MULTIPLE TECHNIQUES CONFIRM ELEVATIONAL DIFFERENCES IN INSECT SIZE THAT MAY INFLUENCE SPIDER SOCIALITY

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Abstract. Social and subsocial spiders of the genus Anelosimus exhibit an altitudinal pattern in their geographic distribution at tropical latitudes in the Americas. Social species, which capture prey cooperatively, occur primarily in the lowland rain forest and are absent from higher elevations, whereas subsocial species are common at higher elevations but absent from the lowland rain forest. Previous studies have suggested that differences in the size of potential insect prey along altitudinal gradients may explain this pattern as insects were found to be, on average, larger in lowland rain forests than at higher elevations. These studies, however, may have under-sampled the insect size composition of each habitat because only one sampling technique was used. Using a number of collection methods we sampled the insect size composition in the environments of social and subsocial spiders in this genus. We found that the average insect size in lowland rain forest habitats was indeed larger than at high-elevation cloud forests in eastern Ecuador. We also found that, even though the various techniques differed in the size of the insects they captured (visual searching and blacklighting yielding larger insects than beating, sweeping, or malaise trapping), they all caught, on average, larger insects in the lowlands. Overall, spider colonies in the lowlands caught larger prey than did spider colonies at higher elevations, paralleling differences in insect size distribution obtained by the various techniques in their respective environments.

Key words: altitudinal gradients; Anelosimus; body size; converse Bergmann rule; inventory; sampling techniques; social behavior; spiders.

INTRODUCTION

The availability of a preferred resource or prey type should be an important influence on the presence or absence of organisms in a particular area (e.g., Olmstead and Wood 1990, Dejong and Ahlen 1991, Kato et al. 2003, Kusch et al. 2004). The geographic distribution of group foraging social organisms, for instance, may be influenced by the size distribution of available prey, as larger prey may be needed to select for cooperative prey capture and provide to all group members (e.g., Caraco and Wolf 1975, Nudds 1978). As such, efficient sampling of the environment is required to identify trends in the size distribution of potential prey that might, in turn, explain patterns in the geographical occurrence of these social organisms. Spiders of the genus Anelosimus Simon, for instance, exhibit an altitudinal pattern in their geographical distribution in tropical America that is associated with their level of social behavior (Agnarsson 2006; Avilés et al., in press). Social species, whose colonies may contain up to tens of thousands of spiders (reviewed in Avilés 1997), occur primarily in the lowland tropical rain forest and are absent from the highest elevations. Subsocial species, whose colonies usually contain the offspring of a single female, have the opposite pattern, being relatively common at high and intermediate elevations, but absent from the lowland rain forests (Avilés et al. 2001, in press, Agnarsson 2006).

Previous studies by Powers and Avilés (2007) and E. Yip and L. Avilés (unpublished data) have suggested that differences in the size distribution of potential insect prey along altitudinal gradients may help explain this geographical pattern. These authors found that low-elevation rain forest sites in eastern Ecuador had a greater abundance of large insects than cloud forest sites where only subsocial species occur. They argue that an abundant supply of large insects, which require multiple individuals for their capture, would provide an incentive for the evolution of cooperative spider societies, while absence of such a supply at high elevations or high latitudes would prevent the establishment of species with large colony sizes in such habitats.

An earlier study by Janzen et al. (1976) also found that insects tend to be larger at lower elevations in the Venezuelan Andes. To our knowledge, only these three studies have explored differences in insect size at varying elevations by sampling entire insect communities (as opposed to looking at trends within single taxa). These earlier studies, however, used a single collection method, either malaise traps (Powers and Avilés 2007; E. Yip and L. Avilés, unpublished data) or sweep nets (Janzen et al.
1976). Different techniques, however, vary in collection efficiency and tend to target different insect types or sizes (e.g., Juillet 1963, Hosking 1979, Disney et al. 1982, Noyes 1989). Therefore, a combination of methods may be required to better appraise the insect fauna of a particular area. In the same manner, because each method may capture different proportions of insect types and sizes than those captured by spiders (Robinson and Robinson 1973, Castillo and Eberhard 1983), exploring different techniques may provide insight into which individual technique, or combination of techniques, better approximates the insect size distribution caught by the spiders. Our goal, however, is neither to find a method that duplicates the prey capture patterns of the spiders nor to determine the exact prey size distribution available to them, as neither of these goals can be realistically attained (e.g., Castillo and Eberhard 1983). Our goal is rather to determine the consistency of different methodologies in assessing size differences in potential insect prey between environments and to determine how well (or how poorly) different methods reflect the prey capture patterns of the spiders themselves. Such an endeavor can guide future efforts in the study of insect size distribution patterns, the composition of insect communities, and the biology of insect-feeding organisms.

In this study, we thus use a variety of insect collection methods to explore differences in the insect size composition in areas of eastern Ecuador where either social or subsocial spiders occur. We attempt to answer three main questions: (1) whether insects at low-elevation tropical rain forests are indeed larger than at higher elevation cloud forests and whether different sampling techniques are consistent in detecting a difference, if a difference exists; (2) how different techniques compare with respect to the mean and range of insect sizes captured by the spiders; and (3) which of a variety of techniques, if any, better approximates what the spiders capture in terms of insect sizes.

Materials and Methods

Study sites and species

This study was conducted in two separate field seasons (May–August 2005 and July 2006) at two low-elevation tropical rain forest and at two high-elevation cloud forest sites in eastern Ecuador, South America. The first low-elevation site was located at the Estación Biológica Jatun Sacha (elevation, 385–410 m; 31°42'0" S, 77°36'36" W) in the Napo province. The station consists of ~2500 ha of mostly primary rain forest, although 30% of it is regenerated secondary forest from logging activities ~30 years ago. The second lowland site was in the Reserva Faunística Cuyabeno (elevation, 200–300 m; 0°1'59" S, 76°19'48" W) in the Sucumbios province. The reserve has an area of ~604 000 ha that consists mainly of primary rain forest. Both of these sites have an annual mean temperature of ~25°C. The first high-elevation cloud forest site was located in the Yanayacu Biological Station in the northeastern slopes of the Ecuadorian Andes in the Napo Province (elevation, 2200 m; 0°36'0" S, 77°52'12" W). The station encompasses ~2500 ha of primary cloud forest and is bordered by roads and disturbed habitats. Here, the annual mean temperature is ~18°C. The second high-elevation site was located in a privately owned ranch ~5 km south of Baeza in the Napo Province (elevation, 2100 m; 0°34'12" S, 77°46'48" W). The ranch consisted of ~30 ha of both primary forest and disturbed habitat. At this second cloud forest site we sampled insects from the environment with only two (swiping and visual searching) of the five techniques used at the other three sites.

At our two low-elevation sites we studied Anelosimus eximius Keyserling, a social species that occurs in lowland tropical rain forests from Panama to southern Brazil (Levi 1963, Aagnarsson 2006). Colonies of this species range in size from a single female plus her offspring to tens of thousands of spiders, with the latter sizes reached after several generations of population growth within expanding nests (Avilés 1997). Colony members cooperate in brood care, prey capture, and web building and maintenance. At our two sites, nests of A. eximius are typically found in the forest interior and along forest and river edges. In this study we only included small- to medium-sized colonies (4–133 cm length of the longest axis), as we studied only colonies inside the forest where they tend to be smaller in size (Purcell and Avilés 2007). Because the size of the insects captured tends to increase with colony size in A. eximius (E. Yip et al., unpublished data), our test is thus conservative with respect to the hypothesis we are testing that the lowland species captures larger prey than the upper elevation species.

At both of our high-elevation cloud forest sites we studied the subsocial Anelosimus baeza Aagnarsson, the most common species in the genus in those areas. A. baeza occurs from Panama to Peru at elevations between 200 and 2500 m (Aagnarsson 2006). In eastern Ecuador, it is rarely found below ~500 m (L. Avilés, unpublished data). Prior to dispersal, colonies of A. baeza in the Yanayacu area contain up to a few dozen individuals (median = 65, range 8–197, N = 26; L. Avilés and J. Purcell, unpublished data), most likely the offspring of a single female. Only occasionally more than one mother may share the same nest (L. Avilés, unpublished data). After hatching, the spiderlings stay together in the maternal nest where they are cared for by their mother. As spiderlings grow, they cooperate in web maintenance and prey capture, but eventually disperse as subadults. Following dispersal, the spiders establish individual webs where mating occurs and adult females deposit their clutch. We studied these spiders during the late stages of their communal period prior to dispersal when the colonies consisted mainly of late juveniles and subadults or subadults and adults. At Yanayacu, colonies were most abundant in a swampy area along
the main road, but they were also common in nearby areas of secondary growth and along road edges. At the Baeza site, colonies were most common in disturbed habitats and pastures. The colonies we studied ranged in size from 13 to 56 cm in length (longest axis), covering most of the range of colony sizes of this species.

Prey capture by spider colonies

At each site, colonies of subsocial and social spiders were surveyed at intervals of 1–1.5 hours in the morning and afternoon. For each colony, we noted the presence of new insects caught in the web or being consumed by the spiders and recorded the body length and taxon of each insect prey (see Plate 1). We surveyed a total of 48 A. eximius colonies between 2005 and 2006, 44 at Jatun Sacha, and 4 at Cuyabeno. We surveyed a total of 30 colonies of the subsocial A. baeza, 17 at Yanayacu, and 13 at the Baeza site.

Size of potential insect prey

Insects present in the environment at each site were sampled simultaneously with prey being caught by the colonies. We used five different insect collecting techniques: no-kill malaise traps, light traps, beating sheets, sweep nets, and visual searching. Except for blacklighting, which was done at night near the field stations, insect surveys were done during the day in the vicinity of the spider colonies. For each insect captured or seen, we recorded taxon and body length. Taxonomic classification was done to order and whenever possible to family. Body length was measured as the length between the most anterior side of the head to the tip of the abdomen. This was done to the nearest millimeter using either a caliper or a ruler. During visual searches, body length was estimated by eye as accurately as possible to the nearest half a centimeter, always by the same scorer. Overall, our data set includes >15,000 insects caught by the various techniques and colonies at the four sites.

Five malaise traps (height = 1.2 m, base = 1.2 m) were set up in five separate areas at —5–10 m away from the spider colonies. Traps were checked daily every three minutes at a time with an entomological heavy duty sweep net (diameter = 38.1 cm). Visual searching involved visually searching for five consecutive minutes insects flying or sitting on or under the surrounding vegetation. Sampling bouts of identical effort and procedure, carried out by the same scorer, were used at the four sites.

Data manipulation and statistical tests

Insect body length data was translated into dry biomass (milligrams) using the length-mass regression equations provided by Sage (1982) for each taxonomic order. These regressions account for the different shapes and length-to-width ratios of different insect groups (Schoener 1980, Sage 1982, Sample et al. 1992).

In our analyses, we used the average size of insects collected or recorded in a sampling bout (one hour blacklighting, one day malaise or colony sampling, three minutes sweeping or beating, and five minutes visual searching) as our response variable, weighted by the number of insects entering in the estimate. Insect sample sizes for each bout ranged from 9 to 219 insects for beating, 47 to 359 insects for blacklighting, 10 to 87 insects for malaise trapping, 20 to insects 514 for sweeping, 9 to 54 insects for visual, and 1 to 21 insects for spider colony catches. We combined the data from the two lowland sites (Cuyabeno and Jatun Sacha) and from the two high-elevation sites (Yanayacu and Baeza), as sites at the same elevations were not significantly different from each other (rain forest, $F_{1,51} = 0.7, P = 0.4$; cloud forest, for the two techniques employed in common, $F_{1,18} = 0.03, P = 0.9$). We tested for differences in average insect size between habitats (cloud forest and rain forest) by fitting a factorial mixed-model ANOVA where the response variable was natural log-transformed mean insect size (mg dry mass) per bout and the factors were “habitat” (cloud forest and rain forest), “technique” (blacklighting, malaise, sweeping, beating, and visual search), and habitat × technique interaction. Because beating, visual, blacklighting, and sweeping samples taken in the same day or malaise samples taken from the same location in different days were not independent from one another, each sampling bout was identified as belonging to a particular day or location and day/location used as a random effect nested within technique × habitat.Tukey’s hsd (honestly significant difference) test was performed for post hoc comparisons among techniques within each habitat and independent contrasts were used to compare the two habitats separately for each technique.

We ran a separate analysis in which we included the spider colonies as an additional technique (daily samples, with colony ID as a random effect) followed by independent contrasts to compare the prey size caught by colonies of the two species with each other and with the yields of each sampling technique. All tests were done using the statistical software JMP IN (SAS Institute 2003).
RESULTS

Are insects at low-elevation sites larger than in the cloud forest and are different techniques consistent in detecting a difference?

The combined data from the two lowland rain forest sites show that the per sample average size of insects captured at the lower elevations is larger than at the high-elevation cloud forests ($F_{1,9} = 52.8$, $P < 0.0001$; Fig. 1). As demonstrated by a nonsignificant interaction between technique and habitat ($F_{4,92} = 0.7$, $P = 0.6$), this pattern was consistent with all the individual techniques, which captured, on average, larger insects in the lowland rain forest than in the cloud forest (independent contrasts, rain forest vs. cloud forest, beating, $F_{1,92} = 4.2$, $P = 0.04$; blacklighting, $F_{1,92} = 10.5$, $P = 0.002$; malaise, $F_{1,92} = 10.3$, $P = 0.002$; sweeping, $F_{1,92} = 20.2$, $P = 0.00002$; visual search, $F_{1,92} = 13.4$, $P = 0.0004$). The average size of insects captured by the spider colonies in the lowlands was also greater than in the cloud forest ($F_{1,180} = 56.2$, $P < 0.0001$; Fig. 1). In terms of insect size range, *A. eximius* colonies captured a much broader range of insect sizes (1–60 mm) than *A. baeza* colonies (1–18 mm). Considering all techniques combined, insects sampled from the rain forest ranged from 1 to 90 mm and from the cloud forest from 1 to 60 mm.

How do the different collection techniques compare to each other with respect to the mean and range of insect size they capture?

At both localities, we found that, for the most part, different techniques captured different average insect sizes and ranges ($F_{4,92} = 89.9$, $P < 0.0001$; Figs. 2 and 3). At any given site, visual search samples had the largest insects (range: cloud forest, 4–35 mm; rain forest, 4–90 mm) (least-square means back-transformed to milligrams: cloud forest, 58.2 mg; rain forest, 177.2 mg).
followed by blacklighting (range: cloud forest, 1–60 mm; rain forest, 1–80 mm) (least-square means back-transformed to milligrams: cloud forest, 17.5 mg; rain forest, 36.7 mg), with these two techniques being significantly different from each other and from the remaining techniques (Tukey’s hsd, $P < 0.05$). Average insect sizes caught by sweeping, malaise, and beating were not significantly different from each other (Tukey’s hsd, $P > 0.05$) either in the cloud forest (sweeping, 4.8 mg; malaise, 3.3 mg; beating, 4.6 mg; range, sweeping, 1–35 mm; malaise, 1–30 mm; beating, 1–25 mm) or the rain forest (sweeping, 10.8 mg; malaise, 7.4 mg; beating, 7.3 mg; range, sweeping, 1–84 mm; malaise, 1–31 mm; beating, 1–60 mm), although there was a trend for sweeping samples to contain on average slightly larger insects than malaise samples in the two environments (Figs. 2 and 3).

*Which of these techniques better approximates what the spiders catch in terms of insect size?*

When individual techniques were compared against insect prey caught by the spiders, we found that beating, malaise, and sweeping caught a similar average insect size as the cloud forest *A. baeza* colonies we studied (independent contrasts, colonies vs. technique, beating, $F_{1,180} = 0.8$, $P = 0.4$; malaise, $F_{1,180} = 0.4$, $P = 0.5$; sweeping, $F_{1,180} = 1.9$, $P = 0.2$; Fig. 2), whereas only sweeping did so relative to the lowland rain forest *A. eximius* colonies we studied (beating, $F_{1,180} = 10.6$, $P = 0.001$; malaise, $F_{1,180} = 10.8$, $P = 0.001$; sweeping, $F_{1,180} = 2.8$, $P = 0.1$; Fig. 2). Blacklighting and visual search, on the other hand, caught much larger insects on average than did our sample of spider colonies in the cloud forest (blacklighting, $F_{1,180} = 51.7$, $P < 0.0001$; visual search, $F_{1,180} = 112.7$, $P < 0.0001$) as well as in the lowlands (blacklighting, $F_{1,180} = 23.9$, $P < 0.0001$; visual search, $F_{1,180} = 144.4$, $P < 0.0001$).

**DISCUSSION**

The combination of all arthropod taxa sampled using different collecting techniques show that, on average, insects in the Ecuadorian lowland rain forest are larger than insects found at adjacent high-elevation cloud forest habitats. These results are comparable to three previous studies (Janzen et al. 1976; Powers and Avilés 2007; E. Yip and L. Avilés unpublished data) that also found a decrease in the average insect size at higher altitudes. Like our study, all three studies surveyed different elevations at the same latitude and involved sampling of all taxa within the insect communities. A number of authors, however, have studied trends within individual taxa or among closely related taxa, often with contradictory results (Hawkins and DeVries 1996, Blackburn et al. 1999, Brehm and Fiedler 2004). The general prediction, based on Bergmann’s rule (Bergmann 1847), that animals will be larger at elevations (or latitudes) where temperatures are lower is generally well supported for birds and mammals (Meiri and Dayan 2003). Evidence for similar trends in the body size of insect fauna, however, is less clear (reviewed for the case of latitudinal clines by Blanckenhorn and Demont 2004). Some insect groups exhibit an increase in body size with increasing altitude (Stalker and Carson 1948, Miller 1991, Smith et al. 2000, De Oliveira et al. 2004), while others appear to be larger at lower elevations (e.g., certain species of grasshoppers, Dingle et al. 1990, Orr 1996, Berner and Blanckenhorn 2006; coleopterans, Krasnov et al. 1996, Sota 1996, Chown and Klok 2003; lepidopterans, Hawkins and DeVries 1996, Brehm and Fiedler 2004; neuropterans, Arnett and Gotelli 1999; and dipterans, Blanckenhorn 1997, Norry et al. 2001), or show mixed patterns or no pattern at all (e.g., Hawkins and DeVries 1996, Brehm and Fiedler 2004). Because these studies have concentrated on trends for specific insect taxa, rather than on entire insect communities, comparing them to our study, however, may have little significance (Blackburn et al. 1999). An alternative to Bergmann’s rule, the converse Bergmann’s rule, has been proposed to explain patterns of increasing size with decreasing elevation (or latitude) (summarized in Mousseau 1997, Blanckenhorn and Demont 2004, Dillon et al. 2006). According to this rule, insects grow to larger sizes at low elevation (or low latitude) because of longer growing seasons in those areas. Our results, as those of Janzen (1976), are compatible with the converse Bergmann’s rule.
A reassuring finding of our study is that, even though the various techniques differed in the size range of insects they caught, all techniques consistently yielded significantly larger average insect sizes in the lowland habitats. It is clear from our results, however, that no technique is likely to yield a complete, much less representative sample of what is available. Different techniques tend to target certain insect groups or sizes more than others or vary in collection efficiency (Kharboutli and Mack 1993). In our study, visual searches yielded, for obvious reasons, much larger insect sizes than any other technique. Although this technique is clearly biased...
toward the largest insects, including it is important as no other technique is likely to reliably sample the largest sized insects present in a habitat. Light traps are effective for attracting night-flying insects (Blomberg et al. 1976), including large moths and beetles as well as smaller insects (Nabli et al. 1999). In our study, blacklighting yielded on average larger insects than the three remaining techniques (beating, sweeping, and malaise trapping), possibly because night-flying insects tend to be larger than diurnal insects (Crouch and Lubin 2000; L. Avilés, unpublished data). Malaise traps, although an efficient technique for sampling flying insects, target mostly small- to medium-sized insects. Similarly, sweep nets, although efficient for collecting hidden insects, often capture small insects in certain taxa (e.g., Kharboutli and Mack 1993). Beating, as our study shows, also tends to capture small insects on average. Therefore, in order to obtain a more or less complete (but not necessarily representative) sample of an insect community, a variety of complementary techniques must be used. Short of censusing an entire community, however, we cannot realistically aspire to uncover the exact size distribution of what is actually there. Even techniques such as insect fogging, that may appear to be better able to census entire communities (e.g., Stork and Hammond 1997), appear to subsample certain arthropod groups (e.g., Store and Blackburn 1993, Yanoviak et al. 2003). Fogging techniques were not available to us and, even if available, would not have been advisable in the vicinity of spider colonies we wished to preserve and study. It is also unclear how representative insect fogging samples would be of the primarily flying insects that are available to spiders.

Because beating, sweeping, and malaise trapping capture comparable average insect sizes as A. baeza colonies in the cloud forest, these three techniques could be used interchangeably to assess potential insect prey corresponding to the preferred size of the spiders. Note, however, that this may not be appropriate if the goal is to assess the taxonomic composition of potential prey, given that different techniques may recover insect groups in proportions different to those caught by the spiders (e.g., Castillo and Eberhard 1983) and from each other (e.g., Kitching et al. 2001). In the case of A. eximius in the rain forest, only sweeping caught insects of similar average size as those caught by our study colonies; malaise and beating yielded slightly smaller insects, while visual and blacklighting yielded considerably larger insects (Fig. 2). Note, however, that because the size of the insects caught is a function of colony size (E. Yip et al., unpublished data), the mean and range of prey sizes in our sample will depend on the size of the colonies surveyed. Thus a greater representation of smaller colonies would result in samples similar to those caught with malaise and beating while greater representation of large colonies should result in samples closer to those obtained with visual searching and blacklighting.

The fact that blacklighting yielded larger insects on average than those caught by the colonies may also be partly related to the fact that we surveyed colonies only
during the day, when flying insects tend to be smaller than at night (Crouch and Lubin 2000; L. Avilés, unpublished data) when blacklighting was performed and spider colonies are also active. Consistent with an observed insect size difference between these time periods, Crouch and Lubin (2000) found that the social spider Stegodyphus mimosarum consumed larger prey at night. One shortcoming of our study is thus absence of night prey capture data for the spiders because not only insect size, but also activity patterns of both insects and spiders may vary between these two periods. Thus, subsocial species may catch proportionally less prey during the night than the day given that lower temperatures at night at higher elevations may restrict the availability of potential insect prey proportionally more than at lower elevations. Colonies of the social spider Stegodyphus mimosarum, for instance, captured more prey during the day, despite the fact that the spiders were more active in the web at night (Crouch and Lubin 2000).

Although an exact assessment of what is available in the environment is not an attainable goal (Robinson and Robinson 1973, Castillo and Eberhard 1983), our study clearly shows that the social and subsocial spiders we studied capture prey that are in line, at least qualitatively, with what is present in their respective habitats. This finding supports the notion that spider social systems are to some extent determined by the insect size composition of their environments. A sufficient supply of large prey items, would, on the one hand, provide an incentive for cooperative prey capture while allowing social spiders to sustain large colonies in the lowland rain forest habitats where they occur. Larger prey items result in increased resources for all colony members and decreased within-colony competition for food (e.g., Ward 1986). Absence of a sufficient supply of large prey at higher elevations may, on the other hand, impose a limit to the maintenance of large social colonies in these habitats and consequently explain the absence of social species at high altitudes (Avilés et al., in press). Other possible factors that may explain the greater occurrence of social species in the lowland tropical forests are the relatively benign climate conditions as well as the year-round prey availability, which may allow for permanent activity and continuous growth of colonies to very large sizes (reviewed in Avilés 1997).

In summary, our study shows that, given the sampling methods used, the average insect size in the Ecuadorian lowland rain forest where social Anelosimus species occur is larger than at higher-elevation cloud forests where subsocial species are found. Because different sampling techniques may vary in their efficiency and the size of insects they capture, a combination of several techniques should better cover the range of insect sizes when sampling entire communities of insects. Finally, the insect size caught by some individual sampling techniques may be comparable to the average size of the prey caught by spiders in the genus Anelosimus in their respective environments. To our knowledge, no previous study has simultaneously used a variety of techniques to sample whole arthropod communities along altitudinal gradients. Because our data is limited to a single latitude and two elevations, however, sampling at more elevations as well as different latitudes is required to further assess the generality of this pattern.

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LITERATURE CITED


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