

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

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## 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).

75

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.

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#### 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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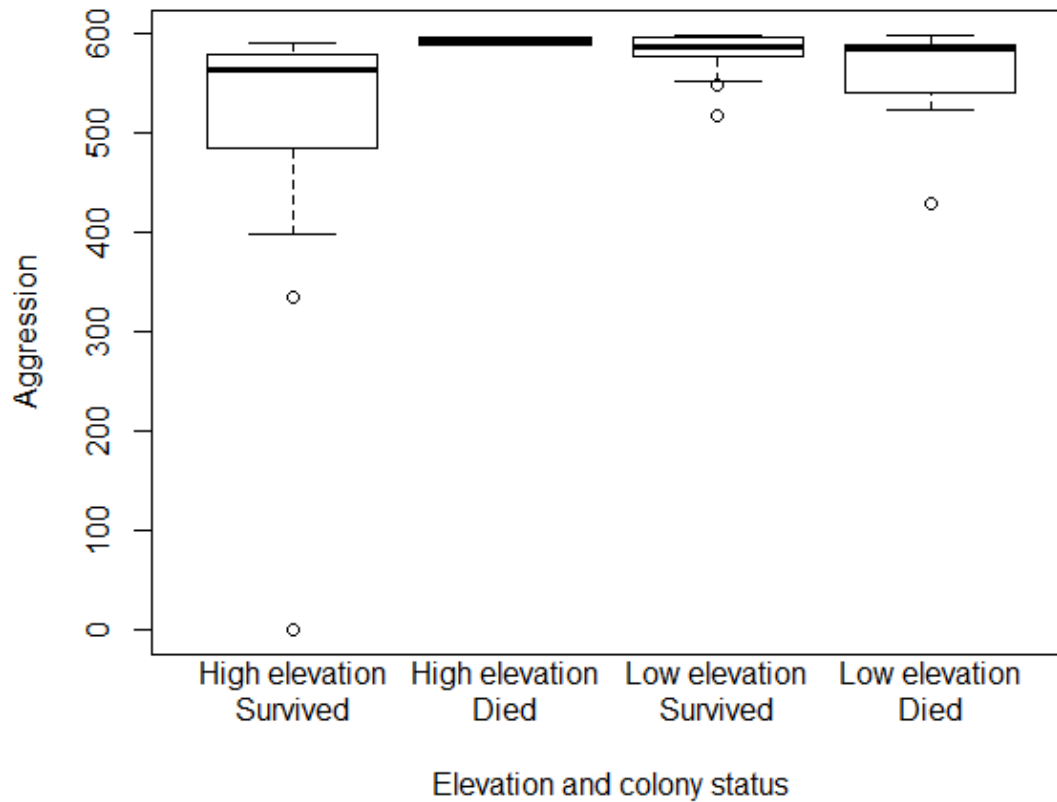
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375 **Figures & Supplementary Figures:**



376

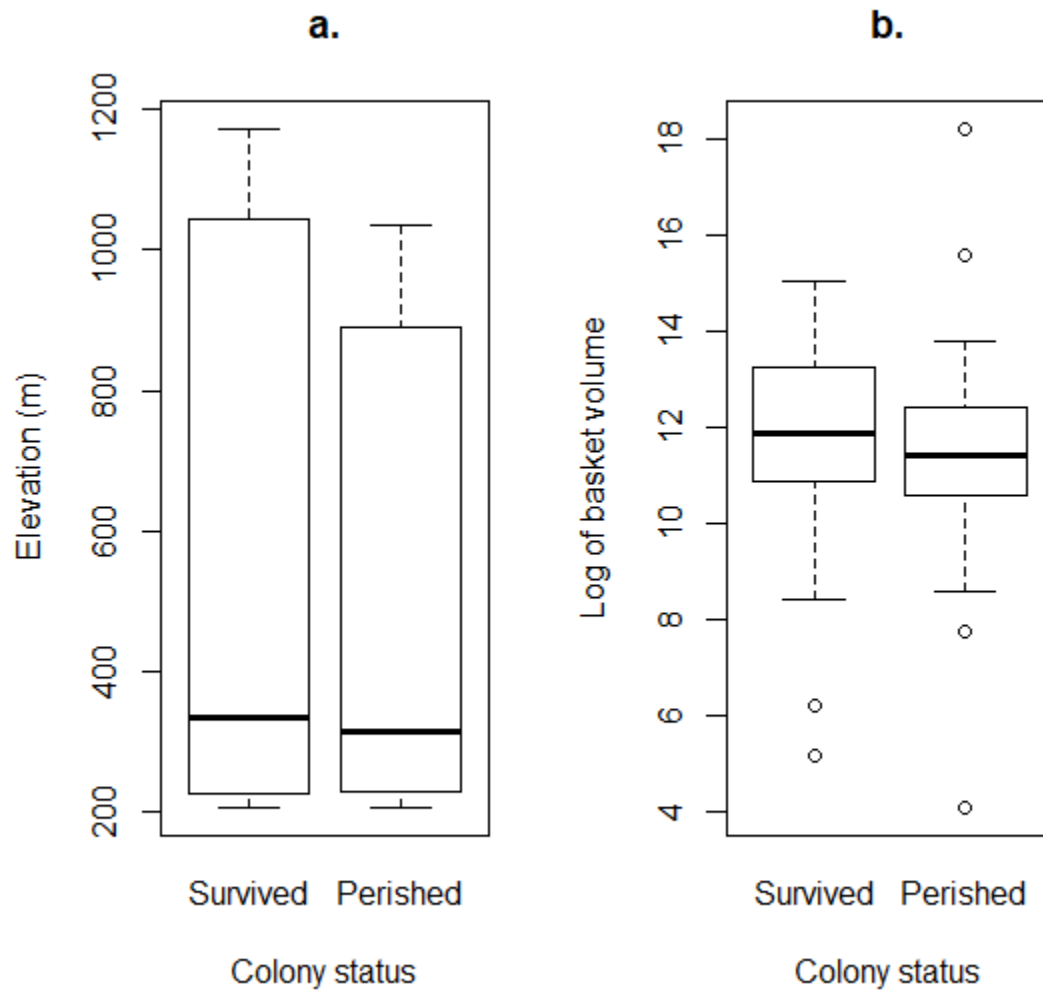
377 **Figure 1.** The aggressiveness of colonies that either survived or died, at low (< 450m) or high

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

379 seconds) hence is unitless.

380





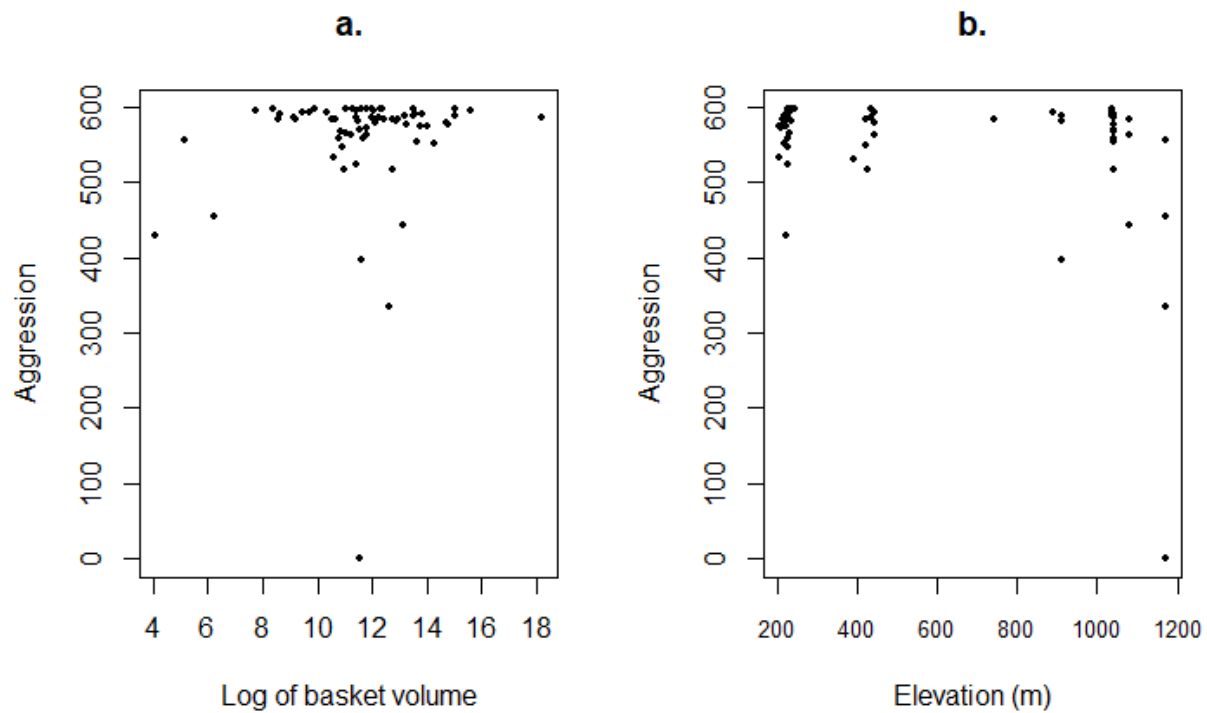
381

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.