Smaller colonies and more solitary living mark higher elevation populations of a social spider

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Summary

1. There appears to be a pattern of decreasing sociality with increasing elevation across social spider species in the genus *Anelosimus* at tropical latitudes. Our data suggest that this pattern holds within a single species, *Anelosimus eximius*, on a smaller altitudinal gradient.

2. In comparing colony size at six different altitudes in north-eastern Ecuador, we find that the lowland *A. eximius* populations tend to have larger colonies and few solitary females. At higher elevations, many of the colonies are small and the proportion of solitary females is greater.

3. Contrary to expectation, we also found no difference in spider density between the upper elevation and lowland populations. This result may be partly due to the fact that upper elevation populations occur only at the forest edge (as opposed to both edge and interior) where populations at all elevations appear more robust.

Key-words: distribution, range, social polymorphism, Theridiidae.

Introduction

Social behaviour can allow an organism to occupy a niche that it may not otherwise be able to access (Wilson 1975; Slobodchikoff 1984; Avilés 1999). Naked mole rats and emperor penguins, for instance, are able to withstand notoriously harsh environmental conditions by either co-operatively searching for new food patches during short and unpredictable windows of time (Jarvis et al. 1994) or by huddling together to maintain warmth during the frigid Antarctic winter (Ancel et al. 1997; Gilbert et al. 2006). Likewise, by foraging in groups, tree killing bark beetles are able to overcome the defences of live trees (Raffa & Berryman 1987) and mammalian carnivores and social spiders are able to catch prey larger than their body size (Macdonald 1983; Nentwig 1989; Rypstra & Tirey 1991). Sociality may also allow for increased defence from predators, as in spider mites (Mori & Saito 2005), swarm-founding wasps (London & Jeanne 2003) and sweat bees (Smith, Wcislo & O'Donnell 2003).

On the other hand, sociality may be unnecessary or even unfavoured under some conditions, as reflected in both the inter- and intraspecific variability in social behaviour observed in a range of species in response to various climatic and habitat-related conditions (Lott 1984; Wcislo & Danforth 1997; Cronin 2001). Within Halictine bee species, for instance, there is an increase in solitary nests with increasing latitude (Packer 1990) and altitude (Eickwort et al. 1996). In both cases, a shorter foraging season is thought to reduce the number of broods produced, thus decreasing the need for workers. Temperate conditions were also cited as a possible factor in reduced sociality across several closely related species of thrips in Australia (Kranz et al. 2002), while the production of fewer broods per generation was thought to cause an increased number of solitary foun- dress colonies in a southern California population of paper wasps (Liebert, Nonacs & Wayne 2005). In a number of bird species, flocking behaviour is reduced in the absence of predators (Beauchamp 2004). In colonial orb-weaving (noncooperative) spiders *Metepeira atascadero* (Uetz & Hieber 1997) individuals occurring in a prey-poor environment live solitarily or in small groups, with relatively large spacing among group members. Closely related *M. incrassata* living in a prey-rich environment occur in much larger groups with less spacing between individuals (Uetz & Hodge 1990). All of these findings indicate that, even though sociality may allow expansion into new ecological niches, in some habitats it may be disadvantageous. Thus, sociality may restrict the geographical distribution of social species to areas where their particular social niche can be realized.
The co-operative social spiders (also known as nonterritorial permanent social) form colonies that may contain hundreds to tens of thousands of spiders and are notoriously restricted to tropical latitudes and, within some regions, to lower elevations (reviewed in Avilés 1997). Related subsocial species, which form colonies containing a single mother and her brood, in contrast, extend into higher latitudes and elevations and may be absent from lowland tropical areas where social species thrive (Aagnarsson 2006; L. Avilés unpublished). In the spider genus Anelosimus (Theridiidae), this pattern may be partly due to the availability of larger insect prey in areas where social species are present relative to where they are absent (Guevara & Avilés, in press; Powers & Avilés, in press). Large insects both require more individuals for their capture (e.g. Nentwig 1985) and are a perishable resource that can be shared (Rypstra & Tirey 1991). Other factors that may be correlated with both latitude and altitude are probably also involved in determining the geographical pattern in this and other genera (Avilés 1997), including rainfall (e.g. Riechert 1985; Riechert, Roeloffs, & Echternacht 1986), temperature (e.g. Jones et al. 2007) and predation rates (e.g. Henschel 1998).

Here we explore whether the pattern of decreasing sociality with increasing elevation found across species in the genus Anelosimus (L. Avilés, unpublished) may also be applicable to differences between populations of a single species across an altitudinal gradient. The social Anelosimus eximius Simon (1891) is amenable to intraspecific investigation as it is found in both lowland rainforests and on the slope of the Andes up to about 1300 m (Levi 1963; Aagnarsson 2006; this paper). If the conditions that allow this species to thrive in lowland tropical rainforest change with elevation, we would expect A. eximius populations at the altitudinal limits of its range to be less social, or to exhibit characteristics more similar to subsocial species at higher elevations. If this is the case, then we expect the upper elevation populations to have a greater proportion of nests with solitary females (prediction 1), smaller average colony sizes (prediction 2) and greater nest density (prediction 3) due to spiders dispersing from their natal nests more readily, and at smaller colony sizes than in lowland populations. As the upper elevation populations are near the limit of the A. eximius species range, we also expect that this habitat may be marginal, which may lead to a lower overall population density than lowland sites (prediction 4). In order to test these predictions, we compared A. eximius populations at different elevations in various regions of Ecuador. Secondarily, we compare forest edge and interior populations at the lowland sites as earlier studies have suggested that the forest interior may be a marginal habitat relative to forest edge for this species (Pasquet & Krafft 1989; Leborgne, Krafft & Pasquet 1994). This comparison then allows us to control for the separate effects of elevation and habitat type (edge vs. interior) in our elevation tests, as upper elevation populations only occurred at the forest edge (see Methods).

### Methods

From May to June 2005 and May to July 2006, Anelosimus eximius nests were mapped in three transects within each of six sites in eastern Ecuador (Table 1). Additionally, data collected by LA (unpublished) from a seventh site in western Ecuador (Endesa, EN; Table 1) were used for one of the tests. The sites studied ranged from lowland rainforest (sites < 700 m) to lower montane rainforest or ‘cloud forest’ (sites > 700 m) (Neill 1999). The Cuyabeno Faunistic Reserve is a primary rainforest site traversed in some areas by trails as well as rivers navigable by motorized canoe. Three transects surveyed the forest interior (CF), while three others mapped the river edge by canoe (CR). The Jatun Sacha Reserve (JS) is a well conserved, though isolated, patch of primary rainforest. Three transects mapped nests in the rainforest interior. EN is an open (disturbed) habitat area in a lumber plantation 6–8 km north of the Km 113 of the Quito–Pto Quito highway. All colonies seen along a 1000 m stretch of road were surveyed. Puyo (PU) transects


<table>
<thead>
<tr>
<th>Location</th>
<th>Province</th>
<th>Coordinates</th>
<th>Elevation</th>
<th>Habitat type</th>
<th>Abbreviation</th>
<th>Av. annual temperature</th>
<th>Av. annual rainfall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cuyabeno Faunistic Reserve</td>
<td>Sucumbios</td>
<td>0-028°S, 76-294°W</td>
<td>225 m</td>
<td>Forest edge</td>
<td>CR</td>
<td>22–29 °C</td>
<td>3000 mm</td>
</tr>
<tr>
<td>Cuyabeno Faunistic Reserve</td>
<td>Sucumbios</td>
<td>0-032°S, 76-321°W</td>
<td>240 m</td>
<td>Forest interior</td>
<td>CF</td>
<td>22–29 °C</td>
<td>3000 mm</td>
</tr>
<tr>
<td>Jatun Sacha Reserve</td>
<td>Napo</td>
<td>1-060°S, 77-617°W</td>
<td>400 m</td>
<td>Forest interior</td>
<td>JS</td>
<td>25 °C</td>
<td>5000 mm</td>
</tr>
<tr>
<td>Endesa: road</td>
<td>Pichincha</td>
<td>0-08°N, 79-07°W</td>
<td>700 m</td>
<td>Forest edge</td>
<td>EN</td>
<td>20 °C</td>
<td>2000 mm</td>
</tr>
<tr>
<td>Puyo area: road</td>
<td>Pastaza</td>
<td>1-5°S, 77-9°W</td>
<td>900 m</td>
<td>Forest edge</td>
<td>PU</td>
<td>20-9 °C</td>
<td>4538 mm</td>
</tr>
<tr>
<td>Via a Loreto: road</td>
<td>Napo</td>
<td>0-703°S, 77-736°W</td>
<td>1000 m</td>
<td>Forest edge</td>
<td>VL</td>
<td>18 °C</td>
<td>1800 mm</td>
</tr>
<tr>
<td>Macas area: road</td>
<td>Morona-Santiago</td>
<td>2-3°S, 78-1°W</td>
<td>1200 m</td>
<td>Forest edge</td>
<td>MA</td>
<td>20 °C</td>
<td>2414 mm</td>
</tr>
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mapped nests along three secondary roads stemming from the highway connecting PU and Macas north of the Pastaza River, along a mid elevation ridge (900 m). The roadside alternates between areas of farmland and relatively intact cloud forest. In this region, we also explored a forest reserve, but did not find any A. eximius nests along the trail system. The highway to Loreto (Via a Loreto, VL) follows the base of the Sumaco volcano, remaining about 1000 m above sea level for the first 50 km, where three transects were mapped. The roadside alternates between farmland and open roadsides with natural vegetation for the first 20–30 m along the road, with cloud forest beyond the road cut. We explored several forested trails in this area, but did not find A. eximius. Macas (MA) transects surveyed nests along two secondary roads stemming from the PU-MA road south of the Pastaza River (1200 m elevation). The roadside is primarily agricultural land, with shrubby vegetation in areas used for grazing livestock.

At all six regular sites, nests were mapped in two random and one nonrandom transect. Random transects were 600 × 5 m at all sites except along Cuyabeno River, where they were 1000 × 5 m. These transects were initiated by generating random points (in Excel 10·0) corresponding to distances along trails, roads or rivers. The T-squared sampling method (Krebs 1999) was then used to find the nearest nest to the nest closest to the random point, thus ensuring that transects were initiated with a random nest. Starting at this random nest, forest transects continued in a fixed direction determined at the start by the direction of the trail near the nest, but diverging thereafter. At the edge sites (CR, VL, PU and MA), transects followed the road or river edge, and the compass direction was noted at every bend. Nonrandom transects were placed in areas of known nest abundance. The length and width of the nonrandom transects varied at each site: 1000 × 5 m along the Cuyabeno River; 150 × 30 m in Cuyabeno Forest; 600 × 5 m and paralleling a trail in JS; 200 × 5 m in PU; 300 × 5 m in MA. In VL, the transect spanned two stretches of roadside habitat interrupted by a heavily degraded construction area, for a total area of 200 × 5 m. In EN, both sides of a 1000 m nonrandom stretch of road were mapped; all nests near the roadside (up to about 10 m) were included. Additionally, we measured the extent of continuous vegetation at random points along each transect as the maximum length of leafy vegetation with gaps of less than 30 cm.

All nests within each transect were measured and sketched (Fig. 1a). Nest cross-section areas (Fig. 1b) were then estimated by tracing irregular shapes into Canvas 3·5 (Deneba Systems Inc.) using a writing tablet or by calculating the area of an ellipse when shapes were regular. Nest contents were inspected for the presence of one or multiple females. For single female nests (with or without their brood), the presence of additional subadult or adult females was ruled out by careful inspection. In a few ambiguous cases where careful inspection was not possible (mostly in VL), nests were excluded from the solitary female comparison.

The regression of number of individuals to nest size (cross-section area) was calculated in JS and both Cuyabeno sites by LA, and in VL by JP (Appendix S1). Entire nests of different sizes, or substantial, well-measured fractions of huge nests, were collected from each site, and the inhabitants were sorted by age and counted. Colony sizes were estimated using these regressions. The VL regression was applied to the PU and MA nests, as these sites were similar in elevation and habitat.

Nest density was calculated by summing the total number of nests per transect and dividing by the surveyed area. Individual density was determined using the nest size regressions (Appendix S1) to estimate total population size in each transect, divided by the surveyed area. Only random transects were included in the density analyses, as nonrandom transects targeted areas of high density.

Nonparametric tests were used whenever our data did not conform to normal assumptions. JMP IN 5·1, R 1·12, Microsoft Excel 10·0, and the website http://faculty.vassar.edu/lowry/binomialX.html were used for statistical analyses. The Kolmogorov–Smirnov test was used to compare the distribution of colony sizes (including solitary females, one-sided). Proportions of nests with solitary females were compared using a binomial exact one-tailed test. Only unambiguous nests where careful inspection of the nest occupants was possible were used in this analysis. In VL, the nonrandom transect nests were excluded from this analysis because they were not carefully viewed. After excluding solitary
females from the distributions, median colony sizes were compared using the Wilcoxon test. For this test, ambiguous nests were categorized as occupied by one or more females, based on the colony size estimate from the nest size regression, and included or excluded accordingly (Appendix S1). Continuous vegetation differences were compared using 95% confidence intervals. Population and nest densities were compared with an ANOVA, followed by independent contrasts to compare upper elevation vs. lowland sites and edge vs. forest interior sites in the lowlands, both planned comparisons. Alpha values were adjusted down using a Bonferroni correction to account for multiple comparisons.

Results

UPPER VS. LOWER ELEVATIONS

Upper elevation sites all had colony size distributions consisting of significantly smaller colonies than at least one of the three lower elevation sites (Kolmogorov–Smirnov one-sided test, Table 2). A large percentage of these small upper elevation colonies contained a solitary female (Fig. 2). Thus EN (700 m), PU (900 m), VL (1000 m) and MA (1200 m) each had significantly more solitary females than any of the lowland sites, except for MA vs. JS (400 m, a forest interior site) (binomial exact one-tailed test, Table 2). When solitary females are excluded from the analyses, the median colony sizes in one of the three upper elevation sites remain smaller.

Fig. 2. In general, upper elevation sites have a significantly higher proportion of solitary females than any of the lowland sites. The following letter coding indicates which sites are significantly different from one another (*P < 0.0001 for both comparisons) in a two-tailed test.

CR, Cuyabeno River; CF, Cuyabeno Forest; EN, Endesa; JS, Jatun Sacha; PU, Puyo; VL, Via a Loreto; MA, Macas.

*Note that for percentage solitary females, PU vs. MA and VL vs. MA were significantly different from one another (*P < 0.0001 for both comparisons) in a two-tailed test.
than those in two of the three lowland sites (Fig. 3). In this case, VL (1000 m) colonies remain significantly smaller than CR (225 m) and CF (240 m) colonies (Wilcoxon test, Table 2). PU appeared to have substantially smaller colony sizes than CR and CF (Fig. 3), but the small sample of nests with more than one female at this site may be responsible for the lack of significance in this comparison. Although nest density was lower (Fig. 4a) and individual density higher (Fig. 4b) when comparing upper elevation sites with lowland sites, these differences were not significant whether we include lowland sites in both edge and interior habitats (ANOVA, Nest Density: $F_{1,10} = 0.51, P = 0.49$; Individual Density: $F_{1,10} = 0.30, P = 0.59$) or only edge populations (ANOVA, Nest Density: $F_{1,6} = 0.44, P = 0.53$; Individual Density: $F_{1,6} = 0.68, P = 0.44$). The power of these density tests, however, is low (adjusted power $= 0.05$ for an $\alpha = 0.05$ given the observed variance and effect size). Upper elevation sites appeared more variable in both nest and individual density.

**Forested Edge Versus Forest Interior**

Along the lowland forest edge (CR), colonies attained larger average sizes than those within the forest (CF and JS) (Fig. 3). Vegetation along the edge tended to be significantly more continuous on the horizontal axis than vegetation inside the forest (length of continuous vegetation, mean $\pm$ 95% confidence intervals: 26 $\pm$ 12-16 m along the forest edge, 1.59 $\pm$ 0.63 m in the forest interior), a pattern that may relate to the differences in average nest sizes between these two habitats (see Discussion). Nest density was similar in the three lowland sites

**Discussion**

The data support our expectation that the altitudinal pattern of sociality known to exist among *Anelosimus* species (L. Avilés unpublished) is mirrored within at least one generalist species. As predicted, colony size distributions are significantly more biased towards smaller colonies at the upper elevations (prediction 2; Fig. 3 and Table 2), to a large extent because solitary females occupy a much greater proportion of nests in the upper elevation sites (prediction 1; Fig. 2). When solitary females are excluded, median colony size is still significantly smaller in one of three upper elevation...
sites relative to two lower elevation sites (prediction 2, Fig. 3). Contrary to our expectations, nest density is not significantly greater in upper elevation sites (prediction 3), although this result should be taken with caution given the low power of our tests (see Results). None the less, two upper elevation transects do have much higher nest density than any lowland transects and the overall mean is in the expected direction (Fig. 4a).

The finding that upper elevation colonies can sometimes grow to large sizes leads us to consider a couple of plausible explanations. First, social species at upper elevations may, in fact, occupy two social niches: one for colonies that tend to remain whole and grow very large and another for small colonies containing one or a few females. In this case, the first niche would mirror the typical social spider strategy from the lowland habitat, while the second would be similar to the lifestyle of subsocial spider species. Alternatively, the attractor (e.g. Avilés 1999) representing the growth trajectory of colonies at the upper elevation sites may have a long tail, thus allowing for the occasional large colony, even though overall it would correspond to smaller colony sizes. The preponderance of solitary females and small colonies at the upper elevation sites also allows for two possible, nonmutually exclusive, explanations: either more females are dispersing and establishing nests solitarily or more solitary dispersers are surviving. Both possibilities may occur simultaneously, with a greater dispersal tendency of females at these sites also partly explaining the paucity of very large colonies at these sites.

Unlike the altitudinal and latitudinal gradients of eusociality in wasps, where length of the reproductive season may be responsible for lower levels of sociality at higher elevations and latitudes (Packer 1990; Eickwort et al. 1996), we cannot yet ascribe the observed patterns to any one particular factor. Among abiotic factors, temperature is clearly correlated with elevation. The pattern we observe, however, is opposite of that expected under the hypothesis that Jones et al. (2007) proposed to explain the increasing occurrence of multiple female nests at higher latitudes (and lower temperatures) in the subsocial spider Anelosimus studiosus in North America (see also Furey 1998). Jones et al. (2007) suggested that lower temperatures slow the developmental rate of the progeny, making the presence of additional caretakers advantageous in the event of the mother’s death. Rainfall, on the other hand, does not vary linearly with elevation (Table 1), but may none the less play a role in spider sociality (Riechert 1985; Riechert et al. 1986). In A. eximius, rainfall and rain intensity may, for instance, influence the frequency and success of colony foundation (Venticinque, Fowler, & Silva 1993) and may partially explain the paucity of small nests in the lowlands.

Among the biotic factors, we have found insect size to be correlated with elevation and latitude, with large insects being more common in the lowland rainforests occupied by social Anelosimus species relative to higher elevations or latitudes where social species are absent (Guevara & Avilés 2007; Powers & Avilés, in press). We have argued that the presence of an abundant supply of large insects provides an incentive for co-operative prey capture and may be necessary to support large colony sizes. A preference for large prey has also been noted in the social species Stegodyphus mimosarum (Crouch & Lubin 2000). Predation rates may also be lower at higher elevations, as suggested by studies that have documented lower species richness and abundance in a range of potential spider predators at higher elevations, including insectivorous birds (Rahbek 1997) and some ants and spiders (Olson 1994). Henschel (1998) found that spiders living in larger groups were less vulnerable to predation by birds, araneophagus spiders, and ants compared with solitary spiders in the social Stegodyphus dumicola in Namibia. Riechert et al. (1986) found a similar pattern in Agelena consociata in Gabon. If predation rates decrease with increasing elevation, we might expect greater dispersal tendencies and/or greater survival of solitary dispersers in upper elevation spiders.

Contrary to expectations (prediction 4), upper elevation sites do not appear marginal for this species based on overall spider density (Fig. 4b) and the occasional presence of very large nests. If these habitats are not marginal, then what factors prevent A. eximius from expanding to even higher elevations? One possibility is that increased competition with subsocial species for resources or space maintains the species boundary. Interspecific competition, however, has been notoriously difficult to demonstrate in spiders, suggesting that competition for resources may rarely be a limiting factor in these organisms (Wise 1993). Another possibility is that the species may not be plastic enough to lose its tendency to produce large colonies as the conditions favourable to large colony size decline with elevation. In either case, it would be interesting to investigate the relative role of plasticity and local adaptation on the dispersal tendencies and the propensity to establish nests solitarily in different populations of this species.

We also find some differences between lowland forest interior and edge habitat, including smaller colonies (Fig. 3) and marginally lower individual density (Fig. 4b) inside the forest. Greater nest sizes along the forest edge (Fig. 3) may result from the more continuous vegetation substrate in this habitat (see Results), while forest interior nests would need to break up once they reach the limit of their current plant substrate. This may also account for the greater individual density in the edge habitat (Fig. 4b), as the per capita rate of growth may not reach maximum levels in colonies constrained to smaller sizes (Avilés & Tufiño 1998). The alternative possibility of a greater availability of insects or greater insect sizes accounting for larger colony sizes at the forest edge has been rejected by recent studies that found no differences in these two aspects across the two habitat types (Guevara & Avilés 2007; Powers & Avilés, in press; E. Yip & L. Avilés, unpublished). While these data are not sufficient to support or refute the suggestion that forest interior habitat may be less favourable for A. eximius (Pasquet & Krafft 1989;
Leborgne et al. 1994), the pattern seems to be stronger at higher latitudes (Pasquet & Krafft 1989; Leborgne et al. 1994) and higher elevations (this study) where A. eximius colonies appear absent from the forest interior.

The relatively broad range of habitats and elevations occupied by A. eximius allows us to investigate the efficacy of its social strategy across different environments. Contrary to our expectation, we found that the upper elevation habitat supports a robust population. While the fact that all upper elevation sites were in edge habitat may contribute to this finding, we suggest that the mechanism leading to higher population density may differ between lowland and upper elevation sites. Whereas an abundance of large nests support the population along the lowland river edge, upper elevation populations seem to be split more evenly between large and small nests, suggesting a more important role for small nests. Our data suggest that the sites on the altitudinal range edge of this species may host a phenotype with some characteristics resembling the subsocial strategy.

As such, this area offers an excellent opportunity to investigate the costs and benefits of several socially intermediate traits. For instance, it would be interesting to explore the fitness of solitary females in this environment, which we might expect to be greater than the fitness of solitary females at lower elevations. Also, we expect dispersal to occur more frequently and at smaller colony sizes in this habitat. Thus it may be interesting to determine how the shape of the per capita reproductive success function (e.g. Avilés & Tufíño 1998) relates to when and how frequently dispersal takes place. Finally, while these observations do not allow us to distinguish the relative influences of phenotypic plasticity and local adaptation in shaping these differences, they do provide an interesting baseline for future investigations.

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References


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**Supplementary material**

The following supplementary material is available for this article.

**Appendix S1.** Regressions of nest cross-section area to number of females per colony for Cuyabeno River (a), Cuyabeno Forest (b), Jatun Sacha (c), and Via a Loreto (d).

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2656.2007.01228.x

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