

1 Individual variation in sexual behaviour is linked to temporal heterogeneity in
2 predation risk

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22 ABSTRACT

23 Variation in predation risk is a major driver of ecological and evolutionary change,
24 and, in turn, geographical variation in behaviour. While it is known that predation risk
25 is rarely constant, the extent to which variation in predation risk shapes individual
26 behaviour in wild populations remains unclear. Here we investigated individual
27 differences in reproductive behavior of a prey species and related the found variation
28 to the risk of predation each population experienced. Our results show that high
29 heterogeneity in predator biomass is linked to individual behavioural diversification.
30 Increased within-population heterogeneity in predator biomass is also associated with
31 behavioural polymorphism. Some individuals adjust the frequency of consensual
32 mating behaviour in direct response to differences in sex ratio context, while others
33 display constantly at elevated frequencies. This pattern is analogous to a “live fast, die
34 young” pace-of-life syndrome. Notably, both high and low mean differences in
35 predator biomass led to a homogenization of individual frequency of consensual
36 mating displays. Overall, our results demonstrate that individual behavioural variation
37 is associated with heterogeneity in predator biomass. We suggest that heterogeneity in
38 predator biomass is an informative predictor of adaptive responses to changes in
39 biotic conditions.

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45 INTRODUCTION

46 Consistent behavioural differences among individuals across time and context are a
47 ubiquitous biological feature of recognized ecological and evolutionary importance
48 (1-3). However, this variation in individual behaviour is expressed in an inconstant
49 world. Ecosystems are dynamic, varying temporally in their physical and biotic
50 conditions. Shifting community composition, particularly when it involves temporal
51 variation in predation risk, has obvious implications for individual behaviour (4). Yet,
52 although individual behavioural variation is omnipresent in most natural populations,
53 partitioning the sources of ecological conditions that fuel individual behavioural
54 differences remains unclear (5-7). Given that the natural world is facing
55 unprecedented change associated to the anthropocene, a clearer understanding of the
56 link between individual behaviour and shifts in the biotic environment is needed. Here
57 we quantify individual behavioural variability across different mating opportunity
58 contexts and ask the question – does individual behavioural variation across contexts
59 increase with increasing environmental heterogeneity? To do this, we use an extensive
60 temporal ecological dataset, and explicitly consider among- and within-individual
61 variation in reproductive behaviour of wild populations of freshwater fish exposed to
62 different levels of predation risk.

63 Fluctuating selection caused by temporal environmental heterogeneity is
64 expected to increase the variance in fitness among individuals in the same population
65 (8, 9). When selection favours different phenotypes at different times, investing in the
66 diversification of individual strategies is adaptive (10-12). As such, individual
67 diversification in behavioural strategies is often more pronounced in temporally
68 heterogeneous conditions than in more homogenous ones (13). Variance in among-
69 individual differences in the tradeoff between current and future fitness expectation is

70 expected to lead to polymorphism in mating strategies (14, 15). The pace-of-life
71 syndrome hypothesis suggests that within a population some individuals will engage
72 in high-risk behaviours, such as greater sexual activity, whereas others exhibit less
73 risk-prone behaviours and prioritize future, over current, reproductive success (16,
74 17). Temporal heterogeneity in environmental conditions is expected to promote
75 among-individual differences in fitness pay-offs leading to diversification in
76 behaviour among individuals. The resulting among-individual diversification in
77 behaviour should be characterised by individuals engaging in high-risk strategies at
78 the extremes of these distributions in the population (18). Empirical evidence for this
79 relationship is, however, lacking.

80 Predation risk is a powerful force shaping individual behaviour and life history
81 strategies (19, 20). Temporal heterogeneity in predation risk modifies the fitness
82 outcome associated with a given prey phenotype, leading to changes in individual
83 behavioural strategies (21-23). For example, among Trinidadian guppies (*Poecilia*
84 *reticulata*), males are behaviourally and phenotypically more conspicuous than
85 females, and hence potentially at greater predation risk. Accordingly, predation
86 pressure has the potential to modify population sex ratio, thereby influencing
87 individual behavioural strategies (21).

88 Given that variation in individual behaviour, also referred as personality, is
89 heritable (24), exposure to constant predator pressure (i.e. always high, or always low)
90 may favour the evolution of reduced variation (greater homogenization) in individual
91 behavioural strategies. In contrast, individuals from populations subject to frequent
92 changes in selection pressure will have no optimal life history strategy, or behaviour.
93 We can thus predict greater among-individual behavioural variation in populations

94 exposed to greater temporal heterogeneity in predation risk (25). To test these
95 predictions, we quantify the frequency of male guppy sexual behaviour across
96 contexts of contrasting operational sex ratio and relate this to temporal heterogeneity
97 in predator biomass, a metric for perceived predation risk in the population. Individual
98 behavioural variation in response to environmental conditions can be partitioned using
99 reaction norms to compare three key components: (1) variation in individual
100 intercepts, (2) in individual slopes, and (3) the covariance between them (26).
101 Variance in the individual intercept of the reaction norm indicates that some
102 individuals have greater mean phenotypes than others. Variance in individual slopes
103 of the reaction norm reveals the variability in the frequency of sexual behaviours in
104 response to differences in sex ratio contexts. Finally, covariance in intercepts and
105 slopes of the reaction norm compares among-individual behaviour in the average
106 context to the variation in other sex ratio contexts. By partitioning the variance in
107 intercepts and slopes across sex ratio contexts and combining this information with
108 environmental data, we can test the hypothesis that temporal heterogeneity in predator
109 biomass promotes diversification in individual behavioural strategies (Figure 1).
110 Based on variance partitioning, we expect that individuals exposed to greater temporal
111 heterogeneity in predator biomass will have greater variance in intercepts (i.e. among-
112 individual variation in the average context) and slopes (i.e. within-individual variation
113 across environments) of the reaction norms (Figure 1 (a)). In contrast, in more
114 temporally homogenous conditions the optimal phenotype is expected to remain less
115 variable, thereby we expect comparatively less individual behavioural variation
116 among- and within-individuals across contexts (Figure 1 (b)). Finally, higher variance
117 in the slopes between individuals is expected when they exhibit contrasting
118 behavioural strategies across sex ratio contexts (Figure 1 (a)).

119 METHODS

120 Male guppies were collected from 16 populations in Trinidad (S1), for which we have
121 detailed temporal information on predator abundance (see below). We quantified
122 individual male reproductive behaviour across a range of sex ratio contexts, and then
123 linked individual behavioural variation to the risk status (i.e. male's native population
124 exposed to high or low temporal changes in predator biomass).

125

126 Assessment of temporal heterogeneity in predator biomass

127 We sampled fish assemblages from 16 sites across the Northern Range of
128 Trinidad (S1) at 3-month intervals over five years – each site was visited 20 times.
129 Each site consisted of a 50-metre stretch of stream, the ends of which were blocked
130 with seine nets before each sampling session.

131 The primary predators of guppies in the Northern Range are the pike cichlid,
132 *Crenicichla frenata* and the wolf fish, *Hoplias malabaricus* (27). A survey of these
133 predators was conducted using hand seining (64 mm mesh) followed by electrofishing
134 (28). On capture, all the individuals were identified, counted, and individually
135 weighed on a portable balance, and finally released unharmed. The combined biomass
136 of individuals of the two main guppy predator species were calculated for each time
137 point at each site. Predator biomass was calculated using guppy predators heavier than
138 two grams.

139

140 Sampling and experimental setup

141 Guppies were collected during the final sampling session (July-August 2015).
142 To prevent atypical behaviour due to guppies being kept in single sex groups, we

143 collected a sample including males, females and juveniles from each of the 16
144 populations (S1). Individuals were transferred to a closed container with aeration and
145 immediately transported to the laboratory. To mitigate stress and reduce mortality,
146 individuals were allocated to settling tanks (90 x 30 x 40 cm) in low-density groups
147 with a sex ratio and water temperature that matched their natural conditions.
148 Additionally, each tank was set up with an aeration system and the bottom covered
149 with gravel and natural plants, which provided shelter. The laboratory was kept on a
150 12L-12D regime.

151 After settling for 48 hours, each focal male was randomly allocated to a test
152 tank containing 15 companion fish. Companion individuals all originated from the
153 lower section of the Tacarigua River in Trinidad and were collected prior to the test
154 individuals. We decided to use companion individuals from the same population in all
155 tests in order to standardize variability in focal behaviour due to inherited intra
156 population behavioural differences. Three sex ratio contexts were used (excluding the
157 focal male): female biased (13 females to 2 males), male biased (3 females to 12
158 males) or even (8 females to 7 males), with two test tanks per treatment (i.e. a total of
159 six test tanks).

160 Each focal male was introduced to his test tank and kept inside a perforated
161 transparent plastic bottle, allowing for both visual and chemical cues. As soon as the
162 focal male appeared acclimatized (i.e. swimming normally), the bottle was removed
163 and the focal male was allowed to interact with the companion individuals.

164 We quantified the type and frequency of sexual displays during a 20-minute
165 period. Male guppies perform two forms of sexual displays: the consensual sigmoid
166 display, favoured by females and more often employed in low predation risk
167 localities, and the sneaking thrust, a coercive form of copulation (29). At the end of

168 the observation period, the focal male was relocated to a new tank (60 x 25 x 30 cm)
169 with individuals from its original population. Unique colour patterns allowed the focal
170 male to be unambiguously recognised. After 24 hours, the same focal male was re-
171 tested as described above in a different sex ratio treatment. This process was repeated
172 so that each focal male was tested in the three sex ratio contexts in a randomised
173 order. The companion individuals were replaced after six observations, and were not
174 re-used during the experiment. At the end of the three trials, the standard length of
175 each focal male was recorded to the nearest millimetre using ImageJ (30). A total of
176 20 focal males per population were tested ($N_{\text{total focal males}} = 320$).

177

178 Statistical analysis

179 The main goal of the study was to test the hypothesis that populations of
180 guppies exposed to greater heterogeneity in predator biomass display greater
181 individual variation in behaviour. Using behavioural reaction norms (31) we explore
182 among- and within-individual variation in sexual displays (i.e. consensual sigmoid
183 displays and sneaking thrusts) across different sex ratios, and related the variation in
184 reaction norms to temporal heterogeneity in predator biomass. We modelled the effect
185 of heterogeneity (i.e. population coefficient of variation (CV) in predator biomass) in
186 generating among-individual variation in behaviour across environments using linear
187 mixed-effects models (LMMs). Mixed random regression models are a suitable
188 analytical tool quantify and test the significance of the relationship between variation
189 in-among individuals and environmental variability (ie. reaction norms) (32). Further,
190 these models yield the highest power to detect variances in individual slopes and
191 intercepts in large data sets, as it is our case (33).

192 The 16 populations were divided into two groups according to their predator
 193 biomass CV values. Populations with a CV value greater than the overall CV mean
 194 were classified as ‘high heterogeneity’, whereas populations with CV values smaller
 195 than the overall mean CV were considered ‘low heterogeneity’. In a separate analysis,
 196 we instead split the populations according to their mean differences in predator
 197 biomass. Using the same reasoning, populations were divided into two groups of
 198 ‘high mean’ and ‘low mean’ predator biomass.

199 LMMs were fitted separately to 1) High CV, 2) Low CV, 3) High mean, 4)
 200 Low mean, predator biomass, to both sexual behaviours (consensual mating display
 201 and sneaking thrust), resulting in eight different models. These models shared a
 202 common form, as follows (eq.1)

203

$$204 \quad \text{eq.1} \quad y_{ij} = \alpha_x + \alpha_1 sr + \alpha_2 sr^2 + f_1(d_i, n, sr) + f_2(p_j, n, sr) + \varepsilon_{ij},$$

205

206 Where y_{ij} is the number of sexual behaviours of individual i of population j , α_u is
 207 the intercept, α_1 and α_2 are fixed effects associated with the slope and curvature of
 208 the sex ratio (sr), f_1 and f_2 are random regression functions on natural polynomials
 209 of order n , at the individual (f_1) and population (f_2) groups. In both f_1 and f_2 , n
 210 was set to 1, allowing for the estimation of random intercepts and slopes. Polynomials
 211 were applied to scaled sex ratios (male biased, even and female biased were assigned
 212 values -1, 0, and 1, respectively) to improve convergence. Finally, normally
 213 distributed heterogeneous residuals by sex ratios were estimated $\varepsilon_{i,j}$, with variance
 214 $D = I\sigma_{di}^2$. d and p vectors with individual and population values respectively, were

215 assumed to follow normal distributions, $d_i \sim \mathcal{N}(0, D)$ and $p_i \sim \mathcal{N}(0, P)$ respectively,
 216 where both $D \frac{1}{3}$ and $P = I\sigma_{pj}^2$ are 2x2 matrices, and σ_{di}^2 and σ_{pj}^2 are the individual
 217 environment and the population effect of individual i and population j . Note that
 218 $D[1, 1]$ and $D[2, 2]$ are the variances in intercepts and slope across sex ratio contexts,
 219 whereas $D[1, 2]$ and $D[2, 1]$ correspond to the covariance between the slope and the
 220 intercept of the reaction norm. Since the distributions of consensual sigmoid displays
 221 and sneak thrust counts were markedly right skewed, the models were fitted to the
 222 logarithm-transformed corresponding variables.

223 We also estimated the effect the variability and the strength of predator
 224 biomass in generating behavioural repeatability. Here, individual repeatability was
 225 calculated using (eq. 2). Low and high CV/mean populations groups were coded as -1
 226 and +1 with the variance arising from the slopes is given by $\left(\frac{x}{-1}\right)^2 D[2, 2]$ in each sex
 227 ratio treatment (and zero in the even sex ratio – defined as the intercept). Therefore,
 228 the variance across sex ratio treatments arising only from slopes is $\frac{2}{3} D[2, 2] + \frac{1}{3}$ in
 229 each sex ratio context ($\sigma_{\varepsilon_{M/E/F}}^2$) as described in eq.2.

230

231 eq.2
$$\frac{D[1,1]}{D[1,1] + \frac{2}{3}D[2,2] + \frac{1}{3}\sigma_{\varepsilon_M}^2 + \frac{1}{3}\sigma_{\varepsilon_E}^2 + \frac{1}{3}\sigma_{\varepsilon_F}^2}$$

232

233 Before fitting these models, we checked how heterogeneous the original
 234 populations were. To address this, we fitted separate linear models to each population,

235 estimating an intercept and a residual variance. The mean and variance were plotted to
236 inform about their variability across population groups.

237 All models were fitted in a Bayesian framework, using MCMCglmm (34).
238 Convergence was checked using trace plots and posterior distribution densities.
239 Inferences on the comparison of reaction norms between populations with low and
240 high CV/mean predator biomass were based on 95% Highest Posterior Density (HPD)
241 credible intervals. To make inferences about differences between population groups,
242 for each posterior sample, we calculated the difference in the estimated parameters
243 between the two populations, which allowed us to obtain a distribution of such
244 differences and therefore (HPD) credible intervals.

245

246 RESULTS

247 Predator biomass

248 Our data revealed a clear differentiation between populations in terms of
249 heterogeneity and mean differences in predator biomass. Temporal differences in the
250 coefficient of variation and in the mean of predator biomass for the 16 populations are
251 shown in Figure 2.

252

253 Consensual sigmoid display

254 There were differences in among-individual variance in the intercepts and
255 slopes of reaction norms between populations of low and high predator biomass CV
256 (Table 1, Figure 3, S2, S5). Individuals from populations with ‘high CV’ in predator
257 biomass showed greater variance in frequency of consensual mating behaviour than
258 individuals from ‘low CV’ populations. In contrast, mean differences in predator

259 biomass affected the variance in intercepts, but not the variance in slopes of the
260 reaction norms (Table 1, Figure 3, S2, S5).

261 There was strong and positive covariance in intercepts and slopes across sex
262 ratio treatments associated with individuals from populations with ‘high’ predator
263 biomass CV values (posterior mode (95% CrI); 0.44 (-0.51: 0.68), S2). By
264 comparison, the covariance in intercepts and slopes across sex ratios was not
265 significantly different from zero in ‘low CV’ populations (posterior mode (95% CrI);
266 -4.93^{-5} (-0.01: 0.005), S2). In terms of mean differences in predator biomass, the
267 values of covariance in intercepts and slopes across sex ratio treatments for both ‘low’
268 and ‘high’ mean populations were small and not significantly different from zero
269 (posterior mode (95% CrI); -0.001 (-0.032: 0.151) for low; 0.0003 (-0.018: 0.024) for
270 high, S2).

271 The fixed effects structure of the model gives information about how the
272 guppy population, as a whole, changes behaviour across contexts. There was no effect
273 of predator biomass in any of the population groups evaluated (Table 1, S2).
274 Regardless of population group (i.e. low and high CV/mean) there was an increase in
275 the frequency of consensual mating behaviour towards the female biased sex ratio
276 context (Table 1, S2). Repeatability of consensual sigmoid display frequency among
277 individuals across sex ratio contexts was low for all four population groups (Table 2).

278

279 Sneaking thrusts

280 There were no differences in among-individual variation in sneaking (thrusts
281 frequency) across sex ratio contexts between populations of ‘low’ and ‘high’ predator

282 biomass CV, or between populations with ‘low’ and ‘high’ mean predator biomass
283 (Table 1, Figure 3, S2, S5).

284 The covariance in intercepts and slopes between individuals was close to zero
285 in ‘low CV’ populations (posterior mode (95% CrI) -0.0006 (-0.029: 0.014), S2), but
286 highly negative in ‘high CV’ populations (posterior mode (95% CrI) -0.733 (-0.081:
287 0.086), S2). In contrast, individual covariance in intercepts and slopes was not
288 significantly different from zero across sex ratio for populations of ‘low’ and ‘high’
289 mean predator biomass (posterior mode (95% CrI); 0.013 (-0.113: 0.082) for low;
290 0.0001 (-0.004: 0.014) for high, S2, S5).

291 There was no evidence of individual adjustment in the frequency of sneaking
292 across sex ratio contexts between populations with ‘low’ or ‘high’ values of predator
293 biomass CV, or between populations with ‘low’ or ‘high’ mean differences in
294 predator biomass. Intercepts and slopes of the fixed structure for all population groups
295 (i.e. low/high CV or mean) were small and not significantly different from zero
296 (Table 1, S2, S5). Repeatability in the frequency of sneaking among individuals
297 across sex ratio contexts was also low for all population groups (Table 2).

298

299 DISCUSSION

300 Our study demonstrates that temporal heterogeneity in predator biomass is key in
301 shaping how prey individuals adjust some of their behavioural strategies in response
302 to changes in sex ratio contexts. Individual guppy males behaved in distinct ways
303 when faced with different sex ratios, and these differences were attributable to the
304 coefficient of variation in predator biomass associated with their original population.
305 We detected a positive relationship between increased heterogeneity in predator

306 biomass and diversification in individual behaviour (Figure 1 (a), S5). In contrast,
307 mean differences in population predator biomass led to a homogenization in the
308 frequency of consensual mating displays (Figure 1 (b), S2, S5). Furthermore, our
309 results provide evidence that increased heterogeneity in predator biomass generates
310 polymorphism in male prey mating behaviour. In populations with a greater
311 coefficient of variation in predator biomass, some individuals expressed high
312 frequencies of consensual mating behaviour across all sex ratio contexts, while others
313 adjusted their behaviour to match the reproductive conditions. This polymorphism in
314 mating behaviour is consistent with the assumptions of the pace-of-life syndrome
315 hypothesis, which is predicted to emerge under heterogeneous environmental
316 conditions (15). Overall, our results reveal that heterogeneity in predator biomass is a
317 vital factor in shaping the frequency of consensual mating displays and individual life
318 strategies. In contrast, changes in mean density of predator biomass have less effect
319 (Figure 1 (d), S5). It is widely recognized that predators play a vital role in structuring
320 ecological communities. The novelty of our study is that the key role of heterogeneity
321 in predation risk in generating behavioural diversity within the prey population is now
322 clear.

323 An individual's personality is traditionally assumed to be constant through
324 time. It follows that individuals with stronger personality should have reduced
325 behavioural flexibility (35). However, under conditions of temporal environmental
326 heterogeneity more than one adaptive strategy may be viable (18, 36). For example,
327 some individuals may respond to changes in conditions, whereas other may not (32).
328 Male guppies from populations with high predator biomass CV showed greater
329 variance in intercepts and slopes in the frequency of consensual mating displays
330 (Figure 3, S5). This indicates greater variability in personality types within these

331 populations (i.e. temporal variation in individual personality). Our result shows that
332 individual personality can vary over time (37), supports the prediction that exposure
333 to environmental heterogeneity favours variation in individual behavioural flexibility
334 across environmental conditions (i.e. variable individual personalities) (38, 39) and
335 emphasises the importance of including individual behavioural variation across
336 contexts in personality studies.

337 We showed an association between the coefficient of variation in predator
338 biomass associated with each population, and the variance in individual intercepts and
339 slopes of the reaction norms. However, when comparing population in terms of mean
340 differences in predator biomass, we detected an effect in individual intercepts of the
341 reaction norm (Figure 3, S5). Male guppies from populations with ‘high mean’
342 predator biomass populations had greater variance in intercepts than individuals from
343 low mean predator biomass populations. This indicates that while changes in
344 heterogeneity lead to diversification in the frequency of consensual mating displays
345 across contexts (Figure 1 (a), S5), differences in means affect only the diversification
346 in the overall frequency of consensual behaviour, but not across contexts (Figure 1
347 (c), S5). This result has obvious ecological and evolutionary consequences, as it
348 shows that our ability to fully understand the effects of biotic interactions on
349 ecosystem structure and function may be constrained by which environmental
350 variable is used to compare populations.

351 Temporal variation in predation risk shapes the link between life history
352 strategies and behaviour by exerting variable selection among males in the same
353 population. Increased variation in predation risk is predicted to generate behavioural
354 polymorphism within the prey population (40). In populations exposed to high
355 heterogeneity in predator biomass, some individuals always displayed consensual

356 sigmoid behaviour at higher rates across all contexts, whereas others adjusted the
357 frequency of behaviour to match the reproductive conditions (S2). Such a pattern
358 correlates with a fast-slow continuum strategy (17, 41). In wild guppy populations,
359 males have potentially greater predation risk than females because of their
360 conspicuous consensual mating behaviour and coloration. As a result, individuals that
361 display constantly at high frequency can be seen as investing in a strategy of short-
362 term fitness returns at the expense of survival.

363 We further note that high or low population differences in mean predator
364 biomass did not generate behavioural polymorphism (S2). When the probability of
365 predation is constant over time and identical among all individuals in the population,
366 selection favours the convergence of individual phenotypes (42). Our study supports
367 this by providing empirical evidence that changes in the population heterogeneity in
368 predator biomass generates polymorphism in behavioural strategies, while changes in
369 population mean lead to homogenization of behaviours across contexts.

370 A common feature of personality studies is their focus exclusively on
371 individual variation in an average context as a measure of individual personality (i.e.
372 individual repeatability) (43-46). We found low repeatability in the frequency of both
373 sexual behaviours across contexts for all four population groups (S3, S4). This is in
374 contrast to the high repeatability in male guppy behaviour reported in other studies
375 (47, 48). While unexpected, difference between studies may be a consequence of a
376 mathematical artefact. Repeatability is commonly measured as the proportion of
377 total variance explained by among-individual differences in the average context (49,
378 50). Our study on the other hand examined both within- and among-individual
379 variation in behaviour across contexts and related this variation to the extent of CV
380 and mean differences in predator biomass associated with the population.

381 Despite the indisputable role of environmental variability as an explanatory
382 metric of individual behavioural variation, its effect of heterogeneity around the mean
383 remains largely overlooked in most studies (51). Our study provides strong empirical
384 and novel evidence for the link between diversification in behavioural strategies
385 within and among individuals and temporal heterogeneity in predator biomass. We
386 showed that changes in CV and in mean predator biomass have distinct effects on
387 individual variation in prey behavioural strategies. The evolution of diversification in
388 behaviour and life history strategies is key in maintaining diversity in ecological
389 communities. Finally, conservation practitioners should be aware of both the mean
390 and variance of predator pressure within communities before establishing plans for
391 conservation priority of populations, as well when removing predators of threatened
392 populations during conservation management (52).

393

394 STATEMENTS

395 Ethics

396 Approval was provided by the University of St. Andrews Animal Welfare and Ethics
397 Committee (2015). The review panel declared no need to obtain Animal Ethics
398 approval.

399 Data accessibility

400 The raw data was supplied and allocated to the following repository
401 <http://datadryad.org/submit?journalID=RSPB&manu=RSPB-2017-1499>.

402 Competing interests

403 The authors declare there are no competing interests.

404 Contribution

405 MB, AED, AEM, IR contributed with funding; MB, AED, AEM conceived the
406 experimental design; MB performed the experiments; MB, MJJ, MBM analyzed the
407 data; MB, MJJ, MBM prepared the figures and tables; MB, AED, MJJ, MBM, AEM
408 wrote the paper. All authors have read and approved the publication.

409

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417

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547 9.

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552 CAPTIONS

553

554 Figure 1 - Predicted pattern of reaction norms for behavioural diversification (a),
555 behavioural homogenization (b and d), and behavioural adjustment (c) scenarios.
556 Each panel shows a hypothetical reaction norm plot for four predation risk
557 populations scenarios (high and low coefficient of variation (a, b), and high and low
558 means (c, d)), across three sex ratio contexts (Male biased (σ), Even ratio (σ/φ) and
559 Female biased (φ)). The lines represent individual reaction norms. Variance in
560 individual intercept indicates that some individuals have greater frequency of sexual
561 behaviour at the average sex ratio context (even-sex ratio), whereas variance in slopes
562 denotes within-individual variability in sexual behaviour across sex ratio contexts.

563

564 Figure 2 - Differences in coefficient of variation (black) and in means (grey) in
565 predator biomass between the 16 populations of Trinidadian guppies. Within-
566 population differences were used to split the populations into groups of low and high
567 CV or mean predator biomass. Error bars denote 95% CrI.

568

569 Figure 3 - Posterior samples of variation in individual intercepts and slopes for the
570 frequency in consensual displays and sneaking thrusts between populations for the
571 four population groups (low and high CV/mean) predator biomass. Error bars denote
572 95% CrI.

573

574 Table 1 - Variation in posterior mode at the fixed and random levels, for the predator
575 biomass of the four population groups (low and high CV/mean). Inference about
576 significant differences was based on 95% credible intervals (CrI) comparisons. Non-
577 overlapping CrI are shaded in grey and denote significant differences between groups.

578

579 Table 2 - Individual repeatability in consensual mating and sneaking thrust across sex
580 ratio contexts for the four population groups (low and high CV/mean). Individual
581 repeatability was calculated as the ratio of the variance among individuals by total
582 variation (i.e. among and within individual variation across sex ratio contexts).

119 ratio contexts (Figure 1 (a)).

Comment [m16]: Reviewer 1 – specific comment 19

120

121 METHODS

122 Male guppies were collected from 16 populations in Trinidad (S1), for which we have
123 detailed temporal information on predator abundance (see below). We quantified
124 individual male reproductive behaviour across a range of sex ratio contexts, and then
125 linked individual behavioural variation to the risk status (i.e. male's native population
126 exposed to high or low temporal changes in predator biomass).

127

128 Assessment of temporal heterogeneity in predator biomass

129 We sampled fish assemblages from 16 sites across the Northern Range of
130 Trinidad (S1) at 3-month intervals over five years – each site was visited 20 times.
131 Each site consisted of a 50-metre stretch of stream, the ends of which were blocked
132 with seine nets before each sampling session.

133 The primary predators of guppies in the Northern Range are the pike cichlid,
134 *Crenicichla frenata* and the wolf fish, *Hoplias malabaricus* (27). A survey of these
135 predators was conducted using hand seining (64 mm mesh) followed by electrofishing
136 (28). On capture, all the individuals were identified, counted, and individually
137 weighed on a portable balance, and finally released unharmed. The combined biomass
138 of individuals of the two main guppy predator species were calculated for each time
139 point at each site. Predator biomass was calculated using guppy predators heavier than
140 2 g.

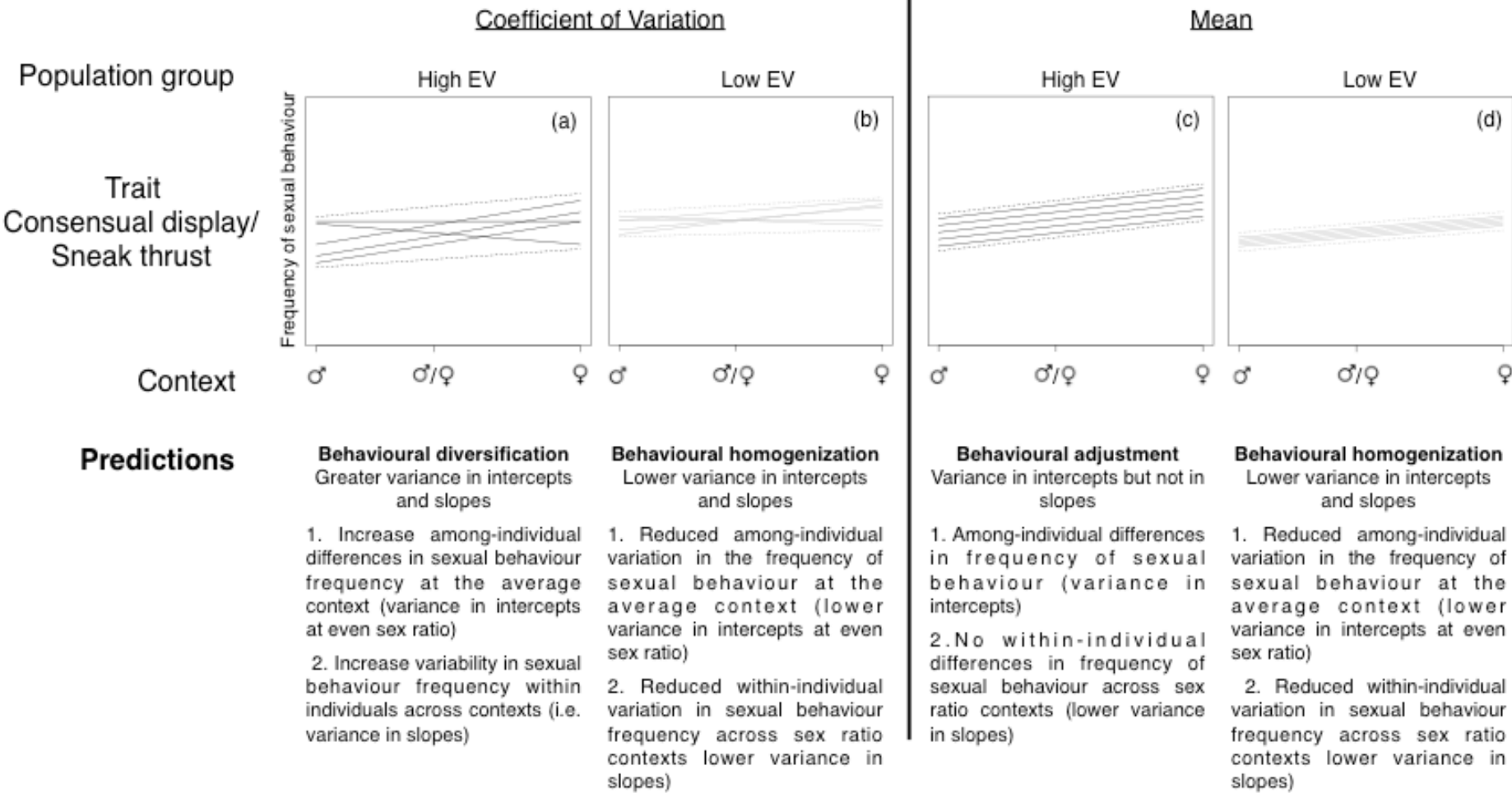
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141

6

Figure 1



8 models: 4 population groups x 2 sexual behaviours

Figure 2

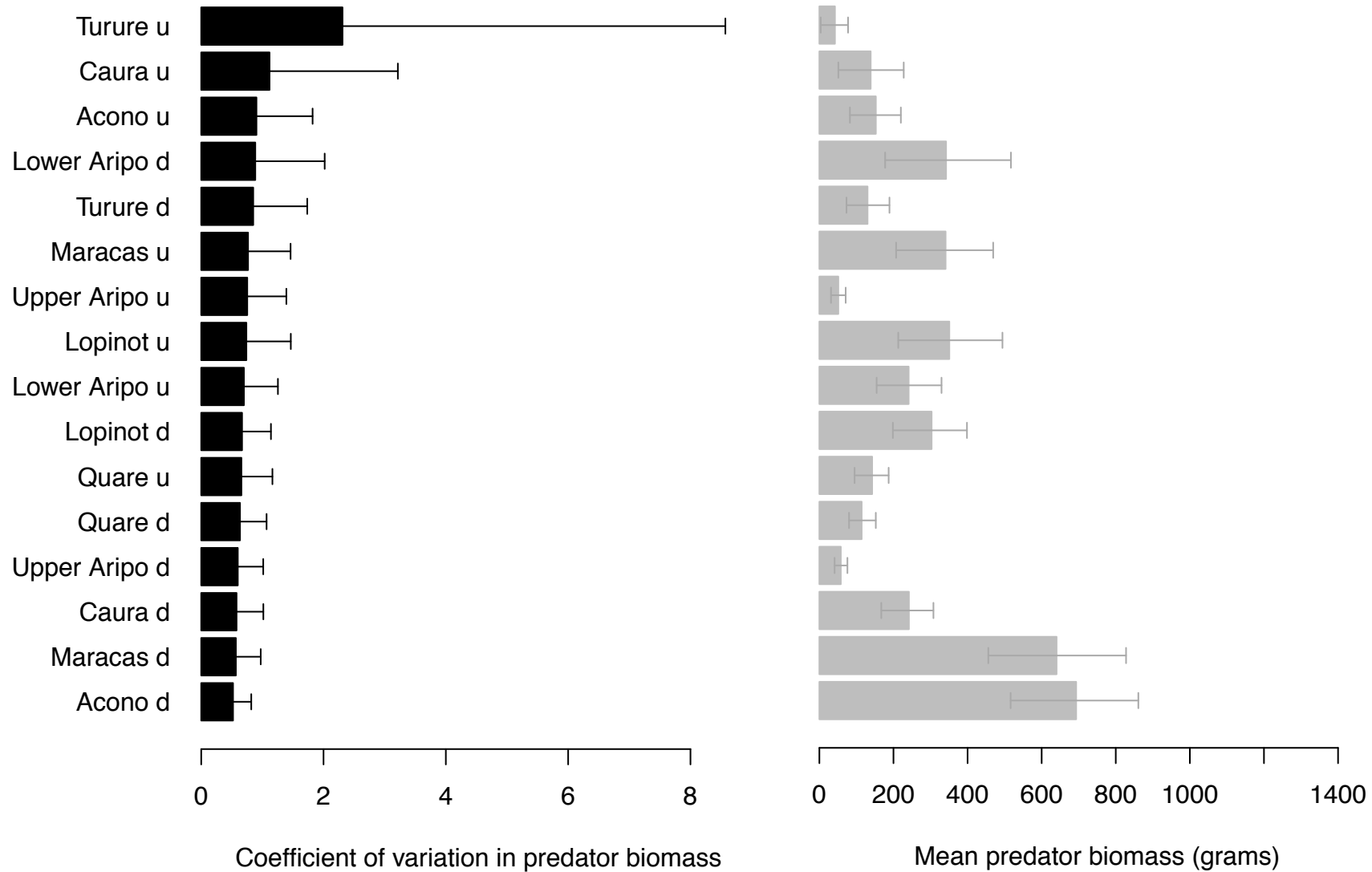


Figure 3

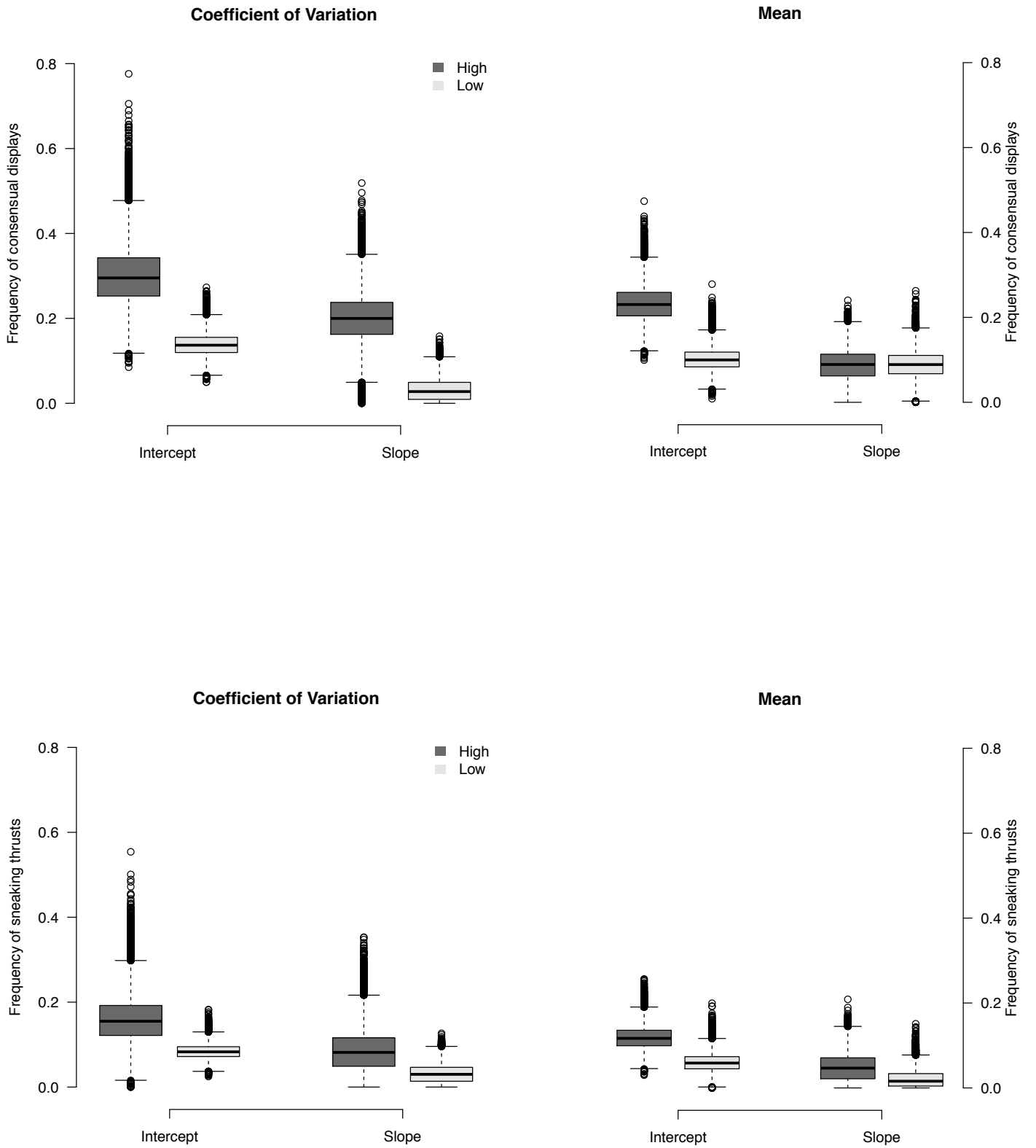


Table 1 –

		Population groups		
		Low Coefficient of Variation	High Coefficient of Variation	
		Posterior mode (\pm CrI)	Posterior mode (\pm CrI)	
Sexual Behaviour	Consensual Mating Display	Fixed effects		
		Intercept	1.772 (1.460: 2.066)	1.598 (0.603: 2.565)
		Slope	0.199 (0.133: 0.272)	0.127 (-0.381: 0.723)
		Random effects		
	Among individuals	0.126 (0.087: 0.191)	0.280 (0.170: 0.440)	
	Within individuals	0.0004 (1.36e ⁻¹⁰ : 0.080)	0.191(0.088: 0.321)	
	Sneaking Thrusts	Fixed effects		
		Intercept	1.754 (1.563: 1.945)	1.315 (0.838: 1.754)
		Slope	-0.069 (-0.168: 0.033)	-0.085 (-0.289: 0.154)
		Random effects		
Among individuals	0.079 (0.050: 0.118)	0.155 (0.059: 0.270)		
Within individuals	0.0003 (1.67e ⁻¹⁰ : 0.068)	0.0004 (9.87e ⁻¹¹ : 0.172)		
		Low Mean	High Mean	
		Posterior mode (\pm CrI)	Posterior mode (\pm CrI)	
	Consensual Mating Display	Fixed effects		
		Intercept	2.053 (1.550: 2.597)	1.506 (1.245: 1.773)
		Slope	0.207 (0.095: 0.342)	0.185 (0.070: 0.278)
		Random effects		
	Among individuals	0.096 (0.052: 0.156)	0.224 (0.154: 0.314)	
	Within individuals	0.084 (0.026: 0.151)	0.089 (2.73e ⁻⁰⁸ : 0.145)	
	Sneaking Thrusts	Fixed effects		
		Intercept	1.851 (1.405: 2.314)	1.512 (1.325: 1.701)
		Slope	-0.126 (-0.357: 0.097)	-0.036 (-0.116: 0.046)
		Random effects		
Among individuals	0.058 (0.017: 0.103)	0.110 (0.067: 0.173)		
Within individuals	0.22e ⁻⁰³ (7.16e ⁻¹³ : 0.062)	0.19e ⁻⁰³ (5.28e ⁻¹⁰ : 0.103)		

Table 2 -

Sexual Behaviour	Population groups	
	Low Coefficient of Variation	High Coefficient of Variation
	Posterior mode (\pm CrI)	Posterior mode (\pm CrI)
Consensual Mating Display	0.349 (0.232: 0.433)	0.478 (0.325: 0.601)
Sneaking Thrusts	0.302 (0.192: 0.391)	0.276 (0.118: 0.417)
	Low Mean	High Mean
	Posterior mode (\pm CrI)	Posterior mode (\pm CrI)
	Consensual Mating Display	-0.001 (-0.032: 0.015)
Sneaking Thrusts	0.013 (-0.113: 0.082)	0.0001 (-0.004: 0.014)