Community-wide body size differences between nocturnal and diurnal insects

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Abstract. Examining community-wide patterns for the most diverse animal group, insects, is fundamental to our understanding of the ecological and evolutionary factors that maintain tropical diversity. Using several sampling techniques (malaise traps, pitfall traps, visual searches, and social spider nest captures), we investigated the day–night community composition of active insects to reveal differences in body size at three elevations in eastern Ecuador. We show that insects active at night are, on average, larger than those active during the day. Even though insect size decreased with increasing elevation, the observed diel pattern was consistent across elevations, and for most insect orders. All sampling techniques consistently detected day–night differences in insect size, except for social spider captures at the two higher elevations, probably due to the reduced range of colony sizes at the higher elevations and possibly lower spider activity at night. We suggest that the observed diel patterns in insect size may be driven by a combination of factors, including increased risk imposed on large insects by diurnal visual predators, mainly insectivorous birds, and physiological responses to diel changes in abiotic conditions.

Key words: Anelosimus; body size; diel patterns; Ecuador; elevational gradients; insects; inventory; social spiders; tropical community.

INTRODUCTION

Insects, through their unparalleled diversity and numerical dominance, play key ecological roles shaping and maintaining local and global biodiversity (Stork 2007). As such, ecologists have long sought to identify and understand patterns in insect diversity, biomass, abundance, activity, and body size (Janzen et al. 1976, Basset and Kitching 1991, Stork and Blackburn 1993). Community-wide insect size distributions are perhaps some of the less explored patterns despite their critical role in many aspects of ecological communities. Most of our knowledge of insect size distributions involves broad-scale geographical clines, including a seemingly general trend for decreasing insect size with increasing elevation and latitude (Janzen et al. 1976, Gaston and Blackburn 2000, Blanckenhorn and Demont 2004, Guevara and Avilés 2007, Powers and Avilés 2007), but there are instances of the reverse trend within certain insect taxa (Gaston and Blackburn 2000, Blanckenhorn and Demont 2004). Insect size distributions at more local scales have been less explored despite the implications in local biotic processes (i.e., predator–prey and other multi-trophic interactions), community structure, and local diversity (Gaston and Blackburn 2000). Existing studies already have revealed vertical stratification in forest insect size. At an Indonesian rain forest site, Stork and Blackburn (1993) found that insects were smaller in the understory, possibly as a result of higher desiccation risk in the canopy. At a Bornean rain forest site, Schulze et al. (2001) found, in contrast, that Lepidopterans were larger in the understory, a pattern presumably due to higher predation risk by birds in the canopy. Local body size shifts may also arise from habitat disturbance, with larger insects being found in less disturbed areas (Shahabuddin et al. 2010). Similar studies revealing local variation in insect size across time and space remain notably scarce. In particular, none has explored day–night patterns.

Day–night variation in local ecological conditions may drive various community-wide insect patterns, including diversity, abundance, and activity (Basset and Springate 1992, Springate and Basset 1996). Similar effects on insect size can be predicted, as body size distributions are largely driven by their interaction with the environment. Environmental differences between day and night may either exert a selective pressure on the size of insects active at different time periods or induce behavioral or physiological responses leading to the ecological sorting of day- and night-active insects.
Relevant environmental factors include differences in predation risk between day and night or diel changes in abiotic factors such as temperature and solar radiation. Larger insects would be expected at night, for instance, under pressure from diurnal visual predators, such as birds, the dominant size-dependent predators of insects (Holmes et al. 1979, Berger and Gotthard 2008). Since large insects are easier to see than smaller ones, birds may be more likely to target them during the day (Curio 1977, Berger et al. 2006). This pressure would be relaxed during the night, allowing increased activity of larger insects. Nightly drops in temperature, particularly at higher elevations, may also favor larger insects at night as larger insects cool more slowly due to their smaller surface area to volume ratio. In such scenarios, insect activity may shift in unison with predation levels (Lima and Dill 1990) or physiological responses to temperature (Somme 2008), thus predicting that nocturnal active insects would be larger than diurnal ones. If desiccation risk, in contrast, is the predominant factor affecting diel patterns in insect size, one might expect larger insects to be active during the day because of their decreased surface-area-to-volume ratio.

With these ideas in mind, we used a combination of sampling techniques that allow comparison of day–night active insects at three sites of varying elevation in eastern Ecuador. Under the first two scenarios described above, one would predict that night active insects would be larger than those active in the daytime, while the third scenario would predict the opposite pattern. We further explored whether diel variation in insect size is consistent across elevations and among insect taxa.

**Methods**

**Study sites**

We collected our data at three nearby sites along an elevation gradient on the eastern slope of the Andes in the Napo Province, Ecuador. All sites occurred along or within a few kilometers of the Baeza-Tena road. Our low-elevation site was the Estación Biológica Jatun Sacha (1.072° S, 77.731° W; elevation 385–410 m), a lowland tropical rain forest consisting mainly of primary forest with some areas of regenerated forest. We conducted insect surveys during July and August 2005–2008. Our mid-elevation site was near the Hollin River (0.695° S, 77.731° W; elevation 950–1100 m), a montane rain forest site consisting of shrubby vegetation and disturbed habitat along the Jondachi-Loreto road. Here, we sampled insects in June and July 2006. Our high-elevation site was in the Cocodrilos area of the Reserva Ecologica Antisana (0.64° S, 77.8° W; elevation 1740–1940 m), a cloud forest site consisting of primary forest, shrubby vegetation and disturbed habitat along the Baeza-Tena road. Here, we performed insect surveys in June and July 2008.

**Insect size surveys**

We surveyed insects using four sampling techniques that target active insects, thus permitting comparison of day–night activity: no-kill malaise traps, pitfall traps, visual searches, and social spider nest captures. The prey-capture webs of social spider nests of the genus *Anelosimus* (Araneae: Theridiidae) serve as a convenient sampling method as they are three-dimensional structures that effectively intercept active flying insects (Avilés 1997). Depending on the species and number of individuals they contain, the nests range from a few centimeters to sometimes a few meters in length for one of the species in the lowland rain forest, hence capturing prey that reflect the local range of insect sizes (Guevara and Avilés 2007) as well as their activity patterns. The four techniques used may target different insect types and size ranges, thus they are complementary and together can provide a better assessment of the insect size composition than a single method. For the purpose of our study, we did not include other popular methods because these may either target sedentary taxa that may not be representative of the taxa active at a given time period (i.e., sweeping and beating) or do not provide a means of comparison between periods (i.e., black lights only sample night-active insects).

We conducted surveys with malaise traps and visual searches at random points in the vicinity of existing spider nests. At each site, we set up malaise traps (height, 1.2 m; base, 1.2 m) in separate areas at approximately 5–10 m away from spider nests (low-elevation $N = 8$ traps in 2005, mid-elevation $N = 7$ traps in 2006, high-elevation $N = 5$ traps in 2008). The traps contained an insect-retention bottle at the top that allowed entry of insects but not their exit. We checked the traps daily in the evening (day sample between 17:00 and 18:00) and early in the morning (night sample between 07:00 and 08:00). We removed the bottles with the insects each time and replaced them with empty bottles of the same size for the next sampling period. We performed visual searches one to six times per day (mode twice a day) at different haphazardly chosen locations within each site. For this, we visually searched for five consecutive minutes active and/or flying insects in the surroundings. We sampled insects using pitfall traps only at our low-elevation site.

We surveyed spider nests every 1–1.5 h in the day (07:15–17:30) and night (18:30–01:00). Each time, we noted the presence of new insects caught in the web or being eaten by the spiders. At the low-elevation site, we surveyed nests of two social spiders belonging to the Family Theridiidae, *Anelosimus eximius* Keyserling and *Anelosimus domingo* Levi (Avilés 1997), along a ~2 km trail in the forest interior and in areas surrounding the field station where they are typically found. At the mid-elevation site, we studied the subsocial *Anelosimus elegans* Agnarsson and a second population of the
social A. eximius. We found nests of both species along the road edge and nearby pastures. At our high-elevation site, we studied the social A. guacamayos Agnarsson (Avilés et al. 2007) and a second population of the subsocial A. elegans. We found nests of both species along an ~2-km transect along the main road. We surveyed a total of 50 A. eximius and 26 A. domingo nests in 2005, 2006, and 2009 at the low-elevation site, 32 A. eximius and 35 A. elegans nests in 2006 at the mid-elevation site, and 73 A. guacamayos and 141 A. elegans nests in 2008 at the high-elevation site.

We measured insect size as the length (to the nearest millimeter) between the most anterior point of the head to the tip of the abdomen. For malaise, pitfall, and most spider nest samples, we used a ruler for length measurements. For visual searches, and sometimes for insects trapped in spider nests, we estimated length by eye to the nearest 0.5 cm, always by the same observer. We classified the specimens to order. In total, our data set included 6427 insects at the three sites.

Data analysis

We conducted three separate analyses where we used as the response variable the log-transformed mean insect size collected in a sampling bout (one day or night malaise, pitfall, visual, or spider catches), weighted by the number of insects in each bout. Number of insects for daytime bouts (across all sites) ranged from 2 to 57 for malaise, 3 to 17 for pitfall, 6 to 74 for visual, and 0 to 27 for spider catches. Number of insects for night bouts ranged from 1 to 41 for malaise, 4 to 12 for pitfall, 6 to 39 for visual, and 0 to 12 for spider catches.

In the first analysis, we tested for overall diel differences in insect size across sites using a linear mixed-effects model where the response variable was the log-transformed mean body size per bout and the fixed effects were period (day, night), site (low-, mid-, high-elevation), and the period × site interaction. We treated spider nest/trap ID as a random effect.

In the second analysis, we tested for differences among techniques within each site using a similar model where period, technique (malaise, pitfall, visual, or spiders), and the period × technique interaction were the fixed effects, and nest/trap ID the random effect. We used independent contrasts to compare day vs. night for each technique at each site, and for comparisons of overall day–night insect size across sites.

In the third analysis, we tested for diel differences in the size of different insect groups. We divided the specimens in each bout into the seven most common taxa plus an “other” category for less common taxa. Our response variable was the log-transformed mean insect size (per taxa) per bout, the fixed effects were period, taxon, and period × taxon interaction, and the random effect was nest/trap ID. All analyses were performed in R 2.14.2 (R Development Core Team 2012), using the lme function in the nlme package (available online).2

Results

At our low-elevation site, nocturnal insects were, on average, larger than diurnal ones ($F_{2,199} = 1733.5$, $P < 0.0001$; Figs. 1 and 2). This pattern was consistent across sampling techniques as shown by a nonsignificant interaction between technique and period ($F_{3,199} = 0.70$, $P = 0.60$; independent contrasts, day vs. night, A. domingo $F_{1,199} = 13.2$, $P = 0.0004$; A. eximius $F_{1,199} = 21.5$, $P < 0.0001$; malaise $F_{1,199} = 4.6$, $P = 0.034$; pitfall $F_{1,199} = 3.1$, $P = 0.008$; visual $F_{1,199} = 5.7$, $P = 0.01$; Fig. 2).

At the two other sites, insects were also larger at night than during the day (mid-elevation $F_{2,205} = 847.4$, $P < 0.0001$; high-elevation $F_{3,352} = 1624.1$, $P < 0.0001$; Fig. 1) for all sampling techniques used, except the spider catches (Fig. 2). This was evidenced by significant interactions between technique and period at the two higher elevations (mid-elevation $F_{2,205} = 2.3$, $P = 0.04$; high-elevation $F_{3,352} = 7.6$, $P = 0.0001$). Thus, differences in insect size between day and night were significant for samples from malaise traps (independent contrasts, day vs. night, mid-elevation $F_{1,205} = 24.3$, $P < 0.0001$; high-elevation $F_{1,352} = 9.8$, $P = 0.002$; Fig. 2) and visual searches (day vs. night, mid-elevation $F_{1,205} = 15.5$, $P = 0.0001$; high-elevation $F_{1,352} = 20.9$, $P < 0.0001$), but not for spider samples at the mid-elevation (A. elegans and A. eximius $P > 0.05$) and high-elevation sites (A. elegans and A. guacamayos $P > 0.05$; Fig. 2).

Although overall insect size decreased with elevation ($F_{2,428} = 120.8$, $P < 0.0001$; Fig. 1), insects were consistently larger at night than during the day at all

2 http://cran.r-project.org/web/packages/nlme/index.html
FIG. 2. Insect sizes (log-transformed body length, mean and 95% CI, measured in mm) for day and night samples obtained by different sampling techniques at three sites of varying elevation in eastern Ecuador (open circles are day samples; solid circles are night samples) and the overall distribution of insect body sizes for each site (open bars are day samples day; black bars are night samples). Abbreviations are, for spider nests samples: *Anelosimus domingi* (dom), *A. eximius* (exi), *A. guacamayos* (gua), and *A. elegans* (ele); malaise trap samples (mal); pitfall trap samples (pit); visual search samples (vis).

**Table 1.** Day and night mean insect body size for the most common insect orders captured with a combination of sampling techniques at three different sites of varying elevations in eastern Ecuador.

<table>
<thead>
<tr>
<th>Order</th>
<th>Low-elevation (385–410 m)</th>
<th>Mid-elevation (950–1100 m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Day</td>
<td>Night</td>
</tr>
<tr>
<td></td>
<td>Body size</td>
<td>n</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>7.3 (5.6–9.4)</td>
<td>175</td>
</tr>
<tr>
<td>Diptera</td>
<td>5.8 (4.5–7.6)</td>
<td>103</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td>7.5 (5.8–9.7)</td>
<td>176</td>
</tr>
<tr>
<td>Hemiptera/Homoptera</td>
<td>6.5 (5.0–8.4)</td>
<td>99</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td>11.9 (9.1–15.7)</td>
<td>77</td>
</tr>
<tr>
<td>Orthoptera</td>
<td>11.4 (8.7–13.0)</td>
<td>89</td>
</tr>
<tr>
<td>Blattaria</td>
<td>16.1 (11.7–22.3)</td>
<td>37</td>
</tr>
<tr>
<td>Other</td>
<td>9.5 (7.1–12.8)</td>
<td>43</td>
</tr>
</tbody>
</table>

Notes: Values represent back-transformed fitted mean body length (mm) with 95% CI. Sample size for the number of bouts in the mean estimate is given by n.
sites (independent contrasts \( P < 0.05 \); Fig. 1). The low-elevation site had the largest insects for both time periods (back-transformed values, means \( \pm 95\% \) CI, day 6.6 \( \pm 1.9 \) mm; night 12.1 \( \pm 2.8 \) mm) followed by the mid- (day 4.4 \( \pm 1.2 \) mm; night 8.6 \( \pm 1.9 \) mm) and high-elevation sites (day 3.5 \( \pm 0.98 \) mm; night 5.8 \( \pm 1.6 \) mm). Although nocturnal insects were on average larger than diurnal ones for the most common orders (low-elevation, \( F_{2,283} = 1283.6, P < 0.0001 \); mid-elevation, \( F_{2,283} = 645.6, P < 0.0001 \); and high-elevation, \( F_{2,497} = 1414.7, P < 0.0001 \); Table 1), this day–night difference did not always hold across insect orders (taxon \( \times \) period, low-elevation, \( F_{7,401} = 3.2, P = 0.003 \); mid-elevation, \( F_{7,283} = 0.6, P = 0.8 \); and high-elevation, \( F_{7,497} = 3.9, P < 0.0001 \)).

### DISCUSSION

We used a combination of techniques to sample the size range of night- and daytime-active insects at three sites of varying elevation in eastern Ecuador. Our data showed that night-active insects were on average larger than insects active in the daytime, a pattern that held across an elevational range, even though insect size decreased with elevation (for the elevational pattern, see also Guevara and Avilés [2007] and Powers and Avilés [2007]). The pattern was also consistent across sampling techniques, with the exception of the social spider captures, which showed day–night insect size differences at the low-elevation rain forest site, but not at higher elevations.

There are several potential ecological, physiological, and evolutionary explanations for the observed day–night insect size pattern that need not be mutually exclusive. Strong diurnal predation pressure, for instance, could drive day–night shifts in insect activity (Lima and Dill 1990), thus potentially influencing shifts in body size if size-dependent predation occurs. Just as palatable caterpillars and other insects may have evolved nocturnal lifestyles to avoid visual diurnal predators (Janzen 1983, Berger and Gotthard 2008),

table 1. extended.

<table>
<thead>
<tr>
<th></th>
<th>Day</th>
<th>Night</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body size</td>
<td>( n )</td>
<td>Body size</td>
</tr>
<tr>
<td>3.8 (2.9–5.2)</td>
<td>141</td>
<td>6.5 (4.6–9.1)</td>
</tr>
<tr>
<td>3.7 (2.8–5.0)</td>
<td>282</td>
<td>4.1 (3.0–5.6)</td>
</tr>
<tr>
<td>5.0 (3.7–6.7)</td>
<td>177</td>
<td>6.2 (4.2–9.0)</td>
</tr>
<tr>
<td>4.7 (3.5–6.3)</td>
<td>250</td>
<td>4.7 (3.4–6.5)</td>
</tr>
<tr>
<td>9.5 (6.8–13.1)</td>
<td>33</td>
<td>15.2 (10.2–22.4)</td>
</tr>
<tr>
<td>10.0 (7.1–14.2)</td>
<td>23.0 (13.8–38.4)</td>
<td>5</td>
</tr>
<tr>
<td>10.1 (6.5–15.9)</td>
<td>7</td>
<td>12.4 (7.4–20.8)</td>
</tr>
<tr>
<td>6.4 (4.6–8.9)</td>
<td>38</td>
<td>8.9 (6.0–13.2)</td>
</tr>
</tbody>
</table>

Day–night body size differences in active insects may also arise if similar predation pressures exist on conspicuously large insects, particularly at tropical latitudes where biotic interactions are notably important (Schemske et al. 2009). Insectivorous birds, which are dominant visual insect predators (Holmes et al. 1979, Cornell and Hawkins 1995), are diurnal foragers known to cause high size-dependent insect mortality. Similarly, ants, which mostly forage during the day, may also exert strong predation pressure due to their high abundance in the tropics (Floren et al. 2002). Some Neotropical ants, for example, use ambush group foraging to specifically target large mobile insects (Morais 1994). Size-dependent predation may influence insect size patterns either via ecological sorting (i.e., more favorable nocturnal conditions for large insects allow for their increased activity at this time) or via natural selection either favoring small insects during the day or allowing insects to become larger at night under relaxed predation. Large nocturnal insects, however, are not completely exempted from nocturnal predation as they may be, for example, more obvious “radar” targets for echo-locating predators (i.e., bats). Thus, the observed patterns should arise only if the relative risk in size-dependent predation is greater in the daytime.

Abiotic factors have also been shown to influence physiological and behavioral responses of insects (Hodkinson 2005). Temperature and solar radiation, for instance, may influence activity regimes associated with body size given the larger ratio of surface area to volume of small insects. Our patterns are consistent with the prediction that larger insects should be active at night, when temperatures are lower, but argue against desiccation risk, which should be greater during the day for small insects, being the predominant factor driving diel patterns in insect activity and size at our study sites. Abiotic factors have been shown to influence physiological and behavioral responses of insects (Hodkinson 2005). Tropical rain forests, in general, exhibit higher nocturnal insect activity compared to temperate forests or higher elevations because night air temperatures remain in warm ranges (Janzen 1967, 1973). As minimum temperatures and relative humidity decrease with elevation, however, diel temperature changes become more pronounced, often alternating from high daytime to very low night temperatures, particularly at the equator (Sarmiento 1986). At mid to upper elevations in the Andes, daily temperature fluctuations often involve 20°C or more. In the lowlands, the daily temperature fluctuation is much lower, closer to about 10°C (Neil and Jorgensen 1999). Smaller-sized insects may be less active at night because they may need to seek shelter to be able to withstand low night temperatures (i.e., they cool faster due to their larger surface area to volume ratios [Somme 2008]). Small-sized insects, particularly tropical ones, may also face great desicca-
tion challenges due to strong daytime insolation that would favor higher daytime activity of larger insects. Although this prediction is not supported by our overall pattern of night-active insects being larger than diurnal ones, the less pronounced difference in day–night insect size at higher elevations (Fig. 1) may be partly explained by a greater daytime desiccation risk of smaller insects at higher elevations. This, in turn, is consistent with abiotic factors playing a greater role at our higher elevation sites and predation potentially playing a greater role at lower elevations. That predation, rather than temperature, may be the primary factor driving the larger size of nocturnal insects is further supported by our finding (see also Guevara and Avilés 2007, Powers and Avilés 2007) that insects are smaller at the higher elevations where temperatures are lower, which is the opposite of what is expected under Bergmann’s rule (i.e., reverse Bergmann’s rule [Lomolino et al. 2010]). A reassuring finding is that diel patterns were for the most part consistent across elevations and across most insect orders.

Diel patterns in insect size obtained by the combination of techniques were also paralleled by spider catches at the low-elevation site. Several reasons may account for the lack of a difference at higher elevations. One possibility is that the spiders at higher elevations may be less active at night than their counterparts at the low-elevation site, as changes in ambient temperature and wind speed may affect spider activity (Crouch and Lubin 2000). High elevation spider populations may thus not be able to take advantage of the larger insects available to them at night. Additionally, in Anelosimus spiders, level of sociality and colony size decrease with elevation, both within (Purcell and Avilés 2007) and among (Avilés et al. 2007) species. The capture of the largest insects by the subsocial A. elegans at the mid- and high-elevation sites, in particular, may thus be constrained by its smaller nests, as colonies consist only of the offspring of a single female (Avilés 1997). A similar explanation may apply to some extent to the social species, A. eximius at the mid-elevation and A. guacamayos at the high-elevation sites, as their populations consist of smaller nests and a greater fraction of solitary females as elevation increases (Avilés et al. 2007, Purcell and Avilés 2007). At the low-elevation site, on the other hand, successful capture of large nocturnal prey is possible due to the large nests and high cooperation levels of the species found at this site (Yip et al. 2008).

Finally, we must mention that each sampling method has limitations. Visual searches, for example, are biased toward larger insects (Guevara and Avilés 2007), particularly at night when small insects may be more difficult to see. We aimed to minimize night–day efficiency biases by performing searches under sufficient night light and by the same observers at each site. We, however, caution interpretation of visual search data as, unlike the other sampling techniques used, the potential for human error is considerable. In addition, visual searches and spider nest surveys were not done during the entire night period, thus possibly excluding variation in insect size due to crepuscular changes in abiotic or biotic factors. Although malaise traps tend to miss large as well as flightless active insects, they should be less prone to night–day efficiency biases. The potential shortcomings of individual techniques, however, should be alleviated by the use of a combination of complementary techniques, including those that target small and large insects or both active sedentary and flying ones. Lastly, we note that although a phylogenetically corrected analysis would be desirable for a strong evolutionary inference of the processes behind the patterns observed, such an analysis is beyond the scope of this paper.

Studies reporting insect size distributions in the tropics are generally scarce. Data on diel insect patterns are, in particular, notably biased toward quantification of species richness, abundance, and activity. To our knowledge, community-wide diel patterns in insect size have not been previously reported for the tropics or other latitudes, thus there are no relevant studies providing means of comparison to our results. We conclude that, given the sampling techniques we used at three elevations in eastern Ecuador, nocturnal insects are larger than diurnal ones, at least at tropical latitudes. Our study gives new insight into day–night shifts in insect body size at local scales and provides testable explanations of the processes creating such pattern.

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LITERATURE CITED


