

1 **Title: Competitive asymmetry and local adaptation in Trinidadian guppies**

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24 **Abstract:**

25 1. The outcome of competition between individuals often depends on body-size. These
26 competitive asymmetries can drive variation in demographic rates, influencing the
27 ecology and evolution of life-histories. The magnitude and direction of such asymmetries
28 differ among taxa, yet little is known empirically about how adaptation to resource
29 limitation alters competitive asymmetries.

30 2. Here, we investigate the relationship between size-dependent competitive ability and
31 adaptation to resource limitation.

32 3. We examined size-dependent competition in two ecotypes of Trinidadian guppy,
33 adapted to high or low levels of resource competition. Using aquaria-based competition
34 experiments, we describe how the size and ecotype of competitors influence somatic
35 growth rate, whilst controlling for the confounding effect of niche differentiation. We
36 replicated our study across two independent evolutionary origins of the 'competitive'
37 ecotype.

38 4. The two 'competitive' ecotypes differed markedly in size-dependent asymmetry,
39 indicating that adaptation to resource limitation alone is insufficient to explain changes in
40 size-dependent competitive asymmetry. For one origin, the ecotype adapted to resource
41 limitation was a superior competitor over a wide range of size pairings.

42 5. The equivalence of competitors varied over five-fold, dependent on size and ecotype;
43 in three of four populations, larger individuals had a competitive advantage.

44 6. Our results demonstrate that competitive asymmetry has strong effects on somatic
45 growth. Because somatic growth contributes to demographic parameters, intraspecific
46 trait variation is likely to play a key role in regulating demographic rates. Our findings imply

47 that the evolution of size-dependent asymmetries under conditions of intense competition
48 is likely to be constrained by niche availability, although further research is needed to
49 verify this.

50

51 **Keywords: density-dependence, ecotypes, individual differences, interaction**
52 **surface, intraspecific competition, size-dependent, somatic growth rate, trait**
53 **variation.**

54

55 **Introduction**

56

57 *“All animals are equal, but some animals are more equal than others” – Animal Farm,*
58 *George Orwell*

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60 Competitive interactions for limited resources have long been thought to play a
61 major role in the regulation of populations (e.g. Gause 1934; Hairston, Smith & Slobodkin
62 1960; Connell 1983). Empirical investigations of competition often envision total numbers
63 of individuals as the important determinant of the level of competition experienced (e.g.
64 Jenkins *et al.* 1999; Svanbäck & Bolnick 2007; Bassar *et al.* 2013). However, individuals
65 are rarely equal in competitive ability. Where individuals differ in competitive ability
66 through phenotypic trait values, competition is said to be asymmetric (Weiner 1990).
67 Differences in competitive ability are frequently described between species (Lawton &
68 Hassell 1981; Schoener 1983) and between distinct life-history stages (Schröder, van
69 Leeuwen & Cameron 2014). Asymmetric competition can significantly alter ecological

70 and evolutionary dynamics. For example, asymmetric competition among life-history
71 stages can modify the age structure of populations and drive life-history evolution (de
72 Roos, Persson & McCauley 2003), whilst asymmetry between species can lead to the
73 extinction or displacement of one species, or an evolutionary 'arms-race' between species
74 (Law, Marrow & Dieckmann 1997).

75 In species without clearly defined life-history stages, asymmetry may result from
76 differences among competitors in the values of quantitative traits. Body size is one such
77 trait (Schoener 1983; Ward, Webster & Hart 2006). Many size-dependent traits relate
78 directly to two factors that determine the competitive ability of an organism: a.) the impact
79 an individual has on local resource availability, and b.) its ability to tolerate resource
80 depletion (Persson 1985; Goldberg 1990; Werner 1994). Larger individuals often have an
81 advantage with respect to a.): they are often better at acquiring resources and are able
82 to outcompete smaller individuals (Weiner 1990). By contrast, smaller individuals may
83 have an advantage with respect to b.): they have lower per capita resource requirements,
84 which may allow them to better tolerate resource depletion (Persson 1985). In the wild,
85 examples exist of both larger individuals being competitively superior (e.g. Jenkins *et al.*
86 1999; Boaventura, Da Fonseca, & Hawkins 2003; Donahue, 2004), and of smaller
87 individuals having a competitive advantage (e.g. Marshall & Keough 1994; Werner 1994;
88 Byström & Andersson 2005). Theoretical work has shown that when competitive
89 asymmetry depends on body size, shifting competitive dominance from small individuals
90 to large ones can lead to a doubling of generation time, through a reduction of growth rate
91 and survival in juveniles, but increased survival and fecundity in adults (Bassar *et al.*
92 2016). Such competitive asymmetry can in turn influence population dynamics and the

93 timescale of evolution (Bassar *et al.* 2016). Despite the significant ecological and
94 evolutionary consequences of size-dependent asymmetry, many studies of natural
95 populations assume that competition is symmetric with respect to body size and model
96 demographic rates as a function of the total population size or density: conspecifics are
97 assumed to be ecologically equivalent (Hassell 1975; Connell 1983; Schoener 1983;
98 Gurevitch *et al.* 1992; Bassar *et al.* 2010a).

99 Of course, competitive ability can evolve. Because species differ in the strength
100 and direction of size-dependent asymmetries, we suggest that the relationship between
101 size and competitive ability may also evolve. Although size-dependent asymmetry is
102 considered a population-level parameter, it ultimately arises from how the competitive
103 ability of individuals changes during growth (Werner 1988). What factors might contribute
104 to the evolution of such ontogenetic changes in competitive ability, and therefore of size-
105 dependent asymmetry? One candidate is resource limitation. Where they exist, size-
106 dependent asymmetries are strongest under conditions of resource limitation (Post,
107 Parkinson & Johnston 1999), yet such conditions alone may not drive the evolution of
108 such asymmetries: if resource acquisition is independent of body size, competition will be
109 size-symmetric by definition. The degree and mode of adaptation to resource limitation
110 may differ among populations: how then does adaptation to resource limitation influence
111 size-dependent competition? To address this question, we compare the degree of size-
112 dependent competitive asymmetry in ancestral and derived populations differentially
113 adapted to conditions of resource limitation.

114 Trinidadian guppies (*Poecilia reticulata*) represent an excellent system for testing
115 how asymmetries within and among populations are influenced by body size and local

116 adaptation to resource limitation. Guppies inhabit streams and rivers throughout Trinidad,
117 along gradients of predation intensity. In downstream regions guppies live in high-
118 predation habitats alongside several predatory species, such as the pike cichlid
119 (*Crenicichla alta*) and the wolf fish (*Hoplias malabaricus*). These large predatory fish are
120 restricted to downstream regions by the presence of barrier waterfalls. Above barrier
121 waterfalls, guppies exist in low-predation habitats with one other fish species present, the
122 killifish (*Rivulus hartii*), a competitor to and occasional predator of guppies. Increased
123 predation rates in downstream localities leads to reduced densities of guppies compared
124 to upstream locations: the absolute density of guppies in low-predation habitats is
125 approximately twice that of high-predation habitats (Reznick & Endler, 1982), whilst
126 differences in population size structure mean that the biomass density of guppies in low-
127 predation habitats is four-fold higher than in high-predation habitats (Reznick, Butler &
128 Rodd 2001). The lack of predators in low-predation locations shifts the nature of
129 population regulation between these populations from top-down, via predation (as in high-
130 predation) to bottom-up regulation through resource competition (as in low-predation)
131 (Torres-Dowdall *et al.* 2012; Bassar *et al.* 2013). Guppies of both ecotypes are
132 omnivorous, consuming invertebrates, detritus, and algae, however low-predation
133 habitats have lower resource availability (Reznick, Butler & Rodd 2001) and lower
134 resource quality, i.e. fewer invertebrate prey available as food for guppies (Zandoná *et al.*
135 2017).

136 These changes in the predation risk and population densities ultimately drive
137 differences in the life histories of these two ecotypes. Low-predation guppies are larger
138 at maturity, commit fewer resources to reproduction, have lower reproductive frequency,

139 and produce a smaller number of larger offspring per litter than high-predation guppies
140 (Reznick & Endler 1982). These differences have a genetic basis (Reznick 1982) and are
141 consistent across independent river watersheds (Reznick, Rodd & Cardenas 1996).
142 Genetic analyses of nuclear and mitochondrial sequences support the parallel,
143 independent evolution of the low-predation ecotype following invasion of guppies from
144 ancestral high-predation habitats across multiple river watersheds in Trinidad (Alexander
145 *et al.* 2006): the life-histories of guppies in low-predation habitats have consistently,
146 repeatedly, and independently diverged from those of the ancestral high-predation
147 guppies. Changes in predation risk alone cannot explain the difference in life-histories
148 between guppy ecotypes; instead, in low-predation guppies the increased population
149 densities and strong density regulation of natural populations support the argument that
150 limited resource availability drives the evolution of the low-predation life-history (Reznick
151 *et al.* 1996; Reznick, Butler & Rodd 2001; Reznick *et al.* 2012; Bassar *et al.* 2013).
152 Furthermore, low-predation guppies are less sensitive to increases in population density
153 than high-predation guppies (Bassar *et al.* 2016), and life-history changes such as larger
154 offspring size confer a competitive advantage at high population densities (Bashey 2008).
155 Thus, the weight of evidence suggests that low-predation guppies are adapted to
156 resource limitation. Several traits that evolve in the low-predation ecotype are size-
157 related, suggesting that increased size plays an important role in adaptation to
158 competition through resource limitation. As such, guppies provide an excellent model for
159 investigating the effect of size and local adaptation to resource limitation on competitive
160 asymmetries.

161 Here, we employ an experimental approach to test whether competitive ability
162 changes dependent on population- and individual-level traits (ecotype and body size,
163 respectively) in Trinidadian guppies. Under the assumption that low-predation guppies
164 are adapted to resource limitation, we expect a population-level competitive advantage
165 of the low-predation ecotype. If adaptation to resource limitation increases size-
166 dependent asymmetry, we would expect low-predation guppies to have a stronger
167 positive relationship between competitive ability and body size. We discuss our findings
168 with respect to potential mechanisms underlying local adaptation to increased levels of
169 competition, and to the ecology and evolution of competitive asymmetry.

170 **Methods**

171 *Experimental design*

172 We performed aquaria-based competition trials to determine if ecotype- and size-
173 based competitive asymmetry operates in Trinidadian guppies, and whether size-based
174 asymmetries differed between high-predation and low-predation ecotypes. We
175 determined competitive asymmetry by the impact of the ecotype and body-size of an
176 individual on the somatic growth rate of its competitor(s). This provides an indirect
177 measure of an individual's trait-dependent impact on resource availability. We chose to
178 measure the effect on somatic growth since fitness and thus demographic rates are very
179 sensitive to this parameter in guppies (Bassar *et al.* 2013). Each tank contained either
180 two or four guppies, simulating the two-fold difference in absolute population densities
181 typical between natural high-predation (low density) and low-predation (high density)
182 populations (Reznick & Endler, 1982; Bassar *et al.* 2013). Guppies were categorized into
183 four size classes ($\pm 1.5\text{mm}$): 10mm, 14mm, 18mm, and 22mm. These size classes broadly

184 represent different life-history stages in female guppies: juveniles (10mm), newly-
185 reproducing adults (14mm), and established, mature adults (18mm and 22mm),
186 representing most of the natural size variation seen in wild populations of guppies of both
187 ecotypes (Rodd & Reznick, 1997). Each tank contained either one or two size classes of
188 fish, and one or both ecotypes, in all possible unique pairings at each density, giving 72
189 competition trials (Fig 1). Note that whilst we describe the experimental design in terms
190 of discrete size-classes, analysis of the effect of individual and competitor body size on
191 somatic growth was performed by regression, i.e. size is analysed as a quantitative trait.
192 Simulation studies have shown that such a design is sufficient to be able to estimate the
193 degree of body size asymmetry in growth rate (Bassar *et al.* 2016). All tanks received the
194 same amount of food which was held constant over the 28-day trial. The tanks provided
195 a homogenous habitat, preventing any size- or ecotype- dependent niche differentiation.
196 This controlled approach allows us to directly quantify competitive asymmetry, which
197 would be confounded by the contrasting effect of niche differentiation in natural
198 environments. We performed the experiment twice, using fish from different watersheds
199 to test the repeatability of the effects across two independent origins of the low-predation
200 guppy ecotype.

201

202 *Fish populations and housing*

203 We collected guppies from two independent watersheds in the Northern Range
204 mountains, Trinidad, representing two independent origins of the guppy ecotypes. In the
205 Aripo watershed, we collected low-predation fish from the Naranjo tributary. We collected
206 high-predation fish from the Aripo river, downstream from Haskin's Falls. In the Quare

207 watershed, we collected low-predation fish from the Quare-2 tributary, and high-predation
208 fish from the main stem of the Quare river, accessed below the pump-house on the Hollis
209 Reservoir Road. These sites are well established examples of low-predation (i.e.
210 resource-limited) and high-predation (i.e. resource-abundant) habitats (Magurran 2005).
211 We collected fish using butterfly nets and returned them to our field station in plastic
212 bottles of medicated water (0.150ml/L of Stress Coat®, Mars Fishcare North America,
213 PA, USA; 0.075ml/L of AmQuel Plus®, Kordon LLC, CA, USA). We treated fish with a
214 salt bath (sea salt 25g/L, for 15 minutes) to rid them of ectoparasitic infections and with
215 antibiotics (either tetracycline at 0.187g per 20L, or furan at 1.25g per 20L) to control
216 bacterial infections. We kept stock fish in glass tanks at densities of approximately 1.5
217 fish per litre of water. We provided constant aeration to each tank under ambient
218 temperature and light levels. We fed stock fish twice daily, with either live *Artemia* brine
219 shrimp nauplii, dried bloodworms or flaked fish food. We replaced the water in each tank
220 every other day.

221

222 *Experimental setup*

223 Only female guppies were selected for the competition trials because they occur
224 over a wider range of body sizes than males; females have indeterminate growth,
225 whereas the growth of males ceases at maturity. Prior to the trials, fish were
226 anaesthetised with MS-222 and given a unique subcutaneous coloured elastomer implant
227 (Northwest Marine Technologies, WA, USA). Standard length (SL) was measured with
228 digital callipers as the distance from the tip of the snout to the hypural plate, recorded in
229 to the nearest 0.01mm. Mass was recorded to the nearest 0.001g. These measurements

230 were recorded at day 0, day 14, and day 28 of the experiment. Guppies give birth to live
231 young and increase in mass significantly during pregnancy. Whilst we visually selected
232 non-gravid females for our trial, guppies are able to store sperm. Thus, pregnancy status
233 was unclear at the end of the trial, which could introduce substantial variation into growth
234 measurements. By contrast, change in SL reflects food resources allocated to growth,
235 rather than reproduction. Initial SL was strongly correlated with the natural log of initial
236 mass (adjusted $R^2=0.96$). Whilst we chose to focus on change in SL as our measure of
237 growth, we also report on change in mass for the purpose of comparison with other
238 studies. For both watersheds, mean initial SL and standard deviation for each size class
239 of fish (N=108 for each size class) were 10mm: mean=10.36mm, s.d.=1.08mm; 14mm:
240 mean=14.31mm, s.d.=1.19mm; 18mm: mean=17.93mm, s.d.=1.01mm; 22mm:
241 mean=21.56mm, s.d.=1.26mm. During the trials, fish were housed in plastic tanks (2L
242 capacity: 120x110x180mm) containing approximately 1.5L of stream water and received
243 constant aeration at ambient temperature and light conditions. Fish were added to tanks
244 according to treatment, in random order. Water was replaced every other day. Offspring
245 produced during the trial were removed from the tank daily. Fish that died or that displayed
246 symptoms of illness during the trial were replaced by another of the same size and
247 ecotype, in order to maintain the treatment within the tank. Growth data from replacement
248 fish were not used in the analysis. Potential variation in feeding behaviour, due to
249 differences in perceived number (or size) of competitors, was controlled by visually
250 isolating tanks from one another with opaque barriers between tanks.

251

252 *Feeding regime*

253 We chose live *Artemia* brine shrimp nauplii as a food source for the competition
254 trials, due to their motility and the ease with which they can be reared and quantified in
255 the lab. Brine shrimp nauplii are a close approximation of the natural invertebrate prey of
256 guppies, and are readily consumed by all size classes of guppy in the lab (personal
257 observation, T. Potter). Brine shrimp were reared in 4L plastic containers of stream water
258 with 25ppt sea salt added, at a starting density of 1g of cysts per litre. Constant aeration
259 was provided, and containers were kept at ambient light and temperature levels. Brine
260 shrimp were harvested 36 hours after initial hydration of cysts, by syphoning into a fine
261 mesh net. Harvested brine shrimp were rinsed with fresh water and allowed to drain. To
262 quantify the food source, rinsed brine shrimp were loaded into a graduated syringe, and
263 added to fresh water to give a stock density of 0.1ml of brine shrimp per ml. During
264 feeding, a homogenous distribution was maintained by constant swirling of the mixing
265 vessel.

266 Each tank, regardless of treatment, received the same quantity of brine shrimp,
267 representing a fixed carrying capacity. The quantity of brine shrimp provided per tank was
268 determined on the basis of previous guppy-diet research (Auer, 2010) and preliminary
269 trials to ensure all brine shrimp could be consumed by the fish in the tank within a few
270 minutes. The trial tanks of two or four 10mm size class fish were fed a range of diets
271 (100-350 μ l of shrimp-water mixture, at 50 μ l increments), with tanks visually inspected for
272 remaining brine shrimp after one hour of feeding. The ration was considered to be limiting
273 if no brine shrimp were observed at this time. The largest limiting ration was 250 μ l, and
274 this ration was deemed appropriate for use in the competition trials. Each tank received
275 250 μ l of shrimp-water mixture in the morning of each day for the duration of the trial. We

276 assumed that competition was exploitative in our experiment. The mode of competition
277 can shift from exploitative to interference with decreasing resource availability (Holdridge,
278 Cuellar-Gempeler & terHorst 2016), which could influence asymmetry. However,
279 environmental homogeneity, and the small size and rapid dispersal of food through the
280 tank in our experiments limited the potential for interference competition.

281

282 *Modelling individual growth*

283 Somatic growth of fish can be described by one of several types of growth curves
284 and the choice of the growth curve assumed may influence the estimates of competitive
285 asymmetry. Therefore we first tested which growth curve most accurately describes
286 somatic growth (length and mass) from a separate experiment where low-predation and
287 high-predation guppies were raised on *ad libitum* food from birth and measured for mass
288 and SL every other day over a sixty day period (see Supplementary Information for
289 details). For both males and females and for mass and length the Gompertz growth model
290 provided the best fit to the growth data.

291 To estimate the degree of competitive asymmetry from the competition
292 experiment, we followed the modelling approach outlined in (Bassar *et al.* 2016) and
293 (Bassar, Travis & Coulson 2017). To begin, we used a growth model that estimates the
294 change in somatic size assuming growth follows a Gompertz curve, including a quadratic
295 term to improve model assumptions of heteroscedasticity. This model is:

$$G_j \left(\ln(z_j') \middle| \ln(z_j) \right) \sim \beta_{0j} + \beta_{zj} \ln(z_j) + \beta_{zj^2} \ln(z_j)^2 \quad \text{Eqn.1}$$

296 where G is the mean change in SL or mass of fish of initial standard-length z and ecotype
297 j at time t . The parameters β_{0j} , β_{zj} , and β_{zj^2} together describe the growth of size z and

298 ecotype j fish in the absence of competitive effects. Adding density dependent growth and
 299 competitive asymmetries means modifying the model to incorporate density effects:

$$G_j(\ln(z_j') | \ln(z_j)) \sim \beta_{0j} + \beta_{zj} \ln(z_j) + \beta_{zj^2} \ln(z_j)^2 + \beta_{Nj} \sum \alpha(z_j, x_j) n_{jx} + \beta_{Nj} \sum \alpha(z_j, x_i) n_{ix}. \text{Eqn.2}$$

300 The parameter β_{Nj} describes the decrease in the growth increment with increasing
 301 density of fish of the same size and ecotype. The interaction surface, $\alpha(z_j, x_i)$, describes
 302 how the strength of competition is modified by different sizes and ecotypes of fish, with z_j
 303 denoting the body size of the focal individual of the j th ecotype and x_i denoting the body
 304 size of a competitor of the i th ecotype. The term n_{jx} is the number of individuals of
 305 ecotype j of size x . The summations in the last two terms are done across all sizes in the
 306 population.

307 We modelled the interaction surface two ways. Both assume that all individuals
 308 compete for the same resources. The first model for the interaction surface is based on
 309 competitive abilities changing linearly on the log scale (Bassar, Travis & Coulson 2017):

$$\alpha_{ji}(z_j, x_i) = \frac{e^{\eta_j + \phi_j(\ln(x_j) - \ln(\nu))}}{e^{\eta_i + \phi_i(\ln(z_i) - \ln(\nu))}} = e^{\eta_{ji} + \phi_j(\ln(\frac{x_j}{\nu}) - \phi_i(\ln(\frac{z_i}{\nu}))}. \text{Eqn.3}$$

310 Equation 3 is derived from the idea that competitive ability within an ecotype (or species)
 311 can be described as a monotonic increasing (or decreasing) function of size z . The
 312 parameter η_j describes the competitive ability of an individual of size ν , which is a
 313 constant set by the researcher, as in covariate centering. The size-competition coefficient
 314 ϕ_j describes how competitive ability increases or decreases with body size. Dividing
 315 ecotype j 's competitive function by the competitive function for ecotype i yields a surface
 316 that describes the proportional change in competitive ability between individuals of

317 different sizes and ecotypes. This new parameter, the ecotype-competition coefficient η_{ji}
318 then represents the difference in competitive ability between the two ecotypes.

319 An alternative formulation of the interaction surface that is common in the plant
320 literature (Weiner 1990) is:

$$\alpha_{ji}(z_j, x_i) = \frac{x_j^{\phi_j}}{z_i^{\phi_i}}. \quad \text{Eqn.4}$$

321 Competitive asymmetry by ecotype can be included by multiplying equation 4 by $e^{\eta_{ji}}$ so
322 that:

$$\alpha_{ji}(z_j, x_i) = e^{\eta_{ji}} \frac{x_j^{\phi_j}}{z_i^{\phi_i}}. \quad \text{Eqn.5}$$

323 The advantage of this formulation is that the ϕ values can be directly interpreted with
324 respect to the trait value. For example, when $\phi = 1$ competitive ability is directly
325 proportional to the trait value.

326

327 *Statistical analysis*

328 Model parameter estimates were obtained by maximum likelihood estimation,
329 using the function *mle2* of the package *bbmle* (Bolker 2017) in the R environment (R Core
330 Team 2017). We tested five hypotheses relating to competitive asymmetry as a function
331 of body size and ecotype: 1. Competition is asymmetric as a function of the ecotypes
332 (η_{ji}), and competitive ability changes with body size differently between ecotypes (ϕ_j
333 and ϕ_i); 2. Competition is asymmetric as a function of the ecotypes (η_{ji}), and there is a
334 common relationship between size and competitive ability among ecotypes (i.e. a single
335 value of ϕ); 3. Competition is symmetric with regards to ecotype, but competitive ability
336 changes with body size differently between ecotypes (ϕ_j and ϕ_i); 4. Competition is

337 symmetric with regards to ecotype, and there is a common relationship between size and
338 competitive ability (ϕ); 5. The null hypothesis, in which we assumed competitive symmetry
339 within and between ecotypes, i.e. individuals are competitively equivalent. For each
340 model, optimal starting values for each parameter were selected by cycling through a
341 range of start values and selecting those which resulted in the lowest global log-likelihood
342 score. In all models, we allowed the parameters describing density-independent growth
343 and the density-dependent parameter to vary based on ecotype. Models were centred at
344 18mm or 0.125g. Model assumptions of heteroscedasticity were confirmed from plots of
345 the residuals against predicted values.

346

347 **Results**

348 *Data collection*

349 In total, we obtained growth data for 281 fish over the course of both sets of
350 competition trials (Aripo = 152; Quare = 129). Somatic growth rates observed were typical
351 of those seen in wild populations (Bassar *et al* 2013), suggesting that the food-level used
352 was generally well-calibrated to reflect natural food availability. The exception was for
353 Quare low-predation fish of the 22mm size class, in which negative growth was observed
354 at high densities (two-tailed z-test, $z=-3.63$, $p<0.001$). In the Aripo trials, fish that died or
355 were replaced due to illness during the experiment were smaller, and from high density
356 treatments (GLM with logit-link function, *density*: Estimate=0.35, S.E=0.17, $P=0.04$; *body-*
357 *size*: Estimate=-0.09, S.E=0.04, $P=0.01$). In the Quare trials, density and body-size had
358 no detectable effect on mortality. Fish that died were more likely to be of the low-predation
359 ecotype (GLM with logit-link function, *ecotypeLP*: Estimate=1.00, S.E=0.29, $P=0.001$).

360 The overall replacement rate of fish that died or were removed due to ill health was 35%.
361 We accept that this rate is high, however the imbalance of design resulting from taking
362 no growth data on replacement fish did not bias model parameter estimates: we simulated
363 the experiment for both watersheds, with a.) the full, balanced design (no replacement),
364 and with b.) the imbalanced designs that arose from replacement of fish in the physical
365 experiments. Model parameter estimates did not differ between a.) and b.) in the
366 simulations, but z-scores were higher in a.). However, this difference did not change the
367 interpretation of results obtained experimentally. On this basis, we conclude that fish
368 replacement did not bias our model parameter estimates.

369

370 *Interaction surface model selection*

371 When considering growth as change in standard length, the proportional form of
372 the interaction surface gave a better fit to the data than the exponential form. This was
373 true for fish from both watersheds (Table 1) (difference in AIC scores between best-fitting
374 proportional form and exponential form: Aripo $\Delta AIC = 4.22$; Quare $\Delta AIC = 3.62$). Further
375 discussion of the results refers to those obtained with the proportional form of the
376 interaction surface, where growth is defined as change in standard length. For
377 comparison with other studies, the Supplementary Information provides results using
378 change in mass as the measure of growth and employing the exponential form of the
379 interaction surface.

380 Including the interaction surface in the model greatly improved the fit of the data
381 compared to the null model, in which we assumed competitive equivalence of guppies

382 both within and between ecotypes (comparisons between poorest-fitting interaction
383 surface model and null model: Aripo: $\Delta AIC = 16.12$; Quare: $\Delta AIC = 8.93$) (Table 1, Fig 2).

384 The best-fitting functional form of the interaction surface differed between
385 watersheds. In the Aripo watershed, the difference in AIC scores between the best and
386 next-best fitting models was small (Table 1), indicating uncertainty with regards to the
387 best fit. However, we argue that selection of the simpler model with the size-competition
388 coefficient ϕ common to both ecotypes (Table 1; hypothesis 4) is justified, since in the
389 larger models (Table 1; hypotheses 1-3) the estimates for the additional parameters (η_{ji} ,
390 ϕ_j , and ϕ_i) were highly non-significant ($P > 0.35$).

391

392 *Interaction surface results: Aripo*

393 In the Aripo watershed, the simplest hypothesis was supported (Table 1:
394 hypothesis 4): ecotypes share a common degree of size-dependent competitive
395 asymmetry, and there is no evidence of ecotype-dependent asymmetry. The size-
396 competitive coefficient is approximately equal to 1 (Table 2: $\phi = 1.089$, S.E = 0.246,
397 $P < 0.001$), meaning that competitive ability increases proportionately to body size in Aripo
398 guppies. As such, competitor size strongly influences individual growth rates at high
399 population density (Fig 3a), but not at low population density (Fig 3b), and this is true for
400 both ecotypes.

401

402 *Interaction surface results: Quare*

403 In the Quare trials, the full model provided the best fit to the data (Table 1:
404 hypothesis 1): ecotypes differed in the degree of size-based competitive asymmetry, and

405 there is asymmetry as a function of ecotype. Low-predation guppies display much weaker
406 size-dependent competitive asymmetry than high-predation guppies (Table 2: $\Delta\phi = -$
407 1.407, S.E = 0.428, $P=0.001$). For high-predation Quare guppies, competitive ability
408 increases more than proportionately to body size (Table 2: $\phi_{HP} = 1.771$, S.E = 0.400,
409 $P<0.001$), whereas for low-predation Quare guppies, competitive ability is essentially
410 symmetric, since it is not statistically different from zero (Table 2: $\phi_{LP} = 0.364$, S.E = 0.226,
411 $P=0.054$). We found statistically significant competitive asymmetry between ecotypes in
412 Quare guppies (Table 2: $\eta_{ji} = 4.136$, S.E = 1.202, $P<0.001$) which interacts with the size-
413 dependent competitive asymmetry of the high-predation ecotype, influencing the growth
414 rates of individual fish at high population densities (Fig 4a, Fig 4b.). For both low- and
415 high-predation guppies, growth is suppressed to a greater extent by low-predation rather
416 than high-predation competitors, when competitors are smaller than ~19mm (Fig 4a, Fig
417 4b).

418 The interaction of the traits (size and ecotype) of a focal individual with those of its
419 competitors means that describing the competitive equivalence of low- and high-predation
420 Quare guppies is quite complex (Fig 5). For example, when the size of competitors varies,
421 the competitive equivalence of a low-predation guppy compared to a high-predation
422 guppy ranges from 0.6 to 3.3, a greater than five-fold difference. Low-predation guppies
423 were competitively superior (equivalence > 1) over approximately two thirds of the
424 potential competitor size pairings in the range of 10mm-22mm.

425

426 **Discussion**

427 We performed size-structured competition trials to determine whether intraspecific
428 trait variation affects somatic growth, which is a key contributor to demographic
429 parameters. We asked how competitive ability changes with body-size in Trinidadian
430 guppies, and whether competitive asymmetry differed between ecotypes adapted to
431 different degrees of competitive intensity. Our results demonstrate the importance of
432 including intraspecific trait variation when estimating demographic rates: including
433 competitive ability via body size significantly improved the fit of our model to the data
434 (Table 1, Fig 2), and had major effects on estimates of somatic growth rates (Fig 3, Fig
435 4). When ecotype effects were present, the equivalence of competitors varied more than
436 five-fold across the range of sizes typically seen in guppy populations (Fig 5).

437 Competitor size has significant effects on growth rate in guppies at high population
438 densities. This was true whether we considered growth as change in standard length or
439 mass, and in trials with guppies from different river watersheds, in three of the four
440 populations we tested (Aripo high- and low-predation, and Quare high-predation). The
441 size competition-coefficient was greater than 1, meaning that larger guppies have a
442 disproportionate competitive effect on smaller guppies. By contrast, smaller guppies have
443 little competitive impact on larger guppies. Asymmetry favouring large individuals can
444 have significant consequences for the ecological dynamics of populations (de Roos &
445 Persson 2003; Bassar *et al.* 2016). Are natural populations of guppies likely to be
446 regulated by asymmetry? The effect of competitor body size on somatic growth was much
447 reduced in the low-density treatments (Fig 3b). This suggests that at low-population
448 densities, typical of natural high-predation populations, the traits of conspecifics have a
449 limited impact on somatic growth and thus fitness in guppies. However, at high population

450 densities, typical of low-predation habitats, strong asymmetry resulted in greater than two-
451 fold variance in somatic growth rates (Fig 3a).

452 Asymmetry favouring larger individuals can modify the age and size structure of
453 populations: juveniles take longer to reach maturity and have a lower probability of
454 surviving the juvenile period and recruiting to maturity; adult life-span and fecundity
455 increase, resulting in a higher ratio of juveniles to adults within the population (de Roos &
456 Persson 2003). How does this theoretical prediction match our measurements of
457 asymmetry, and observations of size-structure in guppy populations from the literature?
458 Low-predation populations typically have an evenly-distributed size- and age-structure
459 (Rodd & Reznick 1997; Reznick, Butler & Rodd 2001), which would correspond to minimal
460 changes in competitive ability with body size. Our results from the Quare low-predation
461 guppies are in agreement with this hypothesis, since competition is essentially symmetric
462 with regards to size in these fish. However, in the Aripo low-predation guppies, we found
463 strong size-dependent asymmetry favouring larger individuals. One possible explanation
464 for this paradox is that Aripo low-predation populations might display ontogenetic niche
465 shifts. When adults and juveniles occupy different niches, competition between life-
466 history stages within a population is reduced (Werner & Gilliam 1984). If adults and
467 juveniles do not compete strongly with each other, then adults would not strongly
468 suppress juvenile growth rates and recruitment. This effect would decouple size-based
469 competition from the life-history stage-dependent dynamics described by de Roos and
470 Persson (2003), and would explain the evenly-distributed population size structure,
471 despite strong size asymmetry. An alternative explanation could be of increased mortality
472 of juveniles in low-predation habitats (i.e. at high population densities), however mark-

473 recapture work has shown that mortality risk for all size classes of guppy are uniformly
474 lower in low-predation habitats (Reznick *et al.* 1996).

475 We found that both ancestral populations (the high-predation ecotypes) displayed
476 strong competitive size-asymmetry, which influenced growth rates at high densities. High-
477 predation guppies have high metabolic requirements, associated with the fast pace of
478 their life-history strategy e.g. high reproductive rate, and continued growth following
479 maturation at a relatively smaller size (Auer *et al.* 2018). As such, the metabolic demands
480 on adult high-predation guppies may select for increased competitive ability with size.
481 How does competitive asymmetry evolve in response to increased population density and
482 resource scarcity? In the low-predation populations, competition was symmetric with
483 regards to size in the Quare population, but strongly asymmetric favouring larger
484 individuals in the Aripo population: the relationship between local adaptation and size-
485 asymmetry was not consistent between ecotype pairs. This indicates that adaptation to
486 resource scarcity alone is insufficient to explain changes in the relationship between
487 competitive ability and body size in guppies.

488 We expected that the low-predation ecotype would have a population-level
489 competitive advantage over the high-predation ecotype. We found contrasting results
490 between watersheds: in the Aripo, we found no evidence of asymmetry as a function of
491 ecotype; in the Quare, the low-predation ecotype were competitively superior over the
492 majority of the range of body sizes considered. Again, these contrasting results between
493 these independent origins of the guppy ecotypes highlight that there are different
494 mechanistic routes to adaptation to resource scarcity, which could result from differences
495 between watersheds in factors such as available genetic variation, or niche availability.

496 In our experiments, we deliberately limited the potential for niche differentiation, so as
497 to accurately quantify size- and ecotype-dependent asymmetries. In natural systems,
498 however, niche differentiation is likely. For example, natural shoals of guppies have been
499 shown to be assorted by body length (Croft *et al.* 2003), generating niche differentiation
500 among size classes. Although we did not test this directly, our results in conjunction with
501 theory suggest that the potential for niche differentiation is likely to play an important role
502 in the evolution of competitive asymmetry. Where competitive ability increases with size,
503 selection should favour ontogenetic niche differentiation, such that different sizes and
504 ages do not compete strongly. Under this scenario, we would expect the Aripo low-
505 predation population (strongly size-asymmetric) to display ontogenetic niche
506 differentiation. However, if there is no potential for niche differentiation, selection should
507 favour a reduction in asymmetry. Under this scenario, we would expect the Quare low-
508 predation guppies (size-symmetric) to display significant niche overlap between ages and
509 sizes. One way to test this idea would be to perform mark-recapture experiments with
510 density manipulation in pairs of Quare and Aripo low-predation streams. The degree of
511 size-dependent niche differentiation ρ_j can be estimated by its inclusion within the
512 interaction surface of the somatic growth model, whilst fixing the size-dependent
513 competition coefficient ϕ_j to the values obtained in this experiment. This approach would
514 allow the disentangling of the contrasting effects of ρ_j and ϕ_j on somatic growth, and
515 could be further verified through stomach content analysis, or behavioural observations
516 of habitat use and foraging in the field.

517 Our experiment was limited to comparisons between two independent evolutionary
518 origins of the low-predation ecotype. We found contrasting patterns between ecotype

519 pairs, suggesting different mechanisms underlying local adaptation to resource limitation.
520 Whilst many ecotype studies consider two origins (e.g. Schluter *et al.* 2004; Bassar *et al.*
521 2010b; Zandonia *et al.* 2011), further replication would allow a better understanding of
522 local factors leading to the differences among sites observed here.

523 In summary, our work highlights the importance of considering intraspecific trait
524 variation and the consequences of asymmetric competition when defining demographic
525 rates and using them to generate predictions about life-history evolution. We found that
526 competitors were not equal: competitive equivalence among individuals varied over five-
527 fold dependent on population- and individual-level traits. Adaptation to resource limitation
528 alone was insufficient to explain differences in size-dependent competitive ability between
529 populations. Our findings raise questions with regards to the role of niche availability in
530 the evolution of competitive asymmetry, and subsequently on demographic rates. We
531 have briefly outlined one experimental approach that could address these questions.

532

533 **Acknowledgements**

534 We wish to thank Andy Van Alst, Charles Boyd, John Ranieri, and Kathryn
535 Chenard for helping to set up the experiments. David Reznick and Tim Coulson provided
536 valuable insight and we thank them for their comments on draft versions of the
537 manuscript. We are grateful for thoughtful and detailed comments from two anonymous
538 reviewers and two editors. This study was funded by NSF DEB-1556884, awarded to JT
539 and RB.

540

541 **Authors' contributions**

542 RDB, JT, and TP conceived the project and TP and RDB designed methodology. TP and
543 LK performed the experiments and collected the data. TP and RDB analysed the data.
544 TP wrote the initial drafts of the manuscript, and all authors contributed critically to drafts
545 and gave approval for publication of the final version.

546

547 **Data accessibility**

548 Data will be made available upon publication to the Dryad Digital Repository.

549

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686

Table 1. Likelihoods and AIC values for the various models of somatic growth, for both watersheds. Lowest AIC scores are given in bold type. The hypotheses tested by the models are: 1. Competition is asymmetric between ecotypes (η_{ji}) and ecotypes differ in how competitive ability changes with size (ϕ_j, ϕ_i); 2. Competition is asymmetric between ecotypes (η_{ji}) and competitive ability changes with size in the same manner between ecotypes (ϕ); 3. Competition is symmetric with regards to ecotype, and ecotypes differ in how competitive ability changes with size (ϕ_j, ϕ_i); 4. Competition is symmetric with regards to ecotype, and competitive ability changes with size in the same manner between ecotypes (ϕ). The null hypothesis is that there is no effect of ecotype or size on competitive ability.

| Hypothesis | Exponential Model | | | Proportional Model | | |
|--------------|---|-----------|----------------|---|-----------|----------------|
| | Model | -2logLike | AIC | Model | -2logLike | AIC |
| <i>Aripo</i> | | | | | | |
| 1 | $e^{\eta_{ji} + \phi_j x_j - \phi_i z_i}$ | -510.20 | -486.20 | $e^{\eta_{ji}} \frac{x_j^{\phi_j}}{z_i^{\phi_i}}$ | -514.50 | -490.50 |
| 2 | $e^{\eta_{ji} + \phi x_j - \phi z_i}$ | -509.35 | -487.35 | $e^{\eta_{ji}} \frac{x_j^{\phi}}{z_i^{\phi}}$ | -513.71 | -491.71 |
| 3 | $e^{\phi_j x_j - \phi_i z_i}$ | -509.62 | -487.62 | $\frac{x_j^{\phi_j}}{z_i^{\phi_i}}$ | -513.82 | -491.82 |
| 4 | $e^{\phi x_j - \phi z_i}$ | -509.02 | -489.02 | $\frac{x_j^{\phi}}{z_i^{\phi}}$ | -513.24 | -493.24 |
| null | null | -492.38 | -474.38 | null | -492.38 | -474.38 |
| <i>Quare</i> | | | | | | |
| 1 | $e^{\eta_{ji} + \phi_j x_j - \phi_i z_i}$ | -486.83 | -464.83 | $e^{\eta_{ji}} \frac{x_j^{\phi_j}}{z_i^{\phi_i}}$ | -490.45 | -468.45 |
| 2 | $e^{\eta_{ji} + \phi x_j - \phi z_i}$ | -476.73 | -456.73 | $e^{\eta_{ji}} \frac{x_j^{\phi}}{z_i^{\phi}}$ | -477.92 | -457.92 |
| 3 | $e^{\phi_j x_j - \phi_i z_i}$ | -474.70 | -454.70 | $\frac{x_j^{\phi_j}}{z_i^{\phi_i}}$ | -476.69 | -456.69 |
| 4 | $e^{\phi x_j - \phi z_i}$ | -474.27 | -456.27 | $\frac{x_j^{\phi}}{z_i^{\phi}}$ | -474.97 | -456.97 |
| null | null | -463.76 | -447.76 | null | -463.76 | -447.76 |

Table 2. Parameter estimates from the best models of the change in standard length (mm) using the proportional form of the interaction surface, for high-predation (HP) and low-predation (LP) ecotypes. β_0 is the model intercept; β_z is the body size coefficient; β_{z^2} is the quadratic body size coefficient; β_N is the density coefficient; ϕ is the size asymmetry coefficient common to both ecotypes; η_{ji} is the ecotype asymmetry coefficient; ϕ_{HP} and ϕ_{LP} are the size asymmetry coefficients for HP and LP ecotypes, respectively; $\Delta\phi$ is the difference between ϕ_{HP} and ϕ_{LP} . N.B. The quadratic term $\beta_{z^2}LP$ for the Quare watershed was not significant, and thus removed from the model. For the Aripo model, adjusted $R^2=0.85$; for Quare, adjusted $R^2=0.90$.

| Parameter | Watershed | | | | | | | |
|------------------|-----------|-------|--------|--------|--------|-------|---------|--------|
| | Aripo | | | | Quare | | | |
| | Est | SE | z | P | Est | SE | z | P |
| β_0 LP | 0.204 | 0.017 | 12.300 | <0.001 | 0.127 | 0.017 | 7.582 | <0.001 |
| β_z LP | -0.305 | 0.035 | -8.790 | <0.001 | -0.312 | 0.022 | -14.457 | <0.001 |
| β_{z^2} LP | 0.291 | 0.075 | 3.877 | <0.001 | - | - | - | - |
| β_N LP | -0.042 | 0.005 | -8.576 | <0.001 | -0.034 | 0.005 | -6.989 | <0.001 |
| β_0 HP | 0.162 | 0.017 | 9.419 | <0.001 | 0.100 | 0.016 | 6.342 | <0.001 |
| β_z HP | -0.247 | 0.035 | -7.001 | <0.001 | -0.270 | 0.029 | -9.415 | <0.001 |
| β_{z^2} HP | 0.422 | 0.079 | 5.374 | <0.001 | 0.397 | 0.056 | 7.028 | <0.001 |
| β_N HP | -0.027 | 0.005 | -5.388 | <0.001 | -0.020 | 0.005 | -4.352 | <0.001 |
| ϕ | 1.089 | 0.246 | 4.435 | <0.001 | - | - | - | - |
| η_{ji} | - | - | - | - | 4.136 | 1.202 | 3.440 | 0.001 |
| ϕ_{HP} | - | - | - | - | 1.771 | 0.400 | 4.424 | <0.001 |
| ϕ_{LP} | - | - | - | - | 0.364 | 0.226 | 1.611 | 0.054 |
| $\Delta\phi$ | - | - | - | - | -1.407 | 0.428 | -3.289 | 0.001 |
| sigma | 0.043 | 0.002 | 17.194 | <0.001 | 0.033 | 0.002 | 15.670 | <0.001 |

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697 **Figure Legends**

698 **Figure 1.** Experimental design of the competition trials. Somatic growth was measured
699 over 28 days, with two ecotypes, low-predation and high-predation, and four size classes
700 of fish tested: 10mm, 14mm, 18mm, and 22mm. Each bold outlined square represents a
701 single tank, housing fish according to either a.) low or b.) high density treatment,
702 respectively. In the low population density treatment, each unique combination of two fish,
703 of each size class and ecotype were paired in a tank. The high population density
704 treatment consisted of four fish, of one or two size classes, and one or two phenotypes.
705 In total, there were seventy-two tanks, in which a total of 216 guppies of a range of sizes,
706 two different ecotypes, and at two different levels of population density were competing
707 for a limited food source. The amount of food provided in each tank was held constant.
708 The experiment was performed twice, using guppies from two independent evolutionary
709 origins of the low-predation ecotype.

710

711 **Figure 2.** Predicted vs observed somatic growth, for guppies from a.) the Aripo, and b.)
712 the Quare, for (i) the best fitting model, and (ii) the null model. Values are corrected for
713 the density independent component of growth (Eqn. 1), and thus describe the effect of
714 competitors on somatic growth.

715

716 **Figure 3.** How is somatic growth influenced by competitor size at low and high population
717 densities? Somatic growth is plotted as a function of competitor body size, simulated from
718 parameter estimates of the best fitting model (solid lines) for the Aripo watershed
719 experiment (Table 2), and from the null model (dashed lines) in which competitive

720 symmetry is assumed. Note that because competition-coefficients did not differ between
721 ecotypes, functions are only shown for the low-predation ecotype, at a.) high, and b.) low
722 population densities, at four initial standard length size-classes:(i) 10mm, (ii) 14mm, (iii)
723 18mm, and (iv) 22mm. Growth is defined as change in standard length (mm) over a 28-
724 day period. Shaded regions represent 95% prediction intervals.

725

726 **Figure 4.** How is somatic growth influenced by both the ecotype and size of competitors?
727 Somatic growth is modelled as a function of competitor body size, with lines denoting
728 whether competitors are homotypic (solid) or heterotypic (dashed) with regards to
729 ecotype. Functions are plotted for a.) the low-predation ecotype (LP) and b.) the high-
730 predation ecotype (HP), at high population density. At low density, there was no effect of
731 competitor traits on growth. Functions are plotted for individuals of size (i) 10mm, (ii)
732 14mm, (iii) 18mm, and (iv) 22mm. Somatic growth is defined as change in standard
733 length (mm) over a 28-day period. Estimates were simulated from model coefficients for
734 somatic growth for the Quare competition trials (Table 2). Shaded regions represent 95%
735 prediction intervals. N.B. Predicted growth for 22mm low-predation guppies was negative
736 at a high density of low-predation competitors, which is unlikely in natural populations.

737

738 **Figure 5.** The competitive equivalence of two ecotypes (low-predation: LP; high-
739 predation: HP) is plotted as a function of the size of competitors. Equivalence is with
740 respect to the LP ecotype: the scale describes the number of high-predation guppies of
741 size x that would be competitively equivalent to one low-predation guppy of size z . Where
742 equivalence is greater than 1, the low-predation ecotype is competitively superior; where

743 equivalence is less than 1, the high-predation ecotype is competitively superior.
744 Competitive equivalence is determined from the interaction surface of the somatic growth
745 model, using the coefficients of ϕ_j , $\Delta\phi_i$, and η_{ji} obtained from the Quare competition trials
746 (Table 2).

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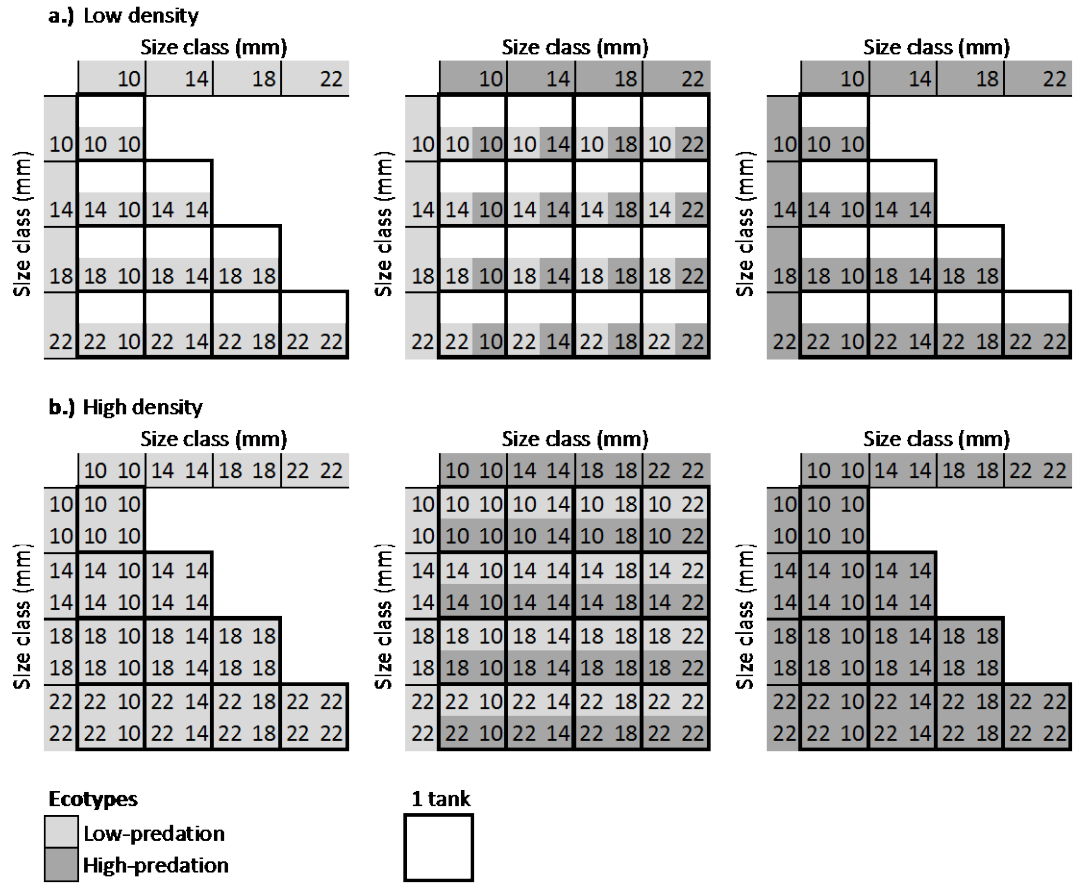
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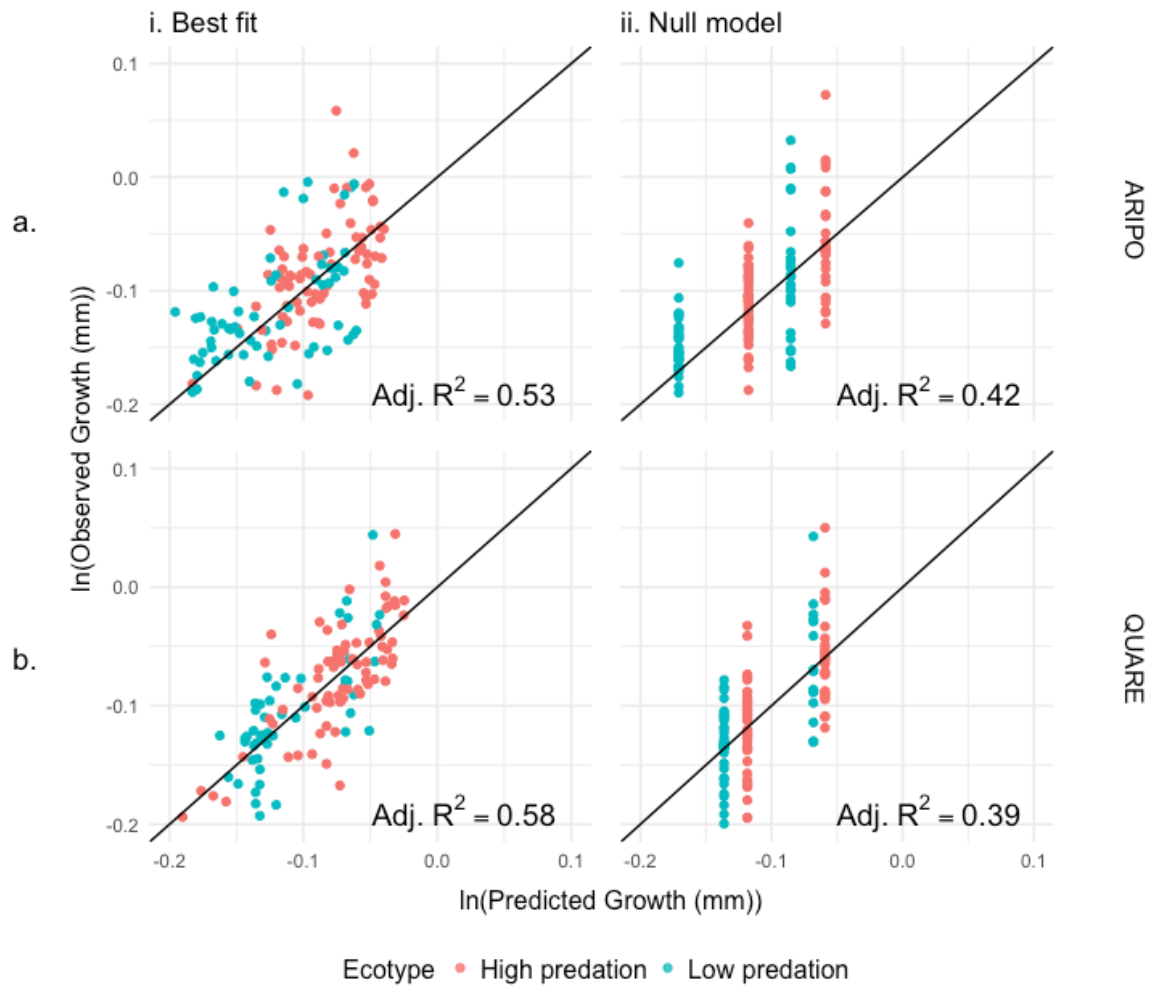
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774 **Figure 2**



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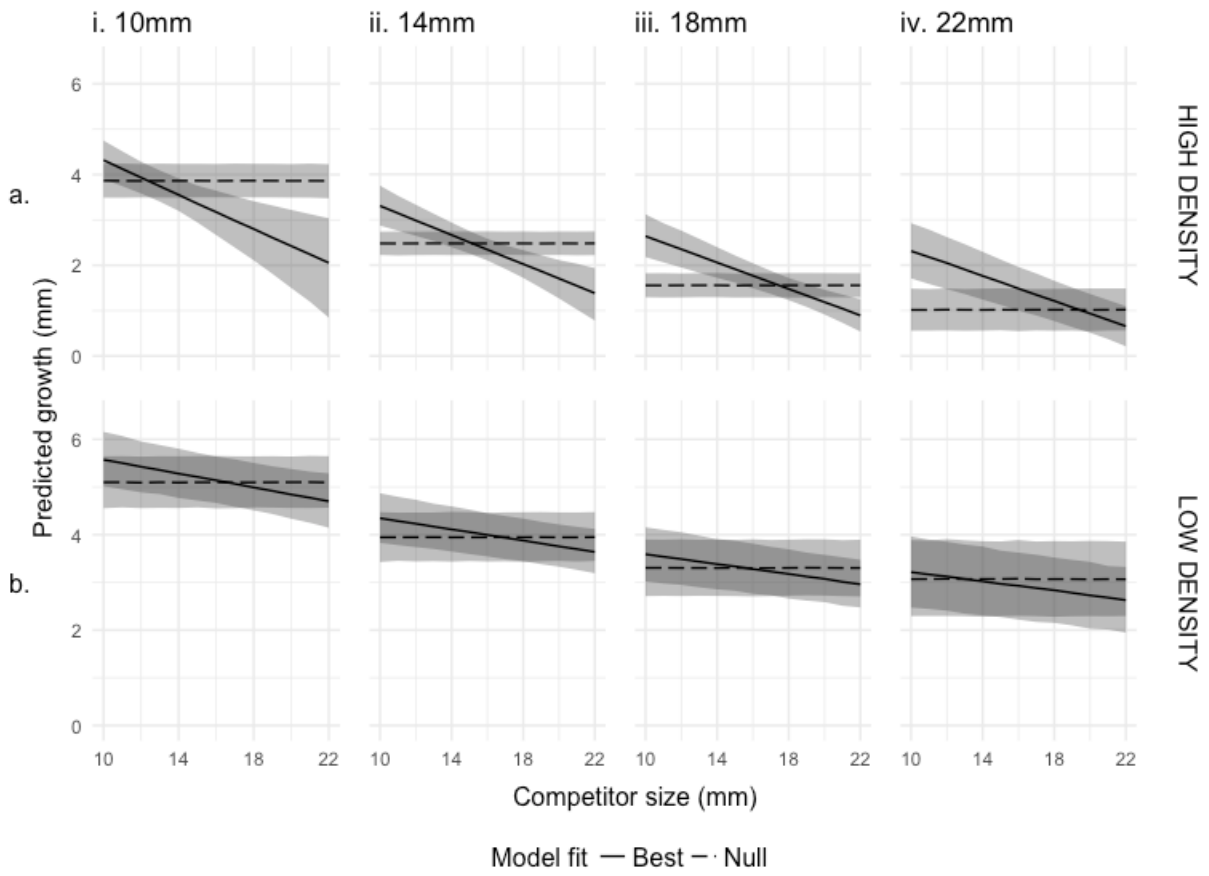
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784 **Figure 3**



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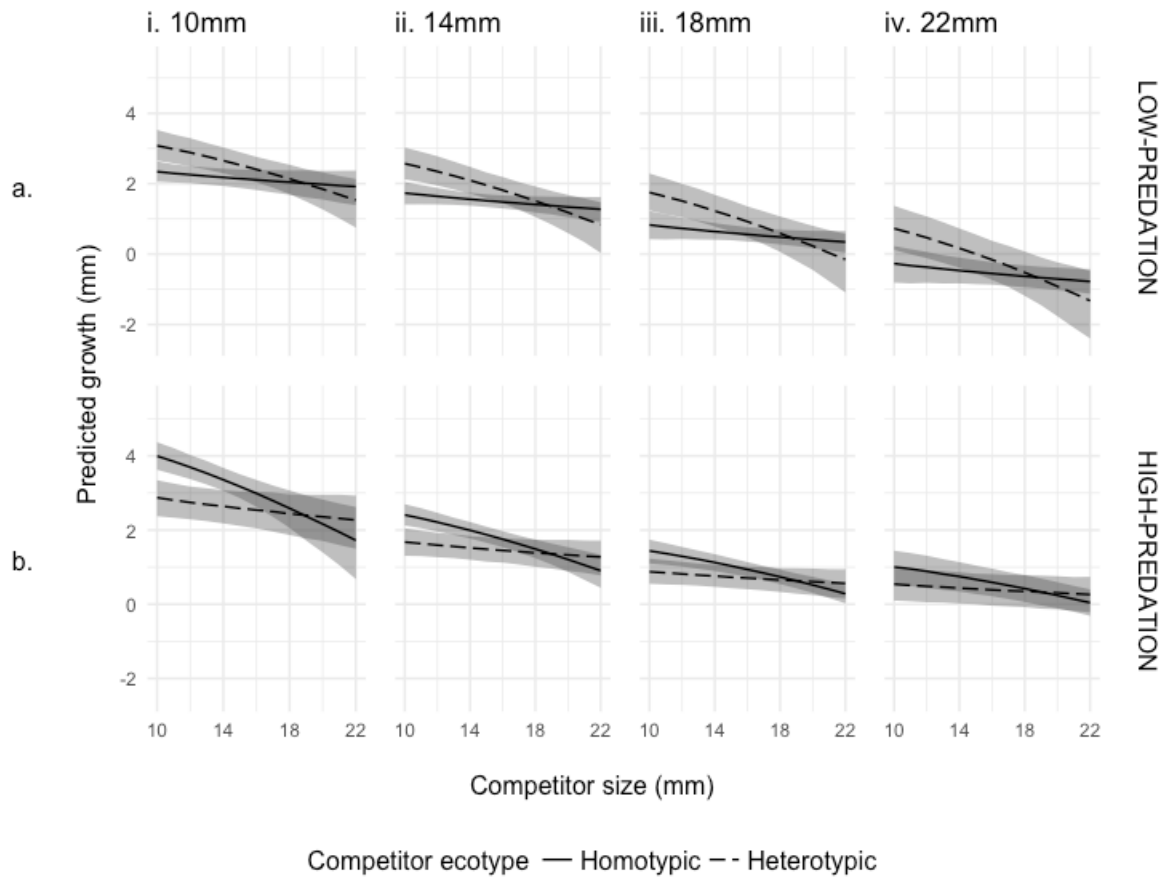
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796 **Figure 4**



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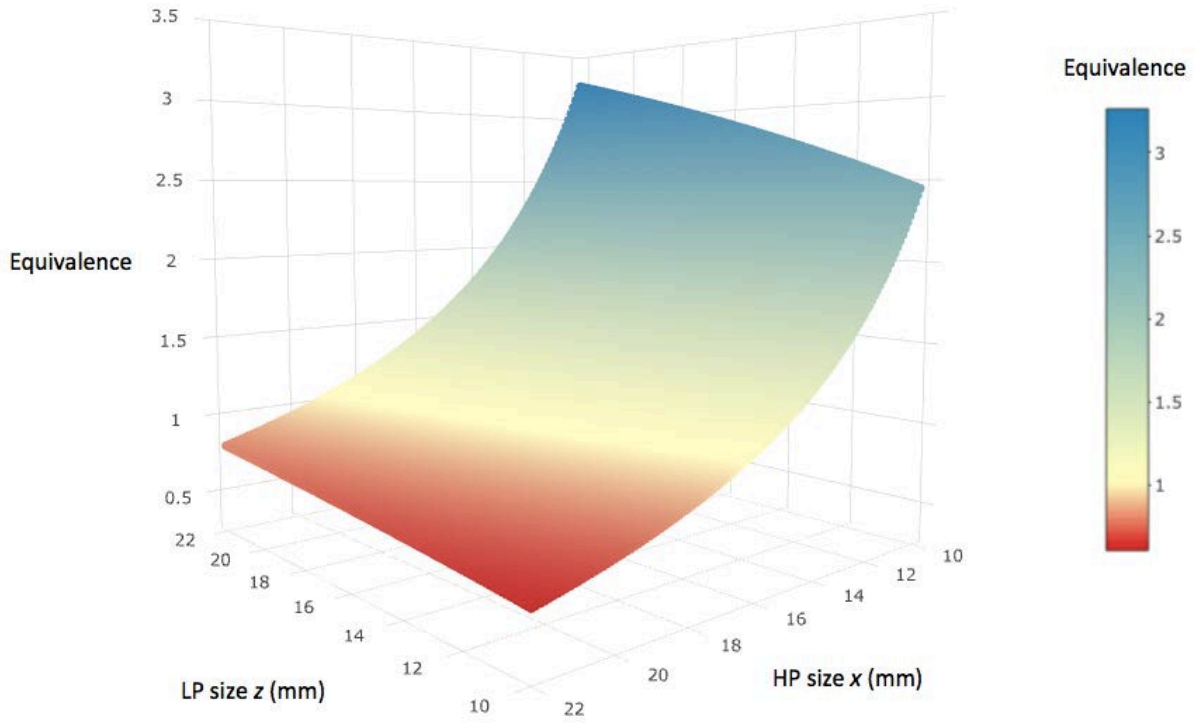
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1 **Figure 5**

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