

Abundance and vertical distribution of a bromeliad-dwelling zygopteran larva, *Mecistogaster modesta*, in a Costa Rican rainforest (Odonata: Pseudostigmatidae)

Michael C. Melnychuk & Diane S. Srivastava¹

Department of Zoology, University of British Columbia,
6270 University Boulevard, Vancouver, B.C., Canada V6T 1Z4.

¹Corresponding Author <srivast@zoology.ubc.ca>

Received 03 October; revised 21 December 2001; accepted 01 January 2002.

Key words: Odonata, dragonfly, phytotelmata, canopy, epiphyte fauna, insect community, habitat size.

Abstract

We compared the larval abundance of *Mecistogaster modesta* between bromeliads at ground level and canopy level in a primary tropical wet forest. Zygopteran abundance correlated strongly with bromeliad diameter at both levels. Although the per-bromeliad zygopteran abundance did not differ between vertical levels, *M. modesta* showed a strong vertical distribution in abundance owing to the variation in bromeliad size and density along a vertical gradient, with more and larger bromeliads closer to ground level than to the canopy. We predict *M. modesta* larval abundance to be 171 ± 65 (s.e.) per hectare, with >80% of larvae below halfway to the lower canopy limit. The total prey abundance or species richness did not differ between ground and canopy bromeliads, further suggesting that apart from bromeliad size, habitat quality for *M. modesta* was similar between vertical levels. Effects of habitat size on larval abundance patterns are addressed by comparing habitat volume and basal resource mass with diameter. Finally, larger-scale spatial patterns in zygopteran abundance are discussed with reference to bromeliad distributions.

Introduction

In general, entomologists know far more about adult life stages of insects than larval stages. Adults are easier to see and catch, especially when insects change from aquatic to terrestrial habitats upon emergence. Equally sparse are detailed insect abundance data on both small and large spatial scales. We often have records of where species occur, the basis of species range maps, but standard sampling techniques are rarely utilized to complement these known distributions with estimates of abundance. Thus, larval abundance is poorly recorded for most insect groups, including odonates.

Ecological processes at early life-history stages generally have a strong effect on insect population dynamics, influencing population size and structure (Cappuccino & Price 1995). Larval stages can also have important regulatory effects on other species through predation or competition (Fincke et al. 1997; Yanoviak 1999). Not only is information on larval abundance important for understanding the structure of insect populations and communities, but it plays a significant role in conservation strategies of some insect species as well (e.g. in odonates, Hawking & New 1999; and in butterflies where caterpillars feed on rare plants, New 1997, 1999).

A first step to understanding larval ecology is to document patterns in larval abundance over time and space, both vertical and horizontal. Secondly, these patterns may hint at the processes involved in creating them. Little is known about the larval abundance of *Mecistogaster modesta* Selys, a pseudostigmatid zygopteran that ranges from Mexico to Venezuela (Tsuda 1991, cited in Hedström & Sahlén 2001). It is the smallest of the helicopter damselflies in Costa Rica (Hedström & Sahlén 2001), a name given to this family from the impressive manoeuvrability of the adults, achieved through asynchronous beating of the wings. Larval development in this family occurs in phytotelmata, or plant-formed containers that harbour distinct aquatic communities, such as tree holes (Fincke et al. 1997), bamboo internodes (Louton et al. 1996), and bromeliads (Calvert 1911; Hedström & Sahlén 2001).

Adult *M. modesta* females oviposit in “multi-tank” bromeliads, in which rain and fallen leaves collect in discrete pools between the bromeliad leaves. Larval development takes place year-round, though emergence occurs primarily between January and March in Costa Rica, based on compiled adult records for the country (Hedström & Sahlén 2001). Bromeliads on the leeward (southwest) side of the Continental Divide can desiccate seasonally, like in tropical dry forests (Rossi et al. 1997). *M. modesta* only occurs on the rainward (northeast) side (Hedström & Sahlén 2001), where the water in bromeliads remains year-round (Calvert 1911). We estimate that larval development takes at least half a year, based on captive growth rates and the distribution of instar sizes over several months (D. Srivastava unpubl.).

This zygopteran larva is the main predator in this community – it consumes all smaller aquatic invertebrates within the bromeliad, including conspecifics (D. Srivastava unpubl. feeding trials and analyses of fecal pellets). Typical prey includes dipterans (Chironimidae, Tipulidae, Culicidae, Ceratopogonidae), coleopterans (Helodidae), and oligochaetes. Tanypodine chironomids and tabanid larvae are the only other aquatic predators in this community, but they are much less common than *M. modesta*.

Bromeliad size has a strong effect on aquatic insects, with larger bromeliads supporting a more diverse and abundant aquatic community (Richardson 1999). The relevant habitat size to *M. modesta* could include: (1) the volume of water contained by the bromeliad, which provides space for the entire community, (2) the quantity of debris trapped between the bromeliad leaves, which provides a resource base for detritivores that *M. modesta* preys upon, and (3) the diameter of the bromeliad, which provides a catchment size that traps fallen leaves and rainfall. These measures of bromeliad size correlate strongly with one another (Richardson 1999), permitting numerous ways of investigating the effects of habitat size on abundance.

M. modesta inhabits wet and moist primary tropical forests (Hedström & Sahlén 2001), but no records exist of larval abundance and vertical distribution. Many changing abiotic and biotic variables are associated with vertical gradients, so abundance might reasonably vary with height above ground. Bromeliads generally occur from the ground to the branches of the upper canopy, and grow on a variety of substrates including the forest soil, tree trunks and branches, vines, and lianas. The abundance and sizes of tank bromeliads are likely to change along this vertical gradient. The quality of bromeliad habitat (e.g. prey density) might equally vary with height, further affecting zygoteran abundance. Productivity mechanisms are thought to differ between high and low-light environments, possibly leading to higher prey densities in canopy than in ground bromeliads. In shade, such as in the forest understory, productivity is usually entirely detritus-based, whereas in exposure to direct sunlight, such as in clearings or the upper forest canopy, productivity also includes primary production of algae, perhaps giving a more productive habitat in total (Laessle 1961; Corbet 1983). Thus, we expect strong vertical patterns in larval abundance, owing to vertical patterns in bromeliad density, bromeliad size, and per-bromeliad zygoteran abundance.

This study has two objectives: (1) to compare larval abundance of *M. modesta* between ground and canopy bromeliads, and (2) to estimate larval abundance per hectare of intact primary forest. To achieve the latter objective, we predict zygoteran abundance as a function of bromeliad size at different heights. We combine these predictions with bromeliad size and density data collected on a vertical gradient in order to predict zygoteran abundance per hectare at different vertical levels. We will compare differences between primary and secondary forests in a companion paper (Srivastava & Melnychuk unpubl. ms).

Methods

Study site

We surveyed bromeliads and their inhabiting aquatic insects in a primary tropical wet forest in northwestern Costa Rica. This forest, adjacent to the Estación Biológica Pitilla (10°59'N, 85°26'W) in the Area de Conservación Guanacaste, was on the northeast slope of the Continental Divide. It was relatively untouched apart from some historical selective logging, hunting, and subsistence farming. An access trail also run through the forest. Representative tree species included *Toxosiphon lindenii* (Rutaceae), *Calophyllum brasiliense* (Guttiferae), *Cinnamomum* sp. (Lauraceae) and *Quiina schippii* (Quiinaceae). There were 72 ± 5 (s.e.) trees per hectare, with the largest exceeding 1 m in DBH (diameter breast height) and over 40 m in height (Srivastava & Melnychuk unpubl. ms). Tree size followed a log series distribution, with 92 % of trees under 10 cm DBH, 6 % between 10 and 30 cm DBH, and 2% over 30 cm DBH (Srivastava & Melnychuk unpubl. ms). The forest floor was semi-open, with the understory dominated by palms, *Heliconia* spp., and ginger (Family: Zingiberaceae) plants. The dominant bromeliad genera were *Guzmania* and *Vriesea*. We sampled bromeliads in October and November 2000 during the wet season, which received approximately 4 m of rain and

lasted from May until February. Our study area – 1.06 ha; 815-883 m a.s.l. – fell within the larger expanse of this forest.

Environmental data collection

We collected temperature and rainfall data at ground level and in the forest canopy over a one-day period (16-17 November) using plastic cups. Although ideally we would have measured temperature and rainfall in the bromeliads themselves, the time required to position the rope and climb several trees to access canopy bromeliads would have introduced large time-of-day effects. For five trees in our study area, we ran a length of twine from the ground over a branch in the lower canopy. We suspended four 150 ml plastic cups, 0.5 m apart, from the twine at canopy level and four cups, 0.5 m apart, at ground level (0-2 m in height). Two cups at each height were left open to collect rainfall, while the other two cups were filled with water and sealed to measure temperature. After 26-27 h, we carefully lowered the cups and immediately recorded the temperature and volume of the water collected. Data for each pair of cups were averaged for the analysis.

Bromeliad census

To estimate bromeliad density in the forest, we counted all bromeliads of the genera *Guzmania* and *Vriesea* in three circular 15 m radius plots. These plots were centered around trees suitable for climbing with rope, harness and ascenders, so that we could census canopy bromeliads on other trees from 16-18 m above ground. To reduce the bias from this non-random sampling technique, we did not count bromeliads located on the central tree. We estimated the diameter of each bromeliad in 5 cm size classes, and only counted those plants with a diameter >15 cm. (Diameter is the maximum distance between any two leaf tips when extended outwards by hand. It can be measured non-destructively, and with experience can be estimated from a distance.) Bromeliads smaller than this are easily obscured by branches and leaves. Further, in four previous field seasons at this site, D. Srivastava has never found *Mecistogaster modesta* larvae in bromeliads <15 cm.

We recorded the height at which each bromeliad was located. As the lower and upper limits of the canopy were not uniform throughout our study area, we standardized bromeliad height by the canopy height instead of measuring distance above the ground. We assigned four vertical height classes relative to the lower limit of the canopy: L₁, 0-2 m above the ground; L₂, 2 m – halfway to the lower canopy limit; L₃, halfway to lower canopy – lower canopy limit; and L₄, lower – upper canopy limit. Using binoculars as required, we counted bromeliads in the lower two height classes from the ground, and bromeliads in the upper two height classes from a canopy vantage point. When a trail ran through a plot, we subtracted its area from that of the plot (trail area <0.5% of plot area) in order to estimate bromeliad abundance on a per-area basis.

Insect surveys

We harvested 15 bromeliads at ground level (L_1), representing a wide range of common diameters (31-157 cm). We used climbing gear to harvest 16 more bromeliads (30-160 cm) on six different trees within 4 m of the lower canopy limit (L_3 and L_4). We cut the bromeliads at the base with a saw and placed each upright in a bucket or plastic bag. We carefully lowered canopy bromeliads in a bucket attached to a rope. Because of time constraints and the difficulties involved with harvesting canopy bromeliads, we would often harvest several bromeliads from the same tree. However, bromeliads were at least 2 m away from each other to ensure greater independence of samples.

The range of canopy heights we encountered while sampling bromeliads was from 15-22 m (average 17.2 m) for the lower canopy limit and from 25-30 m (average 27.0 m) for the top of the canopy. The collection sites, as well as the bromeliad census plots, were widely distributed over the study area. The study was not done during the flowering season which precluded definite bromeliad species identifications, but most bromeliads were of the *Guzmania* genus (14 at both levels), while the others were *Vriesea* spp.

At the field station, we used an 80 cm-wide funnel to collect the water contained in the bromeliad when it was harvested. We measured the maximum water volume that the bromeliad would hold by pouring a known volume into it until all leaves overflowed, then subtracting the overflow. We measured the bromeliad diameter to the nearest centimeter. We separated the bromeliad leaves over the funnel and carefully rinsed off all the debris caught between them. The debris was filtered through 850 and 150 μm sieves. We mixed the $>850 \mu\text{m}$ debris with water in large, white dissection trays (the smallest *M. modesta* stadium is $>1 \text{ mm}$). We thoroughly searched this debris using forceps to turn over dead leaf fragments, and recorded all zygopteran larvae present, before releasing them. For a subset of 10 ground bromeliads and 10 canopy bromeliads, we also identified and counted other aquatic insects, by species, and annelids, by order, from the $>150 \mu\text{m}$ debris. We sorted by eye, only recording insects or annelids $>1 \text{ mm}$ in length, and used a dissecting microscope as required for identification.

After counting and removing insects, we fractionated the debris into size classes of 0.15-0.85 mm and 0.85-20 mm. Leaf parts $>20 \times 20 \text{ mm}$ were excluded from the analysis. The individual debris fractions were dried in envelopes for 1-2 d at ambient temperature and then in an 80°C propane oven for $>8 \text{ h}$ before weighing them on a digital balance.

M. modesta abundance vs bromeliad size, at ground and canopy levels

We used analysis of covariance to test whether the number of *M. modesta* larvae per bromeliad was different between ground and canopy levels, with bromeliad size as the covariate. We used diameter as the primary measure of size in order to combine this information with the bromeliad density data, which were also measured by diameter. We used the natural logarithms of zygopteran abundance and bromeliad diameter in the model, as this fit had a higher r^2 value than the linear variables or log-linear

combinations. We used the program GLIM with a log-link function for the analysis (Crawley 1993), and used a Poisson error structure because *M. modesta* abundance (1) is count data, and (2) was zero in some bromeliads.

We predicted log-abundance values and their associated standard deviations for a series of bromeliad diameters by re-calculating the y-intercept after an appropriate horizontal translation of the regression model (Crawley 1993: 276). These bromeliad diameters corresponded to the midpoints of the size intervals considered in our bromeliad density census. For example, we calculated the predicted log-abundance and standard deviation of *M. modesta* in bromeliads of size 17.5 cm diameter to correspond with the density of bromeliads in our 15-20 cm size interval.

We also used ANCOVA with debris mass and maximum water volume as covariates to investigate whether other measures of bromeliad size were equivalent in comparing zygoteran abundance between ground and canopy-level bromeliads. As the three measures of bromeliad size were not equivalent, we regressed them against one another and compared ground and canopy bromeliads. We used ANCOVA to test whether debris mass or maximum water volume differed between vertical levels for bromeliads of the same diameter.

Estimating M. modesta abundance per hectare of forest

We predicted the number of *M. modesta* larvae per hectare by multiplying the number of zygoterans in bromeliads of different sizes with the density of those bromeliad sizes in the forest. As the (log-log) zygoteran abundance-bromeliad diameter relationship did not differ between ground and canopy bromeliads, we could apply their common ANCOVA fit to all vertical levels of our bromeliad census. We transformed these log-abundance predictions from our ANCOVA model back into linear values for multiplication with the bromeliad density data. We were thus able to predict the *M. modesta* abundance for every bromeliad in our census plots, allowing calculations of zygoteran density at different vertical levels and for the forest as a whole.

We assume that our bromeliad census was accurate, so within-plot variance results from the uncertainty in the log-log relationship of *M. modesta* abundance and bromeliad diameter. We used the Delta method to transform the logarithmic standard deviations associated with each predicted log-abundance value into linear variances:

$$\sigma^2_{\text{linear abundance prediction}} = (e_{\text{ln abundance prediction}})^2 \sigma^2_{\text{ln abundance prediction}}$$

These linear variances were multiplied by the bromeliad density² of their corresponding size classes to calculate the total variance of predicted zygoteran density within each plot. Between-plot variance was due to the difference in *M. modesta* density between our three plots. We added the within-plot and between-plot variances at each vertical level and for all levels combined, then calculated the standard error in the number of *M. modesta* larvae per area of forest.

Prey species richness and abundance

We used ANCOVA with bromeliad maximum water volume as the covariate to test whether abundance and species richness of the prey community were different between ground and canopy bromeliads (annelid orders were treated as species in the richness analysis). Water volume was selected instead of bromeliad diameter as the covariate because (1) abundance and species richness both had stronger correlations with water volume than other measures of habitat size, and (2) unlike the above analysis, we were not interested in combining these data with bromeliad density data (measured by diameter). Only truly aquatic insects were considered in the analyses.

Results

Temperature and rainfall

Both the mean and variance of temperature were similar between the ground and canopy levels (Table 1). Although the mean rainfall appears to have been greater at ground level on the day we collected these data, the difference is not significant (t-test assuming unequal variances, $t_5 = 1.17$, $p > 0.05$). The variance in rainfall was greater at ground level than in the canopy (F-test, $F_4 = 10.2$, $p = 0.023$).

Table 1. Temperature and rainfall at ground and canopy levels over a one-day period ($n = 5$ at each level, mean \pm s.e.).

	Ground	Canopy
Temperature ($^{\circ}\text{C}$)	20.1 \pm 0.12	20.0 \pm 0.10
Rainfall (mm d^{-1})	23.6 \pm 5.0	17.4 \pm 1.6

Bromeliad density

On average, our plots contained $1,085 \pm 511$ (s.e.) bromeliads (>15 cm diameter) per hectare. The vertical distribution of bromeliads was uneven (Fig. 1), with more bromeliads in the lower two levels (21.4% of all bromeliads in L_1 ; 54.4% in L_2) than in the upper two levels (17.2% in L_3 ; 7.0% in L_4). Moreover, these four levels differed in their extent of vertical space: L_1 represents 2 m; L_2 , 5.5-7 m; L_3 , 7.5-9 m; and L_4 , 9-12 m. When the number of bromeliads is standardized by the vertical width of each level, bromeliad density in the lower two levels was even greater (L_1 , 116 bromeliads per hectare per vertical meter; L_2 , 84-107; L_3 , 21-25; L_4 , 6-8).

The bromeliad size distribution was also different among vertical levels. Mean bromeliad size was greater in L_1 (41.2 cm) and L_2 (45.6 cm) than in L_3 (30.4 cm) and L_4 (33.1 cm) (Fig. 1). Bromeliads >83 cm were absent in the uppermost level and uncommon in the other levels. No bromeliads >120 cm occurred in our plots. With all vertical levels combined, the abundance of bromeliads decreased as bromeliad size increased (Fig. 1); 50.2% were 'small' (15-37 cm diameter), 40.9% were 'medium' (38-72 cm), and only 8.8% were 'large' (≥ 73 cm).

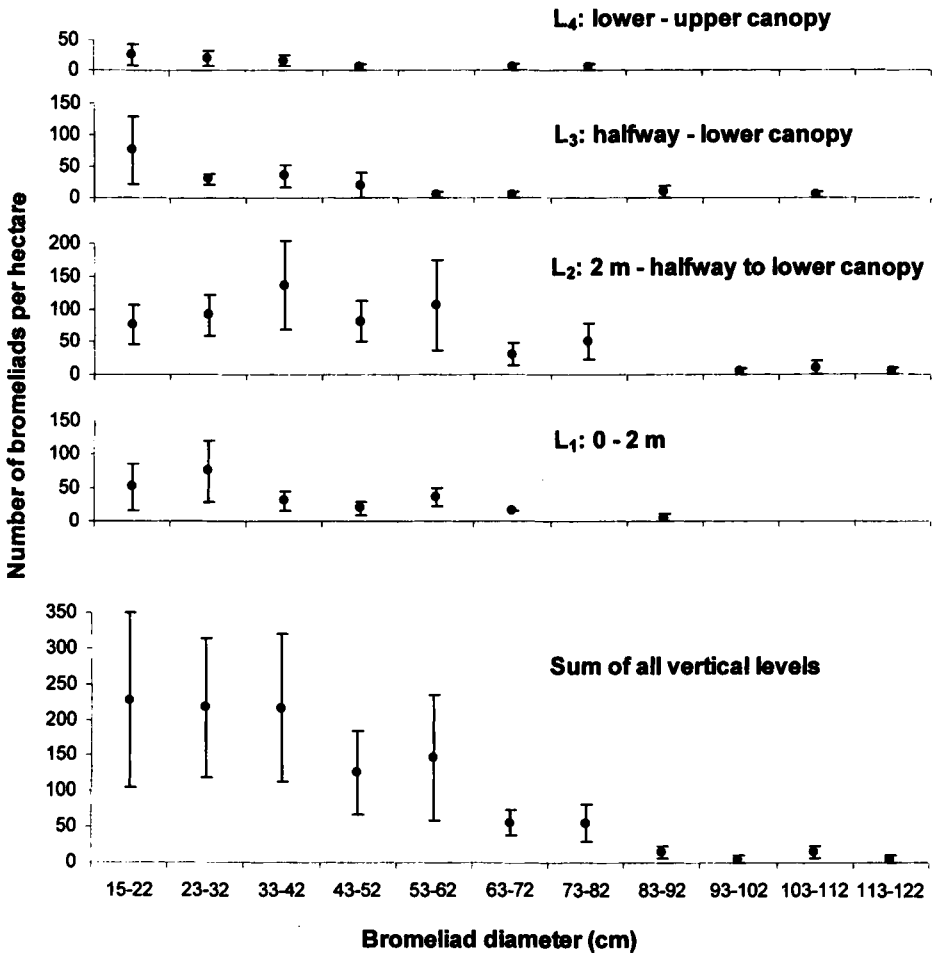


Figure 1. Size distribution of bromeliads (>15 cm) in four vertical height levels and at all heights combined (mean density per size class \pm s.e., $n = 3$).

Mecistogaster modesta abundance vs bromeliad size, at ground and canopy levels

The abundance of *M. modesta* larvae was correlated with bromeliad diameter within both vertical levels (ground, $r = 0.74$; canopy, $r = 0.64$; log-log correlations). With abundance data from both heights combined, bromeliad diameter explained 49% of the deviance (maximum likelihood analog of variance) in larval abundance. Zygopteran larvae were not found in canopy bromeliads <38 cm diameter, while the smallest inhabited bromeliad at ground level was 72 cm diameter (Fig. 2a). On the other hand, the maximum number of *M. modesta* in a ground-level bromeliad was eight, while it was only two in canopy bromeliads. Despite such differences between ground and canopy levels, adding vertical levels as a term to the model only accounted for an additional 5% of the deviance (full model with interaction terms, $r^2 = 0.54$). There was thus no significant difference in *M. modesta* abundance in bromeliads of the same diameter between ground and canopy levels (ANCOVA, neither slopes [$F_{1,27} = 2.757$, $p > 0.05$] nor intercepts [$F_{1,28} = 0.142$, $p > 0.05$] were different in a log-log plot; Fig. 2a).

Other measures of bromeliad size yielded qualitatively different results between ground and canopy levels in the relationship between *M. modesta* abundance and bromeliad size (Fig. 2b,c). Zygopteran abundance was also correlated with debris mass and with maximum water volume at both vertical levels ($r = 0.76$ to 0.91 , log-log correlations). In our models using these other measures of size, we found that *M. modesta* abundance differed between ground and canopy-level bromeliads of the same size. With debris mass as the covariate, slopes of ground and canopy bromeliads did not differ ($F_{1,27} = 3.422$, $p > 0.05$), indicating that zygopteran abundance changes with debris mass at the same rate at both heights. However, they had different intercepts ($F_{1,28} = 6.010$, $p < 0.05$), with 3.8 times more *M. modesta* larvae in ground bromeliads for a given debris mass (i.e. the difference in log-abundance intercepts = 1.326, and $e^{1.326} = 3.8$; Fig. 2b). With maximum water volume as the covariate, slopes were different ($F_{1,27} = 17.225$, $p < 0.001$), indicating there were more zygopterans in ground bromeliads of volumes greater than 282 ml, but more zygopterans in canopy bromeliads of volumes less than 282 ml (Fig. 2c).

Although the size range of bromeliad diameters studied was very similar between ground and canopy levels (Fig. 2a), the size ranges were different between levels for both debris mass (ground, 0.3-39.6 g; canopy, 0.6-169.1 g; Fig. 2b) and maximum water volume (ground, 20-594 ml; canopy, 17-1,844 ml; Fig. 2c).

Different measures of bromeliad size resulted in different outcomes between ground and canopy levels partly because these measures of size were not equivalent at different levels. The proportional effect of bromeliad diameter on debris mass was similar between ground and canopy bromeliads (ANCOVA, $F_{1,27} = 0.027$, $p > 0.05$, same slopes in log-log space). However, canopy-level bromeliads had 2.3 times more debris mass than ground-level bromeliads of the same diameter ($F_{1,28} = 4.524$, $p < 0.05$; Fig. 3a). The maximum water volume for a given bromeliad diameter did not differ between ground and canopy levels (slopes, $F_{1,27} = 2.485$, $p > 0.05$; intercepts, $F_{1,28} = 1.988$, $p > 0.05$; Fig. 3b).

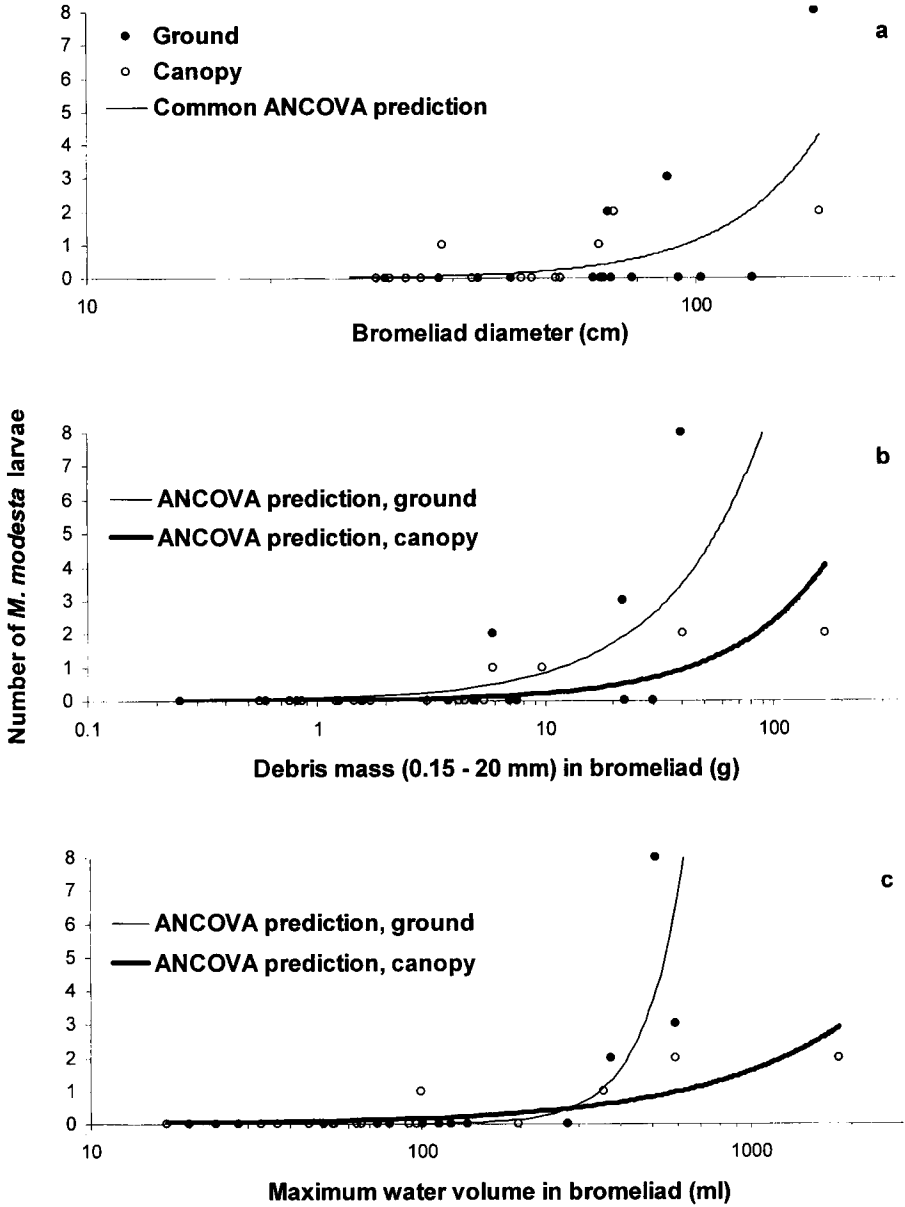


Figure 2. Abundance of *Mecistogaster modesta* larvae in ground and canopy-level bromeliads of differing sizes, measured as (a) diameter, (b) debris mass contained in the bromeliad, and (c) maximum water volume held by the bromeliad. Predicted abundances were generated with a power function from maximum likelihood regression (analysis of covariance). Note that only the x-axes are logarithmic.

Predicted M. modesta abundance per hectare of forest

The total abundance of *M. modesta* larvae in our bromeliad abundance plots is predicted to be 171 ± 65 (s.e.) per hectare (Table 2). Of the four vertical levels, L_2 had the greatest *M. modesta* abundance per hectare (Table 2), even when standardized for vertical space (16.2-20.7 larvae per hectare per vertical meter). The standardized zygopteran density was slightly lower in L_1 (13.0) and much lower in the upper two levels (L_3 , 2.7-3.2; L_4 , 0.6-0.8). With all heights combined, we predict an average density of 6.7 *M. modesta* larvae per hectare for every meter of height from the ground to the top of the canopy.

The predicted zygopteran abundance per hectare of forest depends strongly on bromeliad size. Although more than half of all bromeliads were 15-37 cm diameter (Fig. 1), only 7.8% of all zygopterans are predicted to inhabit these 'small' bromeliads because of the low number of *M. modesta* per bromeliad (Fig. 2a). Similarly, 45.7% of all zygopterans are predicted to inhabit 'large' bromeliads even though these accounted for only 8.8% of all bromeliads.

The total variation in *M. modesta* abundance per hectare was mainly due to between-plot variance in bromeliad size and density (94-99.6% of total variance in each vertical level, 99.2% overall). Very little of the total variance was associated with prediction error from our ANCOVA model (0.8% overall). L_1 and L_3 have similar means of zygopteran abundance per hectare, but the total variance was much higher for L_3 (Table 2). The coefficient of variation increases as we move up vertical levels (L_1 , 0.34; L_2 , 0.60; L_3 , 1.56) until the canopy, where it drops slightly (L_4 , 1.08).

Table 2. Estimated number of *Mecistogaster modesta* larvae per hectare of forest, at different vertical levels ($n = 3$ plots).

Vertical level	Mean	Within-plot variance	Between-plot variance	Total variance	Standard error
L_1 : 0-2 m above ground	26.0	4.8	74.4	79.1	5.1
L_2 : 2 m — halfway to lower canopy	113.7	65.5	4,662.5	4,728.0	39.7
L_3 : halfway to lower canopy — lower canopy	24.1	5.5	1,403.8	1,409.3	21.7
L_4 : lower canopy — upper canopy	7.0	0.9	55.9	56.8	4.4
Sum of all vertical levels	170.8	99.3	12,654.6	12,753.9	65.2

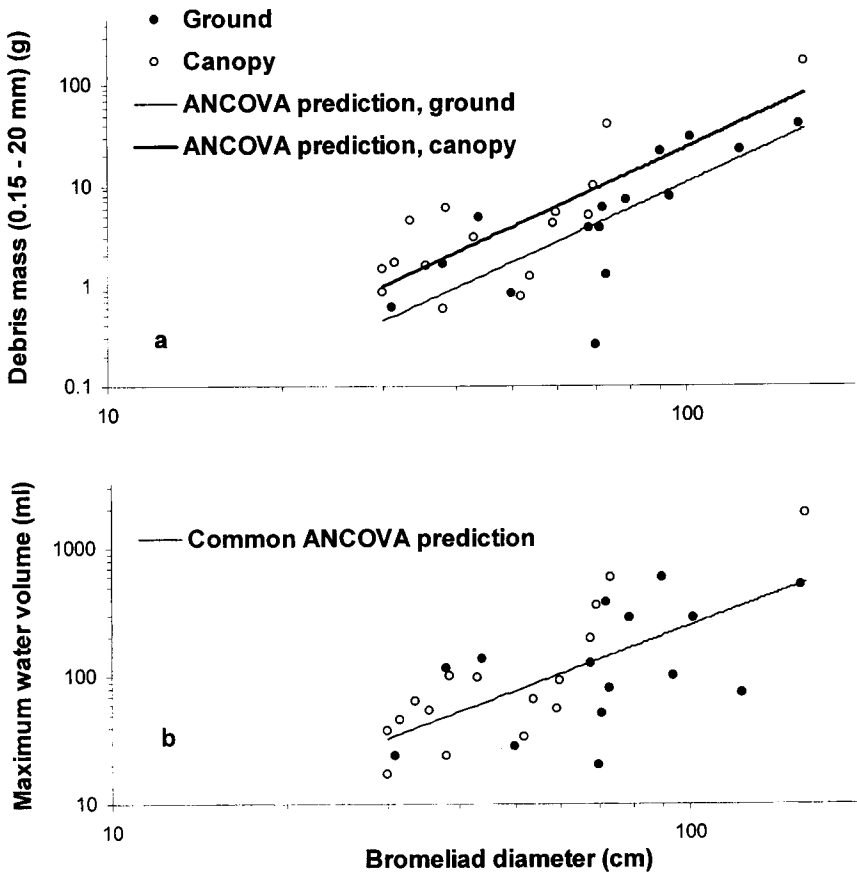


Figure 3. Other measures of habitat size in ground and canopy-level bromeliads of differing diameters – (a) debris mass, (b) maximum water volume. Predicted debris masses and water volumes were generated with a power function from maximum likelihood regression (analysis of covariance). Both axes are logarithmic.

Prey species richness and abundance

There was a strong effect of bromeliad maximum water volume on both total prey abundance (full model, $r^2 = 0.80$; Fig. 4a) and species richness (full model, $r^2 = 0.67$; Fig. 4b). Ground and canopy bromeliads did not differ in either prey abundance (slopes, $F_{1,16} = 1.062$, $p > 0.05$; intercepts, $F_{1,17} = 0.001$, $p > 0.05$; Fig. 4a) or species richness (slopes, $F_{1,16} = 3.673$, $p > 0.05$; intercepts, $F_{1,17} = 0.537$, $p > 0.05$; Fig. 4b).

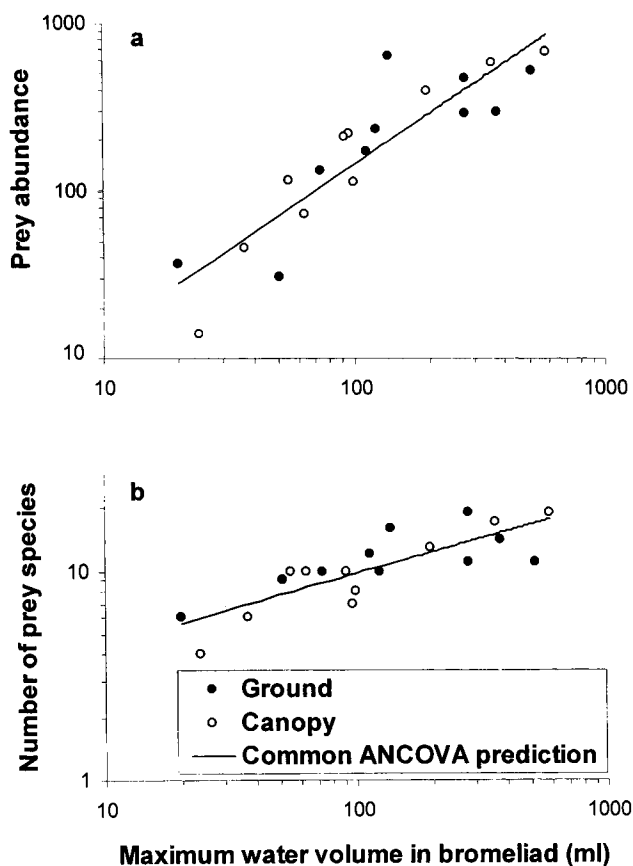


Figure 4. Prey community in ground and canopy-level bromeliads of differing maximum water volumes – (a) total abundance, (b) species richness. Predicted abundances and species richnesses were generated with a power function from maximum likelihood regression (analysis of covariance). Both axes are logarithmic.

Discussion

Vertical effects on zygopteran larval abundance

The differences in predicted abundance of *Mecistogaster modesta* larvae among vertical levels (Table 2) simply follow the bromeliad density and size distributions at different levels (Fig. 1). They are attributed to more and larger bromeliads in the lower two levels

than in the upper two levels. There was no effect of habitat quality differences between vertical levels, as the number of larvae per bromeliad diameter did not differ between the ground and canopy (Fig. 2a). These results are contrary to earlier predictions that in tropical phytotelmata, odonates will occur more frequently and at higher density in relatively exposed situations such as the canopy, as the higher light levels should generally support more productive communities and greater biomass (Corbet 1983). Similar results were recorded for a different phytotelm specialist in Panama, where *Mecistogaster* spp. larvae were found in 40% of understory tree holes but in only 13% of canopy tree holes (Yanoviak 1999). This is likely due to the presence of other top predators excluding *Mecistogaster* spp. in tree holes, unlike our bromeliad system where other predators are uncommon.

The higher coefficient of variation in *M. modesta* abundance in L₃ and L₄ (Table 2) results from a less predictable bromeliad abundance in these upper two levels. This may be a sampling artifact due to our small number of plots (which also explains the high between-plot variance in zygopteran abundance). It could equally reflect the relative unpredictability of the canopy environment, where abiotic conditions such as light, wind, and humidity fluctuate and may limit epiphyte distributions (Benzing 2000). In contrast, our collection cup results suggest a more variable rainfall at ground level over the period of a day, perhaps as a result of higher vegetation redirecting rain. However, rainfall and temperature were measured at only a single point in time, limiting the generality of these results.

Although per-bromeliad zygopteran abundance did not differ between ground and canopy levels, survival or development rates might still differ. For example, survivorship of *M. modesta* could be lower in one level but still result in similar abundances if a higher oviposition rate counteracts the lower survival rate. As well, the total number of zygopteran larvae inhabiting bromeliads in one full year could differ between ground and canopy bromeliads even if we observed similar abundances at any given time if the rate of development differs between vertical levels. Clearly, more research is required to investigate the ecological processes behind these patterns of larval abundance.

Vertical structure of bromeliad communities

In addition to being less predictable, bromeliads the upper two levels were also less abundant (Fig. 1). This is not because of less substrate availability in the canopy, as rainforest canopies typically offer a large surface area of potential attachment for epiphytes than lower down, where the main substrata available are tree trunks which offer a much lower total surface area (Frank 1983). Our results are consistent with bromeliad vertical distributions in another Costa Rican forest, where they were more abundant than expected at 5 m and less abundant than expected at 15 m based simply on available bark surface area (Kernan & Fowler 1995).

Bromeliad density in our plots appears to be intermediate compared with other Neotropical forests at similar altitudes. Rainforests in Venezuela and Brazil had 74 (Nieder et al. 2000) and 447 (Fischer & Araujo 1995) epiphytic bromeliads per hectare, respectively, while a remarkable 51,793 mature epiphytic bromeliads per hectare were recorded in a more arid Columbian forest (Sugden & Robins 1979). In this latter

study, 70% of the bromeliads were located above halfway to the upper canopy, clearly different from our study forest.

Smaller bromeliads were more numerous than larger ones at all vertical levels (Fig. 1), but the relatively larger bromeliad sizes in the lower two levels might be the result of physical constraints on the size of canopy bromeliads. Wind or the breaking of tree limbs may limit bromeliad size, as these are more likely to dislodge heavier bromeliads (Frank 1983). These effects are likely stronger in the canopy, where wind speeds are normally greater and tree limbs are generally thinner, than on the ground.

Differences between habitat size measures

Even though (1) mean bromeliad diameter, (2) the “minimum viable bromeliad diameter” for zygoteran larvae, and (3) the maximum number of zygoteran larvae per bromeliad all differed between ground and canopy levels, per-bromeliad *M. modesta* abundance did not differ between levels. On the other hand, debris mass and maximum water volume as measures of bromeliad size predicted different abundances per bromeliad between the ground and canopy.

Bromeliads of equal diameter contained more debris in the canopy than at ground level (Fig. 3a), which in turn generated a higher predicted zygoteran abundance in ground than in canopy bromeliads of the same debris mass (Fig. 2b). This 3.8-fold difference in abundance was, however, less than cross-habitat effects on *M. modesta*, which we documented in another study: we found 6.2 times as many zygoteran larvae per bromeliad in secondary forest than in primary forest (Srivastava & Melnychuk unpubl. ms). In general, insect abundances in phytotelmata are fairly insensitive to changes in detrital amount of less than an order of magnitude (Srivastava & Lawton 1998; Pimm & Kitching 1987).

Several reasons could explain why the debris mass for a given bromeliad diameter was higher at canopy than at ground level. Canopy bromeliads may experience a smaller detritivore community or a greater rate of detritus input. We can discount the first explanation: neither total abundance nor species richness of the prey community differed between ground and canopy bromeliads. We did not collect detritus input data, but as leaves generally fall from the canopy, these near-canopy bromeliads are expected to encounter dead leaves earlier in their fall path and thus more overall.

Which measure of habitat size is more appropriate to predict zygoteran abundance? Although the range of bromeliad diameters was similar between vertical levels, the range of debris mass (and also of maximum water volume) was much smaller for ground than for canopy bromeliads (Fig. 2). Consequently, ground bromeliads are underrepresented on the large end of this size range, which has likely led to unrealistic extrapolation of zygoteran abundance at very large bromeliad sizes (Figs 2b, 2c). We believe the ground-canopy comparisons with debris mass and water volume are weaker than that with diameter because in both cases the covariate did not share the same size range between treatments.

Spatial patterns in zygopteran abundance

M. modesta is geographically restricted to specific areas in Costa Rica, but where it occurs, it is locally common (Hedström & Sahlén 2001). The range overlaps with that of several other pseudostigmatid zygopterans, but the larvae of these other species occur in tree holes rather than bromeliads (Hedström & Sahlén 2001). Its distribution and abundance may be limited by the range and abundance of tank bromeliads, which are highly dependent on water supply on both regional and local scales (Rossi et al. 1997; Benzing 2000). *Guzmania* sp. and *Vriesea* sp. tend to occur most often in Costa Rican highlands and Atlantic lowlands (Rossi et al. 1997), and the distribution of *M. modesta* is consistent with these bromeliad distributions. However, geographical patterns in larval abundance probably do not simply follow bromeliad distributions. For example, La Selva Biological Station (Atlantic lowlands) has numerous bromeliads but few *M. modesta* larvae (M. Maple pers. comm.; Fincke 1998). Such geographical comparisons would be straightforward with the method we have outlined in this paper, and let us start to unravel the processes behind patterns in distribution.

Acknowledgements

This research was made possible by the generous logistical support of the Area de Conservación Guanacaste personnel, especially Carlos Zuñiga, Maria Marta Chavarria, Roger Blanco, Calixto Moraga and Petrona Rios. We thank Jeremy Huff and Barbara Richardson who helped with data collection. Research funds were provided by a grant from the International Dragonfly Fund with the help of the Worldwide Dragonfly Association, and from NSERC funding to W.E. Neill. D. Srivastava was supported by an NSERC Postdoctoral Fellowship during this work.

References

- Benzing, D.H., 2000. Bromeliaceae: profile of an adaptive radiation. Cambridge University Press, Cambridge.
- Calvert, P.P., 1911. Studies in Costa Rican Odonata II. The habits of the plant-dwelling larvae of *Mecistogaster modestus*. Entomological News 22: 402-411.
- Cappuccino, N. & P.W. Price (eds), 1995. Population dynamics: new approaches and synthesis. Academic Press, San Diego.
- Corbet, P.S., 1983. Odonata in phytotelmata. In: Frank, J.H. & L.P. Lounibos (eds) "Phytotelmata: terrestrial plants as hosts for aquatic insect communities", Plexus, Medford, New Jersey, pp. 29-54.
- Crawley, M.J., 1993. GLIM for ecologists. Blackwell Scientific Publications, Oxford.
- Fincke, O.M., 1998. The population ecology of *Megaloprepus caerulatus* and its effect on species assemblages in water-filled tree holes. In: Dempster, J.P. & I.F.G. McLean (eds) "Insect Populations in Theory and Practice", Kluwer Academic, London, pp.391-416.
- Fincke, O.M., S.P. Yanoviak & R.D. Hanschu, 1997. Predation by odonates depresses mosquito abundance in water-filled tree holes in Panama. Oecologia 112: 244-253.
- Fischer, E.A. & A.C. Araujo, 1995. Spatial organization of a bromeliad community in the Atlantic rainforest,

- south-eastern Brazil. *Journal of Tropical Ecology* 11: 559-567.
- Frank, J.H., 1983. Bromeliad phytotelmata and their biota, especially mosquitoes. In: Frank, J.H. & L.P. Lounibos (eds) "Phytotelmata: terrestrial plants as hosts for aquatic insect communities", Plexus, Medford, New Jersey, pp. 101-128.
- Hawking, J.H. & T.R. New, 1999. The distribution patterns of dragonflies (Insecta: Odonata) along the Kiewa River, Australia, and their relevance in conservation assessment. *Hydrobiologia* 392: 249-260.
- Hedström, I. & G. Sahlén, 2001. A key to the adult Costa Rican "helicopter" damselflies (Odonata, Pseudostigmatidae) with notes on their phenology and life zone preferences. *Journal of Tropical Biology* [Online] 49(3).
- Kernan, C. & N. Fowler, 1995. Differential substrate use by epiphytes in Corcovado National Park, Costa Rica: a source of guild structure. *Journal of Ecology* 83: 65-73.
- Laessle, A.M., 1961. A micro-limnological study of Jamaican bromeliads. *Ecology* 42: 499-517.
- Louton, J., J. Gelhaus & R. Bouchard, 1996. The aquatic macrofauna of water-filled bamboo (Poaceae: Bambusoideae: Guadua) internodes in a Peruvian lowland tropical forest. *Biotropica* 28: 228-242.
- New, T.R., 1997. *Butterfly conservation*. 2nd edition. Oxford University Press, Melbourne.
- New, T.R., 1999. Entomology and nature conservation. *European Journal of Entomology* 96: 11-17.
- Nieder, J., S. Engwald & M. Klawun, 2000. Spatial distribution of vascular epiphytes (including hemiepiphytes) in a lowland Amazonian rain forest (Surumoni Crane Plot) of Southern Venezuela. *Biotropica* 32: 385-396.
- Pimm, S.L. & R.L. Kitching, 1987. The determinants of food chain length. *Oikos* 50: 302-307.
- Richardson, B.A., 1999. The bromeliad microcosm and the assessment of faunal diversity in a Neotropical forest. *Biotropica* 31: 321-336.
- Rossi, M.R., V.H. Mendez & J. Monge-Najera, 1997. Distribution of Costa Rican epiphytic bromeliads and the Holdridge Life Zone System. *Revista de Biología Tropical* 45: 1021-1031.
- Srivastava, D.S. & J.H. Lawton, 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. *American Naturalist* 152: 510-529.
- Sugden, A.M. & R.J. Robins, 1979. Aspects of the ecology of vascular epiphytes in Columbian cloud forests. I. The distribution of the epiphytic flora. *Biotropica* 11: 173-188.
- Tsuda, S., 1991. A distributional list of world Odonata. Privately published, Osaka.
- Yanoviak, S.P., 1999. Community structure in water-filled tree holes of Panama: effects of hole height and size. *Selbyana* 20: 106-115.