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COLLECTIVE AGGRESSIVENESS LIMITS COLONY PERSISTENCE IN HIGH BUT NOT LOW ELEVATION SITES IN AMAZONIAN SOCIAL SPIDERS

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10   **ELEVATION SITES IN AMAZONIAN SOCIAL SPIDERS**

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22   **Authors Contributions**: JLLL and BLM assisted with all aspects of the study pipeline. DTN,

23   EC, CS and JE assisted with data collection. DNF and JNP helped to analyze the data and write

24   the paper.

Anonymized et al. 2

32   **ABSTRACT**

33   Identifying the traits that foster group survival in contrasting environments is important for

34   understanding local adaptation in social systems. Here we evaluate the relationship between the

35   aggressiveness of social spider colonies and their persistence along an elevation gradient using

36   the Amazonian spider, Anelosimus eximius. We found that colonies of A. eximius exhibit

37   repeatable differences in their collective aggressiveness (latency to attack prey stimuli), and that

38   colony aggressiveness is linked with persistence in a site-specific manner. Less aggressive

39   colonies are better able to persist at high-elevation sites, which lack colony-sustaining large-

40   bodied prey, whereas colony aggression was not related to chance of persistence at low-elevation

41   sites. This suggests that low aggressiveness promotes colony survival in high-elevation, prey-

42   poor habitats, perhaps via increased tolerance to resource limitation. These data reveal that the

43   collective phenotypes that relate to colony persistence vary by site, and thus, the path of social

44   evolution in these environments is likely to be affected.

45   **Key words**: Araneae, collective behavior, insect abundance, life history, multilevel selection

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 (Tibbetts & Reeve, 2003, Hahn & Tschinkel, 1997, Aviles & Tufino, 1998). 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 (Jandt et al., 2014, Bengston & Jandt, 2014, Wray & Seeley, 2011). Like individual traits, a growing body of evidence conveys that group traits are often associated with group success (Shaffer et al., 2016, Gordon, 2013, Wray et al., 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 behavior 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 (Keiser et al., 2015, Henschel, 1998), parasitism (Straus & Avilés, 2018, Vollrath, 1987), and fungal outbreak (Henschel, 1998). To avoid these fates, social spiders collectively catch prey, repair webs, 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 (Riechert & Roeloffs, 1993, Aviles, 1993, Henschel

69 et al., 1995), and group success is a major determinant of individuals' inclusive fitness. Here, we

70 explore the degree to which group behavior is linked with group persistence using a highly social

71 spider, the Amazonian spider Anelosimus eximius (Araneae, Theridiidae).

72   This species occurs across a range of habitat types from Panama to Argentina at varying

73 elevations. We use this variation in elevation to examine whether the relationship between group

74 behavior and persistence varies across habitat types and along an elevation gradient. In

75 particular, we hypothesise that collective aggressiveness should be favored at sites with low prey

76 availability (Pruitt et al., 2018). For A. eximius, low-elevation sites are reasoned to be resource

77 and enemy rich because they harbor larger average prey sizes and higher ant densities at our

78 study sites and the surrounding areas (Powers & Aviles, 2007, Guevara & Aviles, 2007, Guevara

79 & Aviles, 2015). High aggressiveness is often needed to capitalize on rare prey capture

80 opportunities and fend off enemies (Riechert, 1993b). Prey biomass does not show a consistent

81 trend with elevation (Guevara & Aviles, 2007, Powers & Aviles, 2007), but reduced prey size is

82 particularly salient for social spiders, because large prey are vital for the maintenance of large

83 social spider colonies (Yip et al., 2008). Further, ants are often major predators of social spiders

84 (Henschel, 1998, Purcell & Aviles, 2008). By contrast, we predict that less aggressive colonies

85 will be favored in high-resource and enemy-rich environments, like lowland rainforests (Purcell

86 & Aviles, 2008). Thus, we predict that selection on collective aggressiveness will mimic the

87 usual patterns observed in solitary spiders and other taxa, where low resources favor heightened

88 aggression and responsiveness towards prey (Riechert, 1993a, Magurran & Seghers, 1991,

89 Dunbrack et al., 1996). If this is so, then it would hint that theory developed for behavioral

90 evolution in solitary organisms can be redeployed to correctly predict patterns of selection

91 occurring at the level of collective traits.

MATERIALS AND METHODS

94

Focal species and sites:

96 We measured collective foraging aggressiveness in colonies of A. eximius across the Ecuadorian

97 Amazon in Oct.-Nov. 2017. A. eximius colonies build basket-shaped nests with large sheet and

98 tangle capture webs where they hunt collectively. We observed colonies at three sites on

99 highway e45 near Archidona (n=14; S 0˚ 46.214, W 77˚ 46.604), highway e20 towards Coca

100 (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).

101 We further sampled two sites: roadsides, forest interiors, and waterways in the Yasuní National

102 Park (n=16; S 0˚ 40.862, W 76˚ 23.152) and waterways near the Cuyabeno Wildlife Reserve

103 (n=21; S 0˚ 1.921, W 76˚ 12.851).

104

Collective aggressiveness:

106 We measured colonies' aggressiveness by placing dummy prey (1cm sections of dead leaf) 4cm

107 from the rim of the nest basket, and vibrating it with a handheld vibratory device until spiders

108 emerged and seized the dummy prey (Pruitt et al., 2017), between 1000-1600 hours. We

109 recorded the latency of the first spider to contact the dummy and the number of spiders moving

110 towards the dummy at this time. If spiders did not contact the dummy within 600s, we terminated

111 the trial and recorded the latency as 600. We subtracted the attack latency from 600 to obtain an

112 aggression index where higher scores correspond to higher aggressiveness (hereafter referred to

113 as "aggressiveness"). We repeated these tests every day for four days on a subset of colonies at

114 Archidona (n=11), Iyarina (n=4), and Yasuní (n=10), to assess the repeatability of colony

Anonymized et al. 6

115   aggressiveness. For all other analyses, only the first measurement was used. For the remaining

116   colonies, aggressiveness was only measured once due to logistical constraints. Latency to attack

117   prey and the number of spiders recruiting to an attack are a common measure of foraging

118   aggressiveness in solitary and social spiders (Riechert & Hedrick, 1993, Pruitt et al., 2013, Kralj-

119   Fiser & Schneider, 2012, Kralj-Fiser et al., 2012), and it tightly linked with prey capture success

120   and foraging performance in several species of group-living spiders (Kamath et al., 2018, Pinter-

121   Wollman et al., 2017, Pruitt & Riechert, 2011).

122

123   Habitat measurements and persistence:

124   Immediately following aggressiveness assays, we also recorded habitat characteristics and

125   marked colonies with aluminium tree tags. First, we recorded colony elevation and GPS

126   coordinates (Garmin eTrex 30x). We assessed carnivorous ant presence by measuring latency of

127   ant recruitment to 35g of tuna within 2m of the web (Hoffman & Avilés, 2017), placed on the

128   forest floor beneath the colony. A subset of colonies was run through two such ant-baiting tests,

129   and microhabitat differences in ant recruit speed were found to be consistent through time even

130   within a specific site (r = 0.86, 95% CI: 0.57-0.96, p < 0.0001, n = 21). Faster ant recruitment

131   times were taken as evidence that the microhabitat immediately around the focal colony had a

132   greater risk of attack by predatory ants. Finally, as an exploratory measure, the canopy cover

133   over each colony was estimated using the iPhone application Canopyapp (Davis et al., 2018).

134   We estimated the volume of web baskets by measuring the size of the smallest possible

135   orthotope that contained the basket, by first approximating the shape of each web (e.g., square

136   base, circle base) and then taking the necessary measurements to compute the web volume. Web

137   volume increases approximately linearly with group size in A. eximius (Yip et al., 2008, Powers

Anonymized et al. 7

138 & Aviles, 2007). To determine colony survival, we returned in Oct. 2018, eleven months later,

139 and recorded whether the colony contained any remaining living individuals. This time interval

140 corresponds to ~2 generations of A. eximius (Vollrath, 1982). All aluminum tags were then

141 removed.

142

143 Statistical methods:

144 We could not satisfactorily fit a generalised linear model simultaneously evaluating the influence

145 of elevation, aggression and colony size on persistence. Moreover, neither colony aggression nor

146 elevation could satisfactorily be transformed towards normality. Finally, aggressiveness was not

147 repeatable within sites, r = 0 (95% CI: 0.0 - 0.157, p = 0.500), indicating that colonies' behavior

148 within each site are relatively independent. Therefore, we compared the elevation,

149 aggressiveness, and web size of colonies that either persisted or not using Mann-Whitney U-

150 tests. We assessed the correlation between elevation and aggressiveness, and aggressiveness and

151 colony size using Spearman rank correlations. We took the log of basket volume as our index of

152 colony size.

153 To determine whether the relationship between colony persistence and aggression

154 depended on the elevation of the colony, we split the data into "high" elevations (above 740m,

155 25 colonies) and "low" elevations (below 450m, 43 colonies). This split demarcates a natural

156 break in our sampling distribution. We then compared the aggressiveness of colonies that

157 persisted or not in each dataset separately using Mann Whitney-U tests. To determine how

158 canopy cover and the presence of predator ants varied with elevation, we performed Spearman

159 rank correlations between elevation and each of canopy cover and the latency for ants to arrive at

160 the tuna bait. There were 71 focal colonies in total. However, three colonies did not have

Anonymized et al. 8

161 elevations recorded. Four colonies had no web size measurements, owing to their residing in

162 relatively inaccessible microhabitats (e.g., suspended over cliffs). Otherwise, sample sizes for

163 each group in each comparison are given below. The repeatability of colonies' aggressiveness

164 and number of attackers were assessed by fitting linear a mixed model with either

165 "aggressiveness" or "number of attackers" as the response variable, and then "colony ID",

166 "site", and "trial iteration" as random effects, using the rptR package (Stoffel et al., 2017). This

167 allows us to estimate the intra-class correlation coefficient of colony ID, while accounting for

168 variance explained by site and trial iteration. We estimated 95% confidence intervals on

169 repeatability estimates by running the linear mixed model though 1000 bootstrap iterations. As

170 mentioned above, we aimed to measure 25 colonies across three sites four times each, although

171 three colonies only received three measurements, giving 97 measurements across 25 colonies in

172 total to assess repeatability. We only assessed the role of behavioural traits in survival if we

173 recovered a repeatability estimate that differed significantly from zero.

174

175 **RESULTS**

176

177 Aggressiveness was repeatable, $r = 0.26$ (95% CI: 0.01 - 0.47, $p < 0.01$), but the number of

178 attackers was not, $r = 0.14$ (95% CI: 0 - 0.33, $p = 0.04$). Therefore, we only consider

179 aggressiveness hereafter. The influence of aggressiveness on persistence depended on elevation.

180 At high elevations, persisting colonies were less aggressive (mean = 505.12 ± 32.63 SE, $n = 19$)

181 compared to colonies that vanished (mean = 592.32 ± 1.59 SE, $n = 6$; Fig. 1; Wilcox test, $W = 2$,

182 $p < 0.001$). At low elevations, colonies that persisted appeared more aggressive (mean = 582.84

183   ± 3.50 SE, n = 27) than colonies that vanished (mean = 566.17 ± 9.96 SE, n= 16), but this

184   difference was not significant (W = 272, p = 0.17).

185   Elevation did not influence colony persistence. The mean elevation of colonies that

186   persisted and vanished was 584m and 479m respectively (Fig. S1; n = 46 & 22 respectively,

187   Wilcox test W = 570, p =0.40). Colony web size did not predict persistence; colonies that

188   persisted were no larger than those than did not. Medians (means are highly biased by a few

189   large value) of volume were 143,918 cm^3 for colonies that persisted and 90,450cm^3 for colonies

190   that vanished, but the median logged values are 11.87 and 11.41 respectively (Fig. S1; n = 46 &

191   21 respectively, Wilcox test, W = 554, p = 0.34).

192   Colonies' aggressiveness was not related to their web size (Fig. S2; n = 67, Spearman

193   rank correlation, S = 47550, rho = 0.05, p = 0.69), but colonies were more aggressive at lower

194   elevations (Fig. S2; n = 68, Spearman rank correlation, S = 65398, rho = -0.25, p = 0.04).

195   Higher elevations were associated with reduced canopy cover (Spearman rank

196   correlation, S = 66623, rho = -0.33, p = 0.01) and the slower recruitment of ants (Spearman rank

197   correlation, S = 21568, rho = 0.26, p = 0.05).

198

199   **DISCUSSION**

200

201   Understanding the forces that enable some groups to persist and proliferate when others crash or

202   disband is helpful for predicting how social evolution proceeds in contrasting environments. For

203   many social animals, this can be thought of as a kind of group-level viability selection. Colonies

204   of the Amazonian social spider A. eximius undergo variation in selection on aggressiveness

205   between low and high elevations. At odds with our a priori predictions, less aggressive colonies

Anonymized et al. 10

206   outperform their aggressive rivals at resource-poor high elevations (Fig. 1). The opposite trend

207   emerges at low elevations, although it was not statistically significant. Given this pattern of

208   selection, one might predict that high elevation A. eximius should be less aggressive overall,

209   either because of local adaptation or via on-going viability selection against aggressive colonies.

210   Consistent with this prediction, we observed that colonies of A. eximius at higher elevation do

211   indeed exhibit lower aggressiveness than their low-elevation counterparts (Fig. S2B). In

212   aggregate, this conveys that site-specific selection on colony aggressiveness could play a role in

213   generating geographic variation in colony behavior, akin to patterns observed in solitary species

214   (Drummond & Burghardt, 1983, Magurran & Seghers, 1991, Riechert, 1993a, Walsh et al.,

215   2016).

216   The mechanisms underlying the success of non-aggressive colonies at high elevation

217   remain elusive. We predicted that low-resource conditions would favor colonies with swifter

218   foraging responses because, in trap-building predators, foraging is a time-sensitive opportunity.

219   Thus, colonies at high elevations should maximize on the limited foraging opportunities that are

220   available to them (Powers & Aviles, 2007, Guevara & Aviles, 2007). This is often the case for

221   individual-level aggressiveness (Riechert, 1993a, Magurran & Seghers, 1991, Dunbrack et al.,

222   1996). Further, it is easier for single spiders to monopolize small prey items (Sharpe & Avilés,

223   2016), which could motivate them to be more aggressive at high elevations. However, it is

224   perhaps equally plausible that low-resource conditions could favor reduced aggressiveness. If

225   more aggressive colonies engage in more infighting, exhibit higher metabolic rates, or are

226   otherwise more susceptible to starvation, then selection may favor less aggressive colonies under

227   low resource conditions because it enables them to persist through times of resource scarcity.

228   This mode of competition is often referred to as *Tilman's R* Rule* (Tilman, 1982). Consistent

Anonymized et al. 11

229   with this hypothesis, there is evidence that both aggressive social Anelosimus (Lichtenstein &

230   Pruitt, 2015) and Stegodyphus (Lichtenstein et al., 2017) are more susceptible to starvation, and

231   that non-aggressive Stegodyphus colonies can outperform their rivals when resources fall below

232   a critical level (Pruitt et al., 2019). Alternatively, smaller average prey sizes at high elevation

233   sites might merely not require the same levels of aggressiveness to subdue than the larger prey of

234   low elevation sites. More detailed work within sites is needed to tease apart the mechanisms

235   responsible for this among-site result.

236   One potential mechanism was the abundance of enemies. We found that ants recruited

237   more quickly to tuna baits at lower elevations, consistent with Hoffman and Avilés (2017). This

238   suggests that the threat of predation from ants, or perhaps the degree of indirect resource

239   competition from ants, will be higher at lower elevations. Either of these could select for higher

240   aggressiveness (or, at least, against docility) in social spiders, which are more frequently attacked

241   by ants at low-elevation sites (Purcell & Aviles, 2008, Hoffman & Avilés, 2017), and this may

242   help to explain the patterns of selection that we observed. We also observed reduced canopy

243   cover at higher elevations. While this seems unlikely to directly influence spider colony survival,

244   it may influence the availability of prey (i.e. decreased cover may decrease the number of flying

245   invertebrates) or increase web damage costs, and thus, have consequences for the benefits of

246   colony aggression.

247   At odds with previous work, group size was not a significant predictor of colony

248   persistence in our field data on A. eximius. The formation of larger coalitions is frequently

249   associated with reduced group failure rate in social arthropods, and this fact is thought to

250   underlie the formation of social life history trajectories like foundress coalitions in wasps and

251   ants (Fewell & Page, 1999, Seppa et al., 2002, Tibbetts & Reeve, 2003, Miller et al., 2018).

Anonymized et al. 12

252 Group size dependent survival has also been documented in a number of social (Bilde et al.,

253 2007, Aviles & Tufino, 1998) and transitionally social species of spiders (Lichtenstein et al.,

254 2018). We reason that this discrepancy between findings is because colonies of the smallest size

255 classes (one to a few dozen spiders) are largely missing from our data set, and the persistence

256 benefits of increasing group size are most pronounced at the smallest colony sizes (Lichtenstein

257 et al., 2018, Aviles & Tufino, 1998).

258   In summary we detected a site-specific relationship between colony aggressiveness and

259 persistence in a social spider. Furthermore, we found a cline in aggression with elevation that

260 suggests that the selective benefits to reduced aggression at higher elevations are strong enough

261 to promote appropriate fit between colony traits and the habitats in which they reside.

262

263 **Ethics**: The studies herein were conducted on invertebrates and were therefore not subject to

264 ethics approval. Field studies were conducted under research permit N°23-17 IC-FAU-

265 DNB/MA.

266 **Data accessibility**: The data for this manuscript can be found on Dryad:

267 https://datadryad.org/review?doi=doi:10.5061/dryad.hr90jf2

268 **Competing Interests**: We declare no competing interests.

269

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414 **Figures & Supplementary Figures:**
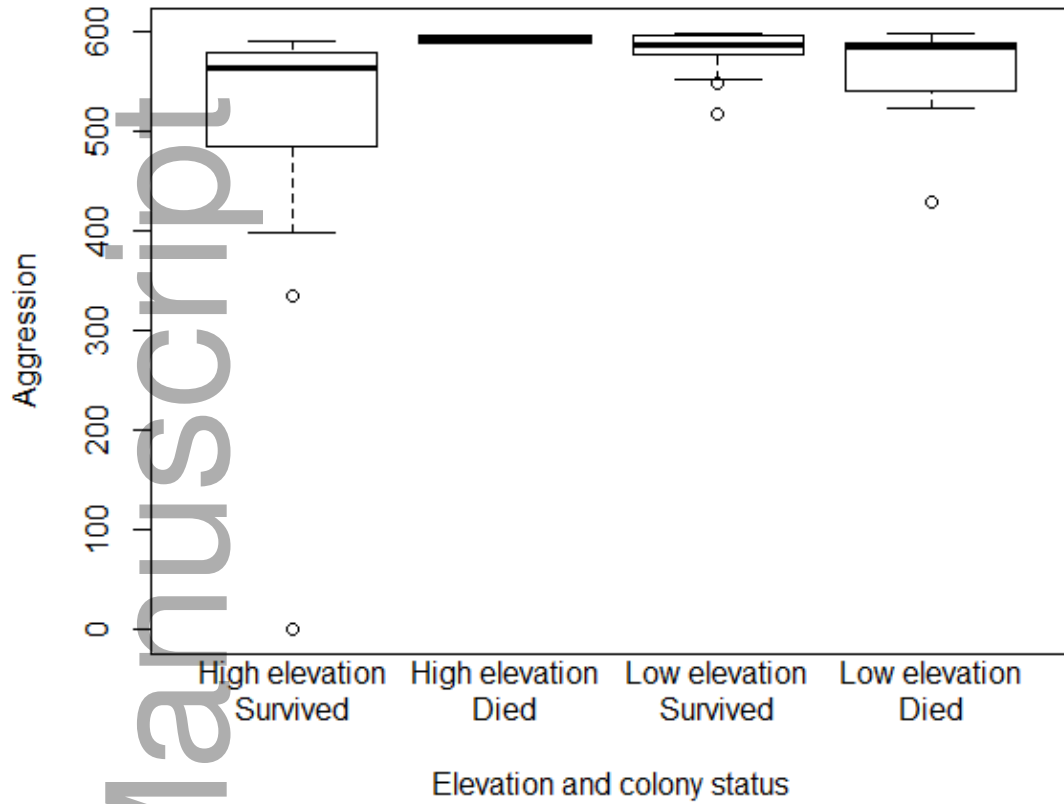
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416 **Figure 1**. The aggressiveness of colonies that either survived or died, at low (< 450m) or high

417 (>740m) elevation sites. Aggression was 600 minus the latency to attack (maximum 600

418 seconds) hence is unitless.

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