pots in a gap formed in 1998 when several emergent trees fell at the site (400 m a.s.l., 10°00′N, 83°27′W), about 2 km east of the NFL.

In altered forest habitats, 25 pots were distributed on scattered trees in open areas in the following four sites (numbered 5–8): (5) 10 pots in a small garden near the NFL (500 m a.s.l., 09°59′N, 83°27′W), surrounded by forest cut in the 1980s; (6) five pots near a logging road (375 m a.s.l., 09°59′N, 83°26′W); (7) five pots in a fruit tree garden at Tapir River Lodge (220 m a.s.l., 09°59′N, 83°26′W), surrounded by primary forest on the west and secondary growth to the north; and (8) five pots in a small fruit tree garden at Kaseri Farm (520 m a.s.l., 10°00′N, 83°27′W), adjacent to primary forest on the north and south and fragmented forest to its west and east, 2 km northwest of the NFL. The latter five pots were censused between September 2000 and January 2003 only.

Because female pseudostigmatids often lay eggs in multiple tree holes encountered at a given site, the eight sites, but not the individual pots, were assumed to be independent observations. Repeated measures General Linear Model (GLM), with site nested within the two forest types, was conducted using the first eight sampling periods (i.e. November 2000 to August 2002) because not all sites in the disturbed sites were sampled for the complete study period. For analysis, proportional data were arcsine square-root transformed, and distance data were log transformed. Throughout, means are given ± SE.

Results

Temporal and spatial distribution of larvae and adults in primary and secondary forest on Barro Colorado Island

Of the 227 unique tree holes sampled, 59% were in primary forest and 41% in secondary forest, not a statistical difference ($F_{1,115}=0.04$, $P=0.84$). The volume of natural tree holes in primary forest (mean $=1.82 \pm 0.37$ liters, $n=134$ holes) did not differ in volume from those in secondary forest (mean $=1.97 \pm 0.46$ liters, $n=93$ holes, $t=-0.26$,

$P=0.79$). Of tree holes checked at least once per year, 151 (67%) were occupied by one or more larval odonate. The probability of occupancy by an odonate did not differ between tree holes in primary and secondary forest ($P=0.58$, Fisher exact test). The distribution of larval *Megaloprepus*, pooled *Mecistogaster* and pooled dragonfly larvae did not differ between primary and secondary forest ($\chi^2=0.59$, df$=2$, $P=0.59$; Figure 1A). Of the 34 *Mecistogaster* larvae that were taken from tree holes as final instars and permitted to emerge in insectaries, there was no significant difference in the distribution of the two species ($P=0.68$, Fisher exact test). Of the eight *Mecistogaster* larvae from primary forest 75% were *M. linearis* and 25% were *M. ornata*. Of the 26 *Mecistogaster* larvae taken from tree holes in secondary forests, 61.5% were *M. linearis* and the remainder *M. ornata*. Adult recruitment of *Megaloprepus*, as measured by the total number of final instars in an occupied hole, varied from 1 to 12 and was positively correlated with tree-hole volume (1982: $r=0.54$, $n=34$, $P<0.001$; 1983: $r=0.64$, $n=17$,

$P<0.001$). Recruitment of dragonflies varied from one to five per hole, and in one year but not the other, was correlated with water volume (1982: $r=0.50$, $n=15$, $P=0.06$; 1983: $r=0.70$, $n=14$, $P=0.006$). In contrast, the correlation for *Mecistogaster* was not significant in either year (1982: $r=0.37$, $n=25$, $P=0.07$, range one to four per hole). In 1983, only one final instar was found in each of the 15 occupied holes.

In contrast to their larvae, adult damselflies were non-randomly distributed with respect to forest type (Figure 1B). Only 23.6% of the sightings of *Mecistogaster linearis* ($n=158$ females, 176 males, 47 sex unknown) and 26% of those of *Mecistogaster ornata* ($n=84$ females, 58 males, 59 sex unknown) were in primary forest whereas 63% of the *Megaloprepus* sightings ($n=171$ females, 259 males) were in primary forest ($P<0.0001$, Fisher exact test). For all three species, habitat use did not differ between the sexes *(Megaloprepus*, $P=0.32$; *Mecistogaster linearis*, $P=0.80$; *Mecistogaster ornata*, $P=0.85$, Fisher exact tests). As shown in Figure 2, territorial male *Megaloprepus* and *Mecistogaster linearis* used the two forest types differently ($P<0.0001$, Fisher exact test). Of the 225 defending *Megaloprepus* males, 69% were in primary forest, whereas 54% of the sightings of non-defending male *Megaloprepus* were in primary forest, a significant difference ($P=0.05$, Fisher exact test). Most (72%) of the 58 holes defended by *Megaloprepus* persisted for only a single season. Twelve holes (21%) persisted over a 2-year span and four (7%) persisted over three seasons. In secondary forest, the 11 sites (23 holes) defended by at least one male were used on average for 1.39 seasons. The 13 defended sites (35 holes) in primary forest were used on average for 1.30 seasons, not a significant difference ($t=-0.47$, $P=0.64$). However, in primary forest a total of 137 unique male *Megaloprepus* were observed at the territorial sites during a total of 852 site checks, disproportionately more than the 88 male *Megaloprepus* observed during 616 checks of defended sites in secondary forest ($\chi^2=4.0$, df$=1$, $P<0.05$). In contrast, of the 19 male *Mecistogaster linearis* seen to defend one of six sites, all were in secondary forest, whereas 86% of non-defending males were observed in secondary forest ($P=0.009$, Fisher exact test). No site was used for more than one season. Although excluded in the above analysis, in 1996 *M. linearis* was seen to briefly defend two sites in primary forest.

Females of all three species were seen to copulate and oviposit in both forest types (Figure 2). Compared with females not seen in reproductive activity, copulating and ovipositing female *Megaloprepus* ($P=0.38$ and $P=0.76$, respectively),
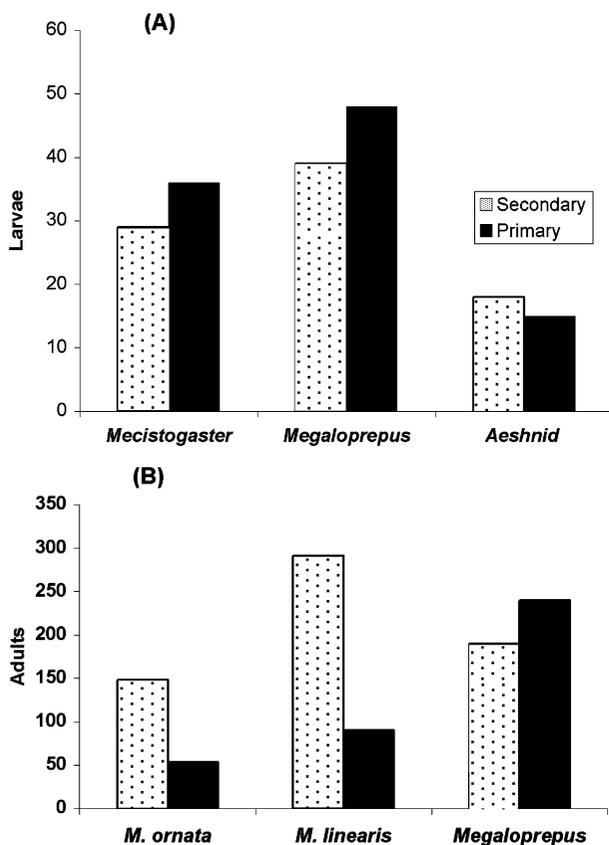

Figure 1. Distribution of odonate individuals observed in secondary and primary forest on BCI, Panama. (A) Odonate larvae (only those that eventually emerged; *Mecistogaster linearis* and *M. ornata* are pooled); (B) adult pseudostigmatids (pooled males and females).
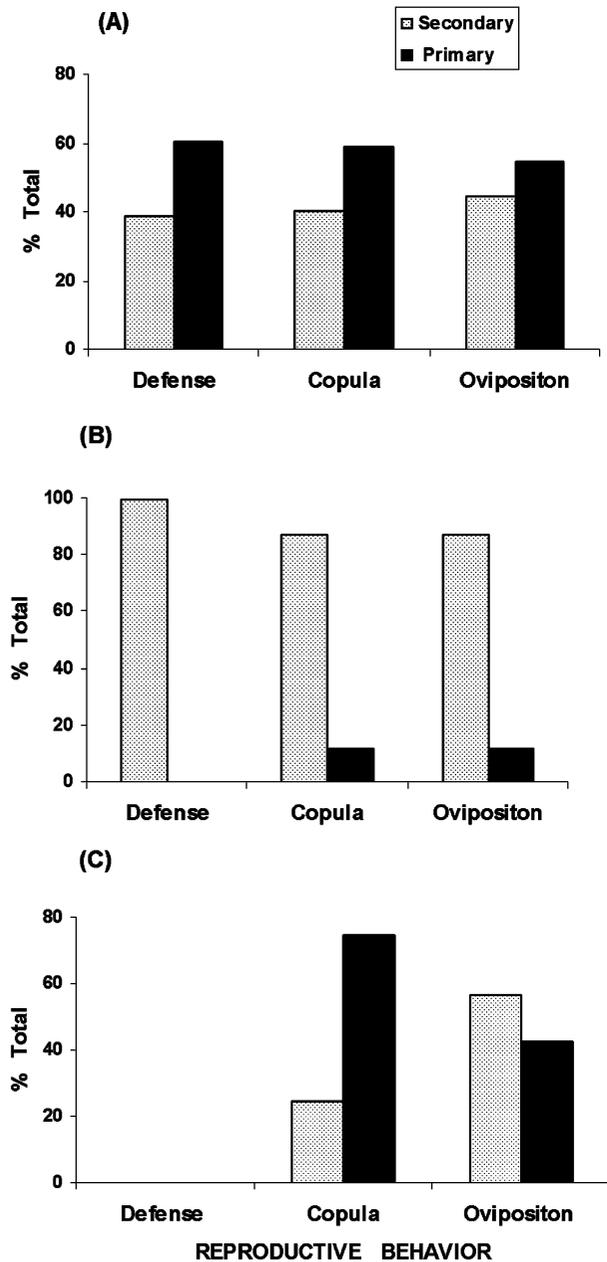
Figure 2. Reproductive activities of the three species of giant damselflies in primary and secondary forests on BCI, Panama. Sample sizes for male defense, copulation and oviposition respectively are: (A) *Megaloprepus*, $n=225$, 42, 78; (B) *Mecistogaster linearis*, $n=19$, 8, 8; (C) *M. ornata*, $n=0$, 5, 7.

Mecistogaster linearis ($P=0.69$ and $P=0.68$ respectively) and *Mecistogaster ornata* ($P=0.38$ and $P=0.38$, respectively, Fisher exact tests) did not differ significantly in their distribution by forest type, but the sample sizes for *Mecistogaster* were small.

Sightings of the two *Mecistogaster* species did not differ from each other by seasonal quartiles ($P=0.1$, Fisher exact test). Seventy-nine percent of adult

Mecistogaster linearis ($n=381$) and 86% of *Mecistogaster ornata* ($n=201$) were sighted during the first two quartiles, a more seasonal distribution than that of *Megaloprepus*, for which only 47% ($n=430$) were sighted in the first two quartiles ($P<0.0001$, Fisher exact test). For all of the copulating male *M. ornata*, the ventral sides of the forewings were black at the tip, a seasonal characteristic not found on any of the males seen before April. The reproductive activities of females of the three species differed significantly with respect to seasonal quartiles ($P<0.0001$, Fisher exact test). All 20 sightings of oviposition behavior of *Mecistogaster ornata* occurred over a 5-month span, between April and August, and all nine copulations (including data collected in 1996) were seen between April and June (Figure 3). Copulation and oviposition by female *M. linearis* were observed between January and July, and January and November, respectively, a significantly longer reproductive span than for *M. ornata* ($P=0.04$, Fisher exact test). *Megaloprepus* copulated and oviposited during all months of the year save for April, when most adults became inactive during the dry season ("siccatated", *sensu* Corbet, 1999). On BCI, the reproductive behavior of *Megaloprepus* was less seasonal than that of *Mecistogaster linearis* ($P<0.0001$, Fisher exact test).

Colonization of pots in primary and altered habitats in Costa Rica

During the 4 years of censuses, a total of 281 pseudostigmatid damselfly larvae were collected from
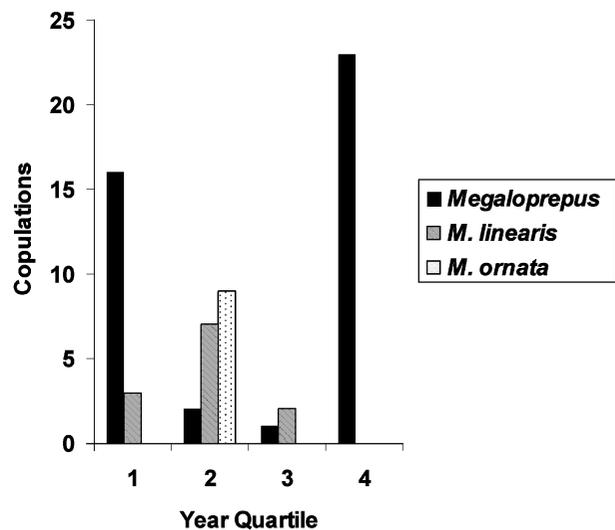

Figure 3. Seasonal distribution of copulations by pseudostigmatids on BCI, Panama (includes 1996 data). Quartiles: (1) January to March, (2) April to June, (3) July to September, (4) October to December.

the tree-hole analogs (Figure 4). Of these, 202 (71.9%) were *Megaloprepus*, which were more than twice as common as the 79 (28%) *Mecistogaster linearis* ($\chi^2=53.9$, df=1, $P<0.001$). Across habitat types, the total number of larvae found was positively correlated with the number of pots at a site, for both *Megaloprepus* ($r=0.74$, $P=0.001$) and *Mecistogaster linearis* ($r=0.87$, $P=0.004$). More than one larva per pot was found on only six occasions (2% of the total 275 censuses). All were *Megaloprepus* and all were in pots in primary forest. No pot contained larvae of both species on any census. *Megaloprepus* larvae were found at all sites and in all but five pots in primary forest, whereas this species was found in only two pots at two of the disturbed sites (5 and 7), the latter located 100 and 5 m, respectively, from primary forest. The only site never colonized by a damselfly was site 8, which was in a grove of fruit trees 200 m from primary forest. *Libellula herculea* (Anisoptera: Libellulidae), an opportunistic colonist of tree holes,

was found on six occasions in pots in primary forest, but never at sites in altered forest.

There was not a significant effect of time on the proportion of pots colonized ($F_{7,84}=1.37$, $P=0.23$). As shown in Figure 5, a greater proportion of pots were colonized in primary forest than in the altered habitats ($F_{1,6}=23.1$, $P=0.003$); the difference was significant across all eight sampling times (all $P<0.05$, Bonferroni tests). More pots were colonized by *Megaloprepus* than *Mecistogaster linearis* ($F_{1,6}=8.5$, $P=0.027$), but there was a significant species × forest type interaction ($F_{1,6}=15.4$, $P=0.008$). *Megaloprepus* colonized a greater proportion of pots in primary forest than in altered forest ($P=0.02$, Bonferroni test). In contrast, the percentage of pots colonized by *M. linearis* did not differ between primary and secondary forest sites ($P=0.16$, Bonferroni test). The percentage of pots colonized by *Megaloprepus* was negatively correlated with the distance of the site from primary forest ($r=-0.83$, $n=8$, $P=0.007$) whereas a similar trend for *Mecistogaster linearis* was not significant ($r=-0.43$, $n=8$, $P=0.28$).

Discussion

Does differential landscape use by adults reflect differential colonization in disturbed sites?

On BCI, where the canopy cover of old secondary forest and the adjacent primary forest was continuous, adult *Megaloprepus* exhibited a preference for primary forest whereas adult *Mecistogaster* were disproportionately found in secondary forest. These differences in landscape use by adults were consistent with the relatively greater colonization by *M. linearis* of sites in disturbed forest patches in Costa Rica
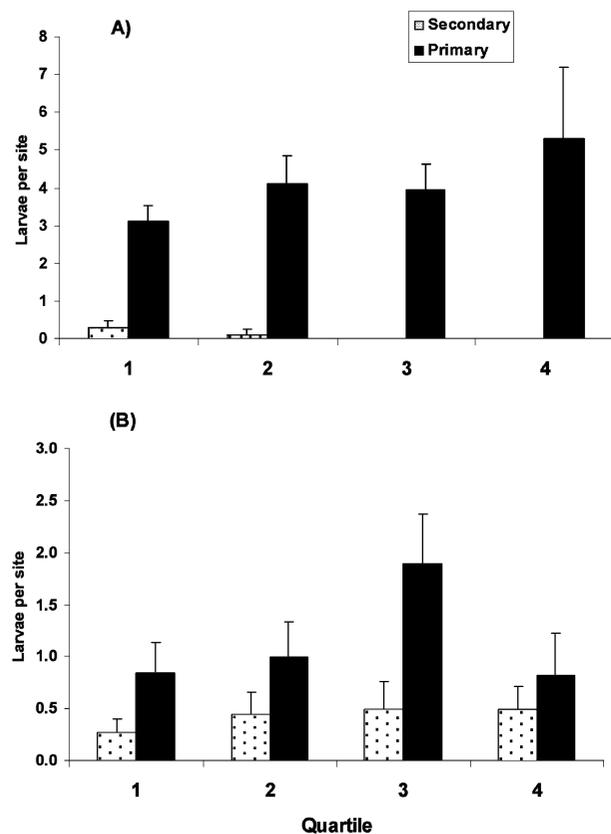

Figure 4. Seasonal distribution of pseudostigmatid damselfly larvae (mean + SE) collected at four sites in primary (total of 50 pots) and four sites in recently altered (i.e. secondary) forest habitats (total of 25 pots) at Barbilla National Park, Costa Rica, between 2000 and 2004. (A) *Megaloprepus*; (B) *Mecistogaster linearis*. Quartiles: (1) January to March, (2) April to June, (3) July to September, (4) October to December.
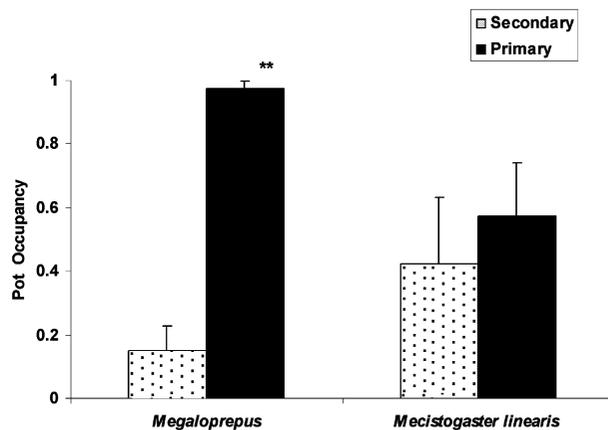
Figure 5. Proportion of pots that were colonized at least once, during 2 years of censuses at four primary forest sites and four altered forest sites at Barbilla National Park, Costa Rica. **$P<0.01$.

(Figure 4). The paucity of larval *Megaloprepus* in pots at the disturbed sites appeared to result from differences in the behavior and/or physiological tolerance of adults, rather than from an inability of its larvae to survive there. First, large *Megaloprepus* larvae were occasionally found at disturbed sites, and many of the pots in the disturbed sites were not colonized by either species. Second, in this aseasonally wet forest where both species laid eggs year round, larvae of *Mecistogaster linearis* would not enjoy the same pre-emptive advantage as they do on BCI by colonizing tree holes early in the wet season and, in small holes, successfully eliminating any later-arriving *Megaloprepus* (Fincke, 1992c). Hence, although *Megaloprepus* were more common overall, the greater abundance of larval *Mecistogaster linearis* at altered sites suggested that female *M. linearis* were more likely than *Megaloprepus* to lay eggs there.

On BCI, even though the three species moved between and reproduced in both forest types, territorial male *Mecistogaster linearis* preferred secondary forest, whereas male *Megaloprepus* were over-represented at defended sites in primary forest. The dichotomy in habitat usage between *Megaloprepus* and *Mecistogaster* on BCI was all the more striking given that the relatively old secondary forest there harbored mature individuals of *Ficus* and *Platypodium elegans*, that once fallen, often provided multiple tree holes (Fincke, 2006). Indeed, this likely explains why the larval distribution of the study species did not differ between secondary and primary forest. In both forest types, occupancy of holes by odonate larvae was below 70%, which suggests that despite searching widely for tree holes, female efficiency at finding them exacerbates the limits to reproductive success of all three species beyond that imposed by larval cannibalism and intra-guild predation (Fincke, 1992a; Fincke & Hadrys, 2001).

The failure of *Megaloprepus* to colonize pots in altered sites could be due to an aversion of crossing gaps >100 m from primary forest, or the conditions in the altered patches themselves. Both seem to play a role. On BCI, *Megaloprepus* was never seen flying across the laboratory clearings, even though males occasionally defended the shaded side of an insectary gutter within 10 m of the forest edge (O. M. Fincke, personal observation). An experiment to measure flight persistence suggested that *Megaloprepus* has low dispersal ability across treeless areas. Females in particular did not fly over open water (Fincke, 2006), and may require vegetation as a flight orientation cue. The high heat and low humidity conditions of open gaps also appear to be problematic for adult *Megaloprepus*. An hour after being placed in a large, sunny greenhouse, males took refuge by perching in deep shade, <0.25 m above the wet floor. Most died within a day, whereas adults are easily kept alive for several days in a shaded insectary (O. M. Fincke, personal observation).

The paucity of *Megaloprepus* that colonized the disturbed Costa Rican sites was consistent with other studies. At Los Tuxtlas field station in Veracruz, Mexico, *Megaloprepus* colonized pots in primary forest and forest edge, but not those in a secondary forest about 1 km away, even though adults were occasionally observed flying along stream corridors and at the forest edge of pastures bordering the reserve (O. M. Fincke & N. Haalboom, unpublished data). In Peruvian Amazonia, where the territorial pseudostigmatid *Microstigma rotundatum* replaced *Megaloprepus* as the top tree-hole predator, larvae of the former were not found in bamboo pots located on small (ca. 1 ha) plantations, although they were found in pots in abandoned plantations (Yanoviak et al., 2006a).

Seasonal differences and co-existence across study sites

Our results suggest that the reproductive physiology of *Megaloprepus* and *Mecistogaster linearis* is sufficiently flexible to respond to seasonal differences in rainfall across their geographic ranges. On BCI, egg laying was seasonal, particularly for the two *Mecistogaster* species. There, *M. linearis* appears to lay diapause eggs that survive the dry season (Fincke, 1992a). However, in the Costa Rican wet forest at Barbilla, both *M. linearis* and *Megaloprepus* oviposited throughout the year. Hatching asynchrony within a single egg clutch is as great as 180 days for *Megaloprepus* (Fincke & Hadrys, 2001), and at least 78 days for *Mecistogaster* (Fincke, 1998; O. M. Fincke, personal observation). Hence, in the colonization experiment, the appearance of larvae between visits was not necessarily evidence of a second oviposition because only the larvae, but not the stick which contained the eggs, were removed between visits. Nevertheless, because the time span between the appearance of larvae in a pot was often greater than 6 months, we conclude that at least several ovipositions occurred in a pot over a year's span.

Sightings of adults at Barbilla were not recorded. Hence, while we cannot dismiss the possibility that adult *Mecistogaster linearis* were rare at that site, its larvae were not uncommon in pots, suggesting that this species was more common than at La Selva field station (Fincke, 1998), another lowland aseasonally wet forest in Costa Rica's Heredia province (10°26′N, 83°59′W). The rarity of both larvae and adults at the latter site supports the hypothesis that when tree holes do not dry out annually, *Megaloprepus* can

competitively exclude *Mecistogaster* from both large and small tree holes (Fincke, 1998). A dry season provides *Mecistogaster* with a pre-emptive advantage in small holes from which usually only one adult emerges per season, as was typically the case on BCI. Results from our colonization experiment challenge the competitive exclusion hypothesis, unless, relative to La Selva, *M. linearis* at Barbilla enjoy more refugia from *Megaloprepus*. One possibility is that natural tree holes in disturbed areas adjacent to primary forest at Barbilla provide effective refugia due to an absence of ovipositing *Megaloprepus*.

Implications for forest conversion

On BCI, old primary forest and much younger secondary forest offered contiguous canopy cover, and importantly for adult recruitment, both forest types harbored large tree holes. More typically however, in Central America and increasingly in South America, as primary forest is cut, remaining patches become surrounded by pastures. Unlike many bats and birds that readily cross between widely separated forest fragments (Estrada et al., 2000; Estrada & Coates-Estrada, 2002), *Megaloprepus* is unlikely to do so. There are no dispersal data available for *Mecistogaster*, and displacement experiments using marked individuals are needed. The negative response by *Megaloprepus*, which rarely reproduced in the man-made clearings, suggested that this species may be more dependent on primary forest, relative to *Mecistogaster linearis*. Although *Megaloprepus* is currently well represented in Costa Rica (Hedström & Sahlén, 2001), the advancing deforestation within most of its distribution area in tropical America raises concern. In the highly fragmented lowland forest surrounding the Los Tuxtlas reserve on the Caribbean coast of southern Veracruz, Mexico where the species approaches the northern limit of its range, the population appears to have decreased within the past decade (O. M. Fincke, unpublished data). In Costa Rica, as abandoned pastures are reforested, the relative abundance of *Mecistogaster linearis* may increase.

Nevertheless, even if *Mecistogaster* is pre-adapted for living in successional forests, as tree-hole specialists, its fate would still depend on access to larval habitats. In our colonization study, the altered sites were supplied with artificial larval habitats, whereas early successional forests are unlikely to provide many natural tree holes. A survey on BCI revealed that only 11% of the total woody species present provided water-filled tree holes, and trees <40 cm dbh rarely harbored a hole with sufficient water

volume (0.1 liters) to support an odonate larva to emergence (Fincke, 2006). Yanoviak et al. (2006b) found that forest conversion increased the abundance of water-filled plant axils and fallen bracts, which were used commonly used by tree-hole mosquitoes, occasionally by the predator, *Toxorhynchites*, but never by the local tree-hole pseudostigmatid, *Microstigma rotundatum*, a finding consistent with pseudostigmatids more generally (Fincke, 1998; Greeney, 2001). Given that the niche of tree-hole disease vectors is broader than that of their natural odonate predators, a decline in tree-hole odonate populations could potentially affect disease transmission rates.

The concept of using aquatic species such as larval odonates as bio-indicators of environmental disturbance (e.g. Rith-Najarian, 1998; Soulé & Kleppel, 1988) or species richness more generally (Sahlén, 1999; Sahlén & Ekestubbe, 2001; Clausnitzer, 2003; Dijkstra & Lempert, 2003; Hedström, 2006) is relatively well established. Our data suggest that, not unlike the spotted owl (*Strix occidentalis*, Strigidae) whose presence is indicative of specific habitat requirements (e.g. Forsman & Meslow, 1986), the presence of the conspicuous giant damselfly *Megaloprepus* is an indication of a healthy predator guild in aquatic tree-hole habitats in wet and moist tropical forests throughout its geographic range. Elsewhere, *Microstigma rotundatum* (Brazil) or the pseudostigmatid, *Coryphagrion grandis* (Africa; Clausnitzer & Lindeboom, 2002; Groeneveld et al. 2007), may serve this role. Based on microsatellite markers for *Megalorpepus* (Hadrys et al., 2005), preliminary analysis suggests considerable genetic divergence between populations of this species in Mexico and Panama (H. Hadrys & O. M. Fincke, unpublished data). Further work is under way to assess the degree to which genetic variation within and between populations of *Megaloprepus* reflect the degree of fragmentation in its forest habitats.

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