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Collective aggressiveness limits colony persistence in high- but not low-elevation sites at Amazonian social spiders

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Abstract

Identifying the traits that foster group survival in contrasting environments is important for understanding local adaptation in social systems. Here, we evaluate the relationship between the aggressiveness of social spider colonies and their persistence along an elevation gradient using the Amazonian spider, *Anelosimus eximius*. We found that colonies of *A. eximius* exhibit repeatable differences in their collective aggressiveness (latency to attack prey stimuli) and that colony aggressiveness is linked with persistence in a site-specific manner. Less aggressive colonies are better able to persist at high-elevation sites, which lack colony-sustaining large-bodied prey, whereas colony aggression was not related to chance of persistence at low-elevation sites. This suggests that low aggressiveness promotes colony survival in high-elevation, prey-poor habitats, perhaps via increased tolerance to resource limitation. These data reveal that the collective phenotypes that relate to colony persistence vary by site, and thus, the path of social evolution in these environments is likely to be affected.

KEYWORDS
araneae, collective behaviour, insect abundance, life history, multilevel selection

1 | INTRODUCTION

Although social evolution provides numerous benefits for group constituents (Krause & Ruxton, 2002), social groups can also vary considerably in their success (ants: Gordon, 2013, social spiders: Aviles, 1986, honey bees: Watanabe, 2008). For a variety of social organisms, many or most of the social groups ever founded will swiftly end in their collective demise (Aviles & Tufino, 1998; Hahn & Tschinkel, 1997; Tibbetts & Reeve, 2003). In some taxa, even social groups in apparent good health can fall victim to colony extinction events (Pruitt, 2012). Thus, any feature that enables groups to persist in their environment is likely to foster their success. Social organisms provide an interesting case study for evolutionary ecologists,

because trait differences occur at both the individual-level and between groups, in terms of their collective traits (Bengston & Jandt, 2014; Jandt et al., 2014; Wray & Seeley, 2011). Like individual traits, a growing body of evidence conveys that group traits are often associated with group success (Gordon, 2013; Shaffer et al., 2016; Wray, Mattila, & Seeley, 2011), and that these links can vary between environments (Pruitt & Goodnight, 2014; Pruitt et al., 2018). Site-specific selection may therefore contribute to biodiversity by promoting intraspecific variation and local adaptation in group-level traits.

Social spiders are a useful model with which to explore the evolutionary ecology of group extinction events and collective behaviour in general. This is because social spider groups emerge and disappear with high frequencies (reviewed in Aviles & Guevara,

2017). Social spider colonies are prone to ant attack (Henschel, 1998; Keiser, Wright, & Pruitt, 2015), parasitism (Straus & Avilés, 2018; Vollrath, 1987) and fungal outbreak (Henschel, 1998). To avoid these fates, social spiders collectively catch prey, repair webs, and raise offspring, and many spiders remain in the colony to breed (Aviles & Guevara, 2017; Bilde et al., 2007). Consequently, groups are inbred and composed of highly related individuals (Aviles, 1993; Henschel, Lubin, & Schneider, 1995; Riechert & Roeloffs, 1993), and group success is a major determinant of individuals' inclusive fitness. Here, we explore the degree to which group behaviour is linked with group persistence using a highly social spider, the Amazonian spider *Anelosimus eximius* (Araneae, Theridiidae).

This species occurs across a range of habitat types from Panama to Argentina at varying elevations. We use this variation in elevation to examine whether the relationship between group behaviour and persistence varies across habitat types and along an elevation gradient. In particular, we hypothesize that collective aggressiveness should be favoured at sites with low prey availability (Pruitt et al., 2018). For *A. eximius*, low-elevation sites are reasoned to be resource and enemy rich because they harbour larger average prey sizes and higher ant densities at our study sites and the surrounding areas (Guevara & Aviles, 2007, 2015; Powers & Aviles, 2007). High aggressiveness is often needed to capitalize on rare prey capture opportunities and fend off enemies (Riechert, 1993b). Prey biomass does not show a consistent trend with elevation (Guevara & Aviles, 2007; Powers & Aviles, 2007), but reduced prey size is particularly salient for social spiders, because large prey are vital for the maintenance of large social spider colonies (Yip, Powers, & Aviles, 2008). Further, ants are often major predators of social spiders (Henschel, 1998; Purcell & Aviles, 2008). By contrast, we predict that less aggressive colonies will be favoured in high-resource and enemy-rich environments, like lowland rainforests (Purcell & Aviles, 2008). Thus, we predict that selection on collective aggressiveness will mimic the usual patterns observed in solitary spiders and other taxa, where low resources favour heightened aggression and responsiveness towards prey (Dunbrack, Clarke, & Bassler, 1996; Magurran & Seghers, 1991; Riechert, 1993a). If this is so, then it would hint that theory developed for behavioural evolution in solitary organisms can be redeployed to correctly predict patterns of selection occurring at the level of collective traits.

2 | MATERIALS AND METHODS

2.1 | Focal species and sites

We measured collective foraging aggressiveness in colonies of *A. eximius* across the Ecuadorian Amazon in October-November 2017. *A. eximius* colonies build basket-shaped nests with large sheet and tangle capture webs where they hunt collectively. We observed colonies at three sites on highway e45 near Archidona (*n* = 14; S 0° 46.214, W 77° 46.604), highway e20 towards Coca (*n* = 10; S 0° 43.421, W 77° 39.993) and near the Iyarina lodge (*n* = 9; S 1° 4.027, W 77° 37.228). We further sampled two sites: roadsides, forest

interiors and waterways in the Yasuní National Park (*n* = 16; S 0° 40.862, W 76° 23.152) and waterways near the Cuyabeno Wildlife Reserve (*n* = 21; S 0° 1.921, W 76° 12.851).

2.2 | Collective aggressiveness

We measured colonies' aggressiveness by placing dummy prey (1 cm sections of dead leaf) 4 cm from the rim of the nest basket, and vibrating it with a handheld vibratory device until spiders emerged and seized the dummy prey (Pruitt et al., 2017), between 1000 and 1600 hr. We recorded the latency of the first spider to contact the dummy and the number of spiders moving towards the dummy at this time. If spiders did not contact the dummy within 600s, we terminated the trial and recorded the latency as 600. We subtracted the attack latency from 600 to obtain an aggression index where higher scores correspond to higher aggressiveness (hereafter referred to as 'aggressiveness'). We repeated these tests every day for four days on a subset of colonies at Archidona (*n* = 11), Iyarina (*n* = 4) and Yasuní (*n* = 10), to assess the repeatability of colony aggressiveness. For all other analyses, only the first measurement was used. For the remaining colonies, aggressiveness was only measured once due to logistical constraints. Latency to attack prey and the number of spiders recruiting to an attack are a common measure of foraging aggressiveness in solitary and social spiders (Kralj-Fiser & Schneider, 2012; Kralj-Fiser et al., 2012; Pruitt, Grinsted, & Settepani, 2013; Riechert & Hedrick, 1993), and it tightly linked with prey capture success and foraging performance in several species of group-living spiders (Kamath et al., 2019; Pinter-Wollman, Mi, & Pruitt, 2017; Pruitt & Riechert, 2011).

2.3 | Habitat measurements and persistence

Immediately following aggressiveness assays, we also recorded habitat characteristics and marked colonies with aluminium tree tags. First, we recorded colony elevation and GPS coordinates (Garmin eTrex 30x). We assessed carnivorous ant presence by measuring latency of ant recruitment to 35 g of tuna within 2 m of the web (Hoffman & Avilés, 2017), placed on the forest floor beneath the colony. A subset of colonies was run through two such ant-baiting tests, and microhabitat differences in ant recruit speed were found to be consistent through time even within a specific site (*r* = .86, 95% CI: 0.57–0.96, *p* < .0001, *n* = 21). Faster ant recruitment times were taken as evidence that the microhabitat immediately around the focal colony had a greater risk of attack by predatory ants. Finally, as an exploratory measure, the canopy cover over each colony was estimated using the iPhone application Canopyapp (Davis, Dobrowski, Holden, Higuera, & Abatzoglou, 2019).

We estimated the volume of web baskets by measuring the size of the smallest possible orthotope that contained the basket, by first approximating the shape of each web (e.g. square base, circle base) and then taking the necessary measurements to compute the web volume. Web volume increases approximately linearly with group size in *A. eximius* (Powers & Aviles, 2007; Yip et al., 2008).

To determine colony survival, we returned in October 2018, eleven months later, and recorded whether the colony contained any remaining living individuals. This time interval corresponds to ~2 generations of *A. eximius* (Vollrath, 1982). All aluminium tags were then removed.

2.4 | Statistical methods

We could not satisfactorily fit a generalized linear model simultaneously evaluating the influence of elevation, aggression and colony size on persistence. Moreover, neither colony aggression nor elevation could satisfactorily be transformed towards normality. Finally, aggressiveness was not repeatable within sites, $r = 0$ (95% CI: 0.0–0.157, $p = .500$), indicating that colonies' behaviour within each site is relatively independent. Therefore, we compared the elevation, aggressiveness and web size of colonies that either persisted or not using Mann–Whitney U tests. We assessed the correlation between elevation and aggressiveness, and aggressiveness and colony size using Spearman rank correlations. We took the log of basket volume as our index of colony size.

To determine whether the relationship between colony persistence and aggression depended on the elevation of the colony, we split the data into 'high' elevations (above 740 m, 25 colonies) and 'low' elevations (below 450 m, 43 colonies). This split demarcates a natural break in our sampling distribution. We then compared the aggressiveness of colonies that persisted or not in each data set separately using Mann–Whitney U tests. To determine how canopy cover and the presence of predator ants varied with elevation, we performed Spearman rank correlations between elevation and each of canopy cover and the latency for ants to arrive at the tuna bait. There were 71 focal colonies in total. However, three colonies did not have elevations recorded. Four colonies had no web size measurements, owing to their residing in relatively inaccessible microhabitats (e.g. suspended over cliffs). Otherwise, sample sizes for each group in each comparison are given below. The repeatability

of colonies' aggressiveness and number of attackers were assessed by fitting linear a mixed model with either 'aggressiveness' or 'number of attackers' as the response variable, and then 'colony ID', 'site' and 'trial iteration' as random effects, using the rptR package (Stoffel, Nakagawa, & Schielzeth, 2017). This allows us to estimate the intra-class correlation coefficient of colony ID, while accounting for variance explained by site and trial iteration. We estimated 95% confidence intervals on repeatability estimates by running the linear mixed model though 1,000 bootstrap iterations. As mentioned above, we aimed to measure 25 colonies across three sites four times each, although three colonies only received three measurements, giving 97 measurements across 25 colonies in total to assess repeatability. We only assessed the role of behavioural traits in survival if we recovered a repeatability estimate that differed significantly from zero.

3 | RESULTS

Aggressiveness was repeatable, $r = .26$ (95% CI: 0.01–0.47, $p < .01$), but the number of attackers was not, $r = .14$ (95% CI: 0–0.33, $p = .04$). Therefore, we only consider aggressiveness hereafter. The influence of aggressiveness on persistence depended on elevation. At high elevations, persisting colonies were less aggressive (mean $= 505.12 \pm 32.63$ SE, $n = 19$) compared to colonies that vanished (mean $= 592.32 \pm 1.59$ SE, $n = 6$; Figure 1; Wilcoxon test, W = 2, $p < .001$). At low elevations, colonies that persisted appeared more aggressive (mean $= 582.84 \pm 3.50$ SE, $n = 27$) than colonies that vanished (mean $= 566.17 \pm 9.96$ SE, $n = 16$), but this difference was not significant (W = 272, $p = .17$).

Elevation did not influence colony persistence. The mean elevation of colonies that persisted and vanished was 584 m and 479 m, respectively (Figure S1; $n = 46$ & 22, respectively, Wilcoxon test $W = 570$, $p = .40$). Colony web size did not predict persistence; colonies that persisted were no larger than those that did not. Medians (means
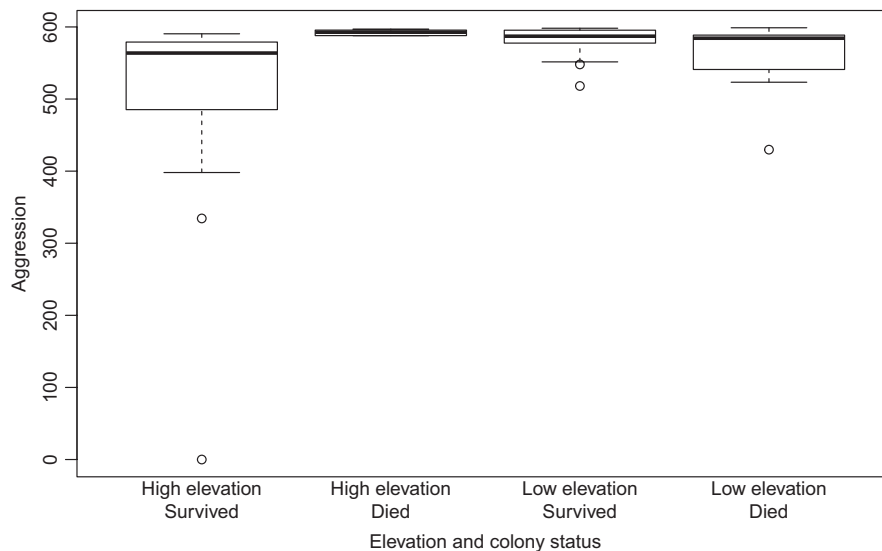
FIGURE 1 The aggressiveness of colonies that either survived or died, at low (<450 m)- or high (>740 m)-elevation sites. Aggression was 600 minus the latency to attack (maximum 600 s) hence is unitless

are highly biased by a few large value) of volume were 143,918 cm^3 for colonies that persisted and 90,450 cm^3 for colonies that vanished, but the median logged values are 11.87 and 11.41, respectively (Figure S1; n = 46 & 21, respectively, Wilcoxon test, W = 554, p = .34).

Colonies' aggressiveness was not related to their web size (Figure S2; n = 67, Spearman rank correlation, S = 47,550, rho = 0.05, p = .69), but colonies were more aggressive at lower elevations (Figure S2; n = 68, Spearman rank correlation, S = 65,398, rho = −0.25, p = .04).

Higher elevations were associated with reduced canopy cover (Spearman rank correlation, S = 66,623, rho = −0.33, p = .01) and the slower recruitment of ants (Spearman rank correlation, S = 21,568, rho = 0.26, p = .05).

4 | DISCUSSION

Understanding the forces that enable some groups to persist and proliferate when others crash or disband is helpful for predicting how social evolution proceeds in contrasting environments. For many social animals, this can be thought of as a kind of group-level viability selection. Colonies of the Amazonian social spider *A. eximius* undergo variation in selection on aggressiveness between low and high elevations. At odds with our *a priori* predictions, less aggressive colonies outperform their aggressive rivals at resource-poor high elevations (Figure 1). The opposite trend emerges at low elevations, although it was not statistically significant. Given this pattern of selection, one might predict that high-elevation *A. eximius* should be less aggressive overall, either because of local adaptation or via ongoing viability selection against aggressive colonies. Consistent with this prediction, we observed that colonies of *A. eximius* at higher elevation do indeed exhibit lower aggressiveness than their low-elevation counterparts (Figure S2b). In aggregate, this conveys that site-specific selection on colony aggressiveness could play a role in generating geographic variation in colony behaviour, akin to patterns observed in solitary species (Drummond & Burghardt, 1983; Magurran & Seghers, 1991; Riechert, 1993a; Walsh, Broyles, Beston, & Munch, 2016).

The mechanisms underlying the success of nonaggressive colonies at high elevation remain elusive. We predicted that low-resource conditions would favour colonies with swifter foraging responses because, in trap-building predators, foraging is a time-sensitive opportunity. Thus, colonies at high elevations should maximize on the limited foraging opportunities that are available to them (Guevara & Aviles, 2007; Powers & Aviles, 2007). This is often the case for individual-level aggressiveness (Dunbrack et al., 1996; Magurran & Seghers, 1991; Riechert, 1993a). Further, it is easier for single spiders to monopolize small prey items (Sharpe & Avilés, 2016), which could motivate them to be more aggressive at high elevations. However, it is perhaps equally plausible that low-resource conditions could favour reduced aggressiveness. If more aggressive colonies engage in more infighting, exhibit higher metabolic rates or are otherwise more susceptible to starvation, then selection may favour less aggressive colonies under low-resource conditions because it enables them to persist through times of

resource scarcity. This mode of competition is often referred to as *Tilman's R* Rule* (Tilman, 1982). Consistent with this hypothesis, there is evidence that both aggressive social *Anelosimus* (Lichtenstein & Pruitt, 2015) and *Stegodyphus* (Lichtenstein et al., 2017) are more susceptible to starvation and that nonaggressive *Stegodyphus* colonies can outperform their rivals when resources fall below a critical level (Pruitt, McEwen, Cassidy, Najm, & Pinter-Wollman, 2019). Alternatively, smaller average prey sizes at high-elevation sites might merely not require the same levels of aggressiveness to subdue than the larger prey of low-elevation sites. More detailed work within sites is needed to tease apart the mechanisms responsible for this among-site result.

One potential mechanism was the abundance of enemies. We found that ants recruited more quickly to tuna baits at lower elevations, consistent with Hoffman and Avilés (2017). This suggests that the threat of predation from ants, or perhaps the degree of indirect resource competition from ants, will be higher at lower elevations. Either of these could select for higher aggressiveness (or, at least, against docility) in social spiders, which are more frequently attacked by ants at low-elevation sites (Hoffman & Avilés, 2017; Purcell & Aviles, 2008), and this may help to explain the patterns of selection that we observed. We also observed reduced canopy cover at higher elevations. Although this seems unlikely to directly influence spider colony survival, it may influence the availability of prey (i.e. decreased cover may decrease the number of flying invertebrates) or increase web damage costs, and thus, have consequences for the benefits of colony aggression.

At odds with previous work, group size was not a significant predictor of colony persistence in our field data on *A. eximius*. The formation of larger coalitions is frequently associated with reduced group failure rate in social arthropods, and this fact is thought to underlie the formation of social life history trajectories like foundress coalitions in wasps and ants (Fewell & Page, 1999; Miller et al., 2018; Seppa, Queller, & Strassmann, 2002; Tibbetts & Reeve, 2003). Group size-dependent survival has also been documented in a number of social (Aviles & Tufino, 1998; Bilde et al., 2007) and transitionally social species of spiders (Lichtenstein, Bengston, Aviles, & Pruitt, 2018). We reason that this discrepancy between findings is because colonies of the smallest size classes (one to a few dozen spiders) are largely missing from our data set, and the persistence benefits of increasing group size are most pronounced at the smallest colony sizes (Aviles & Tufino, 1998; Lichtenstein et al., 2018).

In summary, we detected a site-specific relationship between colony aggressiveness and persistence in a social spider. Furthermore, we found a cline in aggression with elevation that suggests that the selective benefits to reduced aggression at higher elevations are strong enough to promote appropriate fit between colony traits and the habitats in which they reside.

CONFLICT OF INTERESTS

We declare no competing interests.

AUTHORS CONTRIBUTIONS

JLLL and BLM assisted with all aspects of the study pipeline. DTN, EC, CS and JE assisted with data collection. DNF and JNP helped to analyse the data and write the paper.

ETHICAL APPROVAL

The studies herein were conducted on invertebrates and were therefore not subject to ethics approval. Field studies were conducted under research permit N°23-17 IC-FAU-DNB/MA.

DATA ACCESSIBILITY STATEMENT

The data for this manuscript can be found on Dryad: https://datadryad.org/review?doi=doi:10.5061/dryad.hr90jf2

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.