Behavioral dominance interactions between two species of burying beetles (*Nicrophorus orbicollis* and *Nicrophorus pustulatus*)

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Abstract.

Closely related species with ecological similarity often aggressively compete for a common, limited resource. This competition is usually asymmetric and results in one species being behaviorally dominant over the other. Trade-offs between traits for behavioral dominance and alternative strategies can result in different methods of resource acquisition between the dominant and subordinate species, with important consequences for resource partitioning and community structure. Body size is a key trait thought to commonly determine behavioral dominance. Priority effects (i.e., which species arrives at the resource first), however, can also determine the outcome of interactions, as can species-specific traits besides size that give an advantage in aggressive contests (e.g., weapons). Here, we test among these three alternative hypotheses of body size, priority effects, and species identity for what determines the outcome of competitive interactions among two species of burying beetles, *Nicrophorus orbicollis* and *N. pustulatus*. Both overlap in habitat and seasonality and exhibit aggressive competition over a shared breeding resource of small vertebrate carrion. In trials, we simulated what would happen

31   upon the beetles' discovery of a carcass in nature by placing a carcass and one beetle of each

32   species in a container and observing interactions over 13 hour trials ($N = 17$ trials). We recorded

33   and categorized interactions between beetles and the duration each individual spent in contact

34   with the carcass (the key resource) to determine which hypothesis predicted trial outcomes. Body

35   size was our only significant predictor; the largest species won most aggressive interactions and

36   spent more time in contact with the carcass. Our results offer insight into the ecology and

37   patterns of resource partitioning of *N. orbicollis* and *N. pustulatus*, the latter of which is unique

38   among local *Nicrophorus* for being a canopy specialist. *N. pustulatus* is also unique among all

39   *Nicrophorus* in using snake eggs, in addition to other carrion, as a breeding resource. Our results

40   highlight the importance of body size and related trade-offs in ecology and suggest parallels with

41   other coexisting species and communities.

42

43   **Introduction.**

44   Competition among closely related and ecologically similar species is common when reproduction

45   and survival depend on limited resources (Violle et al., 2011). In animals, the resulting competition

46   is often direct and aggressive; the outcomes are usually asymmetric, with one species being

47   consistently dominant over the other (Morse, 1974; Persson, 1985; Martin, Freshwater &

48   Ghalambor, 2017). Body size is one of the most important traits determining dominance in many

49   species, providing a direct benefit in competitive interactions (e.g., greater inertia, muscle mass),

50   and often correlating with traits useful for fighting (e.g., size of mouthparts, fighting appendages,

51   and limbs) (Peters, 1983; Martin & Ghalambor, 2014, 2023). Order of arrival to a resource (priority

52   effects), however, can also determine which species acquires the resource in competitive

53   interactions (Poulos & McCormick 2014; Fukami, 2015). The resource is either claimed before

54   any fighting can occur, or the individual that arrives first is better able to fight for and defend its

55 resource (Fukami, 2015). Alternatively, traits other than size can provide an advantage in

56 competitive interactions, often being inherent to one species (e.g., superior weapons, greater

57 aggression) and allowing that species to consistently outcompete another. Understanding how

58 different traits (body size, weapons) versus priority effects impact competitive outcomes is

59 important for understanding when and why species partition resources in nature (Martin, 2015).

60 *Nicrophorus* burying beetles are an excellent study system for testing among these alternative

61 hypotheses (body size, priority effects, and species identity) to explain the outcomes of

62 interference competition. Seven species co-occur in southeastern Ontario (Anderson & Peck,

63 1985) and aggressively compete for a shared, ephemeral breeding resource—small vertebrate

64 carcasses (Trumbo, 1994). Competition is fierce both within and among species, as breeding pairs

65 rarely share carcasses (Wilson, Knollenberg & Fudge, 1984; Trumbo, 1990a). Coexistence is

66 likely facilitated by different ecological strategies among *Nicrophorus* species that allow them to

67 partition the breeding resource over time (differences in seasonal and diel activity; Anderson,

68 1982; Anderson & Peck, 1985; Trumbo, 1990b; Keller et al., 2019; Wettlaufer et al., 2021, 2023),

69 space (differences in habitat; Anderson, 1982; Anderson & Peck, 1985; Burke et al., 2020), and

70 characteristics of the resource (differences in size of carcass; Trumbo, 1990a). The partitioning

71 observed is thought to reflect the different strategies of dominant and subordinate species. This

72 partitioning may also reflect the trade-offs between the traits linked to behavioral dominance

73 associated with each strategy. These trade-offs are also thought to allow dominant and subordinate

74 species to co-occur rather than compete to the point of competitive exclusion (Grether et al., 2017;

75 Martin & Ghalambor, 2023).

76 While competitive ability among *Nicrophorus* species varies, the outcomes of aggressive

77 contests seem to be strongly influenced by single traits (Wilson, Knollenberg & Fudge, 1984;

78   Trumbo 1990a; Schrempf et al., 2021). Previous work shows that larger size is an excellent

79   predictor of behavioral dominance among *Nicrophorus* species in competitive interactions for

80   carcasses (Wilson, Knollenberg & Fudge, 1984; Otronen, 1988; Trumbo, 1990a, Schrempf et al.,

81   2021). However, when two individuals of similar size compete, the beetle from the larger-on-

82   average species often wins (Otronen, 1988), suggesting that other traits that differ among species

83   also play a role in competitive outcomes. Alternatively, other evidence suggests that the order of

84   arrival influences the ability to remain in possession of a carcass and defend it (Otronen, 1988);

85   however, later arriving dominant species can still usurp a carcass from a subordinate species in

86   some cases (Wilson, Knollenberg & Fudge, 1984; Trumbo, 1990a). Overall, previous evidence

87   from *Nicrophorus* supports a role for each of our three alternative hypotheses influencing the

88   outcome of competition for carcasses.

89   In this study, we test among our three alternative hypotheses using two species of *Nicrophorus*

90   burying beetles that are common and co-occur in southeastern Ontario, Canada: *N. orbicollis* and

91   *N. pustulatus*. *N. orbicollis* is on average the largest and most abundant species at our site (Collard

92   et al., 2021; Wettlaufer et al., 2021). Both species similarly prepare the carcass upon discovery

93   (Scott, 1998) and overlap in breeding season (Anderson & Peck, 1985; Wettlaufer et al., 2021) and

94   habitat. *N. orbicollis* is a habitat generalist (Burke et al., 2020), whereas *N. pustulatus* is likely a

95   canopy specialist (Ulyshen & Hanula, 2007; Wettlaufer et al., 2018). Despite documented use of

96   snake eggs (Trumbo, 2009; Smith, 2007) and even burying of live vertebrates (DeMarco & Martin,

97   2020) for use as breeding resources, *N. pustulatus* uses vertebrate carrion in captivity (Robertson,

98   1992; Rauter & Moore, 2002; Smith et al., 2007) and appears to compete with other *Nicrophorus*

99   species for vertebrate carrion at our sites (Wettlaufer et al., 2021). *N. orbicollis* and *N. pustulatus*

100 are commonly caught in the same traps with the same resource as bait, providing direct evidence

101   for their competitive interactions in nature; at our site in southeastern Ontario, 94 of 118 traps

102   (79.7%) that caught *N. pustulatus* also caught *N. orbicollis*, including 14 of the 16 (87.5%) traps

103   that caught *N. pustulatus* on the ground (Wettlaufer et al., 2021).

104   We used same-sex captive trials involving wild-caught beetles (following Schrempf et al.,

105   2021) that replicate one scenario of what can happen when individuals from *N. orbicollis* and *N.*

106   *pustulatus* come across a carcass in nature. We tested our alternative hypotheses of body size,

107   priority effects and species identity for determining the outcome of interactions for a carcass using

108   summaries of competitive interaction outcomes, where priority is defined as the individual who

109   acquires the resource (carcass) first. We then tested whether the individual that won the most

110   interactions (the dominant) in that trial also spent the most time in contact with the carcass (the

111   resource).

112

Materials & Methods.

113

114   Collection and identification of species

115   We collected *N. orbicollis* and *N. pustulatus* from 2-14 June, 2021 from mixed forest near

116   Glenburnie, Ontario, Canada (44.302408, -76.515571, 125 m elevation). We used wild-caught

117   beetles, rather than captive-bred beetles, because we did not have access to captively bred

118   individuals of both species, and captive breeding can lead to altered behaviors and other traits,

119   including aggression, compared with wild individuals (Price, 1999; Kelley, Magurran & García,

120   2006), which could have altered our results. We set live traps (plastic buckets) baited with raw

121   chicken wings or dead mice set on potting soil and leaf litter in two different locations: *N.*

122   *orbicollis* traps on the ground and *N. pustulatus* traps suspended 4-7 m in the forest canopy

123   (following Wetlauffer et al., 2021). We checked traps every 2-4 days and identified and sexed all

124   captured beetles following, Anderson & Peck (1985). We collected focal beetles and placed them

125   in individual 4 oz clear plastic containers (Reditainer, model no. RTSC100400) containing moist

126   potting soil. To prevent recapture following trials, beetles were marked on their elytra using a

127   black sharpie after each trial and then released 7.5 km away from the initial capture site. Each

128   individual participated in only one trial.

129   We did not know the individual histories of the beetles used in our trials. For example, some

130   of our beetles could have mated previously or had previous experience fighting for carcasses. If

131   previous experience varied with the traits of interest (e.g., larger beetles were more likely to have

132   experience fighting), then our results could be biased, leading to incorrect conclusions (e.g., size

133   impacts the likelihood of experience, which then improves fighting success, rather than a direct

134   benefit of large size in fighting). We revisit some of these limitations in our discussion. The time

135   between a beetle's capture and their participation in a trial averaged 2.8 days (range 2-5 days);

136   beetles in the same trial were usually caught on the same day and held in captivity for the same

137   number of days before trials. We held beetles for at least two days in captivity before trials

138   because we wanted beetles to readjust their behaviors after having been held within the live

139   traps.

140

141   Captive studies

142   The methods for our competitive trials follow Schrempf et al. (2021). Briefly, we conducted

143   trials in clear plastic containers (31.4 x 20.8 x 11.9 cm) with 1-2 cm of fresh topsoil. For each

144   trial, we placed a mouse (*Mus musculus*) carcass (previously frozen, then thawed for 48 hours at

145   ~22 °C; we removed the tail in most trials to facilitate observations of contact with the carcass)

146   in the center of the container on top of the soil. Mice were sourced from the Queen's University

147 Health Sciences breeding facilities, culled using carbon dioxide gas and frozen until used in our

148 study. Mice used in our trials weighed 30.6-46.5 g (mean weight of 38.5g).

149 Beetles were selected for trials based on their sex and collection date – either they were

150 collected on the same day (and thus held for the same amount of time; $N = 16$ trials), or, when

151 this was not possible ($N = 1$ trial), they were collected within one day of each other. Within these

152 groups, we selected beetles haphazardly for trials, without regard to size. Just before the start of

153 each trial, we placed one pair of beetles in a container (one *N. orbicollis* and one *N. pustulatus*).

154 Beetles were introduced to the container at the same time, providing equal opportunity to reach

155 the carcass first. All trials consisted of same-sex pairs (see Table 1) to control for sex as a

156 potential confound; however, previous studies have found no evidence for sex affecting the

157 outcomes of aggressive contests between *Nicrophorus* species (Schrempf et al., 2021; Wettlaufer

158 et al., 2023).

159 Throughout trials, we used a glass pane to cover the container and red bicycle lights (located

160 within the container to avoid reflectance off the glass) to illuminate the trials at night, thereby

161 minimizing disturbance to the beetles. Beetles were exposed to natural light from nearby

162 windows at controlled temperatures ranging from 21-24°C. Trials began at 18:00 and ended at

163 7:00 (13 hours total), and any interactions already underway prior to the start of trials were only

164 timed from 18:00. In total, we conducted 18 trials (one was excluded from analysis because it

165 included beetles of different sexes), each recorded using a Cannon Vixia HF R50 Camcorder

166 (Canon Inc., Tokyo, Japan). We reviewed all trials using VLC media player (www.videolan.org).

167

168 Size measurements

169   We used mass as our estimate of relative size of beetles in our trials. We consider mass to be a

170   good proxy of body size (following Peters 1983; see also Schrempf et al., 2021; Wettlaufer et al.,

171   2023) because different species of *Nicrophorus* may have different morphological proportions

172   that correspond to different ecological strategies unrelated to overall size (Burke, 2017). After

173   each trial was complete, we returned the beetles to their plastic containers and chilled them in a

174   cooler filled with ice for 30-60 minutes. Cooling the beetles slowed their activity, facilitating

175   measurement. Once cooled, we measured each beetle's mass (accuracy of 0.001 grams) using a

176   GEM20 Smart Weigh jewelry scale (Smart Weigh Packaging Machinery Co., Ltd., Zhongshan

177   City, Guangdong Province, China), where mass (g) = weight of the beetle (g) x (10g / weight of

178   the 10g standard (g)).

179

180   Interactions between beetles

181   We considered beetles to be interacting when they were within 1 cm of each other because

182   previous work (Schrempf et al., 2021), suggested that beetles were aware of each other at this

183   distance. Beetles may have been aware of each other at greater distances than 1 cm, but we found

184   it difficult to determine if this was consistently true in our trials. Our 1 cm cutoff may thus

185   underestimate the number of interactions among individuals, but was nonetheless consistently

186   applied across trials. We recorded the duration of each interaction (rounded to the nearest

187   second), and separated interactions between beetles into four categories: (1) Aggressive physical

188   interactions, (2) Avoidance interactions, (3) Neutral interactions, and (4) Other interactions

189   (Schrempf et al., 2021).

190   *(1) Aggressive physical interactions* were defined as instances where we observed direct,

191   aggressive interactions such as grabbing, biting, chasing, or digging after a buried beetle. We

192   separated the outcomes of these interactions into two groups: symmetric outcomes occurred

193   when no beetle won or lost, and asymmetric outcomes occurred when one beetle won and the

194   other lost. Winners were defined as beetles that retained their position after an aggressive

195   interaction; losers were beetles that retreated from the interaction.

196   *(2) Avoidance interactions* were cases where one beetle adjusted its behavior to avoid or

197   accommodate the other, for example, when a beetle altered its path (after coming within 1 cm of

198   the other beetle) to avoid the other. The loser in this case was the individual who adjusted its

199   position to accommodate the other beetle.

200   *(3) Neutral interactions* were defined as cases where individuals were within 1 cm of each

201   other and displayed no signs of aggression or avoidance. These included cases of two beetles

202   passing each other with no alteration of path or apparent aggression, or one beetle passing over

203   another buried beetle without digging after and/or attacking it.

204   *(4) Other interactions* consisted of interactions where we could not observe the details of the

205   interaction but could tell that an interaction had taken place by observing its result. For example,

206   'Other interactions' included a beetle retreating from underneath the carcass where the other

207   beetle was located, where we could infer that an interaction had occurred but could not tell

208   whether it involved avoidance, chasing, or physical contact.

209   When categorizing these interactions, we considered encounters that started as one type and

210   then changed into another type as being two interactions. For example, we recorded a neutral

211   interaction that escalated into a physical one as one neutral interaction and one physical

212   interaction, respectively.

213

214   Contact with the carcass

215   We noted a simple yes/no if the beetle touched the mouse carcass during each minute of the trial.

216   Tails were removed from the majority of trials and contact with the tail in early trials (where the

217   tail was left on) was not counted.

218

219   Priority effects

220   We defined 'priority' as the first individual to acquire the resource (the mouse carcass), following

221   previous resource-centered definitions of priority effects (e.g., Poulos & McCormick, 2014),

222   which differ from community assembly definitions (e.g., which species colonizes a new habitat

223   or environment; Fukami, 2015). Beetles were released into containers at the same time, and

224   typically walked around the outside of the containers before burying into the soil. We recorded

225   which individual was first to make contact with the carcass as our estimate of priority, testing the

226   idea that the first beetle to claim the carcass would be better able to retain possession of the

227   carcass over time. Our definition of priority in our trials does not encompass all ways that

228   priority effects could impact burying beetles in nature. For example, beetles that come into

229   contact with the carcass first could benefit by partially burying the carcass, or quickly attracting a

230   mate and defending the carcass as a pair; our trials did not test for such benefits that could also

231   be important in nature. Nonetheless, our experiments simulate periods of high *Nicrophorus*

232   activity, with beetles arriving at a single carcass in rapid succession. For example, during

233   *Nicrophorus* removal experiments in 2023 at the Queen's University Biological Station near our

234   field site, we recorded rates of arrival at a single mouse carcass of up to 8.4 beetles/hour (*N.*

235   *orbicollis*) and 6.4 beetles/hour (*N. sayi*); the rapid arrival of beetles leads to widespread fighting

236   over carcasses.

237

238   Behavioral dominance

239   We defined the behaviorally dominant beetle in each trial as the individual that won the most

240   interactions (sum of the aggressive physical interactions and avoidance interactions), following

241   Schrempf et al. (2021). We then tested whether relative size (body size hypothesis), being the

242   first to reach the carcass (priority effects hypothesis), or species (species identity hypothesis) best

243   predicted the dominant individuals across trials. We also tested whether the dominant individuals

244   in each trial spent more time in contact with the carcass. We also measured the distance (cm)

245   between each beetle and the mouse carcass at the end of each trial for possible use as an indicator

246   of behavioral dominance in future studies, where the dominant species remains in close contact

247   with the carcass (Wilson et al., 1984; Schrempf et al., 2021).

248

249   Statistical analyses

250   We performed all statistical analyses and plotting in R (version 4.1.1; R Development Core

251   Team, 2021), and followed similar approaches to Schrempf et al. (2021).

252   We tested which of our alternative hypotheses best predicted behavioral dominance using

253   binomial generalized linear models (glm). Our response variable was the proportion of

254   dominance interactions (i.e., aggressive physical interactions, avoidance interactions, and other

255   interactions with an asymmetric outcome; see Table 2) that each species won, combined into one

256   response variable (i.e., cbind(number of interactions won by *N. orbicollis*, number of interactions

257   won by *N. pustulatus*); following Crawley, 2013). We then natural log transformed the mass

258   ratio of our two species (ln(mass in *N. orbicollis*/mass in *N. pustulatus*). Thus, our final models

259   had relative wins by each species as the response variable, and relative mass and first species to

260   the carcass as predictors with their interaction term. We detected overdispersion in our initial

261   models and corrected the standard errors using a quasi-glm model that incorporated a dispersion

262   parameter (Zuur et al., 2009). We further checked the fit of our saturated model by plotting

263   predicted versus fitted values, theoretical quantiles versus standardized Pearson residuals

264   (qqplots), by examining Cook's distance values, and by plotting model residuals accompanied by

265   a Shapiro-Wilk test of normality.

266   In our models, the relative mass predictor tested the body size hypothesis, the first species to

267   the carcass predictor tested the priority effects hypothesis, and the model intercept tested the

268   species identity hypothesis; intercepts above zero indicated that *N. orbicollis* was more likely to

269   win interactions when the species did not differ in mass, and below zero indicated that *N.*

270   *pustulatus* was more likely to win when mass was equal. We ran models with all possible

271   combinations of predictor variables using the *dredge* command from the *MuMIn* package

272   (Bartoń, 2019). We then compared the relative performance of these models using quasi Akaike

273   information criterion values (QAIC), where the model with the lowest QAIC score was

274   determined to be the best performing model. We checked the fit of our best-performing model

275   using the same methods described for the saturated model.

276   We tested whether the dominant individual in a trial spent more time in contact with the

277   carcass using a glm with a Gaussian distribution, with the natural log ratio of time in contact with

278   the carcass, as: ln((time *N. orbicollis* was in contact with the carcass +1)/(time *N. pustulatus* was

279   in contact with the carcass +1)) as the response variable, and the dominant species in the trial

280   (either *N. orbicollis* or *N. pustulatus*) as the sole predictor. We checked model fit by plotting

281   predicted versus fitted values, theoretical quantiles versus standardized Pearson residuals

282   (qqplots), by examining Cook's distance values, by plotting model residuals versus the predictor

283   accompanied by a Bartlett test of homogeneity of variance, and by plotting model residuals

284   accompanied by a Shapiro-Wilk test of normality.

285   We tested if the dominant beetle species in each trial was closest to the carcass at the end of

286   the trial using a glm with a Gaussian distribution, with the natural log ratio of distance to the

287   carcass, as: ln((distance of *N. orbicollis* to the carcass +1)/(distance of *N. pustulatus* to the

288   carcass +1)) as the response variable, and the dominant species in the trial (either *N. orbicollis* or

289   *N. pustulatus*) as the sole predictor. We also tested if beetles interacted more often when

290   competing for larger mouse carcasses using glms, with the number of interactions as the

291   response variable (either all interactions, or just aggressive interactions, in separate models) and

292   mouse mass as the predictor. We checked model fit for these glms using the same methods

293   described for the time in contact with the carcass analysis, described above.

294

Results.

Interactions among species

297   The total number of interactions occurring in each trial varied, however, neutral interactions

298   were the most common (see Table 2). Most aggressive interactions (aggressive physical

299   interactions and avoidance interactions) had asymmetric outcomes, with one beetle emerging as

300   the winner. The duration of interactions varied, with aggressive physical interactions averaging

301   the longest (mean duration of 18.1 seconds +/- 28.1 SD), avoidance interactions the shortest

302   (mean duration of 4.03 seconds +/- 5.74 SD), with neutral (mean duration of 12.1 seconds +/-

303   38.5 SD) and other interactions (mean duration of 6.66 seconds +/- 7.69 SD) falling somewhere

304   in between.

305   Both *N. orbicollis* and *N. pustulatus* initiated interactions with asymmetric outcomes, with *N.*

306   *orbicollis* emerging as the winner more often (*N. orbicollis* 179 wins: *N. pustulatus* 126 wins;

307   see Table 2; Figure 1). Throughout trials, *N. orbicollis* initiated more asymmetric interactions

308   than *N. pustulatus* (198:107; see Table 2). In 14 of 17 trials, the winner of the most asymmetric

309   interactions also spent the most time in contact with the carcass (see Table 2, Figure 2).

310   Additionally, the beetle initiating a contest won 80.0% (244/305) of cases and was

311   significantly more likely to win the contest (estimate = 1.40 +/- 0.35SE, z = 4.0, P = 0.00008).

312   This pattern did not depend on which species initiated the contest (*N. orbicollis*: estimate = 1.45

313   +/- 0.38SE, z = 3.8, P = 0.0001; *N. pustulatus*: estimate = 1.29 +/- 0.44SE, z = 2.9, P = 0.0036).

314   In 14/17 trials, the individual that initiated the most interactions was also the trial winner (i.e.,

315   the winner of the majority of interactions in a trial).

316

317   Factors predicting behavioral dominance

318   Neither priority effects nor species identity were significant predictors of behavioral dominance

319   between *N. orbicollis* and *N. pustulatus*. Larger relative mass was the only significant predictor

320   of behavioral dominance between *N. orbicollis* and *N. pustulatus* (see Table 3) across interaction

321   types (quasibinomial glm, mass: estimate = 5.76 +/- 1.6SE, t = 3.6, P = 0.0025; see Figure 1). As

322   the difference in relative body size increased, so did the difference in number of wins (see Figure

323   1), regardless of species. Restricting the analysis to include only the outcomes of aggressive

324   physical interactions (e.g., fights and chases) resulted in similar results (quasibinomial glm,

325   mass: estimate = 5.85 +/- 1.9SE, t = 3.1, P =0.0076).

326

327   Carcass contact and behavioral dominance

328   Trial winners predicted which individual spent more time in contact with the carcass (deviance =

329   22.46, chi-square P = 0.00005; see Figure 2).

330

331 Behavioral dominance and carcass proximity

332 The trial winner was not more likely to be closest to the carcass at the end of a trial ($F = 0.64$, P

333 $= 0.43$; see Table 2).

334

335 Interactions among beetles and carcass size

336 Larger carcasses did not elicit more interactions among our focal beetles (all interactions, $F =$

337 0.004, $P = 0.95$; aggressive interactions only, $F = 0.057$, $P = 0.82$).

338

339 **Discussion.**

340 Body size predicts behavioral dominance

341 Relative body mass was our single best predictor of contest outcomes between *N. orbicollis* and

342 *N. pustulatus,* making it our only significant trait determining behavioral dominance. We did not

343 know the histories of wild-caught beetles in our trials (e.g., history of fighting, previous mating);

344 if mass covaried with the history of experience for beetles (e.g., larger beetles had more

345 extensive experience with fighting), then it remains possible that this bias impacted our results.

346 In such a case, the impact of mass would be indirect, manifested through different histories of

347 experience (e.g., fighting experience) or condition (mated or not).

348   Our findings were largely consistent with previous work examining behavioral dominance

349 interactions within *Nicrophorus*. We confirm body size as the best predictor of behavioral

350 dominance among competing *Nicrophorus* species, including *N. orbicollis* and *N. defodiens*

351 (Wilson, Knollenberg & Fudge, 1984), *N. vespiloides, N. investigator,* and *N. vespillo* (Otronen,

352 1988), *N. defodiens*, *N. orbicollis*, and *N. sayi* (Trumbo, 1990a; Wettlaufer et al., 2023), as well

353   as *N. orbicollis* and *N. tomentosus* (Schrempf et al., 2021). Results are consistent with previous

354   work in demonstrating that neither species identity (Schrempf et al., 2021) nor order of arrival

355   affects success in competitive interactions over the carcass among species pairs (Trumbo, 1990a;

356   Wilson, Knollenberg & Fudge, 1984; Schrempf et al., 2021; see Otronen, 1988 for an exception).

357

358   Benefits of larger size

359   Aggressive interactions among *Nicrophorus* species typically involve chasing, grappling,

360   digging, and fighting, and thus large size is likely to convey benefits. In all of these cases, greater

361   size could confer greater muscle mass, larger energy reserves, greater inertia, and greater

362   stability when fighting. Large size may also covary with the size and strength of legs and mouth

363   parts that also provide advantages in aggressive interactions by increasing speed, grip, and

364   pushing strength (Pukowski, 1933).

365   Larger relative body size may also signal competitive ability of an individual and play a role

366   prior to the aggressive interactions themselves. The avoidance of larger beetles is supported by

367   the avoidance interactions observed in our trials, where the initiating beetle in avoidance

368   interactions would often turn or adjust its path and move away when approaching within 1 cm of

369   another larger beetle.

370   The importance of large size in determining the outcome of aggressive contests for carcasses

371   between *N. orbicollis* and *N. pustulatus* is consistent with other previous work on *Nicrophorus*

372   (Wilson, Knollenberg & Fudge, 1984; Otronen, 1988; Scott 1998; Trumbo, 1990a; Schrempf et

373   al., 2021; Wettlaufer et al., 2023), suggesting a consistent disadvantage to small size in

374   competitive interactions. The advantage of large size in aggressive contests declines over

375   evolutionary time in other groups (birds), where adaptations, such as novel weapons, allow some

376 small species to dominate larger species, and adaptations to specific challenges, like migration,

377 compromise competitive ability in some larger species (Martin and Ghalambor, 2014). In

378 contrast, we find no similar evidence for a decline in the importance of size in aggressive

379 contests among *Nicrophorus*, suggesting that the costs of small size are difficult to overcome. *N.*

380 *orbicollis* and *N. pustulatus* diverged an estimated 87 million years ago; other species pairs

381 examined to date are also old (> 50 million years diverged) (Sikes & Venables, 2013),

382 suggesting ample time for the evolution of novel traits that could alter the advantage of large

383 size. Large size, however, may play a more important role in fighting in *Nicrophorus*, or other

384 traits that we did not consider in our study, such as cooperative behaviors (Trumbo, 1994), might

385 be key factors providing competitive advantage to some smaller species. Indeed, cooperative

386 behaviors may be more common in smaller species of *Nicrophorus* (Scott, 1998).

387

388 Coexistence of *N. orbicollis* and *N. pustulatus*

389 *N. orbicollis* is larger, on average, than *N. pustulatus* (Collard et al., 2020), suggesting that *N.*

390 *orbicollis* is behaviorally dominant over *N. pustulatus* in most interactions in nature. These

391 results suggest that *N. orbicollis* may preferentially access preferred resources such as the small

392 vertebrate carcasses in the leaf litter of forests, while *N. pustulatus* may be relegated to canopy

393 habitats and alternative resources, such as snake eggs (Blouin-Demers & Weatherhead, 2000;

394 Smith et al., 2007; Trumbo, 2009; Wettlaufer et al., 2018; DeMarco & Martin, 2020). Such

395 partitioning among closely related species may reflect a trade-off between competitive

396 dominance, mediated by size, and the ability to use canopy habitats and carcasses associated with

397 off-ground vertebrate reproduction (environmental tolerance; Martin & Ghalambor. 2023).

398 While our results are consistent with asymmetric dominance interactions creating ecological

399 partitioning among our focal species, we cannot at present rule out alternative hypotheses to

400 explain the pattern, and the factors constraining *N. orbicollis'* success in the canopy remain to be

401 fully explored.

402

Conclusions.

403

404 Our study reveals that body size is the best predictor of who is behaviorally dominant between

405 individuals of *N. orbicollis* and *N. pustulatus* competing for carcasses, and that priority effects

406 (defined by which species arrives at the carcass first) and species identity are either unimportant

407 or minimally important. Our results support previous work and support body size as a key trait in

408 structuring dominance hierarchies and ecological communities.

409
410

Acknowledgements

411

412 Thanks to Chris Eckert, the Martin and Bonier labs, and Eryn Basham for their advice and

413 critique. Thanks to Erin Bolger, Katriona Lane, Emma Schubert, David Griffin, Mary Beazely,

414 and James Yates for their help in data collection. We conducted research on traditional

415 Anishinaabe and Haudenosaunee Territory and are grateful to live and learn on these lands.

416

References

417

418 Anderson RS. 1982. Resource partitioning in the carrion beetle (Coleoptera: Silphidae) fauna of southern Ontario:
419   ecological and evolutionary considerations. *Canadian Journal of Zoology* 60:1314–1325. DOI: 10.1139/z82-
420   178.
421 Anderson RS, Peck SB. 1985. *The carrion beetles of Canada and Alaska. The insects and arachnids of Canada part*
422   *13*. Ottawa: Research Branch: Agriculture Canada.
423 Bartoń K. 2019. *Model inference*. R package version 1.43.6. Available at https://cran. r-
424   project.org/web/packages/MuMIn/index.html.
425 Bestelmeyer BT. 2000. The trade-off between thermal tolerance and behavioural dominance in a subtropical South
426   American ant community. *Journal of Animal Ecology* 69:998–1009.
427 Blouin-Demers G, Weatherhead PJ. 2000. A novel association between a beetle and a snake: parasitism of *Elaphe*
428   *obsoleta* by *Nicrophorus pustulatus*. *Écoscience* 7:395–397.
429 Burke, KW. 2017. Coexistence through morphological divergence in burying beetles (genus: *Nicrophorus*). BSc
430   honours thesis, Queen's University, Kingston, ON, Canada.
431 Burke KW, Wettlaufer JD, Beresford DV, Martin PR. 2020. Habitat use of co-occurring burying beetles (genus
432   *Nicrophorus*) in southeastern Ontario, Canada. *Canadian Journal of Zoology* 98:591–602. DOI:
433   10.1139/cjz-2019-0287.

434 Collard AE, Wettlaufer JD, Burke KW, Beresford DV, Martin PR. 2021. Body size variation in a guild of carrion
435   beetles. *Canadian Journal of Zoology* 99:117–129. DOI: 10.1139/cjz-2020-0171.
436 Crawley MJ. 2013. *The R book*. Chichester, West Sussex, UK: Wiley.
437 DeMarco KVB, Martin PR. 2020. A case of a Pustulated Carrion Beetle (*Nicrophorus pustulatus*, Coleoptera:
438   Silphidae) burying live Tree Swallow (*Tachycineta bicolor*, Passeriformes: Hirundinidae) nestlings under
439   the nest. *The Canadian Field-Naturalist* 134:217–221. DOI: 10.22621/cfn.v134i3.2369.
440 Donadio E, Buskirk SW. 2006. Diet, morphology, and interspecific killing in carnivora. *The American Naturalist*
441   167:524–536. DOI: 10.1086/501033.
442 Fukami T. 2015. Historical contingency in community assembly: integrating niches, species pools, and priority
443   effects. *Annual Review of Ecology, Evolution, and Systematics* 46:1–23. DOI: 10.1146/annurev-ecolsys-
444   110411-160340.
445 Grether GF, Peiman KS, Tobias JA, Robinson BW. 2017. Causes and consequences of behavioral interference
446   between species. *Trends in Ecology & Evolution* 32:760–772. DOI: 10.1016/j.tree.2017.07.004.
447 Hernandez JP, Chalcraft DR. 2012. Synergistic effects of multiple mechanisms drive priority effects within a
448   tadpole assemblage. *Oikos* 121:259–267. DOI: 10.1111/j.1600-0706.2011.19221.x.
449 Hino, T. 2005. Resident males of small species dominate immigrants of large species in heterospecific, winter bird
450   flocks. *Ornithological Science* 4:89–94. DOI: 10.2326/osj.4.89.
451 Hongo Y, Okamoto K. 2013. Interspecific contests between males of two Japanese stag beetle species, *Lucanus*
452   *maculifemoratus* and *Prosopocoilus inclinatus*: what overcomes a body size disadvantage? *Behaviour*
453   150:39–59.
454 Keller ML, Howard DR, Hall CL. 2019. Spatiotemporal niche partitioning in a specious silphid community
455   (Coleoptera: Silphidae *Nicrophorus*). *Die Naturwissenschaften* 106:57. DOI: 10.1007/s00114-019-1653-6.
456 Kelley JL, Magurran AE, García CM. 2006. Captive breeding promotes aggression in an endangered Mexican fish.
457   *Biological Conservation* 133:169-177.
458 Martin PR, Freshwater C, Ghalambor CK. 2017. The outcomes of most aggressive interactions among closely
459   related bird species are asymmetric. *PeerJ* 5:e2847. DOI: 10.7717/peerj.2847.
460 Martin PR, Ghalambor CK. 2014. When David beats Goliath: The advantage of large size in interspecific aggressive
461   contests declines over evolutionary time. *PLoS ONE* 9:e108741. DOI: 10.1371/journal.pone.0108741.
462 Martin PR, Ghalambor CK. 2023. A case for the "Competitive exclusion – tolerance rule" as a general cause of
463   species turnover along environmental gradients. *The American Naturalist* 202:1-17. DOI: 10.1086/724683
464 Martin PR. 2015. Trade-offs and biological diversity: integrative answers to ecological questions. In: *Integrative*
465   *organismal biology*. John Wiley & Sons, Ltd, 291–308. DOI: https://doi.org/10.1002/9781118398814.ch18.
466 Morse DH. 1974. Niche breadth as a function of social dominance. *The American Naturalist* 108:818–830. DOI:
467   10.1086/282957.
468 Otronen M. 1988. The effect of body size on the outcome of fights in burying beetles (*Nicrophorus*). *Annales*
469   *Zoologici Fennici* 25:191–201.
470 Persson L. 1985. Asymmetrical competition: are larger animals competitively superior? *The American Naturalist*
471   126:261–266. DOI: 10.1086/284413.
472 Peters RH. 1983. *The ecological implications of body size*. Cambridge: Cambridge University Press. DOI:
473   10.1017/CBO9780511608551.
474 Poulos DE, McCormick MI. 2014. Who wins in the battle for space? The importance of priority, behavioural history
475   and size. *Animal Behaviour* 90:305-314.
476 Price EO. 1999. Behavioral development in animals undergoing domestication. *Applied Animal Behaviour Science*
477   65:245-271.
478 Pukowski E. 1933. Ökologische Untersuchungen an *Necrophorus* f. Zeitschrift für. *Zeitschrift für Morphologie und*
479   *Ökologie der Tiere* 27:518–586.
480 R Core Team. 2021. *R: a language and environment for statistical computing*. Version 4.1.2. Vienna, R Foundation
481   for Statistical Computing.
482 Rauter CM, Moore AJ. 2002. Quantitative genetics of growth and development time in the burying beetle
483   *Nicrophorus pustulatus* in the presence and absence of post-hatching parental care. *Evolution* 56:96–110.
484   DOI: 10.1111/j.0014-3820.2002.tb00852.x.
485 Robertson IC. 1992. Relative abundance of *Nicrophorus pustulatus* (Coleoptera: Silphidae) in a burying beetle
486   community, with notes on its reproductive behavior. *Psyche: A Journal of Entomology* 99:189–198.
487 Schrempf SD, Burke KW, Wettlaufer JD, Martin PR. 2021. Behavioral dominance interactions between
488   *Nicrophorus orbicollis* and *N. tomentosus* burying beetles (Coleoptera: Silphidae). *PeerJ* 9:e10797. DOI:
489   10.7717/peerj.10797.

490 Scott MP. 1998. The ecology and behavior of burying beetles. *Annual Review of Entomology* 43:595–618. DOI:
491   10.1146/annurev.ento.43.1.595.
492 Sikes DS, Venables C. 2013. Molecular phylogeny of the burying beetles (Coleoptera: Silphidae: Nicrophorinae).
493   *Molecular Phylogenetics and Evolution* 69:552–565.
494 Smith G, Trumbo ST, Sikes DS, Scott MP, Smith RL. 2007. Host shift by the burying beetle, *Nicrophorus*
495   *pustulatus*, a parasitoid of snake eggs. *Journal of Evolutionary Biology* 20:2389–2399. DOI:
496   https://doi.org/10.1111/j.1420-9101.2007.01404.x.
497 Trumbo ST. 1990a. Reproductive success, phenology and biogeography of burying beetles (Silphidae,
498   *Nicrophorus*). *The American Midland Naturalist* 124:1–11.
499 Trumbo ST. 1990b. Interference competition among burying beetles (Silphidae, *Nicrophorus*). *Ecological*
500   *Entomology* 15:347–355.
501 Trumbo ST. 1994. Interspecific competition, brood parasitism, and the evolution of biparental cooperation in
502   burying beetles. *Oikos* 69:241–249.
503 Trumbo ST. 2009. From gravedigger to assassin: how the habits of one species of burying beetle have changed.
504   *Natural History* 118:34–35.
505 Ulyshen MD, Hanula JL. 2007. A comparison of the beetle (Coleoptera) fauna captured at two heights above the
506   ground in a North American temperate deciduous forest. *The American Midland Naturalist* 158:260–278.
507 VideoLan. 2006. *VLC media player*. Retrieved from https://www.videolan.org/vlc/index.html.
508 Violle C, Nemergut DR, Pu Z, Jiang L. 2011. Phylogenetic limiting similarity and competitive exclusion:
509   phylogenetic relatedness and competition. *Ecology Letters* 14:782–787.
510 Wallace MP, Temple SA. 1987. Competitive interactions within and between species in a guild of avian scavengers.
511   *The Auk* 104:290–295.
512 Wettlaufer JD, Burke KW, Beresford DV, Martin PR. 2021. Partitioning resources through the seasons: abundance
513   and phenology of carrion beetles (Silphidae) in southeastern Ontario, Canada. *Canadian Journal of*
514   *Zoology* 99:961–973.
515 Wettlaufer JD, Burke KW, Schizkoske A, Beresford DV, Martin PR. 2018. Ecological divergence of burying beetles
516   into the forest canopy. *PeerJ* 6:e5829.
517 Wettlaufer JD, Ye A, MacMillan HA, Martin PR. 2023. A test of the competitive ability – cold tolerance trade-off
518   hypothesis in seasonally breeding beetles. *Ecological Entomology* 48:55–68.
519 Wilson DS, Knollenberg WG, Fudge J. 1984. Species packing and temperature dependent competition among
520   burying beetles (Silphidae, *Nicrophorus*). *Ecological Entomology* 9:205–216.
521 Young KA. 2003. Evolution of fighting behavior under asymmetric competition: an experimental test with juvenile
522   salmonids. *Behavioral Ecology* 14:127–134.

Table 1. Sex and morphological measurements of beetles used in experiments.

The sex of each participating beetle, as well as its mass, elytra length, and pronotum width.

Trial	Trial start date	N. orbicollis sex	N. pustulatus sex	Mass of N. orbicollis (g)	Mass of N. pustulatus (g)	Elytra length of N. orbicollis (mm)	Elytra length of N. pustulatus (mm)	Pronotum width of N. orbicollis (mm)	Pronotum width of N. pustulatus (mm)
1	04-Jun	male	male	0.440	0.239	11.2	9.2	6.5	5.7
2	07-Jun	female	female	0.301	0.435	9.9	10.2	5.4	7.3
3	07-Jun	female	female	0.804	0.299	13.8	9.4	7.7	6.0
4	08-Jun	male	male	0.458	0.365	11.8	9.8	6.6	6.3
5	08-Jun	female	female	0.556	0.600	12.1	11.6	7.1	7.7
6	09-Jun	female	female	0.916	0.318	15.7	9.9	8.6	6.2
7	10-Jun	male	male	0.509	0.484	12.4	11.4	7.5	7.1
8	10-Jun	female	female	0.379	0.458	10.9	11.3	6.4	7.0
9	11-Jun	male	male	0.687	0.352	13.0	9.8	7.7	6.2
10	11-Jun	male	male	0.212	0.375	8.7	10.4	4.8	6.4
11	12-Jun	male	male	0.427	0.378	11.0	10.0	6.7	6.8
12	12-Jun	male	male	0.515	0.710	12.1	12.6	7.5	7.8
13	13-Jun	male	male	0.354	0.650	10.2	12.6	6.1	8.3
14	13-Jun	female	female	0.763	0.503	12.8	10.9	8.1	7.2
15	14-Jun	male	male	0.617	0.275	13.1	9.1	7.9	5.8
16	14-Jun	female	female	0.705	0.529	13.5	10.4	7.5	7.2
17	16-Jun	male	male	0.529	0.455	12.4	10.6	7.1	7.1

Table 2. Frequency of interactions among beetles, order of arrival, time spent in contact with carcass, and end distance to carcass.

We ran our statistical analyses using the winners of all interactions with asymmetric outcomes as the response variable.

Trial	Trial start date	Aggressive physical interactions *	Avoidance interactions *	Neutral interac- tions	Other interac- tions *	Total number of interac- tions	Initiator of asym- metric interac- tions^	First to carcass	Contact with carcass (minutes) ^
1	04-Jun	18 (17, 0)	8 (8, 0)	59	2 (1, 0)	87	(21, 4)	orbicollis	(521, 30)
2	07-Jun	4 (0, 4)	4 (0, 4)	0	8 (0, 8)	16	(5, 3)	pustulatus	(158, 299)
3	07-Jun	18 (15, 0)	2 (2, 0)	11	0	31	(16, 3)	orbicollis	(154, 88)
4	08-Jun	14 (14, 0)	5 (3, 1)	12	0	31	(14, 4)	pustulatus	(307, 138)
5	08-Jun	9 (0, 9)	1 (0, 1)	8	0	18	(9, 1)	pustulatus	(116, 397)
6	09-Jun	5 (5, 0)	1 (1, 0)	10	0	16	(6, 0)	orbicollis	(285, 18)
7	10-Jun	6 (0, 6)	3 (0, 3)	9	1 (1, 0)	19	(6, 4)	pustulatus	(1, 123)
8	10-Jun	25 (1, 22)	7 (2, 5)	53	18 (0, 11)	103	(6, 35)	orbicollis	(173, 334)
9	11-Jun	20 (20, 0)	2 (2, 0)	8	0	30	(20, 3)	orbicollis	(504, 83)
10	11-Jun	5 (1, 4)	0 (0, 0)	6	0	11	(2, 3)	pustulatus	(286, 315)
11	12-Jun	28 (24, 0)	10 (5, 3)	14	0	52	(30, 2)	pustulatus	(492, 88)
12	12-Jun	16 (6, 4)	11 (0, 11)	22	2 (1, 0)	51	(7, 15)	pustulatus	(156, 344)
13	13-Jun	16 (1, 15)	10 (0, 10)	13	5 (0, 5)	44	(4, 22)	pustulatus	(89, 454)
14	13-Jun	28 (24, 2)	3 (3, 0)	1	0	32	(26, 3)	pustulatus	(307, 383)
15	14-Jun	12 (11, 1)	2 (2, 0)	18	5 (2, 0)	37	(13, 0)	orbicollis	(221, 259)
16	14-Jun	2 (0, 2)	11 (1, 10)	11	3 (0, 0)	27	(6, 5)	pustulatus	(157, 604)
17	16-Jun	7 (7, 0)	0	24	0	31	(7, 0)	orbicollis	(367, 442)

Note: * Number of asymmetric interactions won by: (*N. orbicollis* and *N. pustulatus*)
^ Values for: *N. orbicollis, N. pustulatus*

Table 3. Comparison of model performance for quasibinomial generalized linear models.

We evaluated and compared different predictors corresponding to our alternative hypotheses for their ability to predict behavioral dominance among *N. orbicollis* and *N. pustulatus*. The response variable was the proportion of aggressive contests won by *N. orbicollis* or *N. pustulatus* (n = 17). Models are ranked by QAICc scores. Values are intercept estimates or effect sizes for predictor variables.

Model	Intercept	Relative mass	df	logLik	QAIC	ΔQAIC	weight
outcome~ relative.mass	-0.2659	5.763	2	-60.205	20.6	0	0.824
outcome~relative.mass+first.to.carcass	-0.4649	5.746	3	-59.926	24.1	3.43	0.149
outcome~relative.mass*first.to.carcass	-0.4596	8.746	4	-56.558	27.5	6.83	0.027
outcome~1	0.2662	na	1	-171.009	41.2	20.55	0
outcome~first.to.carcass	0.9416	na	2	-159.139	41.7	21.02	0

Figure 1

Figure 1. Comparison of alternative hypotheses predicting the outcomes of asymmetric interactions

Graph showing trial outcome (winner as individual who won the most asymmetric interactions; all interactions with asymmetric outcomes included) being significantly predicted by relative mass of individuals. Blue shading represents 95% confidence interval. Points represent trials (n = 17) and color of points indicates which species was first to the carcass in each trial (red = *N. orbicollis* first, blue = *N. pustulatus* first).
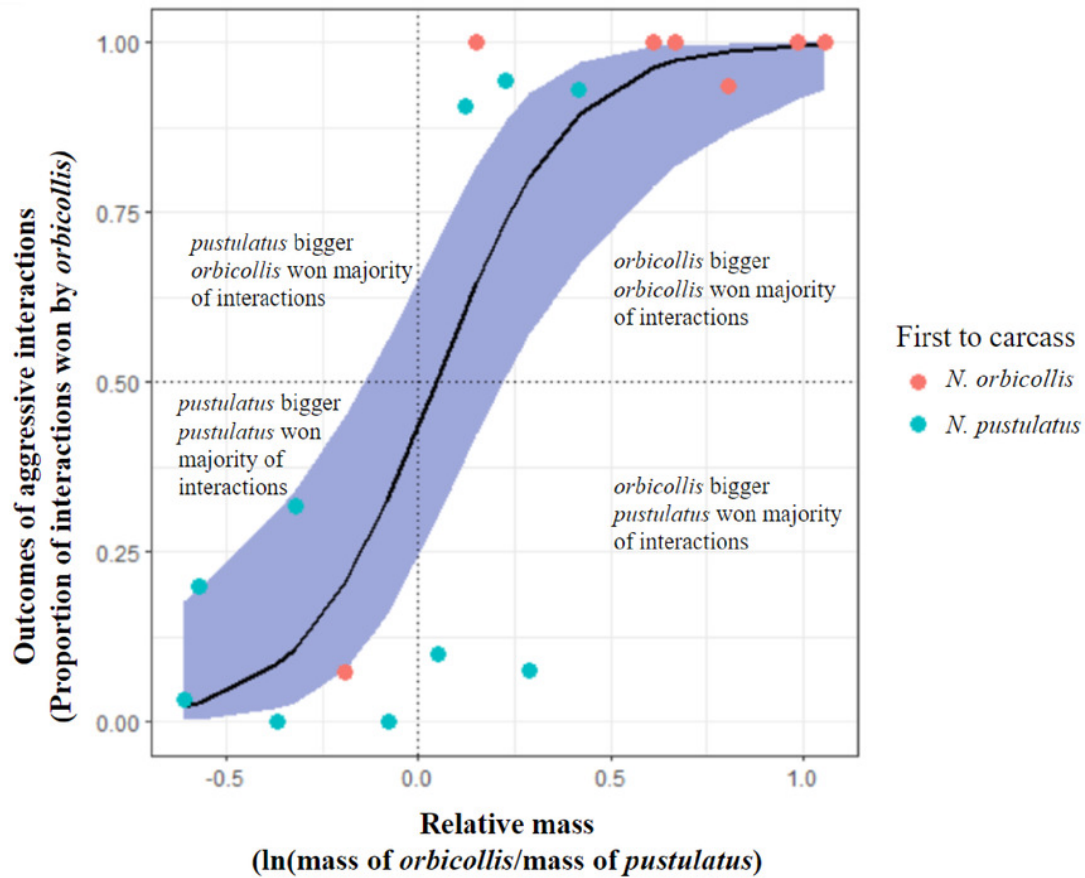
Figure 2

Figure 2. Species that won the most interactions spent more time in contact with the carcass.

All interactions with asymmetric outcomes included (see Table 2). *N. orbicollis* has 9 trial wins and *N. pustulatus* has 8 trial wins (n = 17). Boxes encompass data from the first quartile to the third. Center lines represent the median. Whiskers above and below represent variability of data outside the upper and lower quartiles. Outlined n values indicate how many trials each species won.