

1           **COLLECTIVE AGGRESSIVENESS LIMITS COLONY PERSISTENCE IN HIGH BUT NOT LOW**

2                           **ELEVATION SITES IN 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, 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 resistance to resource limitation through docility promotes colony survival at high elevations. 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.

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

27 **INTRODUCTION**

28 Although social evolution provides numerous benefits for group constituents (Krause & Ruxton,  
29 2002), social groups can also vary considerably in their success (ants: Gordon, 2013, social  
30 spiders: Aviles, 1986, honey bees: Watanabe, 2008). For a variety of social organisms, many or  
31 most of the social groups ever founded will swiftly end in their collective demise (Tibbetts &  
32 Reeve, 2003, Hahn & Tschinkel, 1997, Aviles & Tufino, 1998). In some taxa, even social groups  
33 in apparent good health can fall victim to colony extinction events (Pruitt, 2012). Thus, any  
34 feature that enables groups to persist in their environment is likely to foster their success. Social  
35 organisms provide an interesting case study for evolutionary ecologists, because trait differences  
36 occur at both the individual level and between groups, in terms of their collective traits (Jandt et  
37 al., 2014, Bengston & Jandt, 2014, Wray & Seeley, 2011). Like individual traits, a growing body  
38 of evidence conveys that group traits are often associated with group success (Shaffer et al.,  
39 2016, Gordon, 2013, Wray et al., 2011), and that these links can vary between environments  
40 (Pruitt & Goodnight, 2014, Pruitt et al., 2018). Site-specific selection may therefore contribute to  
41 biodiversity by promoting intraspecific variation and local adaptation in group-level traits.

42 Social spiders are a useful model with which to explore the evolutionary ecology of  
43 group extinction events and collective behavior in general. This is because social spider groups  
44 emerge and disappear with high frequencies (reviewed in Aviles & Guevara, 2017). This, and  
45 because groups are inbred and composed of highly related individuals (Riechert & Roeloffs,  
46 1993, Aviles, 1993, Henschel et al., 1995), means that group success is a major determinant of  
47 individuals' inclusive fitness. Here we explore the degree to which group behavior is linked with  
48 group persistence using a highly social spider, the Amazonian spider *Anelosimus eximius*  
49 (Araneae, Theridiidae). This species occurs across a range of habitat types from Panama to

50 Argentina at varying elevations. We use this variation in elevation to examine whether the  
51 relationship between group behavior and persistence varies along an elevation gradient. In  
52 particular, we hypothesise that collective aggressiveness should be favored at sites with low prey  
53 availability (Pruitt et al., 2018). For *A. eximius*, high-elevation sites are reasoned to be resource-  
54 limited because they harbor smaller average prey sizes (Yip et al., 2008, Powers & Aviles, 2007,  
55 Guevara & Aviles, 2007, Guevara & Aviles, 2015). By contrast, we predict that less aggressive  
56 colonies will be favored in high-resource and enemy-rich environments, like lowland rainforests  
57 (Purcell & Aviles, 2008). Thus, we predict that selection on collective aggressiveness will mimic  
58 the usual patterns observed in solitary spiders and other taxa, where low resources favor  
59 heightened aggression and responsiveness towards prey (Riechert, 1993, Magurran & Seghers,  
60 1991, Dunbrack et al., 1996). If this is so, then it would hint that theory developed for behavioral  
61 evolution in solitary organisms can be redeployed to correctly predict patterns of selection  
62 occurring at the level of collective traits.

63

## 64 MATERIALS AND METHODS

65

### 66 *Focal species and sites:*

67 We measured collective foraging aggressiveness in colonies of *A. eximius* across the Ecuadorian  
68 Amazon in Oct.-Nov. 2017. *A. eximius* colonies build basket-shaped nests with large capture  
69 webs where they hunt collectively. We observed colonies at three sites on the e45 near  
70 Archidona (n=14; S 0° 46.214, W 77° 46.604), the e20 towards Coca (n=10; S 0° 43.421, W 77°  
71 39.993), and near the Iyarina lodge (n=9; S 1° 4.027, W 77° 37.228). We further sampled two  
72 sites: roadsides, forest interiors, and waterways in the Yasuní National Park (n=16; S 0° 40.862,

73 W 76° 23.152) and waterways near the Cuyabeno Wildlife Reserve (n=21; S 0° 1.921, W 76°  
74 12.851).

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76 *Collective aggressiveness:*

77 We measured colonies' aggressiveness by placing dummy prey (1cm sections of dead leaf) 4cm  
78 from the rim of the nest basket, and vibrating it with a handheld vibratory device until spiders  
79 emerged and seized the dummy prey (Pruitt et al., 2017), between 1000-1600 hours. We  
80 recorded the latency of the first spider to contact the dummy. We subtracted the attack latency  
81 from 600 to obtain an aggression index where higher scores correspond to higher aggressiveness.  
82 We repeated these tests every day for four days on a subset of colonies at Archidona (n=11),  
83 Iyarina (n=4), and Yasuní (n=10), to assess the repeatability of colony aggressiveness. For the  
84 remaining colonies, aggressiveness was only measured once due to logistical constraints.  
85 Latency to attack prey is a common measure of foraging aggressiveness in solitary and social  
86 spiders (Riechert & Hedrick, 1993, Pruitt et al., 2013, Kralj-Fiser & Schneider, 2012, Kralj-Fiser  
87 et al., 2012), and it tightly linked with prey capture success and foraging performance in several  
88 species of group-living spiders (Kamath et al., 2018, Pinter-Wollman et al., 2017, Pruitt &  
89 Riechert, 2011).

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91 *Habitat measurements and persistence:*

92 Immediately following aggressiveness assays, we also recorded habitat characteristics and  
93 marked colonies with aluminium tree tags. First, we recorded colony elevation and GPS  
94 coordinates (Garmin eTrex 30x). Then, the canopy cover over each colony was estimated with  
95 using the iPhone application Canopyapp (Davis et al., 2018). We assessed carnivorous ant

96 presence by measuring latency of ant recruitment to 35g of tuna within 2m of the web (Hoffman  
97 & Avilés, 2017), placed on the forest floor beneath the colony. A subset of colonies was run  
98 through two such ant-baiting tests, and microhabitat differences in ant recruit speed were found  
99 to be consistent through time even within a specific site ( $r = 0.86$ , 95% CI: 0.57-0.96,  $p < 0.0001$ ,  
100  $n = 21$ ). Faster ant recruitment times were taken as evidence that the microhabitat immediately  
101 around the focal colony had a greater risk of attack by predatory ants.

102 We estimated the volume of web baskets by measuring the size of the smallest possible  
103 orthotope that contained the basket, by first approximating the shape of each web (e.g., square  
104 base, circle base) and then taking the necessary measurements to compute the web volume. Web  
105 volume increases approximately linearly with group size in *A. eximius* (Yip et al., 2008, Powers  
106 & Aviles, 2007). To determine colony survival, we returned in Oct. 2018, eleven months later,  
107 and recorded whether the colony contained any remaining living individuals. This time interval  
108 corresponds to ~2 generations of *A. eximius* (Vollrath, 1982). All aluminum tags were then  
109 removed.

110

#### 111 *Statistical methods:*

112 We could not satisfactorily fit a generalised linear model simultaneously evaluating the influence  
113 of elevation, aggression and colony size on persistence. Moreover, neither colony aggression nor  
114 elevation could satisfactorily be transformed towards normality. Finally, aggressiveness was not  
115 repeatable within sites,  $r = 0$  (95% CI: 0.0 - 0.157,  $p = 0.500$ ), indicating that colonies' behavior  
116 within each site are relatively independent. Therefore, we compared the elevation,  
117 aggressiveness, and web size of colonies that either persisted or not using Mann-Whitney U-  
118 tests. We assessed the correlation between elevation and aggressiveness, and aggressiveness and

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

121 To determine whether the relationship between colony persistence and aggression  
122 depended on the elevation of the colony, we split the data into “high” elevations (above 740m,  
123 25 colonies) and “low” elevations (below 450m, 43 colonies). This split demarcates a natural  
124 break in our sampling distribution. We then compared the aggressiveness of colonies that  
125 persisted or not in each dataset separately using Mann Whitney-U tests. To determine how  
126 canopy cover and the presence of predator ants varied with elevation, we performed Spearman  
127 rank correlations between elevation and each of canopy cover and the latency for ants to arrive at  
128 the tuna bait. There were 71 focal colonies in total. However, three colonies did not have  
129 elevations recorded. Four colonies had no web size measurements, owing to their residing in  
130 relatively inaccessible microhabitats (e.g., suspended over cliffs). Otherwise, sample sizes for  
131 each group in each comparison are given below. The repeatability of colonies’ aggressiveness  
132 was assessed by fitting linear a mixed model with “aggressiveness” as the response variable,  
133 “colony ID”, “site”, and “trial iteration”, using the rptR package (Stoffel et al., 2017). This  
134 allows us to estimate the intra-class correlation coefficient of colony ID, while accounting for  
135 variance explained by site and trial iteration. We estimated 95% confidence intervals on  
136 repeatability estimates by running the linear mixed model though 1000 bootstrap iterations. As  
137 mentioned above, we aimed to measure 25 colonies across three sites four times each, although  
138 three colonies only received three measurements, giving 97 measurements across 25 colonies in  
139 total to assess repeatability.

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## RESULTS

142  
143 The influence of aggression on persistence depended on altitude. At high elevations, persisting  
144 colonies were less aggressive (mean = 505, n = 19) compared to colonies that vanished (mean =  
145 592, n = 6; Fig. 1; Wilcox test,  $W = 2$ ,  $p < 0.001$ ). At low elevations, colonies that persisted were  
146 more aggressive (mean = 582, n = 27) than colonies that vanished (mean = 562, n = 16) but this  
147 difference was not significant ( $W = 272$ ,  $p = 0.165$ ). Although we could not satisfactorily fit a  
148 glmm to our data, the results of a glmm analysis qualitatively matched the results presented here  
149 (model predicting colony survival [*aggression x elevation*]: Est =  $-13.9 \pm 6.30$ ,  $z = -2.21$ ,  $p =$   
150 0.027).

151 Elevation did not influence colony persistence. The mean elevation of colonies that  
152 persisted and vanished was 584m and 479m respectively (Fig. S1; n = 46 & 22 respectively,  
153 Wilcox test  $W = 570$ ,  $p = 0.404$ ). Colony web size did not predict persistence; colonies that  
154 persisted were no larger than those that did not. Medians (means are highly biased by a few  
155 large value) of volume were  $143,918 \text{ cm}^3$  for colonies that persisted and  $90,450 \text{ cm}^3$  for colonies  
156 that vanished, but the median logged values are 11.87 and 11.41 respectively (Fig. S1; n = 46 &  
157 21 respectively, Wilcox test,  $W = 554$ ,  $p = 0.344$ ).

158 Colonies' aggressiveness was not related to their web size (Fig. S2; n = 67, Spearman  
159 rank correlation,  $S = 47550$ ,  $p = 0.691$ ,  $\rho = 0.051$ ), but colonies were more aggressive at lower  
160 elevations (Fig. S2; n = 68, Spearman rank correlation,  $S = 65398$ ,  $p = 0.041$ ,  $\rho = -0.248$ ).  
161 Colony aggression was repeatable,  $r = 0.26$  (95% CI: 0.012 - 0.474,  $p = 0.003$ ).

162 Higher elevations were associated with reduced canopy cover (Spearman rank  
163 correlation,  $S = 66623$ ,  $p = 0.006$ ,  $\rho = -0.329$ ) and the slower recruitment of ants (Spearman  
164 rank correlation,  $S = 21568$ ,  $p = 0.050$ ,  $\rho = 0.263$ ).



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## DISCUSSION

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168 Understanding the forces that enable some groups to persist and proliferate when others crash or  
169 disband is helpful for predicting how social evolution proceeds in contrasting environments. For  
170 many social animals, this can be thought of as a kind of group-level viability selection. Colonies  
171 of the Amazonian social spider *A. eximius* exhibit clinal variation in selection on aggressiveness.  
172 At odds with our *a priori* predictions, less aggressive colonies outperform their aggressive rivals  
173 at resource-poor high elevations. The opposite trend emerges at low elevations, although it was  
174 not statistically significant. Given this pattern of selection, one might predict that high elevation  
175 *A. eximius* should be less aggressive overall, either because of local adaptation or via on-going  
176 viability selection against aggressive colonies. Consistent with this prediction, we observed that  
177 colonies of *A. eximius* at higher elevation do indeed exhibit lower aggressiveness than their low-  
178 elevation counterparts. In aggregate, this conveys that site-specific selection on colony  
179 aggressiveness could play a role in generating geographic variation in colony behavior, akin to  
180 patterns observed in solitary species (Drummond & Burghardt, 1983, Magurran & Seghers,  
181 1991, Riechert, 1993, Walsh et al., 2016).

182 The mechanisms underlying the success of non-aggressive colonies at high elevation  
183 remain elusive. We predicted that low-resource conditions would favor colonies with swifter  
184 foraging responses because, in trap-building predators, foraging is a time-sensitive opportunity.  
185 Thus, colonies at high elevations should maximize on the limited foraging opportunities that are  
186 available to them (Powers & Aviles, 2007, Guevara & Aviles, 2007). This is often the case for  
187 individual-level aggressiveness (Riechert, 1993, Magurran & Seghers, 1991, Dunbrack et al.,

188 1996). However, it is perhaps equally plausible that low-resource conditions could favor reduced  
189 aggressiveness. If more aggressive colonies engage in more infighting, exhibit higher metabolic  
190 rates, or are otherwise more susceptible to starvation, then selection may favor less aggressive  
191 colonies under low resource conditions because it enables them to persist through times of  
192 resource scarcity. This mode of competition is often referred to as *Tilman's R\* Rule* (Tilman,  
193 1982). Consistent with this hypothesis, there is evidence that both aggressive social *Anelosimus*  
194 (Lichtenstein & Pruitt, 2015) and *Stegodyphus* (Lichtenstein et al., 2017) are more susceptible to  
195 starvation, and that non-aggressive *Stegodyphus* colonies can outperform their rivals when  
196 resources fall below a critical level (Pruitt et al., in press). Alternatively, smaller average prey  
197 sizes at high elevation sites might merely not require the same levels of aggressiveness to subdue  
198 than the larger prey of low elevation sites. More detailed work within sites is needed to tease  
199 apart the mechanisms responsible for this among-site result.

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

210 At odds with previous work, group size was not a significant predictor of colony  
211 persistence in our field data on *A. eximius*. The formation of larger coalitions is frequently  
212 associated with reduced group failure rate in social arthropods, and this fact is thought to  
213 underlie the formation of social life history trajectories like foundress coalitions in wasps and  
214 ants (Fewell & Page, 1999, Seppa et al., 2002, Tibbetts & Reeve, 2003, Miller et al., 2018).  
215 Group size dependent survival has also been documented in a number of social (Bilde et al.,  
216 2007, Aviles & Tufino, 1998) and transitionally social species of spiders (Lichtenstein et al.,  
217 2018). We reason that this discrepancy between findings is because colonies of the smallest size  
218 classes (one to a few dozen spiders) are largely missing from our data set, and the persistence  
219 benefits of increasing group size are most pronounced at the smallest colony sizes (Lichtenstein  
220 et al., 2018, Aviles & Tufino, 1998).

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

225

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

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

230 <https://datadryad.org/review?doi=doi:10.5061/dryad.hr90jf2>

231 **Authors Contributions:** JLLL and BLM assisted with all aspects of the study pipeline. DTN,  
232 EC, CS and JE assisted with data collection. DNF and JNP helped to analyze the data and write  
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## REFERENCES

- 244 Aviles, L. 1986. Sex-ratio bias and possible group selection in the social spider *anelosimus-*  
245 *eximius*. *American Naturalist* **128**: 1-12.
- 246 Aviles, L. 1993. Interdemic selection and the sex-ratio - a social spider perspective. *American*  
247 *Naturalist* **142**: 320-345.
- 248 Aviles, L. & Guevara, J. (2017) Sociality in spiders. In: *Comparative social evolution*,  
249 (Rubenstein, D. R. & Abbot, P., eds.). pp. 188-223. Cambridge University Press,  
250 Cambridge.
- 251 Aviles, L. & Tufino, P. 1998. Colony size and individual fitness in the social spider *anelosimus*  
252 *eximius*. *American Naturalist* **152**: 403-418.
- 253 Bengston, S. & Jandt, J. M. 2014. The development of collective personality: The ontogenetic  
254 drivers of behavioral variation across groups. *Frontiers in Ecology and Evolution* **2**: 81.
- 255 Bilde, T., Coates, K. S., Birkhofer, K., Bird, T., Maklakov, A. A., Lubin, Y. & Aviles, L. 2007.  
256 Survival benefits select for group living in a social spider despite reproductive costs.  
257 *Journal of Evolutionary Biology* **20**: 2412-2426.
- 258 Davis, K., Dobrowski, S. Z., Holden, Z. A., Higuera, P. E. & Abatzoglou, J. T. 2018.  
259 Microclimatic buffering in forests of the future: The role of local water balance.  
260 *Ecography*.
- 261 Drummond, H. & Burghardt, G. M. 1983. Geographic-variation in the foraging behavior of the  
262 garter snake, *thamnophis-elegans*. *Behavioral Ecology and Sociobiology* **12**: 43-48.

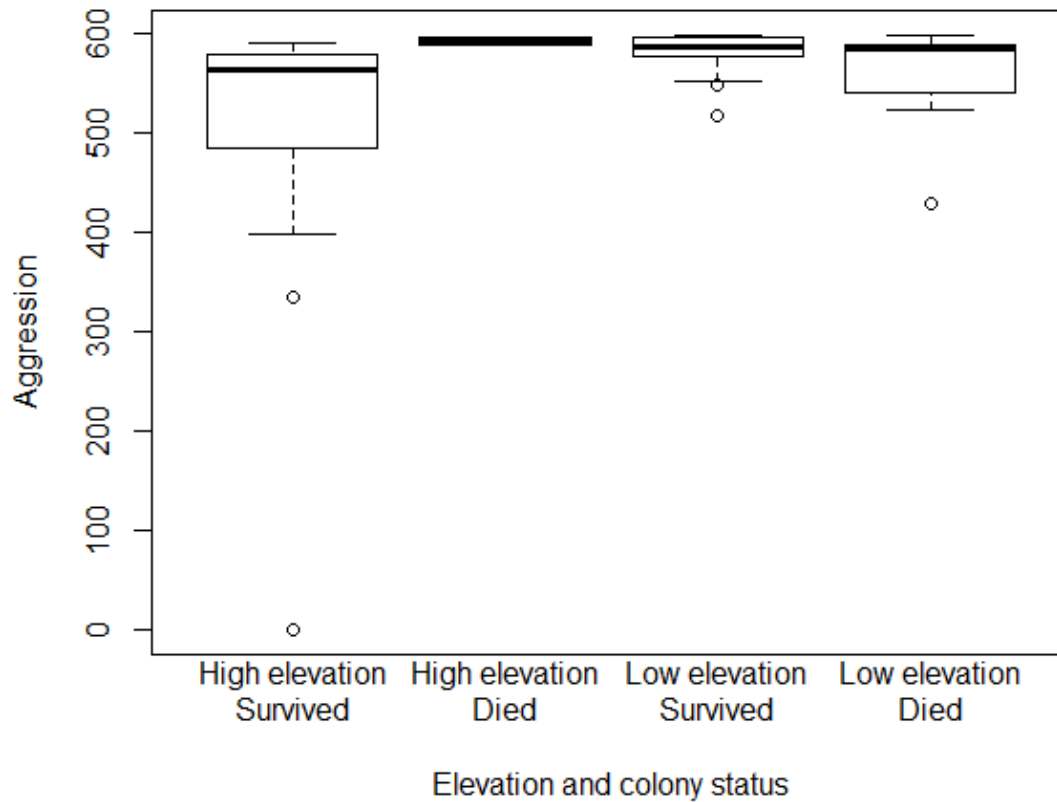
- 263 Dunbrack, R. L., Clarke, L. & Bassler, C. 1996. Population level differences in aggressiveness  
264 and their relationship to food density in a stream salmonid (*salvelinus fontinalis*). *Journal*  
265 *of Fish Biology* **48**: 615-622.
- 266 Fewell, J. H. & Page, R. E. 1999. The emergence of division of labour in forced associations of  
267 normally solitary ant queens. *Evolutionary Ecology Research* **1**: 537-548.
- 268 Gordon, D. M. 2013. The rewards of restraint in the collective regulation of foraging by  
269 harvester ant colonies. *Nature*.
- 270 Guevara, J. & Aviles, L. 2007. Multiple techniques confirm elevational differences in insect size  
271 that may influence spider sociality. *Ecology* **88**: 2015-2023.
- 272 Guevara, J. & Aviles, L. 2015. Ecological predictors of spider sociality in the americas. *Global*  
273 *Ecology and Biogeography* **24**: 1181-1191.
- 274 Hahn, D. A. & Tschinkel, W. R. 1997. Settlement and distribution of colony-founding queens of  
275 the arboreal ant, *crematogaster ashmeadi*, in a longleaf pine forest. *Insectes Sociaux* **44**:  
276 323-336.
- 277 Henschel, J. R., Lubin, Y. D. & Schneider, J. 1995. Sexual competition in an inbreeding social  
278 spider, *stegodyphus-dumicola* (araneae, eresidae). *Insectes Sociaux* **42**: 419-426.
- 279 Hoffman, C. R. & Avilés, L. 2017. Rain, predators, and spider sociality: A manipulative  
280 experiment. *Behavioral Ecology* **28**: 589-596.
- 281 Jandt, J. M., Bengston, S., Pinter-Wollman, N., Pruitt, J. N., Raine, N. E., Dornhaus, A. & Sih,  
282 A. 2014. Behavioral syndromes and social insects: Multiple levels of personality.  
283 *Biological Reviews* **89**: 48-67.
- 284 Kamath, A., Primavera, S. D., Wright, C. M., Doering, G. N., Sheehy, K. A., Pinter-wollman, N.  
285 & Pruitt, J. N. 2018. Collective behavior and colony persistence of social spiders depends  
286 on their physical environment.
- 287 Kralj-Fiser, S. & Schneider, J. M. 2012. Individual behavioural consistency and plasticity in an  
288 urban spider. *Animal Behaviour* **84**: 197-204.
- 289 Kralj-Fiser, S., Schneider, J. M., Justinek, Z., Kalin, S., Gregoric, M., Pekar, S. & Kuntner, M.  
290 2012. Mate quality, not aggressive spillover, explains sexual cannibalism in a size-  
291 dimorphic spider. *Behavioral Ecology and Sociobiology* **66**: 145-151.
- 292 Krause, J. & Ruxton, G. D. 2002. *Living in groups*. Oxford Press, Oxford UK.
- 293 Lichtenstein, J. L. L., Bengston, S., Aviles, L. & Pruitt, J. N. 2018. Female-biased sex ratios  
294 increase colony survival and reproductive output in the spider *anelosimus studiosus*. *The*  
295 *American Naturalist*.
- 296 Lichtenstein, J. L. L. & Pruitt, J. N. 2015. Similar patterns of frequency-dependent selection on  
297 animal personalities emerge in three species of social spiders. *Journal of Evolutionary*  
298 *Biology*.
- 299 Lichtenstein, J. L. L., Wright, C. M., Luscuskie, L. P., Montgomery, G. A., Pinter-Wollman, N.  
300 & Pruitt, J. N. 2017. Participation in cooperative prey capture and the benefits gained  
301 from it are associated with individual personality. *Current Zoology* **63**: 561-567.
- 302 Magurran, A. E. & Seghers, B. H. 1991. Variation in schooling and aggression amongst guppy  
303 (*poecilia-reticulata*) populations in trinidad. *Behaviour* **118**: 214-234.
- 304 Miller, S. E., Blucher, S. E., Bell, E., Cini, A., da Silva, R. C., de Souza, A. R., Gandia, K. M.,  
305 Jandt, J., Loope, K., Prato, A., Pruitt, J. N., Rankin, D., Rankin, E., Southon, R. J., Uy, F.  
306 M. K., Weiner, S., Wright, C. M., Downing, H., Gadagkar, R., Lorenzi, M. C., Rusina,  
307 L., Sumner, S., Tibbetts, E. A., Toth, A. & Sheehan, M. J. 2018. Waspnest: A worldwide  
308 assessment of social polistine nesting behavior. *Ecology* **99**: 2405-2405.

- 309 Pinter-Wollman, N., Mi, B. R. & Pruitt, J. N. 2017. Replacing bold individuals has a smaller  
310 impact on group performance than replacing shy individuals. *Behavioral Ecology* **28**:  
311 883-889.
- 312 Powers, K. S. & Aviles, L. 2007. The role of prey size and abundance in the geographical  
313 distribution of spider sociality. *Journal of Animal Ecology* **76**: 995-1003.
- 314 Pruitt, J. N. 2012. Behavioural traits of colony founders affect the life history of their colonies.  
315 *Ecology Letters* **15**: 1026–1032.
- 316 Pruitt, J. N. & Goodnight, C. J. 2014. Site-specific group selection drives locally adapted colony  
317 compositions. *Nature* **28**: 1248-1256.
- 318 Pruitt, J. N., Grinsted, L. & Settepani, V. 2013. Linking levels of personality: Personalities of the  
319 'average' and 'most extreme' group members predict colony-level personality. *Animal*  
320 *Behaviour* **86**: 391-399.
- 321 Pruitt, J. N., McEwen, B. S., Cassidy, S. T., Najm, G. A. & Pinter-wollman, N. in press.  
322 Experimental evidence of frequency-dependent selection on group behaviour. *Nature*  
323 *Ecology and Evolution*.
- 324 Pruitt, J. N. & Riechert, S. E. 2011. How within-group behavioral variation and task efficiency  
325 enhance fitness in a social group. *Proceedings of the Royal Society Biological Sciences*  
326 *Series B* **278**: 1209-1215.
- 327 Pruitt, J. N., Wright, C. M., Lichtenstein, J. L., Chism, G. T., McEwen, B. L., Kamath, A. &  
328 Pinter-Wollman, N. 2017. Selection for collective aggressiveness favors social  
329 susceptibility in social spiders. *Current Biology* **28**: 100-105.e4.
- 330 Pruitt, J. N., Wright, C. M., Lichtenstein, J. L. L., Chism, G. T., McEwen, B. L., Kamath, A. &  
331 Pinter-Wollman, N. 2018. Selection for collective aggressiveness favors social  
332 susceptibility in social spiders. *Current Biology* **28**: 100-+.
- 333 Purcell, J. & Aviles, L. 2008. Gradients of precipitation and ant abundance may contribute to the  
334 altitudinal range limit of subsocial spiders: Insights from a transplant experiment.  
335 *Proceedings of the Royal Society B-Biological Sciences* **275**: 2617-2625.
- 336 Riechert, S. & Roeloffs, R. (1993) Inbreeding and its consequences in the social spiders. In: *The*  
337 *natural history of inbreeding and outbreeding*, (N, T., ed.). pp. 283-303. University of  
338 Chicago Press, Chicago.
- 339 Riechert, S. E. (1993) The evolution of behavioral phenotypes - lessons learned from divergent  
340 spider populations. In: *Advances in the study of behavior*, vol 22, Vol. 22. pp. 103-134  
341 *Advances in the study of behavior*.
- 342 Riechert, S. E. & Hedrick, A. V. 1993. A test for correlations among fitness-linked behavioral  
343 traits in the spider *agelenopsis-aperta* (araneae, agelenidae). *Animal Behaviour* **46**: 669-  
344 675.
- 345 Seppa, P., Queller, D. C. & Strassmann, J. E. 2002. Reproduction in foundress associations of  
346 the social wasp, *polistes carolina*: Conventions, competition, and skew. *Behavioral*  
347 *Ecology* **13**: 531-542.
- 348 Shaffer, Z., Sasaki, T., Haney, B., Janssen, M., Pratt, S. C. & Fewell, J. H. 2016. The foundress's  
349 dilemma: Group selection for cooperation among queens of the harvester ant,  
350 *pogonomyrmex californicus*. *Scientific Reports* **6**.
- 351 Stoffel, M. A., Nakagawa, S. & Schielzeth, H. 2017. Rptr: Repeatability estimation and variance  
352 decomposition by generalized linear mixed-effects models. *Methods in Ecology and*  
353 *Evolution* **8**: 1639-1644.

- 354 Tibbetts, E. A. & Reeve, H. K. 2003. Benefits of foundress associations in the paper wasp  
355 polistes dominulus: Increased productivity and survival, but no assurance of fitness  
356 returns. *Behavioral Ecology* **14**: 510-514.
- 357 Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press,  
358 Princeton NJ.
- 359 Vollrath, F. 1982. Colony foundation in a social spider. *Zeitschrift Fur Tierpsychologie-Journal*  
360 *of Comparative Ethology* **60**: 313-324.
- 361 Walsh, M. R., Broyles, W., Beston, S. M. & Munch, S. B. 2016. Predator-driven brain size  
362 evolution in natural populations of trinidadian killifish (rivulus hartii). *Proceedings of the*  
363 *Royal Society B-Biological Sciences* **283**.
- 364 Watanabe, M. E. 2008. Colony collapse disorder: Many suspects, no smoking gun. *Bioscience*  
365 **58**: 384-388.
- 366 Wray, M. K., Mattila, H. R. & Seeley, T. D. 2011. Collective personalities in honeybee colonies  
367 are linked to colony fitness. *Animal Behaviour* **81**: 559-568.
- 368 Wray, M. K. & Seeley, T. D. 2011. Consistent personality differences in house-hunting behavior  
369 but not decision speed in swarms of honey bees (apis mellifera). *Behavioral Ecology and*  
370 *Sociobiology* **65**: 2061-2070.
- 371 Yip, E. C., Powers, K. S. & Aviles, L. 2008. Cooperative capture of large prey solves scaling  
372 challenge faced by spider societies. *Proceedings of the National Academy of Sciences of*  
373 *the United States of America* **105**: 11818-11822.
- 374



375 **Figures & Supplementary Figures:**



376

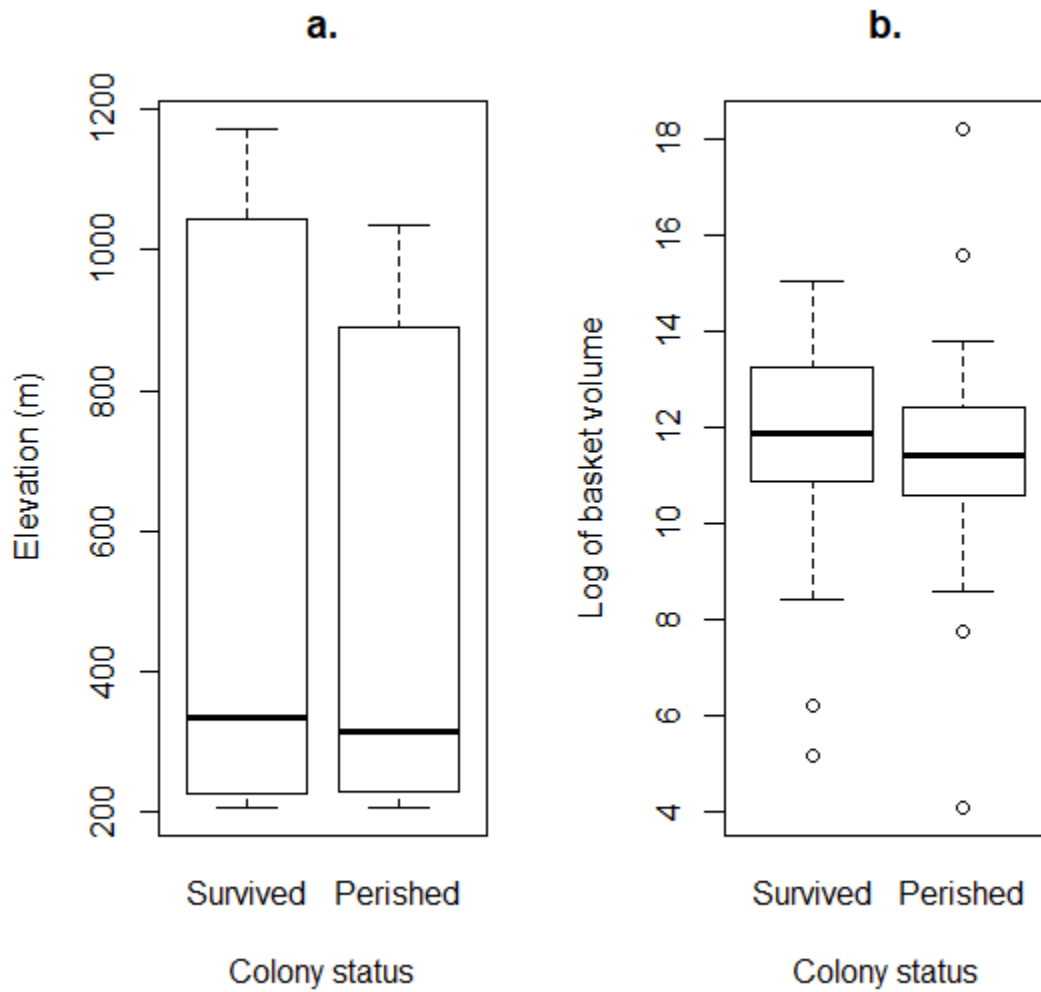
377 **Figure 1.** The aggressiveness of colonies that either survived or died, at low (< 450m) or high

378 (>740m) elevation sites. Aggression was 600 minus the latency to attack (maximum 600

379 seconds) hence is unitless.

380





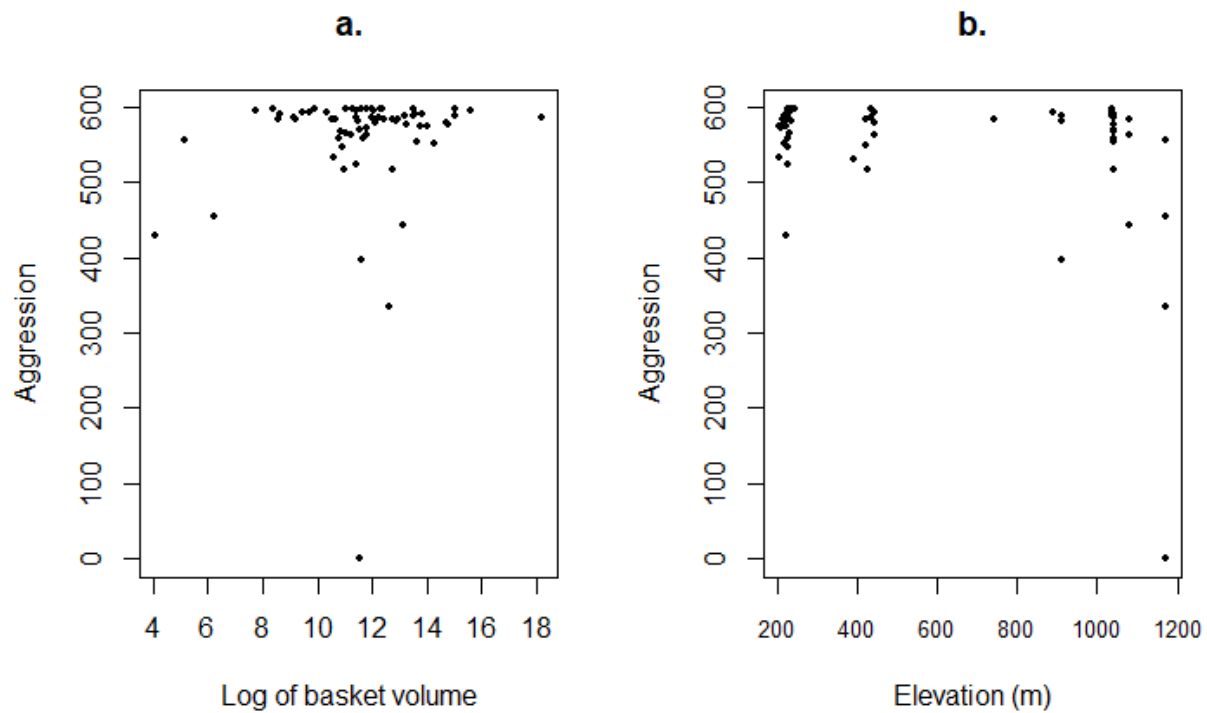
381

382 **Figure S1.** The difference in elevation (metres, a.) and colony size (the log the basket volume,

383 b.) of colonies that either survived or perished. Neither elevation nor colony size differed

384 between colonies that survived or perished.

385



386

387 **Figure S2.** The relationship between colony aggression and colony size (log of basket volume,

388 a.), and elevation (metres, b.). Aggression was not related to colony size, while it is weakly

389 negatively correlated with elevation.