

Landscape variation in the larval density of a bromeliad-dwelling zygopteran, *Mecistogaster modesta* (Odonata: Pseudostigmatidae)

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ABSTRACT

In the premontane rain forests of northwest Costa Rica, patches of secondary forest can contain high densities of large *Vriesea* spp. bromeliads. Such patches contain an average of $6,470 \pm 1,080$ (s.e.) larvae ha^{-1} of the bromeliad-dwelling pseudostigmatid, *Mecistogaster modesta*, ca 36x higher than larval densities that we previously reported for adjacent primary forest. Using a new method to partition landscape variation in populations, we show that secondary forest has higher larval densities than primary forest because of higher bromeliad abundance (13% of effect), greater bromeliad size (33%), and greater larval abundance in bromeliads of similar size (54%). The last effect reflects additional effects of forest type after accounting for differences in the quantity of larval habitat. We use surveys of prey communities in bromeliads and adult densities in the two forest types to show that these additional effects of forest type are more likely due to adult behaviour, not larval resource limitation. This study demonstrates that certain areas of secondary forest can be disproportionately important for *M. modesta* populations, and has implications for estimating effects of forest loss and conversion on *M. modesta*.

INTRODUCTION

While most odonate larvae are found in large freshwater habitats such as ponds and streams, a number of tropical species are found in small container habitats such as bromeliads and tree holes (Kitching 2000). Around the world, at least 11 species of odonates have been found as larvae in bromeliads (Kitching 2000). In Costa Rica, the only odonate routinely found in bromeliads is *Mecistogaster modesta* Selys (Pseudostigmatidae) (Hedström & Sahlén 2001).

Costa Rican rainforests could potentially harbour high densities of larval *M. modesta*. The Costa Rican range of *M. modesta*, a ca 50 km wide strip running along the northeast side of the Continental Divide (Hedström & Sahlén 2001), is largely classified as tropical and premontane wet and rain forests (Holdridge 1967). Such forest types contain many tank-forming bromeliad species, almost all within the genera *Guzmania* and *Vriesea* (Rivas Rossi et al. 1997). Bromeliad tanks contain

high densities of detritivore insects, which are potential prey for zygopterans (Cotgreave 1993; Richardson 1999; Richardson et al. 2000; Melnychuk & Srivastava 2002). Large bromeliads can contain water year-round, unlike seasonal ponds, and represent a large proportion of the total standing water in rainforests.

We have previously estimated *M. modesta* larval densities of 171 ± 65 (s.e.) per ha of primary premontane rainforest in northwest Costa Rica (Melnychuk & Srivastava 2002). However, all rainforest areas may not be equal in producing pseudostigmatids. The most obvious reason is high spatial heterogeneity in the quantity of larval habitat, affected by both the density and size of bromeliads. Habitat quality may also vary spatially, for example, in the density of prey per bromeliad or desiccation frequency of bromeliads. Finally, oviposition rates may vary spatially, even when the quantity and quality of bromeliad habitat are taken into account. In Panama, adults of other pseudostigmatid species occur at higher densities in light gaps in the forest than in the forest understory, and, in the case of one species, *Megaloprepus coerulatus*, this leads to greater oviposition rates in tree holes in light gaps (Fincke 1992a, 1992b). Together, these factors could cause substantial differences in larval *M. modesta* production across forest types, complicating estimates of the effects of deforestation on populations.

In this study, we first document high spatial heterogeneity in *M. modesta* larval abundance per hectare of rainforest, and then use a new approach to partition this variance into effects of bromeliad density, average bromeliad size, and forest type. The forest type effect could include spatial heterogeneity in prey biomass or oviposition frequency, and we use survey data of both prey and adults to distinguish between these possibilities.

MATERIALS AND METHODS

Study site and forest types

The forest around Estación Biológica Pitilla (10°59'N, 85°26'W) was protected in 1989, first as part of Parque Nacional Guanacaste and subsequently as part of the larger Area de Conservación Guanacaste. Since this time, many areas of former pastureland have been allowed to regenerate, such that primary forest – uncut for at least the last 70 years – abuts with secondary forest – logged partially or completely in the 20 years prior to 1989. This study compares zygopteran larval density between typical areas of primary forest with areas of secondary forest that clearly have higher bromeliad densities, larger bromeliads, and very different forest characteristics (hereafter simply “secondary forest”). We intentionally chose to compare very different patches of rainforest to allow us maximum power to tease apart the factors of bromeliad density, size and forest habitat in creating spatial differences in zygopteran density. Secondary forest is highly variable in bromeliad densities, and the particular type of secondary forest we chose for this comparison should not be seen as representative of all secondary forest in the vicinity of Pitilla. We present new survey data from the secondary forest to evaluate whether the algorithms previously described for primary forest (Melnychuk & Srivastava 2002) differed in this new habitat. As much of the primary forest data (except prey biomass) have already been described elsewhere (Melnychuk & Srivastava 2002), we present primary forest data only as needed for this comparison.

The secondary forest was dominated by early-succession tree species such as *Psychotria berteriana* (Rubiaceae), *Conostegia xalapensis* (Melastomataceae), *Vernonia triflosculosa* (Asteraceae), and *Piper sancti-felisis* (Piperaceae). Trees in this area rarely exceeded 6-7 m in height. More than 80% of the trees had a DBH (diameter 1.5 m above ground) < 5 cm, and no trees exceeded 20 cm DBH (Fig. 1; all tree data collected 17-18 November 2000.). The canopy was relatively open, with only $31.5\% \pm 2.8\%$ s.e. canopy cover ($n = 10$ circular plots of 78.5 m^2). By contrast, the primary forest had canopy cover values of $65.5\% \pm 3.7\%$ ($n = 10$), and trees up to 40 m in height. These mature trees (DBH > 20 cm) dominated the primary forest, although a well-developed understory of small saplings, palms and forbs was also present (Fig. 1; Melnychuk & Srivastava 2002).

Effects of bromeliad size on *Mecistogaster* abundance and prey biomass

M. modesta larvae were censused in 31 bromeliads from the primary forest and 15 bromeliads from the secondary forest, between 12 October and 12 November 2000, following methods detailed in Melnychuk & Srivastava (2002). Bromeliads were selected to encompass a wide gradient in sizes. Bromeliad size was measured as diameter, the maximum distance between any two leaf tips when extended by hand, and capacity, the maximum volume of water the bromeliad could contain. The bromeliads were carefully dissected leaf by leaf, and all water and detrital contents searched in white trays for *M. modesta* larvae.

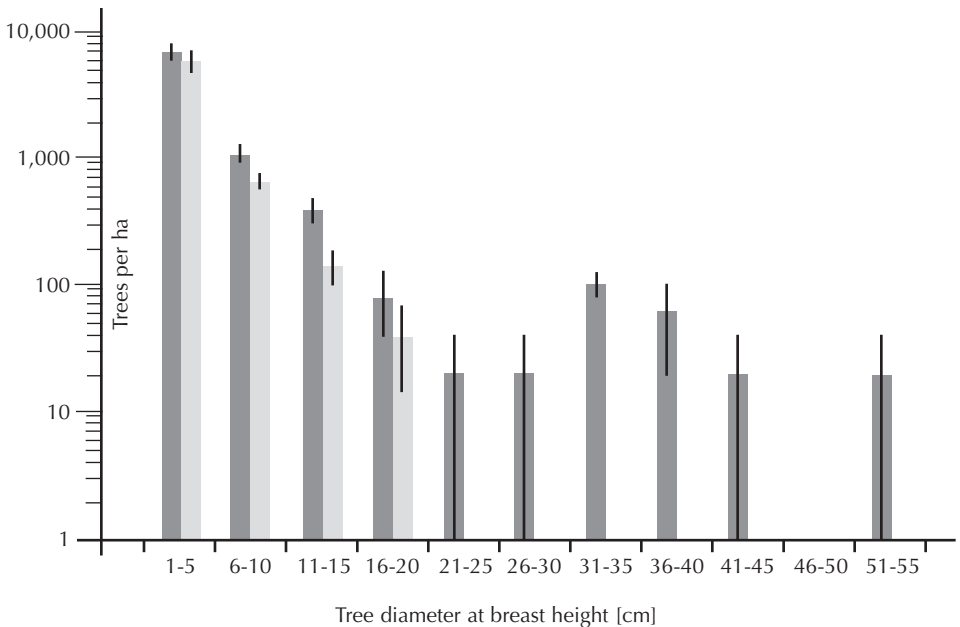


Figure 1: Primary (dark grey bars) and secondary (light grey bars) forest areas differ in tree density and size. Error bars are \pm s.e. ($n = 10$).

In 2000, prey species were also completely counted in 20 primary forest bromeliads, but not in secondary forest bromeliads. We did, however, quantify prey communities in 20 secondary forest bromeliads in 1997 and in 18 secondary forest bromeliads in 2002. In all cases, prey were identified to species or morphospecies, and abundances were recorded separately for instars of different body lengths. To calculate prey biomass, we used allometric equations (power functions, r^2 from 0.88 to 0.98) between body length and wet mass determined separately for chironomids, tipulid larvae, mosquitoes, tabanid larvae, other Diptera larvae and scirtid beetle larvae. We did not consider prey composition in our analyses, as feeding trials and fecal dissections have shown that *M. modesta* larvae can and do consume all other aquatic insects in bromeliads (D. Srivastava and J. Ware pers. obs.). We used capacity as the covariate in the analysis of differences in prey biomass, as capacity was more highly correlated with prey biomass than other measures of bromeliad size, such as diameter.

Bromeliad abundances

We determined bromeliad abundance in circular plots of 707 m² (i.e. 30 m diameter) in areas of secondary forest with high bromeliad density ($n = 3$), and in areas of primary forest ($n = 3$), between 12 October and 12 November 2000. Greater sample size would have increased the power to detect differences in density (37% statistical power in post-hoc power analysis) but we were limited by the number of similar, high-density secondary patches. To demonstrate how high the densities of bromeliads were in such patches, we surveyed bromeliad abundances in five more circular plots in typical low-density secondary forest within 100 m of our high-density patches on 15 November 2002. The survey methods for the secondary forest were identical to those in the primary forest (Melnychuk & Srivastava 2002). The diameter of all bromeliads > 15 cm wide in each abundance plot was estimated in 5 cm size classes. In eight years of fieldwork at this site, zygopteran larvae have never been found in bromeliads < 15 cm. We used bromeliad diameter as a measure of bromeliad size in this survey, as it could be easily estimated from afar even for inaccessible canopy bromeliads. Bromeliads were recorded irrespective of substrate, which included ground, tree trunks and branches, and vines and lianas.

Estimates of *Mecistogaster* abundance per hectare of secondary forest

We estimated *M. modesta* abundance for secondary forest following the same method as for the primary forest, described in full in Melnychuk & Srivastava (2002). Briefly, there were four steps in this calculation. (1) We determined the relationship between bromeliad diameter and abundance of *M. modesta* larvae per bromeliad. (2) We used this relationship to predict the number of *M. modesta* in each bromeliad encountered in each bromeliad abundance plot. (3) Expected numbers of *M. modesta* per bromeliad were summed over all bromeliads in each abundance plot and expressed on a per hectare basis. The linear variance associated with steps (1-3) was calculated using the Delta method, as described in Melnychuk & Srivastava (2002). (4) Finally, we calculated the average density between the three plots. The variance associated with the average density estimate combined within-plot and between-plot variances.

All generalized linear regression models using abundance as the dependent variable were based on Poisson errors, as is appropriate with count data, and used the program GLIM with a log-link function (Crawley 1993). Generalized linear models can circumvent the problem of log-transforming zero values (undefined) by using link functions. The *M. modesta* larval abundance data were moderately overdispersed compared with a Poisson distribution (ratio of residual deviance to residual df = 1.85 compared to 1 if perfectly Poisson). We corrected for this using an empirically-derived scale parameter (1.77) following Crawley (1993). The primary forest *M. modesta* data included bromeliads collected both close to the ground as well as within the canopy. Previous analysis of these data showed no significant effect of bromeliad height when bromeliad diameter was used as a covariate (Melnichuk & Srivastava 2002) and this was verified by a preliminary ANCOVA on the combined primary and secondary forest data (ANCOVA with log diameter as covariate; height within primary: $F_{1,42} = 0.097$, $p = 0.76$). Therefore, bromeliad height is ignored in our analyses.

Differences in larval density between secondary and primary forest

We compared *M. modesta* density between primary and secondary forest plots using the Smith-Satterthwaite test, a modification of the t-test for uneven variances (test-statistic T , Devore 1982).

We were able to separate differences in density between the two forest types into effects of differing bromeliad abundance, differing bromeliad size, and differing *M. modesta* abundance per bromeliad. This method relied on a power function between *M. modesta* abundance per bromeliad (m) and bromeliad diameter (d_b) that we will demonstrate in the Results section:

$$\log m = c \log d_b + k \quad \text{or equivalently:} \quad m = d_b^c e^k \quad (\text{eq. 1})$$

Both c and k are constants (slope and intercept, respectively, when plotted in log-log space). The total number of *M. modesta* larvae (Σm) predicted to occur in an abundance plot with a total of B bromeliads is:

$$\Sigma m = \sum_{b=1}^B (d_b^c) e^k \quad (\text{eq. 2})$$

where d_b is the diameter of a particular bromeliad b on the plot. The term $\Sigma (d_b)$ is influenced by both the number of bromeliads (B) and their individual sizes. We can separate these effects if we define: $\bar{s} = \text{mean } (d_b) = \Sigma (d_b) / B$, such that \bar{s} is an estimation of mean bromeliad size. We will show that c , the slope of the log-log regression, has the same value of 2.79 for both primary and secondary forests, thus $s = d_b^{2.79}$. Note that this working definition of size is a power function of bromeliad diameter just as area and volume are power functions (exponent 2 and 3 respectively) of linear dimensions in general. Given the structural complexity of bromeliads, we would not expect that its size would be well-approximated by either a plane (exponent 2) or a cube (exponent 3) but rather something in between these exponents, such as $c = 2.79$. The equation thus becomes simply:

$$\Sigma m = B \bar{s} e^k = B \overline{d_b^{2.79}} e^k \quad (\text{eq. 3})$$

The ratio of *M. modesta* abundance in secondary (subscript 2) to primary (subscript 1) forests is therefore related to the ratios of bromeliad abundance, size, and larvae per bromeliad:

$$\frac{\sum m_2}{\sum m_1} = \frac{B_2 \bar{s}_2 e^{k_2}}{B_1 \bar{s}_1 e^{k_1}} \quad (\text{eq. 4})$$

Adult *Mecistogaster modesta* abundances

Adult *M. modesta* abundances were quantified from 29 April to 3 May 2004 in the same areas of the primary and secondary forest surveyed for larval abundances. In both the primary and secondary forest areas, an observation route was set up with 20 stations spaced at least 6 m apart. The stations had either no bromeliad within 3 m of the station (10 stations) or were centered on a single bromeliad with no other bromeliads within 3 m (10 stations). Bromeliad sizes were matched between routes. Each route had 2 bromeliads in each of the following ranges of water capacity: 1-20 ml, 30-60 ml, 60-100 ml, 100-200 ml or 300-400 ml. Capacity was estimated from leaf number and width using a previously-determined allometric equation ($r^2 = 0.92$). Each station was visited by an observer for 5 min between 10:30 h and 15:30 h for each of the five continuous days. Observations were not conducted in rainy or heavily overcast conditions. The number and sex of *M. modesta* seen at each station were recorded. Pseudostigmatids were caught with a hand net on first sighting, and numbered on the forewing with an indelible ink marker, following the methods of Fincke (1992a). We analyze here only differences between habitats; effects of bromeliad capacity and isolation on adult behaviour will be examined as part of a larger study.

RESULTS

In our rainforest study site in northwestern Costa Rica, secondary forest contained areas with large bromeliads at high densities (Fig. 2). At Pitilla, such areas were dominated by *Vriesea sanguinolenta*, *V. gladioliflora* and *Guzmania donnellsmithii*, with the *Vriesea* species obtaining maximum diameters of 1 to 2 m. These high-density patches of secondary forest contained $1,600 \pm 510$ (s.e.) bromeliads ha^{-1} , a value 1.5x higher than that for primary forests: $1,085 \pm 211$ (s.e.) bromeliads ha^{-1} . The patches occurred in a matrix of secondary forest that had much lower densities of bromeliads (5.1 ± 1.3 s.e. bromeliads ha^{-1}). By combining survey information on bromeliad diameters and abundances (Fig. 2) with estimates of *Mecistogaster modesta* abundance in bromeliads of differing diameter (Fig. 3), we predicted that these secondary forest patches contained approximately $6,470 \pm 1,080$ (s.e.) *M. modesta* larvae ha^{-1} . This is significantly higher (Smith-Satterthwaite test, $T = 5.83$, adjusted $\text{df} = 2.02$, $p = 0.028$) than our simultaneous prediction of $178 (\pm 69)$ *M. modesta* larvae ha^{-1} in typical areas of nearby primary forest (Fig. 4). We now turn to a detailed examination of this 36-fold difference in predicted densities (see Methods for details of calculations).

We first compared the effect of bromeliad diameter on larval abundances per bromeliad (Fig. 3); diameter, not capacity was used as a measure of size here to be consistent with the diameter survey data. Bromeliad diameter was a strong predictor of zygopteran abundances (ANCOVA, log diameter: $F_{1,43} = 60.74$, $p < 0.0001$). There was no significant difference between habitats in the exponent (2.79) of the power function between zygopteran abundances and bromeliad size (ANCOVA, habitat* log diameter $F_{1,42} = 0.015$, $p = 0.90$), allowing us to directly compare habitat differences in abundance per bromeliad using log-diameter as a covariate. Bromeliads in secondary forest contained 6.2-fold (-1 s.e. = 4.3, +1 s.e. = 8.8) more *M. modesta* larvae than bromeliads of the same diameter in the primary forest (ANCOVA, habitat effect $F_{1,42} = 35.62$, $p < 0.0001$; difference in the log-abundance intercepts = 1.82 and $e^{1.82} = 6.2$). Finally, if we define diameter^{2.79} to be a measure of bromeliad size (see Methods) then we can attribute the 36-fold difference in *M. modesta* abundances between the two habitats to 3.8-fold greater bromeliad “size” in the secondary forest patches, 1.5-fold higher bromeliad abundance in the secondary forest, and 6.2-fold greater larval abundance in bromeliads of similar size.

Prey biomass could not be compared between primary and secondary forests in the same year, as prey species were not examined in the secondary forest in 2000. However, we compared primary forest data from 2000 with secondary forest data from 1997 and 2002, with the proviso that differences between forest types may be year-specific. Prey biomass differed between the three datasets ($F_{2,54} = 8.52$,

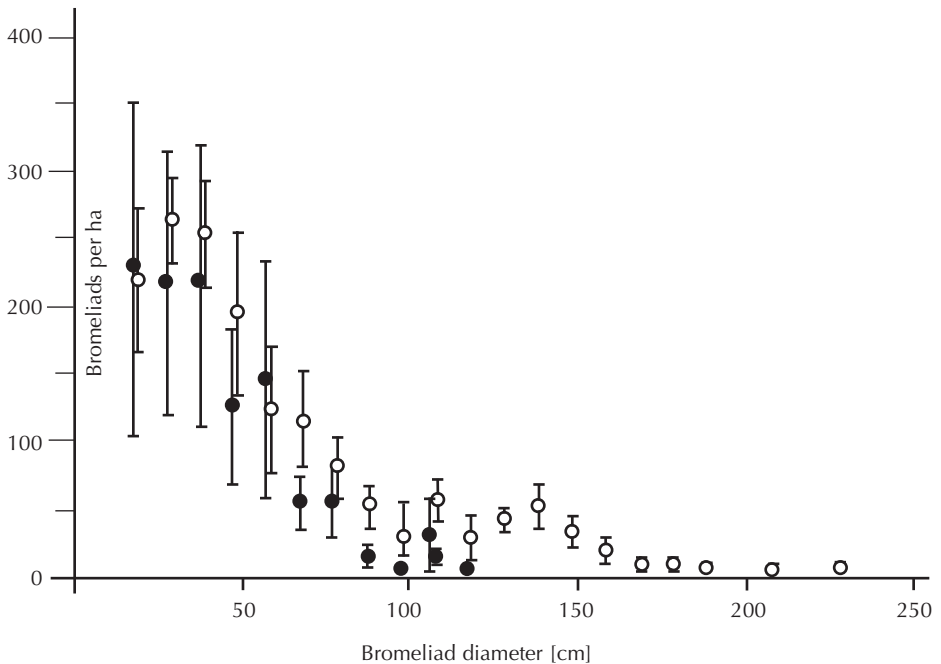


Figure 2: Secondary forest (white circles) can have higher bromeliad densities than primary forest (black circles), particularly in the larger size classes. The data for the primary forest are reprinted from Melnychuk & Srivastava (2002). Error bars are \pm s.e. ($n = 3$).

$p = 0.0006$) after accounting for bromeliad capacity (Fig. 5; log-capacity: $F_{1,54} = 123$, $p < 0.0001$; log-capacity x year interaction not significant: $F_{3,52} = 0.28$, $p = 0.84$). Compared with the primary forest in 2000, bromeliads in the secondary forest either had marginally less prey (2002 data, $F_{1,54} = 3.4$, $p = 0.07$) or the same amount of prey (1997 data, $F_{1,54} = 0.16$, $p = 0.69$).

Adult *M. modesta* were regularly seen in April 2004. In the secondary forest area, with high bromeliad densities, we observed an average of 4.6 ± 0.8 s.e. *M. modesta* adults per day at observation stations (100 min of observations d^{-1}). In contrast, no adult *M. modesta* were seen in the primary forest over the same period. In the secondary forest, approximately 2/3 of the adults seen were females. Males (Fig. 6a) were observed defending the largest *Vriesea* bromeliads from other males, and the same male was repeatedly observed at the same bromeliad over successive days. Females (Fig. 6b) were observed mating with males primarily in the vicinity of defended bromeliads, and ovipositing in bromeliads both in the presence and absence of males (D. Srivastava pers. obs.).

DISCUSSION

We documented a 36-fold difference in larval *Mecistogaster modesta* density (larvae ha^{-1}) in patches of secondary forest with high densities of large *Vriesea* bromeliads compared with nearby primary forest. Note that our estimate of *M. modesta* abundance in the primary forest, 178 (± 69 s.e.) larvae ha^{-1} , differed very slightly

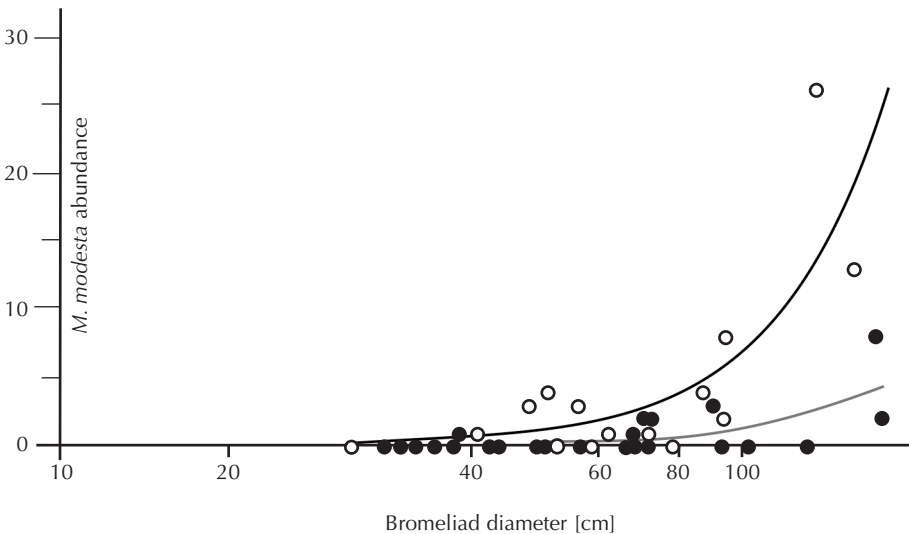


Figure 3: The number of *Mecistogaster modesta* larvae per bromeliad is influenced by both bromeliad diameter and forest type. Note that this is a semi-log graph; the numerous zero abundance values prevent us from log-transforming the y-axis. The data for the primary forest are reprinted from Melnychuk & Srivastava (2002). Black circles: primary forest; white circles: secondary forest.

from our previously published estimate of 171 ± 65 s.e. larvae ha^{-1} (Melnychuk & Srivastava 2002) for purely statistical reasons; when the secondary forest data are added to Figure 3 the insignificant shift in the combined ANCOVA slope is enough to change the calculations slightly. Despite large differences in the number of bromeliads between the two forest types (Fig. 2) only 13% of the 36-fold difference in larval density was due to differences in bromeliad number. Bromeliads were generally much larger in the secondary forest (Fig. 2), in part because the bromeliad species that dominated the secondary area, *Vriesea sanguinolenta* and *V. gladioliflora*, have a higher maximum size than the *Guzmania* species that dominated the primary forest (*G. scherzeriana*, *G. desautelsii* and *G. donnellsmithii*). This difference in bromeliad mean size accounted for 33% of the 36-fold difference in larval densities (Figs 2, 4). This leaves 54% of the difference between forest types unexplained, corresponding to a 6.2 fold difference in larvae per bromeliad after controlling for bromeliad size (Fig. 3). We are confident that this is a real difference between forest types. For example, the relationship between *M. modesta* larval abundance and bromeliad size seen in the secondary forest in 2000 is identical to that seen in an additional 19 bromeliads collected from the secondary forest in 2002 (D. Srivastava pers. obs.). We now examine two possible explanations for this difference: limitations to larval survival in the bromeliad, or limitations to the colonization rate of bromeliads through oviposition.

It has been suggested that resource-limitation of larval survival will create differences between forest types. Corbet (1983) predicted that bromeliads in open forests should contain more odonates than those in shaded forest, as higher algal production in the former will promote greater prey biomass. Our data give partial support for this hypothesis: *M. modesta* larval abundance per bromeliad was higher in the secondary forest, even when we accounted for differences in bromeliad size and density. However, evidence for a resource-limitation mechanism is missing. First, if zygopteran larvae were distributed strictly according to prey availability, as implied by the hypothesis, the ideal free distribution predicts that larvae in primary and secondary forests would have the same per capita availability of prey, requiring 6.2 fold more total prey in the secondary forest bromeliads (as equal-sized bromeliads have 6.2 times more zygopteran larvae in the secondary forests). However there is no hint of greater prey biomass in the secondary forest; depending on the years compared there is either the same or less biomass in secondary forest (Fig. 5). Second, if algal production is important for *M. modesta* abundances, we would expect greater prey and *M. modesta* abundances in the more illuminated canopy-level bromeliads than ground-level bromeliads, but previous work has shown no difference (Melnychuk & Srivastava 2002). Larval survival might also differ between forest types because of differences in desiccation frequencies, though such differences were not obvious to us in the course of fieldwork.

It is more likely that oviposition decisions drive differences between forest types. We observed no adult *M. modesta* in the primary forest, but 4.6 ± 0.8 [s.e.] adults per 100 min of observation in the secondary forest. Obviously there must be some adult individuals in the primary forest over the course of the year, given that their larvae are found there. We chose to carry out the adult observations in mid-April as most of the voucher specimens of adult *M. modesta* from the premontane areas

of Costa Rica have been collected in March and April (Hedström & Sahlén 2001). However, April 2004 was an unusually rainy and overcast dry season, weather conditions known to reduce adult zygopteran activity (Fincke 1992a; D. Srivastava pers. obs.), and so the adult sighting rate reported in this study is probably lower than in more typical years.

Differences in the number of adult *M. modesta* observed between forest types cannot reflect simple differences in the number and size of bromeliads observed, for our sampling scheme standardized both of these variables between forest types. However, there may be additional effects of bromeliad density. Females may be attracted to high densities of bromeliads, as it facilitates comparison of either oviposition sites or territorial males. Males may disproportionately occur in areas of high bromeliad density, because as a group they are more effective at attracting females, similar to the dynamic seen in lekking bird species. Alternatively, differences in adult abundance may simply reflect thermal constraints of foraging adults. The ground layer of the secondary forest floor received more sunlight than that of the primary forest floor. In a related species of pseudostigmatid zygopteran, *Megaloprepus coerulatus*, adult foraging is restricted to areas with direct sunlight such as forest gaps (Fincke 1992a). Finally, prey density may also differ between forest types. Adult *M. modesta* females in the secondary forest foraged exclusively on web-building spiders during the study period, though they are known to also take other insects (C. Esquivel pers. comm.).

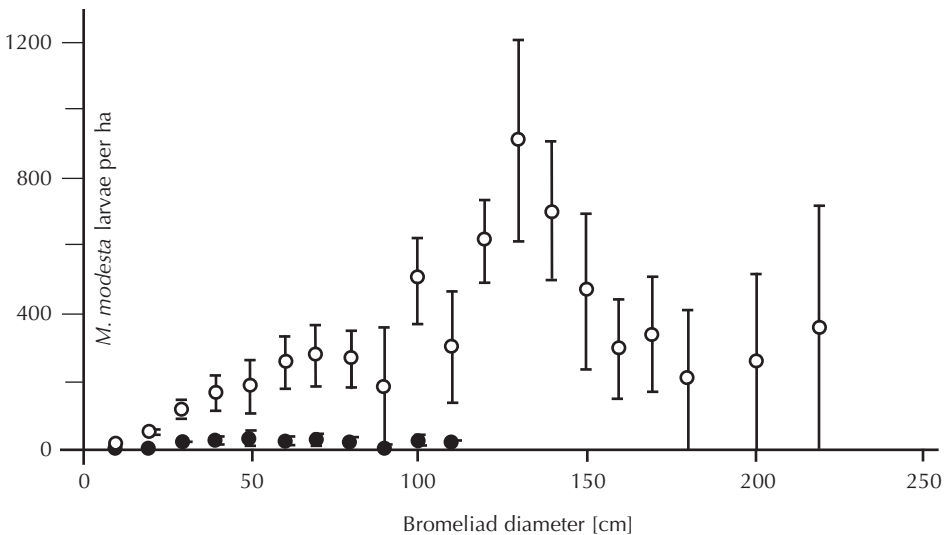


Figure 4: Predicted distribution of *Mecistogaster modesta* larvae in bromeliads of differing sizes, per hectare of forest, obtained by combining bromeliad density data (Fig. 2) with estimates of *M. modesta* abundance from differently-sized bromeliads (Fig. 3). Note that differences in larval density between forest types are predicted for all sizes of bromeliads, but are particularly affected by the presence of large bromeliads in the secondary forest. Black circles: primary forest; white circles: secondary forest.

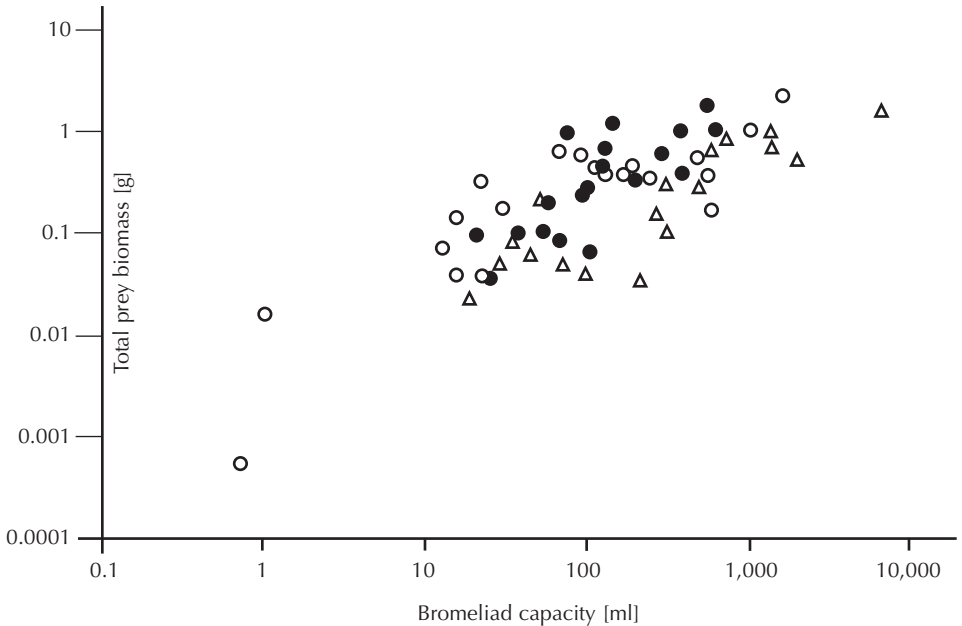


Figure 5: The relationship between bromeliad capacity and prey biomass is similar between years for the same area of secondary forest, and between the primary and secondary forests in different years. Black circles: primary forest 2000; white circles: secondary forest 1997; white triangles: secondary forest 2002.

In summary, this study demonstrates that both bromeliad size and forest type affected the number of *M. modesta* larvae within a bromeliad. Similarly, Fincke (1992a, 1992b) found that *M. coerulatus* larvae were more frequent in large than small tree holes in Panama, and in forest gaps than the understory. As in *M. modesta*, the difference in larval abundance between forest types is correlated with differences in adult abundances (Fincke 1992a). Finally, both *M. coerulatus* and *M. modesta* adult males are territorial, defending, respectively, large tree holes (Fincke 1984) and large bromeliads (D. Srivastava pers. obs.). Females of both species also prefer to oviposit in larger container habitats (Fincke 1992a, 1992b; D. Srivastava pers. obs.). By contrast, in the same Panamanian tree holes, two other species of pseudostigmatids, *Mecistogaster ornata* and *M. linearis*, do not show any preference for either large tree holes or forest gaps (Fincke 1992b), and male territorial behaviour is either limited or absent (Fincke 1984). Differences in larval abundance and male behaviour in the treehole-dwelling *Mecistogaster* are hypothesized to arise from competitive displacement at the larval stage by the larger *M. coerulatus* (Fincke 1992a). Our study shows that, in the absence of a competitive dominant, *M. modesta* shows characteristics more similar to *M. coerulatus* than its congeners *M. ornata* and *M. linearis*.

This study has implications for population monitoring of *M. modesta* and similar species. High spatial variability in *M. modesta* abundance means that it is difficult to estimate effects of deforestation by simply extrapolating estimates based on one part of the forest to another. Two types of error can occur with such extra-

polation. First, different areas of the rainforest differ substantially in bromeliad morphology, size and abundance. Some of this difference is fairly deterministic, reflecting light-limitations and substrate requirements of bromeliads. However, we have noticed that even apparently identical areas of secondary forest can differ substantially in bromeliad density and composition, suggesting that chance founder effects and metapopulation dynamics may also influence bromeliad densities. In this study we compared *M. modesta* abundance in primary forest only with patches of secondary forest with high bromeliad densities. Bromeliad density can also be extremely low in secondary forest. Estimating mean *M. modesta* densities for secondary forest will require detailed information from multiple patch types of secondary forest. Second, even if differences in bromeliad size and abundance are known, preferences of adults for different forest types may add additional error to estimates of larval abundance. In particular, if forest patches with exceptionally high adult activity are lost from rainforests, effects on *M. modesta* populations may be substantial.

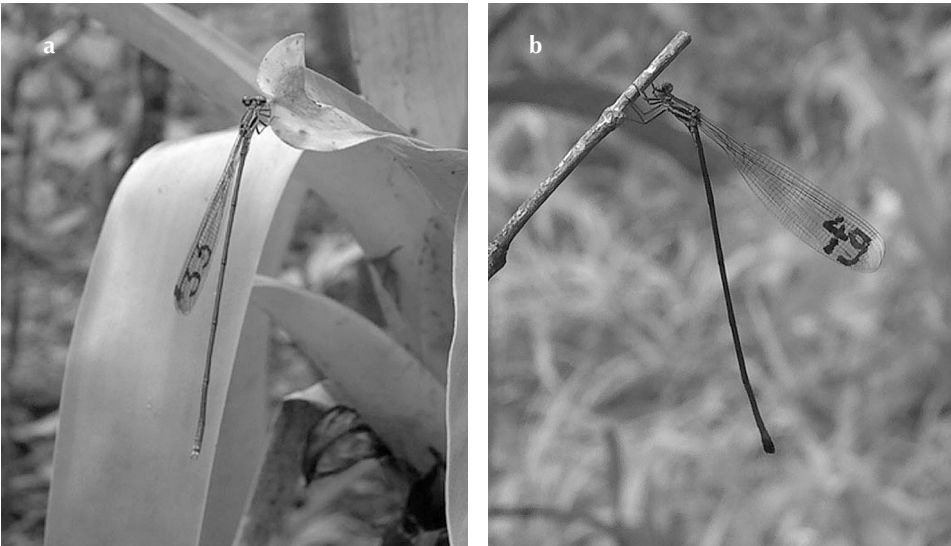


Figure 6: Individuals of *Mecistogaster modesta* with marked wings. — (a) male; (b) female. Estacion Pitilla, Guanacaste, Costa Rica. Photos by Diane Srivastava.

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