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The effect of heterospecific and conspecific competition on inter-individual differences in tungara frog tadpole (Engystomops pustulosus) behavior

OPEN ACCESS

1   <u>Title</u>

2   The effect of heterospecific and conspecific competition on inter-individual

3   differences in tungara frog tadpole (*Engystomops pustulosus*) behavior

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23
24

25   <u>Running header</u>

26   Effect of competition on variation in tadpole behavior.

27

28   <u>Key Words</u>

29   Animal personality, competition, conspecific, heterospecific, inter-individual

30   differences, tadpole, variance partitioning, behavioral syndrome

31   Abstract

32   Repeated social interactions with conspecifics and/or heterospecifics during early

33   development may drive the differentiation of behavior among individuals. Competition

34   is a major form of social interaction and its impacts can depend on whether interactions

35   occur between conspecifics or heterospecifics and the directionality of a response could

36   be specific to the ecological context that they are measured in. To test this, we reared

37   tungara frog tadpoles (*Engystomops pustulosus*) either in isolation, with a conspecific

38   tadpole or with an aggressive heterospecific tadpole, the whistling frog tadpole,

39   *Leptodactylus fuscus*. In each treatment, we measured the body size and distance focal

40   *E. pustulosus* tadpoles swam in familiar, novel and predator risk contexts six times during

41   development. We used univariate and multivariate hierarchical mixed effect models to

42   investigate the effect of treatment on mean behavior, variance among and within

43   individuals, behavioral repeatability and covariance among individuals in their behavior

44   between contexts. There was a strong effect of competition on behavior, with different

45   population and individual level responses across social treatments. Within a familiar

46   context, the variance in the distance swam within individuals decreased under

47   conspecific competition but heterospecific competition caused more variance in the

48   average distance swam among individuals. Behavioral responses were also context

49   specific as conspecific competition caused an increase in the distance swam within

50   individuals in novel and predator risk contexts. The results highlight that the impact of

51   competition on among and within individual variance in behavior is dependent on both

52   competitor species identity and context.

53

<u>Introduction</u>

Among-individual (co)variation in the behavior of animals is now well characterized (Sih

et al. 2004; Réale et al. 2010; Dingemanse and Dochtermann 2013). Animal personality

is used to describe instances of among individual variation in the mean behavioral

response of a population (e.g. variation in the average daily distance each individual

travels). Whereas behavioral syndromes describe among individual correlations of a

behavioral response measured across discrete ecological contexts (e.g. the daily average

distance individuals travel in a familiar vs a novel context). Animal personality is thought

to be driven by intrinsic differences in state between individuals and may be maintained

by genetic variation, phenotypic changes to the genotype to different environments,

and equal fitness payoffs associated with different behavioral strategies (Stamps 2007;

Wolf et al. 2008; Mathot et al. 2012).

In ecology, the niche specialization hypothesis uses comparable statistical and biological

concepts to understand how conspecific and heterospecific competition for food and

space may drive among individual differences in dietary preference, to allow limited

resources to be partitioned among individuals (Bolnick et al. 2003; Araújo et al. 2011).

These behavioral and ecological frameworks are now becoming integrated through the

social (Bergmüller and Taborsky 2010; Montiglio et al. 2013) and behavioral niche (Kent

and Sherry 2020) hypotheses, which predict that conspecific and heterospecific

competition will increase among individual differentiation in behavior to reduce conflict

over resources. These multi-species interactions are important for understanding the

proximate causes of animal personality and behavioral syndromes as well as individual

interactions which promote the coexistence of conspecifics at high density and co-occurrence of multiple species with similar resource needs (Bolnick et al. 2003; Pfennig et al. 2006; Pfennig et al. 2007; Briffa and Sneddon 2016; Kent and Sherry 2020; Sherry et al. 2020).

Under competition, there may be two ways in which individual changes in behavior may lead to consistent differences among individuals in their behavior and resource use. (Figure 1). Individuals may diverge in their average behavior, so that a broader range of behavioral strategies can be used to acquire a more diverse set of resources (Figure 1a; Prati et al., 2021; Preisser, Bolnick, & Grabowski, 2009). For example, less competitive individuals may be forced to forage at less optimal times of day or in less profitable foraging locations (Rychlik 2005; Frere et al. 2008; Harrington et al. 2009; Wauters et al. 2019). This would be detectable as an increase in the variance among individuals as individuals diverge in their average behavior.

Alternatively, competition for resources may also affect how consistent individuals are in their behavioral strategy, by influencing how variable individuals are within themselves (Stamps et al. 2012; Westneat et al. 2015). Here individuals may specialize in a particular microhabitat by showing greater consistency in their foraging behavior (Figure 1b; Beaulieu & Sockman, 2012; Newell et al., 2014; Sherry et al., 2020). For example, each individual may specialize in foraging at a specific time of day within the most optimal foraging hours for that species. Therefore, individuals would diverge in their behavior as they become less variable within themselves (Dingemanse and

100   Dochtermann 2013) and would be detectable as a decrease in the variance within

101   individuals. Consequently, under competition individuals may behave differently from

102   each other either because variation in behavior among individuals increases or because

103   variation within individuals decreases. The repeatability statistic can be used to

104   understand when competition may be driving differences among individuals and where

105   individuals also show high consistency in their behavior within themselves (Bell et al.

106   2009). The individual variance components used to calculate repeatability can then be

107   used to determine whether it is variability among or within individuals which is

108   responsible for this change (Bell et al. 2009; Nakagawa and Schielzeth 2010; Jäger et al.

109   2019). Repeatability will be high when variance among individuals is high relative to

110   within individual variance or when within individual variance is low relative to among

111   individual variance (Nakagawa and Schielzeth 2010; Dochtermann and Royauté 2019).
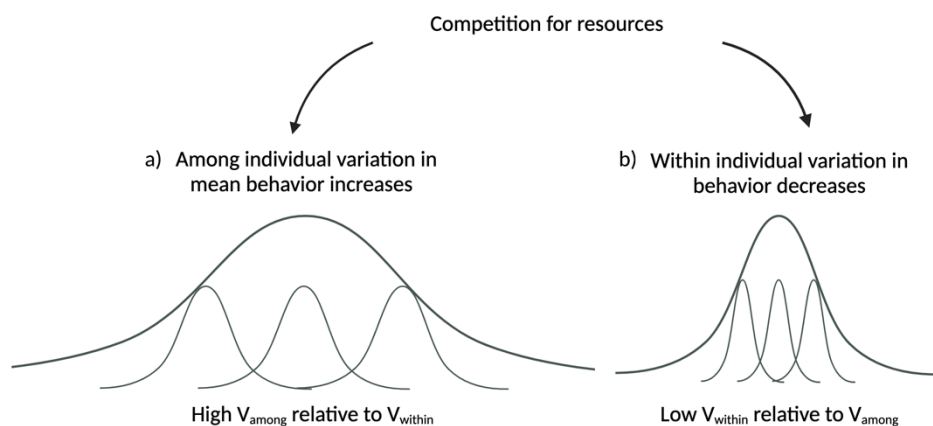
Figure 1. Conceptual illustration of two potential effects on individual level differences in behavior in response to competition. The thin lighter lines are the behavioral responses of individuals and the darker thicker lines are the behavioral response of the population. The repeatability ($R = V_{among} / V_{among} + V_{within}$) of plots a) and b) is the same. In plot a) individuals diverge in their behavioral strategy via an increase in among individual variation in mean behavior. In plot b) individuals diverge in their behavioral strategy via a decrease in within individual variation. Created with BioRender.

112   Behavioral repeatability may also change across ecological contexts (Stamps and

113   Groothuis 2010; Arvidsson et al. 2017; Mitchell and Houslay 2021). This is because novel

114   and risky contexts may result in potentially bolder or more cautious behaviors compared

115   to familiar, low risk contexts (Carter et al. 2013; Perals et al. 2017; Kelleher et al. 2018).

116   An individual's perception of risk may further be dependent on the extent and type of

117   competition they are exposed to during development (Urszán et al. 2015; Han and

118   Dingemanse 2017; He et al. 2017; Castellano et al. 2022). Increased competition for

119   resources may mean that individuals which are in greater need of resources may be

120   prepared to take more risks and travel further distances in unfamiliar contexts

121   (McNamara and Houston 1987; McNamara and Houston 1994; Anholt and Werner 1995;

122   Anholt and Werner 1998). Therefore, patterns of behavioral repeatability may be

123   influenced by the competitive environment as well as be context specific.

124

125   Different competitive environments may also favor specific combinations of behavioral

126   responses across different ecological contexts (Bell 2005; Dingemanse et al. 2007;

127   Fischer et al. 2016). In the absence of competition, there may only be a weak association

128   between an individual's behavioral response in familiar, novel or risky contexts (Bell and

129   Sih 2007; Dingemanse et al. 2007). However, exposure to competition may require

130   individuals to up- or down-regulate their foraging activity across a range of contexts to

131   secure additional resources (Bergmüller and Taborsky 2010). Consequently, conspecific

132   and heterospecific competition may cause individuals to change their behavior across

133   multiple contexts which would be detectable as a behavioral syndrome, that is,

134   correlations between context specific behavioral responses at the among individual

135   level (Garamszegi and Herczeg 2012; Dingemanse and Dochtermann 2013).

136

137   In this study, we investigate the effect of conspecific and heterospecific competition in

138   the tungara frog tadpole (*Engystomops pustulosus*) which can be frequently found

139   inhabiting the same temporary pools with the whistling frog tadpole (*Leptodactylus*

140   *fuscus*) in Trinidad (Downie and Nicholls 2004). Both species have a similar development

141   time of three weeks and occupy a similar ecological niche, suggesting a high level of

142   resource overlap (Murphy et al. 2018; Santana et al. 2019; Atencia et al. 2020). The

143   superior competitive ability of *L. fuscus* is thought to be attributed to its larger starting

144   size and higher activity rates (Downie and Nokhbatolfoghahai 2006; Downie et al. 2008).

145   Amphibian larvae represent an ideal life stage and group of organisms in which to

146   investigate the effects of competition on animal personality and behavioral syndromes

147   (Urszán et al. 2015; Urszán et al. 2018; Castellano et al. 2022). Across a variety of

148   species, tadpoles compete with both conspecifics and heterospecifics for access to

149   resources to fuel fast growth and development prior to metamorphosis and many of

150   these interactions involve asymmetrical competition between species (Werner 1992;

151   Bardsley and Beebee 2001; Richter-Boix et al. 2004; Smith et al. 2004; Richter-Boix et al.

152   2007; Ramamonjisoa and Natuhara 2017; Castellano et al. 2022).

153

154   The behavioral traits we investigated were the total distance individuals travelled in a

155   set period across three ecological contexts, namely, the total distance travelled in a

156   familiar context, novel context and predatory risk context. We will refer to the total

157 distance travelled in each context as activity behavior, exploration behavior and

158 predatory risk-taking behavior respectively. In a familiar context, we predicted that

159 conspecific and heterospecific competition would increase the repeatability of

160 swimming behaviors through an increase in among individual variance in mean behavior

161 and/or decrease in within individual variance. We also predicted that the repeatability

162 of behavior would differ between the three contexts and that behavioral differentiation

163 would be greater under heterospecific compared to conspecific competition. Finally,

164 we predicted that competition with conspecifics and heterospecifics would lead to

165 correlations in behavioral responses between contexts at the among individual level,

166 which may not be present in the absence of competition.

167

168 Methods

169 *Study species and collection sites*

170 We collected a total of 31 *E. pustulosus* and 25 *L. fuscus* foam nests

171 from Lopinot Village, Trinidad (DMS: 10°41'21.7"N, 61°19'26.9"W) between June and

172 July 2019, across four separate collection trips (see experimental design). We collected

173 nests from pools located along a 400-meter length of road where both species are

174 known to co-occur (Downie 2004; Figure 2). We placed each *E. pustulosus* nest into a

175 separate container (dimensions: 145 x 100 x 55mm) containing water from the

176 collection site and each *L. fuscus* nest into containers lined with a damp paper

177 towel. As *L. fuscus* tadpoles rely on heavy rainfall to be washed into larval pool, they

178 can suspend their development after hatching in the absence of water (Downie 1984;

179 Downie 1994). However once submerged in water, their development continues as

180   normal. Consequently, eight of the 25 *L. fuscus* nests collected had already hatched but

181   had not developed beyond Gosner stage 27-28 (Gosner 1960).
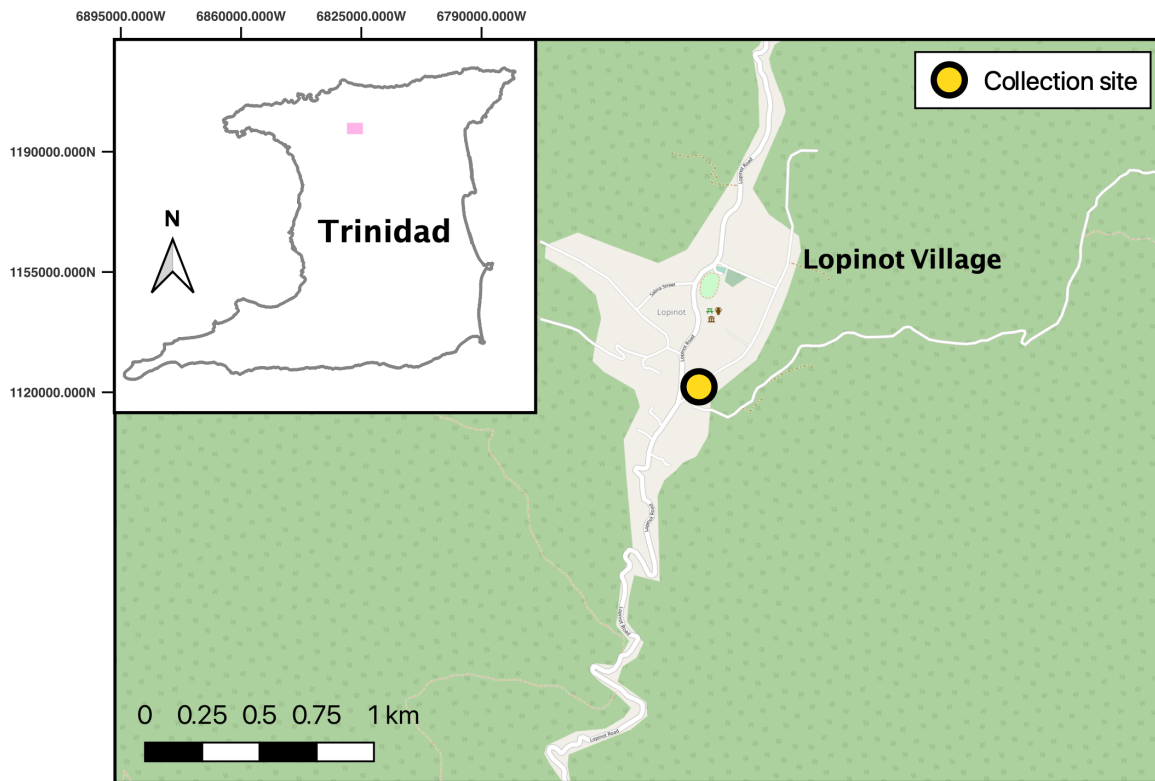
Figure 2.   Map displaying the collection site of *Engystomops pustulosus* and *Leptodactylus fuscus* foam nests in Lopinot Village, Trinidad.

182   We transported the nests back to the William Beebe Tropical Research Station,

183   "Simla", (DMS10°41'30.7"N 61°17'26.4"W) located in Trinidad's Northern Range, within

184   two hours of collection. *E. pustulosus* tadpoles emerged from their eggs between 24

185   and 48 hours after collection. *L. fuscus* tadpoles from nests which had not already

186   hatched were more variable in their emergence time, emerging between 24 to 96 hours

187   post collection. We exposed nests and tadpoles to a 12.5L : 11.5D photoperiod and

188   ambient temperatures ranging between 23.4 °C and 27.9°C (24.8°C ± 0.02 SD).

189

190   *Experimental design*

191   We established three ontogenetic treatment groups to examine the impact of

192   conspecific and heterospecific competition on *E. pustulosus* tadpole behavior: 1) The

193   "heterospecific   treatment"   contained   one *E. pustulosus* tadpole   and

194   one *L. fuscus* tadpole (Figure 3A); 2) the "conspecific treatment" contained

195   two *E. pustulosus* tadpoles, each from different nests (Figure 3B) and 3) the "no

196   competition treatment" which contained an *E. pustulosus* tadpole housed in isolation
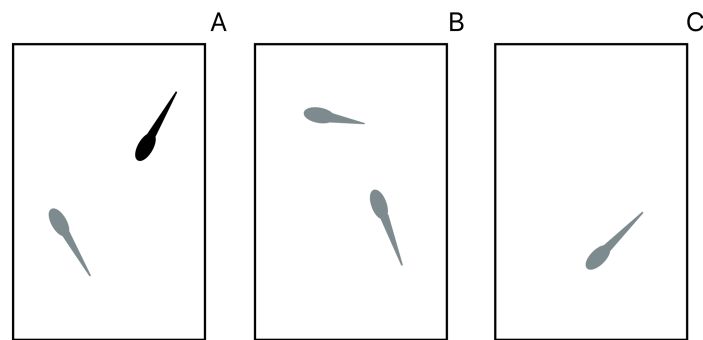
197   (Figure 3C).

198

Figure 3. Illustration of treatment regimes. A: heterospecific treatment containing one *E. pustulosus* (grey) and one *L. fuscus* (black) tadpole. B: conspecific treatment containing one focal (full tail) and non-focal (shortened tail) *E. pustulosus* tadpoles. C: no competition treatment containing a solitary *E. pustulosus* tadpole.

199

200

201

202   We repeated the experiment over four consecutive batches, corresponding to the four

203   collection trips. In each batch, we collected between 3 and 10 *E. pustulosus* foam nests

204   3 to 4 days before assigning tadpoles to their experimental treatments. *L. fuscus* nests

205   were collected slightly earlier, 5-6 days prior to treatment assignment, due to the longer

206   development time of *L. fuscus* eggs.

207

208   Within each batch, we assigned 15 focal *E. pustulosus* tadpoles to each of the three

209   treatment groups, which were chosen at random from two *E. pustulosus* foam nests

210   which hatched on the same day. This was to ensure that focal *E. pustulosus* tadpoles

211   were the same age across each of the three treatment groups. Within the conspecific

212   treatment, tadpoles from the two *E. pustulosus* nests were assigned as the focal or non-

213   focal tadpole. To avoid potential weaker competitive dynamics among related

214   individuals (Pakkasmaa and Aikio 2003; Yu and Lambert 2017), we obtained the non-

215   focal tadpole in the conspecific treatment from the other nest to ensure that

216   competitors were not siblings. To distinguish focal tadpoles in the conspecific

217   treatment, we removed 1/3 of the non-focal tadpole's tail under MS-222 anesthesia

218   (Segev et al. 2015; Clarke et al. 2019). This distinguishing feature quickly disappeared,

219   due to tail regeneration, so we subsequently distinguished focal tadpoles by visual

220   differences in snout-vent-lengths that became apparent 3-4 days after the treatment

221   commenced.

222

223   Focal and non-focal *E. pustulosus* tadpoles were at Gosner stage 25-26 when they were

224   added to their treatment groups. The *L. fucus* tadpoles were more developed (Gosner

225 stage 27-28) than the *E. pustulosus* tadpoles in the heterospecific treatment, reflecting

226 the natural circumstances of *L. fuscus* tadpoles in the wild typically entering breeding

227 pools at a later stage of development (Downie 1984; Downie and Nicholls 2004).

228

229 We housed tadpoles in all treatments in plastic tanks (dimensions: 100 x 65 x 37mm),

230 filled with 150ml of de-chlorinated, aerated tap water. We covered the tank sides in

231 opaque tape, so tadpoles were not influenced by visual cues from tadpoles in adjacent

232 tanks. We fed each tadpole in batches two through four with 7mg of ground fish food

233 (TetraMin Tropical Fish Food Flakes) per day in the first week and 10mg in the second

234 week. Due to a smaller initial size, we fed tadpoles in batch one with 3mg of food in the

235 first week and 7mg in the second week. As there were two tadpoles per tank in the

236 conspecific and heterospecific treatments, the amount of food provided in these

237 treatments was doubled. We left tadpoles undisturbed for five days following their

238 assignment to treatments to allow them to acclimate and develop under their new social

239 environment before starting behavioral assays. The experiment took 15 days from

240 *E. pustulosus* hatching to the completion of the behavioral assays (Figure 4). This

241 represents 60% of the larval period under ideal growth conditions. Tadpoles were

242 returned to their sites of origin within 7 days of completing their final behavioral assay.

243

244 Across the four experimental batches, we collected data from 54 tadpoles in the no

245 competition treatment, 56 focal tadpoles in the conspecific treatment and 51 tadpoles

246 in the heterospecific treatment. 40 tadpoles across the three competition treatments

247 died during the experiment which we did not include in the final tadpole count

248   (supplementary material). We returned unused tadpoles and nests to their sites of origin

249   within 7 days of collection.

250
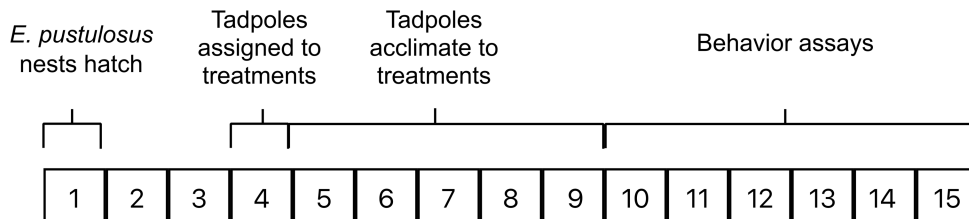
Figure 4. Summary timeline for an experimental batch. Numbers represent 24-hour days.

251

252   *Behavioral assays*

253   We recorded the behavior of each tadpole in three behavioral assays named the activity,

254   exploration, and predator risk-taking assays to record the total distance tadpoles swam

255   in familiar, novel and predator risk contexts respectively. We recorded each individual's

256   behavior on six separate occasions over six consecutive days for each of the three

257   assays. We recorded assays in the same order (activity, exploration and predatory risk-

258   taking) to limit the carry-over effects of the more disruptive exploration and predatory

259   risk-taking assays (Bell 2013). There was a total of 960, 993 and 909 trials recorded

260   from the no competition, conspecific and heterospecific treatments respectively. We

261   removed partial recordings from tadpoles that died before completing all 6 trials and

262   recording errors (e.g., due to power outages) which were identified in 36/2898 trials.

263

264   We recorded all assays using one of four Canon Legria HF R86 camcorders, which we

265   fixed in position (height: 450mm) above the activity tanks and exploration/predatory

266   risk-taking arenas. We could film two tadpoles in separate, adjacent tanks/arenas

267   simultaneously under one camera. The tanks/arenas could be positioned and removed

268   from under the camera but were held in a fixed position during trials to assist with

269   automated tracking software (see video processing). We filmed all the assays in a room

270   adjacent to the laboratory where we performed husbandry procedures, under the same

271   temperature and lighting conditions, to ensure that tadpoles would be undisturbed

272   during filming.

273

274   *Activity assay*

275   To measure activity levels in a familiar context, we filmed the movement of focal *E.*

276   *pustulosus* tadpoles in their home/rearing tanks over a 10-minute period. In the

277   heterospecific and competition treatments, we removed non-focal tadpoles and placed

278   them in a small cup of water from their home tank prior to starting the assay. All

279   tadpoles were left undisturbed for 10 minutes prior to filming to allow them to

280   acclimatize.

281

282   *Exploration assay*

283   To quantify individual exploration of a novel context, we filmed focal tadpole

284   movements in a novel arena (dimensions: 29.8 x 19.5 x 4.9 mm; iDesign, UK), filled with

285   500ml of aerated tap water and warmed to lab temperature. The arena consisted of an

286   acclimation zone (AZ) which opened to a central corridor with four compartments on

287   both the left- and right-hand sides (Figure 5). To start a trial, we transferred one focal

288   tadpole to the AZ and left them to acclimate for 10 minutes. We covered the top of

289   the AZ with an opaque barrier to prevent disturbance from the investigator, and during

290   acclimation we sealed the entrance to the corridor with an opaque removeable

291   barrier. After acclimation, the investigator lifted the front portion of the barrier (the top

292   barrier remained in position), providing the tadpole with access to the arena, and the

293   tadpole's movements were recorded over 15 minutes. The arena was cleaned between

294   trials using tap water and fresh water was used for each new trial and tadpole.

295
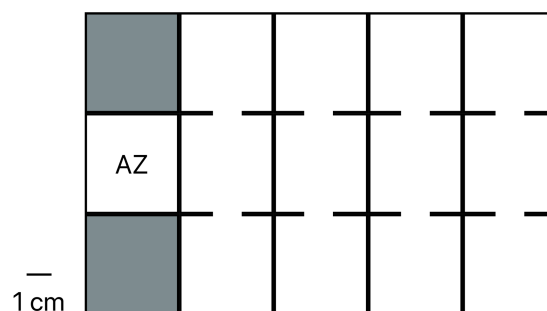
Figure 5. Diagram of the exploration arena. Tadpoles started the trial in the acclimation zone (AZ), spending 10 minutes behind an opaque barrier. After acclimation, tadpoles were free to explore the central corridor zones and adjacent zones to the left and right over 15 minutes. Shaded areas represent unused sealed zones.

296

Predator risk-taking assay

298   To quantify predatory risk taking behavior in a high risk context, we recorded tadpole

299   movements in the presence of visual and olfactory cues from a dragonfly larvae predator

300   (family: Gomphidae) in a novel arena (dimensions: 17 x 12.5 x 4.6; Western Boxes,

301   UK). Each arena consisted of a covered acclimation zone (AZ), an open zone (OZ) in

302   which the tadpole could explore and a predator zone (PZ) which was transparent to

303   allow visual cues of the predator in the OZ (Figure 6). To start a trial, a dragonfly larva

304 was placed into the arena PZ and the focal tadpole was placed into the arena AZ. The

305 AZ was sealed with an opaque barrier to allow tadpoles to acclimate. 10ml of predator

306 conditioned water was also added into the OZ to act as an additional predator olfactory

307 cue after tadpoles and predators were added to the AZ and PZ respectively. Tadpoles

308 were given 10 minutes to acclimate within the AZ before the barrier between the AZ and

309 OZ was removed, we then recorded tadpole movements over 15 minutes. The arena

310 was cleaned between trials using tap water and fresh water was used for each new trial

311 and tadpole. Dragon fly larvae were collected from the Aripo Savannah in Trinidad,

312 where both *E. pustulosus* and *L. fuscus* were also observed to co-occur alongside the

313 dragonfly larvae. When not used in assays, we housed the dragonfly larvae in an 11L

314 Perspex tank and we fed them with four *E. pustulosus* tadpoles (which had died of

315 natural causes) each morning.

316
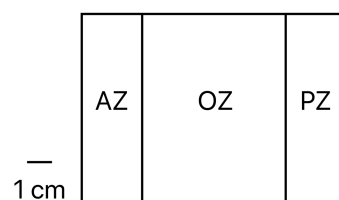
Figure 6. Diagram of the predation arena. AZ represents the acclimation zone where tadpoles acclimated to assay conditions for 10 minutes. PZ represents the predator zone which contained a live dragonfly larval predator. OZ represents the open zone where the tadpole could explore when the opaque AZ barrier was removed for 15 minutes. The barrier between the OZ and PZ was transparent and to allow visual predator cues to pass into the OZ.

317

318

319   *Video processing*

320   Post filming, to reduce storage space and increase processing speed, all videos were re-

321   sized to 640x360 pixels and the activity and exploration assay videos were reduced from

322   25fps to 1fps, using the command line tool ffmpeg (Tomar 2006). The predation assay

323   trials were reduced to a higher frame rate of 5fps to capture the faster movements of

324   tadpoles in this assay. In all three assays, we measured the total distance a tadpole

325   travelled in pixels using a custom-written tracking tool (written by CB) developed in

326   Python v3.0 and using the OpenCV v4.4 library. The tracking tool code can be found on

327   Github (see data availability).   In the exploration and predatory risk-taking assays,

328   tadpoles that did not leave the acclimation zone received a distance score of 0.

329

330   *Morphological measures*

331   The snout vent length (SVL) of each tadpole was measured in FIJI v2.0 (Schindelin et al.

332   2012) to the nearest 0.1mm from the activity assay recordings as a measure of body

333   size. Measurements were taken from each activity trial to give six SVL measurements

334   for each tadpole.

335

336   All procedures were approved by the University of Edinburgh ethics committee, under

337   the   assessment pwalsh1-0001.   Permits   to   collect *E. pustulosus* and *L. fuscus* were

338   obtained from Trinidad's Forestry and Wildlife Division.

339

340

341

Statistical Analysis

343 We estimated the effect of treatment on tadpole body size and tadpole behavior in two

344 separate models using a Bayesian approach.

345

346 *Treatment effects on tadpole body size*

347 To estimate the effect of treatment on tadpole body size we fitted a

348 univariate linear mixed model with a Gaussian error distribution (Dingemanse and

349 Dochtermann 2013). We included a fixed effect of treatment (no competition,

350 conspecific and heterospecific treatment) to estimate the effect the social environment

351 had on the average body size of tadpoles. We also included a fixed effect of trial (fitted

352 as a continuous covariate, coded from 0 to 5) to estimate how body size changed from

353 trial one to six and a random effect of tadpole egg mass ID in the model. To investigate

354 whether treatment affected tadpole growth rates, we included a treatment-specific

355 interaction between trial order (coded from 0 to 5) and size in a random slope model.

356 The random slope model allowed us to determine whether tadpoles in each treatment

357 showed variance amongst individuals in their initial size by fitting a random intercept at

358 trial zero for each tadpole and whether there was variance amongst individuals in their

359 growth rates by fitting a random slope between trial zero and trial five for each tadpole.

360 *Treatment effects on tadpole behavior*

361 To estimate the effect of social treatment on i) the population mean behavior, ii)

362 variance among individuals and iii) variance within individuals, we fitted a multivariate

363 generalized linear mixed model (Dingemanse and Dochtermann 2013) of total distance

364 travelled in a familiar context (activity behavior), a novel context (exploration behavior)

365 and predation risk context (predatory risk-taking behavior). The multivariate model

366 allowed all parameters i-iii to be estimated the total distance travelled in each context

367 simultaneously as well as the pairwise correlations between parameter ii in each context

368 using trial order as the pairing criteria. Given that total distance travelled is a variable

369 constrained to be positive and can be bounded to zero in some contexts, we used a log-

370 normal distribution. As there were a high proportion of exploration and predation-risk-

371 taking assay trials where tadpoles never left the acclimatization zone (54% and 56% of

372 trials respectively), we used a hurdle lognormal distribution for these assays (Hsu and

373 Liu 2008). A hurdle log-normal distribution is in fact a mixture distribution combining a

374 binomial process and a log-normal process. This is adequate for the exploration and

375 predation-risk assays, where the tadpoles decide to leave the acclimation zone or not

376 and then explore the arena. One of the advantages of the hurdle log-normal distribution

377 is that it additionally allowed us to look at a final population level parameter which was

378 iv) the probability that tadpoles remained in the acclimation zone. We used the log-

379 normal distribution for the activity data so that the distance measures in all three

380 contexts could be estimated on the same log scale and aid the comparison of results

381 between the three contexts in the multivariate model.

382

383 To estimate population differences in whether tadpoles left the acclimation zone or not

384 for each treatment, we fitted a treatment specific fixed effect to the hurdle model for

385 the novel, exploration and predatory risk contexts.

386

387   The same fixed effect structure used in the body size univariate model was fitted to the

388   familiar, novel and predator risk contexts in the multivariate model. We fitted two

389   models, one where scaled body size was fitted as a fixed effect and one where scaled

390   body size was not fitted to the model. However, the inclusion of body size did not

391   change the study conclusions and thus was kept in the model. Fitting a fixed effect of

392   treatment allowed us to estimate the overall mean distance tadpoles swam in each

393   treatment and each context.

394

395   To estimate the effect of treatment on the variance among individuals in each context,

396   we included a treatment specific effect for tadpole identity. To estimate the effect of

397   treatment on the variance within individuals we included a treatment specific fixed

398   effect to the residuals. To estimate the effect of treatment on the probability that

399   tadpoles remained in the acclimation zone, we fitted a treatment specific fixed effect to

400   the hurdle model for the novel and predator risk contexts.

401

402   To determine the effect of treatment on the repeatability of tadpole behavior, a

403   separate repeatability estimate was computed for each treatment in the familiar, novel

404   and predator risk contexts. This gave a total of 9 repeatability estimates. Relatabilities

405   were computed using posterior variance estimates of among individual variance and

406   within individual variance obtained from the multivariate mixed model.   As such our

407   treatment specific estimates of repeatability also controlled for body size and trial order,

408   making them estimates of adjusted repeatability (Nakagawa and Schielzeth 2010).

409

410   Estimating among individual variance in mean behavior in the familiar, novel and

411   predator risk contexts provided a 3x3 covariance matrix allowing us to estimate the

412   individual correlations in mean behavior between each context for each of the three

413   treatments. Given that tadpoles were only exposed to one social treatment, we could

414   not estimate the correlation across treatments at the individual level. We converted all

415   covariance estimates into correlations to aid the interpretation of the results.

416

417   To determine whether overall mean body size, variance among individuals in initial body

418   size and variance among individuals in growth rate differed between treatments, we

419   compared the posterior estimates of each parameter across each of the three

420   treatments. To further determine the effect of treatment on behavior, we compared

421   the posterior estimates of mean behavior, variance among individuals, variance within

422   individuals, repeatability, probability of remaining in the acclimation zone and

423   correlations between the average distance swam in each context between the three

424   treatments. Treatment comparisons were calculated as no competition minus the

425   conspecific treatment, no competition minus the heterospecific competition treatment

426   and conspecific minus the heterospecific competition. We have reported the posterior

427   mean for each parameter and treatment comparison with the highest posterior density

428   interval (HPDI) at 95%.

429

430   All models were fitted using the brms package v2.15 (Bürkner 2018) within RStudio

431   2021.09.1+. Brms displays posterior group effect estimates (variation among

432   individuals, variation within individuals and variation among egg masses) as standard

433 deviations which we converted to variances. Furthermore, as brms displays the

434 posterior residual variance of log-normal and hurdle log-normal distribution models on

435 the log scale, the exponential of the posterior residual variance was taken to obtain

436 estimates of within individual variance on their original scale. This provided us with

437 estimates of among and within individual variance which were on the same scale for

438 estimating repeatability. Finally, we converted posterior hurdle model estimates from

439 the logit scale to probability estimates to aid interpretation.

440

441 The univariate and multivariate models used four chains with 8500 iterations and a burn

442 in period of 1000 iterations and a thinning interval of 100. We used uninformative or

443 weak priors on all parameters (Gelman et al. 2013) which included wide normal priors

444 for fixed effects, Half-Student priors for variance parameters and LKJ correlation priors

445 for correlations. The models met all assumptions on convergence and autocorrelation

446 and posterior predictive checks were used to determine if the model fitted the observed

447 data (Gelman et al. 2013).

448

449 Results

450 *The effect of treatment on body size*

451 Tadpoles from the no competition treatment were larger than tadpoles from the

452 heterospecific treatment and marginally larger than tadpoles in the conspecific

453 treatment (Table 1 & 2, Figure 7 & S1). Tadpoles experiencing conspecific competition

454 were also larger than individuals experiencing heterospecific competition (Table 1 and

455 2, Figure 7 & S1). Tadpole body size increased from trial 1 though to trial 6 and there

was no among individual variance associated with Egg Mass ID (Table 1). Across all three

treatments, tadpoles showed among individual variance in their initial body size (Table

1, Figure S2) but this variance did not differ between treatments (Table 2, Figure S2).

Tadpoles did not show among individual variance in their growth rates in any treatment

(Table 1, Figure S3) and this variance did not change between treatments (Table 2, Figure

S3).
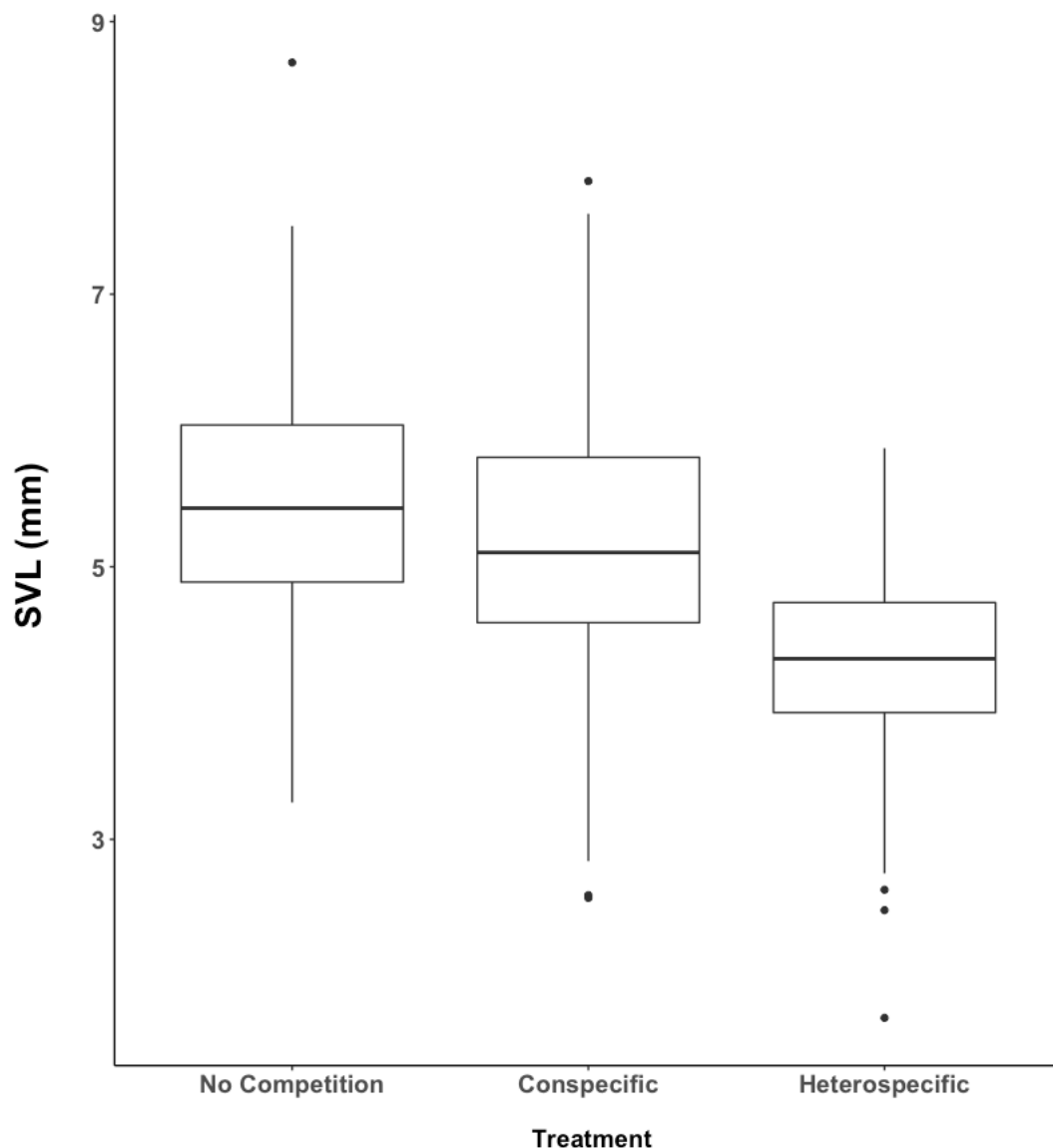
Figure 7. Box and whisker plot of mean tadpole snout vent length (SVL) in the no competition, conspecific and heterospecific treatment groups.

Table 1. Posterior estimates for treatment effects on mean body size (population means), variance among individuals in their initial body size and variance among individuals in their growth rate over the course of the six trials. Also displayed are population mean estimates for trial and variance in body size among egg masses. Estimates are displayed alongside their 95% credible intervals (CI).

| | **Body size** | | |
| | | 95% CI | |
	Mean	2.5	95.7
Population means			
No competition	5.285	4.988	5.588
Conspecific	5.014	4.714	5.339
Heterospecific	4.168	3.865	4.478
Trial	0.056	0.035	0.079
Variance among egg masses			
Egg mass ID	0.149	0.000	0.441
Variance among individuals in initial body size			
No competition	0.288	0.105	0.504
Conspecific	0.404	0.204	0.621
Heterospecific	0.406	0.162	0.705
Variance among individuals in growth rate			
No competition	0.004	0.000	0.010
Conspecific	0.008	0.000	0.017
Heterospecific	0.006	0.000	0.014

462

Table 2. Posterior estimates of the treatment differences on mean body size, variance in initial body size among individuals and variance in the change in body size over the six trials. Estimates are displayed alongside their 95% credible intervals (CI).

	Body size		
		95% CI	
	Mean	2.5	95.7
Population means			
No competition - conspecific	0.273	0.040	0.494
No competition - heterospecific	1.117	0.869	1.377
Conspecific - heterospecific	0.846	0.584	1.105
Variance among individuals in initial body size			
No competition - conspecific	0.148	0.000	0.349
No competition - heterospecific	0.194	0.000	0.495
Conspecific - heterospecific	0.156	0.000	0.395
Variance among individuals in change in body size			
No competition - conspecific	0.005	0.000	0.013
No competition - heterospecific	0.004	0.000	0.011
Conspecific - heterospecific	0.005	0.000	0.013

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468   *The effect of treatment on behavior*

469   At a population level, treatment did not affect the average distance tadpoles swam in a

470   familiar context (Table 3 & 4, Figure S4). In a novel context, tadpoles in the no

471   competition treatment were more exploratory than tadpoles in both the heterospecific

472   and conspecific treatments (Table 3 & 4, Figure S4). In a predator risk context, tadpoles

473   in the no competition treatment swam further than tadpoles in the conspecific

474   treatment (Table 3 & 4, Figure S4).

475

476   In a familiar context, only tadpoles in the heterospecific treatment show variance among

477   individuals in the distance swam and this variance was found to be larger than that

478   observed in the no-competition treatment (Table 3 & 4, Figure S5). Tadpoles did not

479   show among individual variation in the distance swam in the novel and predator risk

480   contexts (Table 3, Figure S5) and these did not change between treatments (Table 4,

481   Figure S5).

482

483   Concerning patterns of within individual (residual) variance, tadpoles showed within

484   individual variance in the distance swam across all three contexts (Table 3, Figure S6).

485   In a familiar context, tadpoles in the conspecific treatment were more consistent in the

486   distance they swam than tadpoles in the no competition treatment (Table 4, Figure S6).

487   In novel and predator risk contexts, tadpoles in the conspecific treatment were less

488   consistent in the distance they swam than tadpoles in the no competition and

489   heterospecific treatments (Table 4, Figure S6).

490

491   In a familiar context, the distance tadpoles swam was only repeatable within the

492   heterospecific treatment and was greater than the amount of repeatability observed

493   within the no competition treatment (Table 5 & 6, Figure S7). The distance tadpoles

494   swam was not repeatable in any treatment within novel and predator risk contexts and

495   did not change between treatments (Table 5 & 6, Figure S7).

496

497   In novel contexts, tadpoles in the conspecific treatment were the most likely to remain

498   in the acclimation zone compared to tadpoles in the no competition and heterospecific

499   treatments (Table 3 & 4, Figure S8). The predator risk context was similar, with tadpoles

500   in the conspecific treatment being more likely to remain in the acclimation zone than in

501   the heterospecific treatment (Table 3 & 4, Figure S8).

502

503   There was no correlation in the average distance individual tadpoles swam between

504   contexts (Table S1). These correlations also did not differ between treatment regimes

505   (Table S2).

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Table 3. Posterior estimates for the treatment effects on population means, variance among individuals, variance within individuals and the probability that tadpoles remained in the acclimation zone for activity, exploration and predatory risk-taking (predation) behaviours. Also displayed are population mean estimates for body size (SVL) and trial number as well as variance among egg masses. Estimates are displayed alongside their 95% credible intervals (CI).

	Activity			Exploration			Predation		
		95% CI			95% CI			95% CI	
	Mean	2.5	97.5	Mean	2.5	97.5	Mean	2.5	97.5
Population means									
No competition	6.228	5.849	6.624	6.819	6.391	7.230	6.141	5.740	6.521
Conspecific	6.221	5.833	6.550	6.212	5.744	6.725	5.849	5.422	6.273
Heterospecific	6.319	5.907	6.744	5.854	5.367	6.355	5.852	5.443	6.289
SVL	-0.088	-0.225	0.052	-0.227	-5.000	-0.069	-0.010	-0.200	0.187
Trial	-0.114	-0.173	-0.061	-0.186	-0.267	-0.089	-0.068	-0.154	0.025
Variance among egg masses									
Egg Mass ID	0.157	0.000	0.429	0.137	0.000	0.443	0.054	0.000	0.194
Variance among individuals									
No competition	0.193	0.000	0.455	0.129	0.000	0.440	0.144	0.000	0.483
Conspecific	0.175	0.000	0.389	0.863	0.000	1.745	0.493	0.000	1.181
Heterospecific	0.686	0.303	1.176	0.403	0.000	1.008	0.127	0.000	0.384
Variance within individuals									
No competition	2.796	2.332	3.285	2.773	2.247	3.418	2.703	2.142	3.360
Conspecific	1.770	1.465	2.073	3.466	2.574	4.455	2.788	2.026	3.520
Heterospecific	2.316	1.897	2.724	2.736	2.045	3.446	2.773	2.195	3.387
Probability remained in acclimation zone									
No competition	NA	NA	NA	0.375	0.321	0.426	0.450	0.394	0.505
Conspecific	NA	NA	NA	0.512	0.458	0.565	0.508	0.457	0.560
Heterospecific	NA	NA	NA	0.432	0.380	0.489	0.416	0.362	0.472

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Table 4. Posterior estimates of the treatment differences on population means, variance among individuals, variance within individuals and the probability that tadpoles remained in the acclimation zone for activity, exploration and predatory risk taking (predation) behaviors. Estimates are displayed alongside their 95% credible intervals (CI).

	Activity			Exploration			Predation		
		95% CI			95% CI			95% CI	
	Mean	2.5	97.5	Mean	2.5	97.5	Mean	2.5	97.5
Population means									
No competition - Conspecific	0.121	0.000	0.297	0.607	0.159	1.111	0.312	0.001	0.662
No competition - Heterospecific	0.178	0.000	0.438	0.965	0.457	1.450	0.315	0.000	0.685
Conspecific - Heterospecific	0.173	0.000	0.418	0.383	0.000	0.804	0.186	0.000	0.469
Variance among individuals									
No competition - Conspecific	0.145	0.000	0.368	0.751	0.000	1.640	0.411	0.000	1.062
No competition - Heterospecific	0.499	0.015	0.963	0.333	0.000	0.918	0.149	0.000	0.439
Conspecific - Heterospecific	0.513	0.000	0.976	0.594	0.000	1.465	0.409	0.000	1.054
Variance within individuals									
No competition - Conspecific	1.026	0.462	1.602	0.749	0.001	1.700	0.408	0.001	0.990
No competition - Heterospecific	0.500	0.000	1.013	0.379	0.000	0,938	0.352	0.000	0.876
Conspecific - Heterospecific	0.549	0.000	0.999	0.794	0.001	1.786	0.405	0.001	0.985
Probability remained in acclimation zone									
No competition - Conspecific	NA	NA	NA	0.136	0.058	0.206	0.060	0.000	0.122
No competition - Heterospecific	NA	NA	NA	0.059	0.000	0.123	0.043	0.000	0.101
Conspecific - Heterospecific	NA	NA	NA	0.080	0.003	0.146	0.092	0.014	0.164

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Table 5. Posterior estimates of repeatability for activity, exploration and predatory risk-taking behaviors (predation) in the no competition, conspecific and heterospecific treatments. Estimates are displayed alongside their 95% credible intervals (CI).

	Activity			Exploration			Predation		
		95% CI			95% CI			95% CI	
	Mean	2.5	97.5	Mean	2.5	97.5	Mean	2.5	97.5
No competition	0.064	0.000	0.148	0.044	0.000	0.140	0.050	0.000	0.166
Conspecific	0.089	0.000	0.187	0.195	0.000	0.364	0.146	0.000	0.319
Heterospecific	0.226	0.107	0.345	0.125	0.000	0.293	0.043	0.000	0.127

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Table 6. Posterior estimates of the treatment differences on repeatability for activity, exploration and predatory risk taking (predation) behaviors. Estimates are displayed alongside their 95% credible intervals (CI).

	Activity			Exploration			Predation		
		95% CI			95% CI			95% CI	
	Mean	2.5	97.5	Mean	2.5	97.5	Mean	2.5	97.5
No competition - Conspecific	0.060	0.000	0.150	0.159	0.000	0.331	0.119	0.000	0.290
No competition - Heterospecific	0.163	0.016	0.296	0.101	0.000	0.266	0.050	0.000	0.146
Conspecific - Heterospecific	0.140	0.000	0.280	0.124	0.000	0.294	0.118	0.000	0.285

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Discussion

We exposed tadpoles to no competition, conspecific competition and heterospecific competition during their development and measured the total distance they swam over multiple trials in familiar, novel and predator risk contexts. We found that conspecific and heterospecific competition resulted in different patterns of among and within individual variation which impacted the repeatability of behavior across the three contexts. Within a familiar context and under heterospecific competition, we found that there was among individual variance in the average distance tadpoles swam, leading to repeatable differences in activity behavior. However, under conspecific competition, there was a decrease in the variance within individuals, but this did not lead to any increase in behavioral repeatability. There was also an increase in within individual variance in the distance swam in novel and predator risk contexts. Our results show that the impact of competition on among and within individual variance as well as behavioral repeatability is dependent on competitor species identity and is context specific.

Ecological theory predicts that individuals can alleviate competition for resources through feeding specialization (MacArthur 1958; Bolnick et al. 2003). Changes in foraging behavior may also be important in promoting co-existence where there is high resource overlap (Pfennig et al. 2006; Pfennig et al. 2007; Kent and Sherry 2020; Sherry et al. 2020). In our experiment, conspecific and heterospecific competition affected the among and within individual components of tadpole activity behavior independently and this suggests that behavioral mechanisms for reducing conflict over contested resources may be different for single and multispecies interactions. The increase in

576   among individual variance and repeatability under heterospecific competition may have

577   provided a mechanism by which food resources could be consistently partitioned

578   between focal and non-focal tadpoles (Sherry et al. 2020; Prati et al. 2021). Therefore,

579   the diversification of behavior in the presence of a heterospecific competitor may

580   promote diversification in how resources are acquired and may be a mechanism which

581   promotes species coexistence (Pfennig et al. 2006; Pfennig et al. 2007). For example, by

582   diverging in the average distance they swam, focal tadpoles may have adjusted their

583   foraging behavior to target the single dietary resource, fish flakes, via different

584   behavioral mechanisms and reduce conflict with *L. fuscus* individuals (e.g. foraging on

585   the water surface vs at the bottom of the tank). Equally, among individual variance in

586   activity behavior may also reflect differences in the susceptibility of *E. puslulosus*

587   tadpoles to heterospecific competition due to individual differences in body size or

588   metabolic rate (Careau et al. 2008; Biro and Stamps 2010; Kelleher et al. 2017). For

589   example, less competitive individuals may have had to forage more intensely than more

590   competitive individuals. Alternatively, differences in morphology and/or behavior

591   among *L. fucus* individuals may have contributed to the diversity of behavioral responses

592   observed in the focal *E. pustulosus* tadpoles via indirect effects (Wolf et al. 1998; Wilson

593   et al. 2009; Jäger et al. 2019).

594

595   In the conspecific treatment, the decrease in within individual variance without the

596   corresponding change in behavioral repeatability suggests that individuals were not

597   partitioning resources through behavioral specialization. A more likely explanation is

598   that the increased consistency in swimming movements was to allow focal tadpoles to

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599   behave more similarly to the non-focal tadpole (Herbert-Read et al. 2013). This may be

600   beneficial for promoting increases in foraging gains through group foraging (Rook and

601   Penning 1991; Rands et al. 2014), reduce the costs of locomotion (Marras et al. 2015) or

602   provide increased protection from predators (Landeau and Terborgh 1986; Szulkin et al.

603   2006). In fish shoals, individuals may conform in their behavior to produce coordinated

604   changes in direction and bursts of speed (Jolles et al. 2018; Sankey et al. 2019; Jolles et

605   al. 2020). This may be mediated by a decrease in behavioral variation both between

606   each other and within themselves (Webster et al. 2007; Magnhagen and Bunnefeld

607   2009; Herbert-Read et al. 2013). Whilst shoaling behavior has not been reported in *E.*

608   *pustulosus* tadpoles, other larvae of anuran species such as cane toads (*Rhinella marina*)

609   and common toads (*Bufo bufo*) are known to form dense aggregations (Wassersug et al.

610   1981; Griffiths and Foster 1998) where behavioral conformity may be important. To

611   elucidate whether the decrease in within individual variance in response to conspecifics

612   was driven by competition over resources or behavioral conformity, future studies could

613   record the behavior of both focal and non-focal individuals. If both individuals show

614   similar patterns of behavior and low within individual variance, this will indicate

615   behavioral conformity over behavioral specialization.

616

617   In addition to the species identity of a competitor impacting the variance in behavior

618   among and within individuals, we found the effect of competitive treatment was highly

619   context dependent. In particular, the level of within and among individual variation in

620   the distance swam in home tanks had no relation to the level of among or within

621   individual variation within novel or high predation risk contexts. Consequently, studies

622   which only consider individual level behavioral responses in a single context are likely to

623   miss elements of behavioral variation that could be relevant in other ecological contexts.

624   There was also no evidence that competition could alter the structure of behavioral

625   syndromes within a population.

626

627   Since low numbers of tadpoles left the acclimation zone in the novel and predator risk

628   contexts, our power to detect differences in the repeatability of behavior between

629   treatments was limited (Martin et al. 2011; Dingemanse and Dochtermann 2013).

630   Nevertheless, tadpoles in the conspecific treatment were the least likely to leave the

631   acclimation zone across both the novel and predator risk contexts compared to tadpoles

632   housed in isolation or with a heterospecific. This provides further support for our

633   findings that behavioral responses to competition were both context specific and

634   dependent on the species of the competitor. Jolles et al (2016) suggested that testing

635   fish in isolation when they had previously been housed in groups may induce stress

636   (Gallup and Suarez 1980) compared to individuals which had always been housed

637   alone. This may contribute to a reduced tendency for individuals to take risks (Jolles et

638   al. 2016). A similar mechanism could explain the high number of tadpoles in the

639   conspecific treatment which remained in the acclimation zone in the present study,

640   compared to the increased exploration levels in the no competition treatment.

641

642   When tadpoles did leave the acclimation zone in the conspecific treatment, individuals

643   were found to be less consistent in novel and predator risk contexts compared to the no

644   competition and heterospecific treatments. Low consistency in behavior has been

645 suggested as an adaptive strategy to reduce an individual's susceptibility to predation

646 (Maye et al. 2007; Stamps et al. 2012; Biro and Adriaenssens 2013; Briffa 2013).

647 Consequently, when tadpoles took risks to leave the acclimation zone, their increased

648 unpredictability in swimming movements may have been to offset the increased chance

649 of predation in riskier contexts.

650

651 Conclusions

652 This study shows that both conspecific and heterospecific competition can impact

653 individual differences in behavior but may be mediated through different mechanisms,

654 affecting among and within sources of individual variation independently. As

655 highlighted by the effect of conspecific competition on the consistency of behavior in

656 familiar and novel contexts, this study also demonstrates that responses to competition

657 is context dependent. Future investigations should consider how individual variation in

658 behavior may change in response to early life conditions depending on the behaviors

659 and contexts investigated.

660

661 Funding

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673   <u>Data availability</u>

674   Analyses reported in this article can be reproduced using the data provided by Author

675   CB https:// doi:10.5061/dryad.p8cz8w9tn. The code for the tadpole tracking tool has

676   been provided by CB and can be accessed via GitHub

677   https://github.com/cammybeyts/Tadpole_tracker.

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