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

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ABSTRACT

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

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

Fluctuating selection caused by temporal environmental heterogeneity is expected to increase the variance in fitness among individuals in the same population (8, 9). When selection favours different phenotypes at different times, investing in the diversification of individual strategies is adaptive (10-12). As such, individual diversification in behavioural strategies is often more pronounced in temporally heterogeneous conditions than in more homogenous ones (13). Variance in among-individual differences in the tradeoff between current and future fitness expectation is
expected to lead to polymorphism in mating strategies (14, 15). The pace-of-life
syndrome hypothesis suggests that within a population some individuals will engage
in high-risk behaviours, such as greater sexual activity, whereas others exhibit less
risk-prone behaviours and prioritize future, over current, reproductive success (16,
17). Temporal heterogeneity in environmental conditions is expected to promote
among-individual differences in fitness pay-offs leading to diversification in
behaviour among individuals. The resulting among-individual diversification in
behaviour should be characterised by individuals engaging in high-risk strategies at
the extremes of these distributions in the population (18). Empirical evidence for this
relationship is, however, lacking.

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

Given that variation in individual behaviour, also referred as personality, is
heritable (24), exposure to constant predator pressure (i.e. always high, or always low)
may favour the evolution of reduced variation (greater homogenization) in individual
behavioural strategies. In contrast, individuals from populations subject to frequent
changes in selection pressure will have no optimal life history strategy, or behaviour.
We can thus predict greater among-individual behavioural variation in populations
exposed to greater temporal heterogeneity in predation risk (25). To test these predictions, we quantify the frequency of male guppy sexual behaviour across contexts of contrasting operational sex ratio and relate this to temporal heterogeneity in predator biomass, a metric for perceived predation risk in the population. Individual behavioural variation in response to environmental conditions can be partitioned using reaction norms to compare three key components: (1) variation in individual intercepts, (2) in individual slopes, and (3) the covariance between them (26).

Variance in the individual intercept of the reaction norm indicates that some individuals have greater mean phenotypes than others. Variance in individual slopes of the reaction norm reveals the variability in the frequency of sexual behaviours in response to differences in sex ratio contexts. Finally, covariance in intercepts and slopes of the reaction norm compares among-individual behaviour in the average context to the variation in other sex ratio contexts. By partitioning the variance in intercepts and slopes across sex ratio contexts and combining this information with environmental data, we can test the hypothesis that temporal heterogeneity in predator biomass promotes diversification in individual behavioural strategies (Figure 1).

Based on variance partitioning, we expect that individuals exposed to greater temporal heterogeneity in predator biomass will have greater variance in intercepts (i.e. among-individual variation in the average context) and slopes (i.e. within-individual variation across environments) of the reaction norms (Figure 1 (a)). In contrast, in more temporally homogenous conditions the optimal phenotype is expected to remain less variable, thereby we expect comparatively less individual behavioural variation among- and within-individuals across contexts (Figure 1 (b)). Finally, higher variance in the slopes between individuals is expected when they exhibit contrasting behavioural strategies across sex ratio contexts (Figure 1 (a)).
METHODS

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

Assessment of temporal heterogeneity in predator biomass

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

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

Sampling and experimental setup

Guppies were collected during the final sampling session (July-August 2015). To prevent atypical behaviour due to guppies being kept in single sex groups, we
collected a sample including males, females and juveniles from each of the 16 populations (S1). Individuals were transferred to a closed container with aeration and immediately transported to the laboratory. To mitigate stress and reduce mortality, individuals were allocated to settling tanks (90 x 30 x 40 cm) in low-density groups with a sex ratio and water temperature that matched their natural conditions. Additionally, each tank was set up with an aeration system and the bottom covered with gravel and natural plants, which provided shelter. The laboratory was kept on a 12L-12D regime.

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

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

We quantified the type and frequency of sexual displays during a 20-minute period. Male guppies perform two forms of sexual displays: the consensual sigmoid display, favoured by females and more often employed in low predation risk localities, and the sneaking thrust, a coercive form of copulation (29). At the end of
the observation period, the focal male was relocated to a new tank (60 x 25 x 30 cm) with individuals from its original population. Unique colour patterns allowed the focal male to be unambiguously recognised. After 24 hours, the same focal male was re-tested as described above in a different sex ratio treatment. This process was repeated so that each focal male was tested in the three sex ratio contexts in a randomised order. The companion individuals were replaced after six observations, and were not re-used during the experiment. At the end of the three trials, the standard length of each focal male was recorded to the nearest millimetre using ImageJ (30). A total of 20 focal males per population were tested ($N_{\text{total focal males}} = 320$).

**Statistical analysis**

The main goal of the study was to test the hypothesis that populations of guppies exposed to greater heterogeneity in predator biomass display greater individual variation in behaviour. Using behavioural reaction norms (31) we explore among- and within-individual variation in sexual displays (i.e. consensual sigmoid displays and sneaking thrusts) across different sex ratios, and related the variation in reaction norms to temporal heterogeneity in predator biomass. We modelled the effect of heterogeneity (i.e. population coefficient of variation (CV) in predator biomass) in generating among-individual variation in behaviour across environments using linear mixed-effects models (LMMs). Mixed random regression models are a suitable analytical tool quantify and test the significance of the relationship between variation in-among individuals and environmental variability (ie. reaction norms) (32). Further, these models yield the highest power to detect variances in individual slopes and intercepts in large data sets, as it is our case (33).
The 16 populations were divided into two groups according to their predator biomass CV values. Populations with a CV value greater than the overall CV mean were classified as ‘high heterogeneity’, whereas populations with CV values smaller than the overall mean CV were considered ‘low heterogeneity’. In a separate analysis, we instead split the populations according to their mean differences in predator biomass. Using the same reasoning, populations were divided into two groups of ‘high mean’ and ‘low mean’ predator biomass.

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

\[
y_{ij} = \alpha + \alpha_1sr + \alpha_2sr^2 + f_1(d_i,n,sr) + f_2(p_j,n,sr) + \varepsilon_{ij},
\]

Where \( y_{ij} \) is the number of sexual behaviours of individual \( i \) of population \( j \), \( \alpha \) is the intercept, \( \alpha_1 \) and \( \alpha_2 \) are fixed effects associated with the slope and curvature of the sex ratio (\( sr \)), \( f_1 \) and \( f_2 \) are random regression functions on natural polynomials of order \( n \), at the individual (\( f_1 \)) and population (\( f_2 \)) groups. In both \( f_1 \) and \( f_2 \), \( n \) was set to 1, allowing for the estimation of random intercepts and slopes. Polynomials were applied to scaled sex ratios (male biased, even and female biased were assigned values -1, 0, and 1, respectively) to improve convergence. Finally, normally distributed heterogeneous residuals by sex ratios were estimated \( \varepsilon_{ij} \), with variance

\[
D = I\sigma^2_d.\ d \text{ and } p \text{ vectors with individual and population values respectively, were}
\]

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assumed to follow normal distributions, $d_i \sim \mathcal{N}(0, D)$ and $p_i \sim \mathcal{N}(0, P)$ respectively,

where both $\frac{1}{3} D$ and $P = I \sigma_{pj}^2$ are 2x2 matrices, and $\sigma_{ai}^2$ and $\sigma_{pj}^2$ are the individual environment and the population effect of individual $i$ and population $j$. Note that $D[1, 1]$ and $D[2, 2]$ are the variances in intercepts and slope across sex ratio contexts, whereas $D[1, 2]$ and $D[2, 1]$ correspond to the covariance between the slope and the intercept of the reaction norm. Since the distributions of consensual sigmoid displays and sneak thrust counts were markedly right skewed, the models were fitted to the logarithm-transformed corresponding variables.

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

$$\text{eq.2} \quad \frac{D[1,1]}{D[1,1] + \frac{2}{3} D[2,2] + \frac{1}{3} \sigma_{\epsilon d}^2 + \frac{1}{3} \sigma_{\epsilon c}^2 + \frac{1}{3} \sigma_{\epsilon y}^2}$$

Before fitting these models, we checked how heterogeneous the original populations were. To address this, we fitted separate linear models to each population,
estimating an intercept and a residual variance. The mean and variance were plotted to inform about their variability across population groups.

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

RESULTS

**Predator biomass**

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

**Consensual sigmoid display**

There were differences in among-individual variance in the intercepts and slopes of reaction norms between populations of low and high predator biomass CV (Table 1, Figure 3, S2, S5). Individuals from populations with ‘high CV’ in predator biomass showed greater variance in frequency of consensual mating behaviour than individuals from ‘low CV’ populations. In contrast, mean differences in predator
biomass affected the variance in intercepts, but not the variance in slopes of the reaction norms (Table 1, Figure 3, S2, S5).

There was strong and positive covariance in intercepts and slopes across sex ratio treatments associated with individuals from populations with ‘high’ predator biomass CV values (posterior mode (95% CrI); 0.44 (-0.51: 0.68), S2). By comparison, the covariance in intercepts and slopes across sex ratios was not significantly different from zero in ‘low CV’ populations (posterior mode (95% CrI); -4.935 (-0.01: 0.005), S2). In terms of mean differences in predator biomass, the values of covariance in intercepts and slopes across sex ratio treatments for both ‘low’ and ‘high’ mean populations were small and not significantly different from zero (posterior mode (95% CrI); -0.001 (-0.032: 0.151) for low; 0.0003 (-0.018: 0.024) for high, S2).

The fixed effects structure of the model gives information about how the guppy population, as a whole, changes behaviour across contexts. There was no effect of predator biomass in any of the population groups evaluated (Table 1, S2).

Regardless of population group (i.e. low and high CV/mean) there was an increase in the frequency of consensual mating behaviour towards the female biased sex ratio context (Table 1, S2). Repeatability of consensual sigmoid display frequency among individuals across sex ratio contexts was low for all four population groups (Table 2).

**Sneaking thrusts**

There were no differences in among-individual variation in sneaking (thrusts frequency) across sex ratio contexts between populations of ‘low’ and ‘high’ predator
biomass CV, or between populations with ‘low’ and ‘high’ mean predator biomass (Table 1, Figure 3, S2, S5).

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

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

DISCUSSION

Our study demonstrates that temporal heterogeneity in predator biomass is key in shaping how prey individuals adjust some of their behavioural strategies in response to changes in sex ratio contexts. Individual guppy males behaved in distinct ways when faced with different sex ratios, and these differences were attributable to the coefficient of variation in predator biomass associated with their original population. We detected a positive relationship between increased heterogeneity in predator
biomass and diversification in individual behaviour (Figure 1 (a), S5). In contrast, mean differences in population predator biomass led to a homogenization in the frequency of consensual mating displays (Figure 1 (b), S2, S5). Furthermore, our results provide evidence that increased heterogeneity in predator biomass generates polymorphism in male prey mating behaviour. In populations with a greater coefficient of variation in predator biomass, some individuals expressed high frequencies of consensual mating behaviour across all sex ratio contexts, while others adjusted their behaviour to match the reproductive conditions. This polymorphism in mating behaviour is consistent with the assumptions of the pace-of-life syndrome hypothesis, which is predicted to emerge under heterogeneous environmental conditions (15). Overall, our results reveal that heterogeneity in predator biomass is a vital factor in shaping the frequency of consensual mating displays and individual life strategies. In contrast, changes in mean density of predator biomass have less effect (Figure 1 (d), S5). It is widely recognized that predators play a vital role in structuring ecological communities. The novelty of our study is that the key role of heterogeneity in predation risk in generating behavioural diversity within the prey population is now clear.

An individual’s personality is traditionally assumed to be constant through time. It follows that individuals with stronger personality should have reduced behavioural flexibility (35). However, under conditions of temporal environmental heterogeneity more than one adaptive strategy may be viable (18, 36). For example, some individuals may respond to changes in conditions, whereas other may not (32). Male guppies from populations with high predator biomass CV showed greater variance in intercepts and slopes in the frequency of consensual mating displays (Figure 3, S5). This indicates greater variability in personality types within these
populations (i.e. temporal variation in individual personality). Our result shows that individual personality can vary over time (37), supports the prediction that exposure to environmental heterogeneity favours variation in individual behavioural flexibility across environmental conditions (i.e. variable individual personalities) (38, 39) and emphasises the importance of including individual behavioural variation across contexts in personality studies.

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

Temporal variation in predation risk shapes the link between life history strategies and behaviour by exerting variable selection among males in the same population. Increased variation in predation risk is predicted to generate behavioural polymorphism within the prey population (40). In populations exposed to high heterogeneity in predator biomass, some individuals always displayed consensual
sigmoid behaviour at higher rates across all contexts, whereas others adjusted the frequency of behaviour to match the reproductive conditions (S2). Such a pattern correlates with a fast-slow continuum strategy (17, 41). In wild guppy populations, males have potentially greater predation risk than females because of their conspicuous consensual mating behaviour and coloration. As a result, individuals that display constantly at high frequency can be seen as investing in a strategy of short-term fitness returns at the expense of survival.

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

A common feature of personality studies is their focus exclusively on individual variation in an average context as a measure of individual personality (i.e. individual repeatability) (43-46). We found low repeatability in the frequency of both sexual behaviours across contexts for all four population groups (S3, S4). This is in contrast to the high repeatability in male guppy behaviour reported in other studies (47, 48). While unexpected, difference between studies may be a consequence of a mathematical artefact. Repeatability is a commonly measured as the proportion of total variance explained by among-individual differences in the average context (49, 50). Our study on the other hand examined both within- and among-individual variation in behaviour across contexts and related this variation to the extent of CV and mean differences in predator biomass associated with the population.
Despite the indisputable role of environmental variability as an explanatory metric of individual behavioural variation, its effect of heterogeneity around the mean remains largely overlooked in most studies (51). Our study provides strong empirical and novel evidence for the link between diversification in behavioural strategies within and among individuals and temporal heterogeneity in predator biomass. We showed that changes in CV and in mean predator biomass have distinct effects on individual variation in prey behavioural strategies. The evolution of diversification in behaviour and life history strategies is key in maintaining diversity in ecological communities. Finally, conservation practitioners should be aware of both the mean and variance of predator pressure within communities before establishing plans for conservation priority of populations, as well when removing predators of threatened populations during conservation management (52).

STATEMENTS

Ethics

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

Data accessibility

The raw data was supplied and allocated to the following repository


Competing interests
The authors declare there are no competing interests.

**Contribution**

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

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**REFERENCES**


Oke KB, Rolshausen G, LeBlond C, Hendry AP. How Parallel Is Parallel Evolution? A Comparative Analysis in Fishes. Am Nat. 2017;0(0):000-.


CAPTIONS

Figure 1 - Predicted pattern of reaction norms for behavioural diversification (a), behavioural homogenization (b and d), and behavioural adjustment (c) scenarios. Each panel shows a hypothetical reaction norm plot for four predation risk populations scenarios (high and low coefficient of variation (a, b), and high and low means (c, d)), across three sex ratio contexts (Male biased (♂), Even ratio (♂/♀) and Female biased (♀)). The lines represent individual reaction norms. Variance in individual intercept indicates that some individuals have greater frequency of sexual behaviour at the average sex ratio context (even-sex ratio), whereas variance in slopes denotes within-individual variability in sexual behaviour across sex ratio contexts.
Figure 2 - Differences in coefficient of variation (black) and in means (grey) in predator biomass between the 16 populations of Trinidadian guppies. Within-population differences were used to split the populations into groups of low and high CV or mean predator biomass. Error bars denote 95% CrI.

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

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

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

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

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Figure 1

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Predictions

**Behavioural diversification**
- Greater variance in intercepts and slopes
- 1. Increase among-individual differences in sexual behaviour frequency at the average context (variance in intercepts at even sex ratio)
- 2. Increase variability in sexual behaviour frequency within individuals across contexts (i.e. variance in slopes)

**Behavioural homogenization**
- Lower variance in intercepts and slopes
- 1. Reduced among-individual variation in the frequency of sexual behaviour at the average context (lower variance in intercepts at even sex ratio)
- 2. Reduced within-individual variation in sexual behaviour frequency across sex ratio contexts (lower variance in slopes)

**Behavioural adjustment**
- Variance in intercepts but not in slopes
- 1. Among-individual differences in frequency of sexual behaviour (variance in intercepts)
- 2. No within-individual differences in frequency of sexual behaviour across sex ratio contexts (lower variance in intercepts at even sex ratio)

**Behavioural homogenization**
- Lower variance in intercepts and slopes
- 1. Reduced among-individual variation in the frequency of sexual behaviour at the average context (lower variance in intercepts at even sex ratio)
- 2. Reduced within-individual variation in sexual behaviour frequency across sex ratio contexts (lower variance in slopes)

8 models: 4 population groups x 2 sexual behaviours
Figure 3

**Coefficient of Variation**

- **Mean**
  - High
  - Low

**Frequency of consensual displays**

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**Coefficient of Variation**

- **Mean**
  - High
  - Low

**Frequency of sneaking thrusts**

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Table 1 –

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<td>1.598 (0.603: 2.565)</td>
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<tr>
<td>Slope</td>
<td>0.199 (0.133: 0.272)</td>
<td>0.127 (-0.381: 0.723)</td>
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<tr>
<td>Random effects</td>
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<tr>
<td>Among individuals</td>
<td>0.126 (0.087: 0.191)</td>
<td>0.280 (0.170: 0.440)</td>
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<tr>
<td>Within individuals</td>
<td>0.0004 (1.36e-10: 0.080)</td>
<td>0.191 (0.088: 0.321)</td>
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<tr>
<td>Sneaking Thrusts</td>
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<td>Fixed effects</td>
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<tr>
<td>Intercept</td>
<td>1.754 (1.563: 1.945)</td>
<td>1.315 (0.838: 1.754)</td>
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<tr>
<td>Slope</td>
<td>-0.069 (-0.168: 0.033)</td>
<td>-0.085 (-0.289: 0.154)</td>
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<tr>
<td>Random effects</td>
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<tr>
<td>Among individuals</td>
<td>0.079 (0.050: 0.118)</td>
<td>0.155 (0.059: 0.270)</td>
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<td>Within individuals</td>
<td>0.0003 (1.67e-10: 0.068)</td>
<td>0.0004 (9.87e-11: 0.172)</td>
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<tr>
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<tr>
<td>Intercept</td>
<td>2.053 (1.550: 2.597)</td>
<td>1.506 (1.245: 1.773)</td>
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<tr>
<td>Slope</td>
<td>0.207 (0.095: 0.342)</td>
<td>0.185 (0.070: 0.278)</td>
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<tr>
<td>Among individuals</td>
<td>0.096 (0.052: 0.156)</td>
<td>0.224 (0.154: 0.314)</td>
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<td>Within individuals</td>
<td>0.084 (0.026: 0.151)</td>
<td>0.089 (2.73e-08: 0.145)</td>
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<tr>
<td>Intercept</td>
<td>1.851 (1.405: 2.314)</td>
<td>1.512 (1.325: 1.701)</td>
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<td>Slope</td>
<td>-0.126 (-0.357: 0.097)</td>
<td>-0.036 (-0.116: 0.046)</td>
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<tr>
<td>Among individuals</td>
<td>0.058 (0.017: 0.103)</td>
<td>0.110 (0.067: 0.173)</td>
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<td>Within individuals</td>
<td>0.22e-03 (7.16e-13: 0.062)</td>
<td>0.19e-03 (5.28e-10: 0.103)</td>
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Table 2 -

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<tr>
<th>Sexual Behaviour</th>
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<td>Posterior mode (±Crl)</td>
<td>Posterior mode (±Crl)</td>
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<td>Consensual Mating Display</td>
<td>0.349 (0.232: 0.433)</td>
<td>0.478 (0.325: 0.601)</td>
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<tr>
<td>Sneaking Thrusts</td>
<td>0.302 (0.192: 0.391)</td>
<td>0.276 (0.118: 0.417)</td>
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<table>
<thead>
<tr>
<th>Sexual Behaviour</th>
<th>Low Mean</th>
<th>High Mean</th>
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<tbody>
<tr>
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<td>Posterior mode (±Crl)</td>
<td>Posterior mode (±Crl)</td>
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<tr>
<td>Consensual Mating Display</td>
<td>-0.001 (-0.032: 0.015)</td>
<td>0.0003 (-0.018: 0.024)</td>
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<tr>
<td>Sneaking Thrusts</td>
<td>0.013 (-0.113: 0.082)</td>
<td>0.0001 (-0.004: 0.014)</td>
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