Predation as a driver of behavioural variation and trait integration: effects on personality, plasticity, and predictability

David J. Mitchell[1,2,*], Christa Beckmann[2,3,4] & Peter A. Biro[2]

1: Department of Zoology/Ethology, Stockholm University, Svante Arrheniusväg 18B. SE-10691, Stockholm, Sweden

2: Centre for Integrative Ecology, School of Life & Environmental Sciences, Deakin University, 75 Pigdons Road, Geelong VIC 3216, Australia

3: School of Science, Western Sydney University, Locked Bag 1797, Penrith, NSW, 2751, Australia

4: Hawksbury Institute for the Environment, Western Sydney University, Penrith, NSW, 2750, Australia

*Corresponding: david.mitchell@zoologi.su.se

Abstract

Predation is increasingly viewed as an important driver in maintaining ecological and phenotypic diversity. In contrast to classic evolutionary theory which predicts that predation will shift trait means and erode variance within prey species, several studies indicate higher behavioural trait variance and integration in high predation populations. These results come predominately from field-sampled animals that cannot isolate the role of predation from other ecological factors such as density. Here, we study the role of predation on behavioural trait (co-)variation in density-controlled populations of guppies (*Poecilia reticulata*) living with and without a benthic ambush predator. At 2.5yrs post introduction of the predators (up to 10 overlapping generations), 40 males were sampled from each of the six populations and extensively assayed for activity rates, water-column use and voracity. Individual variation was pronounced in both treatments, with substantial individual variation means, temporal plasticity and predictability. The effects of predation were subtle. Predators had little effect on mean behaviour, though predator-exposed fish spent more time at the surface in early trials, which decreased to the same as controls with time. Predators did however affect the integration of behavioural traits. In predator exposed ponds, guppies that were higher in the water-column fed slower and had a reduced positive correlation with activity, relative to control populations. Predators also affected the integration of personality and plasticity – leading to changes in among-individual variances through time in water-column use and activity – which was absent in controls. Our results contrast with the extensive guppy literature showing rapid evolution in trait means, and shows maintenance of behavioural variance under predation.

Key words: Behavioural syndromes, animal personality, predator-prey interactions, temporal plasticity, residual model, behavioural reaction norms

Introduction

Predators play a vital role in regulating prey communities, both by shaping the ecology of the environment (Estes et al. 2011) and exacting directional selection on a broad range of traits (Endler 1980; Lapiedra et al. 2018; Reznick et al. 1990). By modulating the relative abundance of prey species (Crooks and Soulé 1999), age and sex demographics (Reznick et al. 2001) and habitat usage (Ripple and Beschta 2004), predators promote ecosystem stability with effects that cascade down trophic levels (Mooney et al. 2010). An extension of these well studied effects of predation is the potential that predators may encourage trait variation in prey species (Bolnick et al. 2011).

While evidence for directional selection on traits such as life-history (Reznick et al. 1990; Spitze 1991), colouration (Endler 1980) and behaviour (Lapiedra et al. 2018; Magurran et al. 1992) are plentiful, the effect of predation on trait variance has received less attention. While long-standing theory suggests that strong selective pressures like predation should shift the population mean and reduce variance (e.g. Hoffmann and Merilä 1999; Levene 1953), a handful of more recent studies have suggested prey may exhibit greater levels of phenotypic variance in populations exposed to high- versus low-predation (Dhellemmes et al. 2020; Dingemanse et al. 2009). This increased variance may result from a couple of factors; negative frequency-dependent selection between predators and prey (Belgrad and Griffen 2016) or learned foraging strategies to target common prey phenotypes (Clarke 1969) may selectively remove the common phenotype and lead to diversifying selection. Alternatively, predators may open niches in the ecological and social environment, leading to increased variance in the prey populations to occupy these niches (Ioannou et al. 2017).

The possibility that predation might increase trait variance is most apparent at the developmental level, where exposure to predation cues in early ontogeny can increase expressed behavioural variation later in life (Edenbrow and Croft 2013; Tariel et al. 2019; Urszán Tamás et al. 2018). For instance, tadpoles exposed to olfactory alarm cues showed greater among-individual variance in activity rates as adults (Urszán Tamás et al. 2018) and similar results have been found in the boldness of aquatic snails (Tariel et al. 2019). While these studies do not speak directly to the role of predation in promoting variation across generations, they do point to a gene-by-environment architecture that promotes variance when exposed to risk, a pattern consistent with the general increase in phenotypic variance when animals are exposed to environmental stress (Rowiński and Rogell 2017). Further, these effects of predation extend to promoting phenotypic integration across traits (Adriaenssens and Johnsson 2013; Bell and Sih 2007; Dhellemmes et al. 2020; Spitze et al. 1991). In sticklebacks (*Gasterosteus aculeatus*), boldness and aggression were not correlated prior to exposure to predation, but were correlated after exposure to predation that included predation selection (Bell and Sih 2007).

While these examples point to an inflation of among-individual variance in mean behaviour (i.e. 'personality'), predation history can also affect individual variation in plasticity (Urszán Tamás et al. 2018). The existence of variance in plasticity implies that personality differences are not fully maintained across environmental gradients or through time (Biro et al. 2010; Brommer 2013) and further imply that trait covariances may be context dependent (Class and Brommer 2015; Stearns et al. 1991). This is particularly apt in an acclimation or habituation context, where the conditions which initially induced a stress response subside with continued exposure. When in high predation environments, habituation rates are reduced due to the increased potential costs of any errors (Brown et al. 2013). At the individual level, this may also change alter the costs and benefits underlying traits, and thus ultimately effect how these traits covary with other traits.

Predation might also favour greater variance within individuals, to reduce the predictability of an individual's behaviour by predators (Briffa 2013; Domenici et al. 2008). Individuals commonly vary in their residual intraindividual variance (rIIV) (Stamps et al. 2012), often termed 'behavioural predictability'. This unpredictability could be particularly advantageous for individuals with a high-risk personality (Highcock and Carter 2014), leading to correlations between personality and predictability when exposed to risk. While variation in personality, plasticity and predictability have different biological causes and consequences, they can also conflate the estimation and interpretation of the other factors. As such, it is important to take a hierarchical and integrated approach to study the effect of predation on behavioural variance.

The evolutionary ecology of predator-prey interactions has been particularly well studied in the guppy (*Poecilia reticulata*). In the native Trinidadian range, guppies live either side of waterfall barriers that confine predators to downstream regions (Endler 1978; Magurran 2005). This natural variation is replicated across multiple, parallel flowing streams. This has led to a rich body of comparative work, where samples of the high predation (downstream) populations are compared to the low predation (upstream) populations, yielding insights into the evolution of life-history traits (Reznick and Endler 1982), behaviour (Harris et al. 2010; Seghers 1974), colouration (Endler 1978) and anatomy (Kotrschal et al. 2017; Reddon et al. 2018). The use of translocation experiments has effectively complemented this work to demonstrate evolution, where high predation guppies were moved to previously guppy-free low predation locations (Endler 1980; Magurran et al. 1992; Reznick et al. 1990).

However, these two methods of study are limited in their ability to control for the secondary effects of predation, which may help to explain the low predation phenotype. Low predation guppies grow slower, reproduce later and give birth to fewer fry (Reznick et al. 1990), while also senescing faster (Reznick et al. 2004). These traits all seem detrimental, raising the question of what maintains the low predation phenotype? Recent insights have been gleaned from a long-term introduction experiment, where low predation populations were monitored with high temporal resolution (Travis et al. 2014). This allowed the researchers to track temporal change in selection pressures resulting from natural density regulation (Reznick et al. 2019). What this work has made clear is the important role of density in the evolution of the low predation phenotype, with populations at carrying capacity favouring slower growth and fecundity (Reznick et al. 2019). Such dynamics also affect behavioural traits, as high density stimulates dispersal in these same populations (De Bona et al. 2019).

While secondary effects of predation – such as density regulation – may be important in promoting trait variance, these factors make it hard to distinguish the direct effects of predation from the secondary effects. Here, we report results from an experimental study where replicated populations of guppies were established and exposed to predators over the course of up to 10 overlapping generations in six semi-natural mesocosms. During this time, the density of control ponds was culled every 6 months to negate the effect of density. After 2.5yrs post-introduction of the predators, we sampled a total of 240 male guppies and repeatedly assayed activity, water-column use and voracity of fish, to better understand how predators affect the mean behaviour, phenotypic variance and phenotypic integration of behavioural traits in their prey. We expected to see predator exposed fish to have reduced activity rates, spend more time high in the water-column and acclimate to the novel conditions slower. Further, we predicted predation to promote trait variances and covariances in the three traits.

Methods

Populations and husbandry

Guppies (*Poecilia reticulata*) used in this experiment were descendants of wild-caught fish collected in 2009 from Alligator Creek, Queensland (Guevara-Fiore 2012). Laboratory stock fish were used to create six populations, which were placed in six replicate ponds (3m × 1.5m × 0.6m deep). Each pond was progressively seeded with a total of 54 mature females, 42-43 mature males, and 22-24 unsexed juvenile guppies from May to August of 2015. Populations were allowed to breed naturally until the 26th of October 2015, when a subset of fish were shuffled between all ponds to further reduce the potential for founder effects. Fifty fish were haphazardly collected from each pond and divided into groups of 10 (five males and five females). Each pond then received one group of 10 from each of the other ponds, for a total of 50 additional fish per pond. Jaguar guapotes (*Parachromis managuensis*) were then added to three ponds (i.e. treatment ponds) on November 26 2015, while the other three remained predator free controls. Cichlids were rotated between the 3 treatment ponds once a month, to control for effects of predator identity. As use of the native Trinidadian pike cichlid (*Crenicichla frenata*) is not permitted in Australia due to quarantine restrictions, we used the jaguar guapote, a cichlid native to Nicaragua where they cooccur with other *Poeciliids*. This is an ambush predator with a large gape that facilitates hunting of evasive prey (Hulsey and García de León 2005). The cichlids were highly cryptic during the day, and became more active during periods of reduced light, while background light went off each evening.

Guppies in each pond were provided a complete refuge, whereby one third of the tank was partitioned off with 16mm plastic mesh that allowed guppies to pass but not the cichlid. Late in the day prior to lights out, guppies increasingly used the refuge, and at night few fish were outside the refuge (D.J.M & P.A.B, *pers obs.*). Cichlids readily fed on guppies as evidenced from 60% increases in mass over the first year. Further, biomass of guppies was lower as a result of predation (see below for details). Guppies were also provided live plants (Java moss) and plastic plants for refuge throughout the mesocosm. All replicates contained a cannister filter (Sicce Whale 500: 1200L/hr), a heater set to 25°C, and gravel substrate. Ponds were illuminated with plant growth spectrum light to stimulate plant growth, natural primary production and foraging resources, and were kept in 12:12 hr light:dark photoperiod (7am-7pm day). Water quality and temperature checks were conducted weekly to ensure all replicates were kept under the same stable conditions. Food was also provided to supplement natural foraging, controlled by automatic feeders that dispensed approximately 0.5 g of a combination of crushed commercial fish flake and dried shrimp into the ponds in the region outside the refuge. All populations were fed three times daily, though treatment populations were reduced to twice daily from August 2016 on due to a decrease in guppy biomass and voracity.

In order to maintain similar population densities between the two treatments, we reduced densities by wet mass in the control ponds every 6 months by culling a random sample of fish (see sampling section below for details). Guppy total biomass was nearly two-fold greater in control than in predator ponds prior to each cull; this, in combination with substantial growth of the predators indicated substantial predation. The measures employed to standardise food availability and density thus allowed us to better focus on the effect of predation, controlling for other density-related factors which are known to contribute to the evolved changes between high and low predation populations in the natural Trinidadian streams (Travis et al. 2014).

Sampling

Ponds were sampled in pairs of control and treatment, with 40 individual males sampled from each pond. To sample, we first caught all fish in each pond (to the best of our ability), while standardising sampling effort between the ponds. Filtration, and heaters were turned off and the cichlids, plants and any other obstacles removed prior to sampling. A fine mesh divide was introduced to the far end of the predator exposed section and was slowly shuffled across to coerce all fish into the refuge area. To standardise sampling effort, we performed three passes of the section with a custom-built seine net, which was the width of the tank, then two more passes using two large square-shaped dip nets.

To select fish for trials, the large tub containing the fish was gently stirred by hand, then a random scoop of fish was taken, the wet mass of the group recorded and then temporarily placed in a holding tank. This was done exhaustively until all fish were caught. Holding tanks were then chosen at random to be a) sampled from, b) culled to reduce density, or c) returned to the pond. Males were sampled exhaustively from the tanks allocated for sampling.

Fish were moved to 1.25L home tanks (length: 25cm, width: 6cm, height: 15cm) in which they resided for housing and for all behavioural assays. Once on the recirculation system, all fish were fed to help them recover from handling and left overnight undisturbed to acclimate. The tanks were placed on a recirculation system, which was held under stable conditions (Temperature = 24.7 ± 0.2 °C, pH = 7.9–8.1, kH = 100– 120 ppm, salinity = 1.1–1.35 ppt) that were the same as in the ponds.

Behavioural observations

Latency to feed

Latency to feed trials, a measure of voracity, were recorded daily for 20 days and began the day after relocation to the lab. Each fish was provided 0.5mL of brine *nauplii* and the latency to commence feeding was recorded to a maximum latency of 150 seconds. This maximum latency was recorded in only 4.5% of observations, and was spread across many individuals and through time. Trials were conducted daily in the afternoons. Due to poor yields in hatching brine, trials were not conducted on some days, and fish instead received a standard ration of flake. In total, 4188 trials were conducted.

Activity and water-column use

Video recorded trials began after fish had acclimated for one week and were designed to create minimal disturbance. Each individual’s home tank was moved from the biorecirculation system to the vertical filming stage (located in the same small constant temperature room) for activity and water-column use assays. The 12-arena stage was backlit with infrared lighting. Once all individuals for a trial had been moved onto the stage, the next set of 12 individuals were fed flake rations in preparation for their trial and to standardise hunger. The experimenter then left the room, and a camera located 2.6m from the stage was set to record remotely. Trials lasted for 22mins, and were live-tracked with EthoVision XT9. The first 2mins were discarded to negate residual effects of movement of the experimenter in the room. From the tracks, we extracted the cumulative distance moved in the 20min tracking period (activity) and the proportion of time in the top half of the tank (water-column use). As tanks were thin (6cm), movement occurred predominately in 2-dimensions. At the conclusion of each trial housing tanks were returned to the recirculation system. Trials were run between 9am and 1pm, began after one week of acclimation post-sampling, and were conducted daily for 14 consecutive days. One day was not run due to a power outage, so a handling effect control (where fish were moved on/off the stage to simulate the protocol) was run in the afternoon.

At the conclusion of all behavioural trials, fish were culled with an overdose of MS-222, dabbed dry with a KimWipe, and weighed to the nearest 0.001g. Due to a small amount of mortality, the final sample size was 237 fish, with 3239 video trials and 4188 latency to feed trials. Activity data from control fish has been used previously by Mitchell et al. (2020) as an example data set to illustrate statistical methods.

All procedures conformed to the standard for animal ethics at Deakin University (B39-2014).

Statistical methods

Data was analysed using double-hierarchical generalised linear models (DHGLM) (Cleasby et al. 2015). These models allow for the simultaneous analysis of a mean and residual model, the latter in log-linked standard deviations. Both are linear models, allowing for fixed and random effects. Full descriptions of these models and formulas can be seen elsewhere (Cleasby et al. 2015; Mitchell et al. 2016; Westneat et al. 2013), so we will not go into great detail here. In contrast to previous models however, we ran these models in a multivariate framework, to assess among-individual correlations between traits. Analyses were implemented through the Bayesian software ‘brms’ (Bürkner 2017).

Distance moved (in 2 dimensions) was square-root transformed and latency to feed was log-transformed to achieve normality of residuals. Proportion of time spent in the top half of the tank was left raw. After transformation to normality, the three response variables were Z-transformed to simplify prior specification and avoid large variance differences which can cause problems when estimating covariance matrices. Fish mass was also log-transformed, then z-transformed to aid specification of priors.

To aid linearity, number of days post-sampling (hereafter just ‘time’) was log-transformed for latency to feed and left-centred time was log-transformed for water-column use. No transformation to time was required for activity. As we were primarily interested in pre-acclimation scores, we left all predictors left-centred.

Both the mean and residual models for all three traits were fit with the fixed effects of treatment, batch, fish mass and time, with interactions between treatment and time, and treatment by batch (see Table 1a in results for full list of terms). The batch variable is a 3-level factor, denoting the pair of treatment and control ponds which were concurrently sampled. Together, the treatment by replicate interaction uses the 5 degrees of freedom required to separate each of the six populations.

Mean models were additionally fit with random intercepts and slopes of time, to assess individual variance in mean behaviour and acclimation rates. A random intercept was specified in the residual model to account for individual differences in rIIV (i.e. individual variation in predictability). As there was a modest ceiling effect in latency to feed trials (150secs, 4.5% of observations), we suggest some caution in interpretation of these results as this may truncate variance slightly (Stamps et al. 2012).

To assess covariances among traits, random effects were fit to an unstructured variance-covariance matrix, which calculates the correlation of all combinations of mean intercepts and slopes, and residual intercepts (rIIV) across the three traits. As we were interested in the effect of predation on trait variances and the integration of traits, we separated random effect (co)variances by treatment. Variance in random slopes indicates that individuals vary in the change of behaviour through time, meaning individual differences in behaviour are not fully maintained through time (Brommer 2013). Therefore, among-individual variances in predicted trait scores and covariances between traits also change with time (Brommer and Class 2015; Stearns et al. 1991).

Repeatability was calculated at the intercept through the standard equation; $R = \frac{\sigma_{int}^2}{\sigma_{int}^2 + \sigma_{\varepsilon}^2}$, though here the residual variance (σ_{ε}^2) is estimated at the midpoint between batches and calculated for each treatment using the residual side model (see supplementary material for more detail). Together, the random effect variance-covariance matrix infers changes in among-individual variances (Eq. 1), cross-time covariances within a behavioural trait (Eq. 2) and covariances between traits (Eq. 3):

$$\sigma^2_{Pred1}[x_1] = \sigma^2_{int1} + 2cov_{int1,slp1}x_1 + \sigma^2_{slp1}x_1^2 \quad (1)$$

$$cov_{Pred1[x1],Pred1[x2]} = \sigma^2_{int1} + cov_{int1,slp1}x_1 + cov_{int1,slp1}x_2 + \sigma^2_{slp1}x_1x_2 \quad (2)$$

$$cov_{Pred1,Pred2}[x_1, x_2] = cov_{int1,int2} + cov_{int1,slp2}x_2 + cov_{int2,slp1}x_1 + cov_{slp1,slp2}x_1x_2 \quad (3)$$

Where numbers in the subscript denote trait 1 or 2, '*Pred*' refers to predicted values, '*int*' to intercepts and '*slp*' to slopes. The predictor '*x*' refers to time, and can be specified separately for the two traits, to account for the differing transformations. These calculations are done for each iteration of the MCMC chain, yielding the credible distribution of the estimate. The implementation of these equations can be found in the supplements, including functions allowing easy generalisation to other datasets analysed with brms. Due to heterogeneous residual variances and that latency to feed trials were separated by 1-8hrs from the video trials, we did not deem it appropriate to try to assess residual covariances.

Models were fit with uninformative priors and ran across 6 chains for 3000 iterations, with a warmup of 500 iterations. Rhats for all parameters were within 1±0.01 indicating convergence. We quote mean effect sizes as the best estimate and confidence intervals based on quartiles for the estimations of 95% credible intervals.

Results

Population effects

As expected, there was evidence of acclimation effects in activity (increase over time) and in latency to feed (decrease over time), but acclimation rates did not differ between treatments (treatment*time effect, NS; Table 1). Treatments also did not differ in mean activity or latency to feed. Predator exposed fish were initially higher in the water-column, and decreased with time to converge with control fish, indicated by the interaction effect (Table 1a, Fig. 1). Larger fish were more sedentary and spent more time towards the bottom. There was also an effect of batch in the three behaviours, which likely results from either population differences among the ponds, or small differences in conditions.

Residual variance in activity decreased over time, meaning fish became more predictable, however the opposite was observed for latency to feed (Table 1b). Residual variance was largely unaffected by other predictors, although again there were some population effects on latency to feed indicated by the batch, and batch-by-treatment interactions.

		Activity			Water-column Use			Latency to Feed		
		Est.	**Q2.5**	**Q97.5**	**Est.**	**Q2.5**	**Q97.5**	**Est.**	**Q2.5**	**Q97.5**
a) Mean model	*Intercept*	-0.148	-0.415	0.114	-0.112	-0.352	0.128	1.184	0.965	1.405
	Batch 2	-0.167	-0.499	0.163	0.159	-0.150	0.468	**-0.549**	**-0.809**	**-0.288**
	Batch 3	0.251	-0.096	0.591	0.206	-0.107	0.527	**-0.285**	**-0.555**	**-0.013**
	Treatment	-0.079	-0.445	0.287	**0.488**	**0.117**	**0.856**	0.218	-0.069	0.507
	Mass	**-0.247**	**-0.348**	**-0.145**	**-0.185**	**-0.281**	**-0.090**	0.030	-0.041	0.100
	Time	**0.030**	**0.017**	**0.043**	-0.006	-0.082	0.071	**-0.447**	**-0.505**	**-0.390**
	Batch 2*Trt	-0.049	-0.536	0.444	-0.189	-0.658	0.281	-0.135	-0.486	0.218
	Batch 3*Trt	-0.393	-0.904	0.111	**-0.573**	**-1.055**	**-0.089**	-0.071	-0.432	0.289
	Trt*Time	0.012	-0.006	0.031	**-0.138**	**-0.250**	**-0.026**	-0.019	-0.095	0.059
b) Residual model	*Intercept*	-0.728	-0.866	-0.589	-0.522	-0.691	-0.354	-0.499	-0.621	-0.375
	Batch 2	-0.063	-0.231	0.104	-0.034	-0.200	0.130	**-0.107**	**-0.206**	**-0.007**
	Batch 3	-0.067	-0.240	0.105	0.001	-0.174	0.177	-0.002	-0.104	0.097
	Treatment	-0.107	-0.306	0.095	0.021	-0.210	0.251	**-0.188**	**-0.371**	**-0.007**
	Mass	-0.020	-0.070	0.030	0.022	-0.026	0.072	-0.022	-0.053	0.010
	Time	**-0.023**	**-0.034**	**-0.013**	-0.023	-0.083	0.037	**0.090**	**0.045**	**0.134**
	Batch 2*Trt	0.220	-0.020	0.454	0.188	-0.044	0.421	**0.231**	**0.076**	**0.388**
	Batch 3*Trt	0.076	-0.174	0.321	0.061	-0.184	0.302	0.062	-0.096	0.222
	Trt*Time	0.004	-0.012	0.020	-0.024	-0.110	0.062	0.026	-0.037	0.089

N_{ID} = 237 N_{obs} = 3239 N_{obs} = 3239 N_{obs} = 4188

Table 1: *Displayed are parameter estimates of the fixed effects in the mean (a) and residual (b) models, with the upper and lower bound of the confidence intervals. Parameters in bold denote no overlap with 0, indicating significance in the traditional sense. The control treatment and batch 1 are reference groups.*

Among-individual variances

There was strong evidence for personality differences in all three behaviours. At the intercepts there was very high repeatability for activity (control: R = 0.79 [0.71, 0.85], predation: R = 0.8 [0.73, 0.86]). Repeatability was slightly lower for water-column use (control: R = 0.64 [0.51, 0.75], predation: R = 0.76 [0.67, 0.84]), and latency to feed (control: R = 0.65 [0.55, 0.74], predation: R = 0.68 [0.57, 0.77]). Further, individuals differed in their temporal plasticity, indicating differential responses during acclimation to experimental conditions. Reaction norm variance in all traits lead to large changes in rank order, though individual differences in means from the start of the trials were partially maintained for all traits. In activity rates, the correlation of predicted values of the first and last days were moderately high (control: *r* = 0.56 [0.42, 0.69], predation: *r* = 0.59 [0.44, 0.71]). In water-column use these were lower (control: *r* = 0.32 [0.12, 0.52], predation: *r* = 0.4 [0.21, 0.58]), as they were for latency to feed (control: *r* = 0.39 [0.18, 0.58], predation: *r* = 0.41 [0.18, 0.62]). Finally, individuals also showed strong differences in predictability (coefficients of variance ranging from 0.13 to 0.34; see supplements), demonstrating that some individuals were more consistent in their behavioural scores than others (Table 2). However, these variances did not differ between treatments, with very similar variance estimates and large overlap in the credible distributions between the two treatments.

Change in trait variances through time

The effect of the treatment on trait variances appeared dependent on time. In activity, among-individual standard deviation did not change from the first day (σ = 0.9 [0.79, 1.03]) to the last day (σ = 0.92 [0.81, 1.05]) in control fish (Fig. 1a), but the reaction norms fanned out in the predator exposed fish to expand variation from σ = 0.82 [0.71, 0.94] to σ = 1.04 [0.91, 1.18] (Fig. 1d). In water-column use, among-individual variances increased from a low at the start of trials in controls (σ = 0.72 [0.59, 0.86]) to a high at the end (σ = 0.89 [0.77, 1.03]; Fig. 1b); by contrast, predator exposed fish showed much higher variance initially (σ = 0.99 [0.83, 1.16]) and then converging to lower variance that was similar to the control (σ = 0.83 [0.72, 0.97]; Fig. 1e). By contrast, variance changes over time in latency did not differ among treatments. Reaction norms converged through time in latency to feed trials, from σ = 0.72 [0.61, 0.84] to 0.62 [0.52, 0.72] in control, and from σ = 0.63 [0.53, 0.75] to 0.55 [0.47, 0.65] in treatment. This pattern was consistent across the two treatments (Fig. 1c,f), as indicated by the very similar intercept-slope correlations (Table 2).

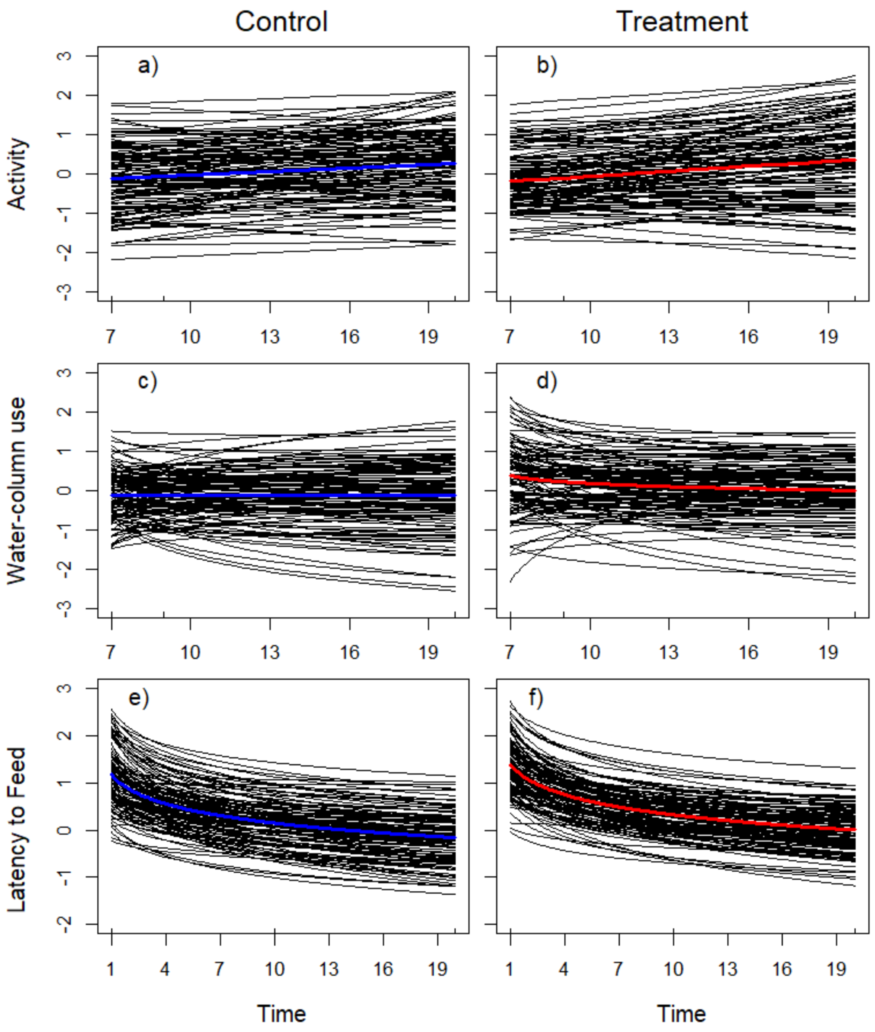

Figure 1: *Displayed are reaction norm plots for individual activity (a,b), water-column use (c,d) and latency to feed (e,f. Control are displayed on the left and predation on the right. Coloured lines correspond to mean level trend, and black lines are individual level predictions. Upward ticks correspond to centring in Fig. 2. Time is shown on the raw scale, back transformed from the log-transformed data used in analysis in c through f, creating the non-linear trends.*

Effects on covariances among traits

There was some evidence that predators affected phenotypic integration of traits (Table 2). These differences appeared to centre on correlations with water-column use, with the treatment fish that were previously exposed to the benthic jaguar guapote appearing to rest near the surface. In both treatments, individuals that were more active were also more likely to be higher in the water column, and this covariance increased with time (Fig.1a). Control fish tended to be at the surface more when active, though effects were slight and only appeared different around day 10 (Fig. 2a). Further, there appeared to be a consistent difference in the correlations of water-column use and latency to feed between treatments, with top-dwelling fish having higher latency to feed in predation ponds, but not control (Fig. 2c). Among-individual correlations between water-column use and latency were small in treatment populations and non-significant in control populations (fig 2c).

There was additionally strong temporal dependence of the trait covariances. Activity and water-column use started weakly or uncorrelated, but were relatively highly correlated in later trials (Fig. 2a). With activity and latency to feed, a small negative correlation disappeared with time (Fig. 2b), while water-column and latency to feed correlation seemed largely stable through time (Fig. 2c).

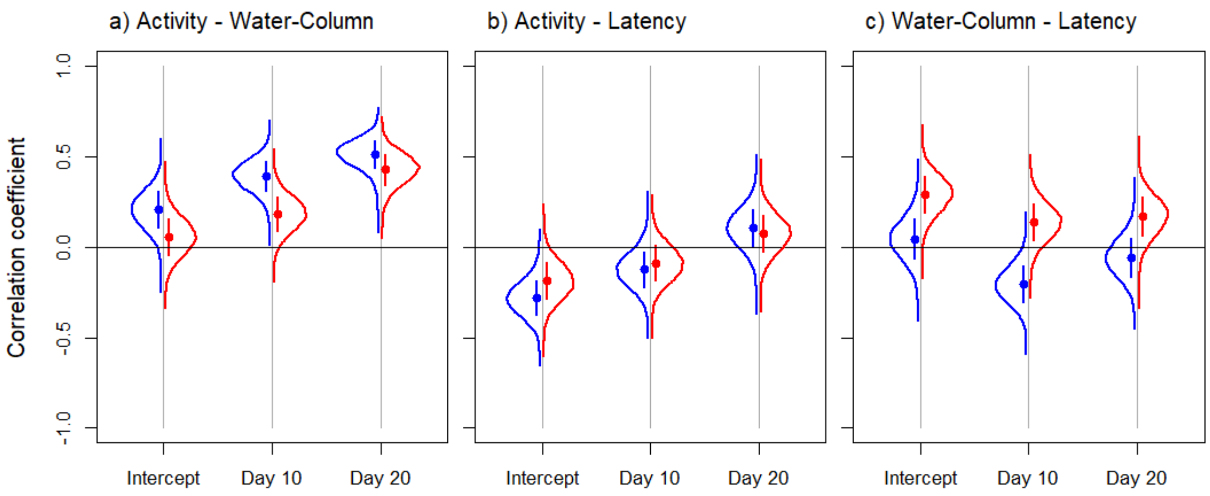

Figure 2: *Displayed are the 3 pairwise trait correlations at three different values of time. Density plots of the posterior estimate are displayed, with controls shown in blue and predator exposed fish in red. As latency to feed observations begun prior to the activity and water-column use assays, the 'left-centre' refers to a correlation of first assay of latency (1 day after sampling) and first assay of the tracking trials (7 days after sampling). Other correlations are on matched days post sampling from ponds.*

Control

	Act[int]	Act[time]	Act[rIIV]	WC[int]	WC[time]	WC[rIIV]	Lat[int]	Lat[time]	Lat[rIIV]
Act[int]	0.903								
ε	0.062								
Act[time]	**-0.447**	0.066							
ε	**0.077**	0.005							
Act[rIIV]	-0.165	**0.471**	0.332						
ε	0.105	0.095	0.032						
WC[int]	**0.203**	**-0.408**	-0.074	0.723					
ε	**0.101**	**0.095**	0.116	0.067					
WC[time]	**0.288**	**0.363**	0.102	**-0.453**	0.359				
ε	**0.098**	**0.096**	0.118	**0.095**	0.033				
WC[rIIV]	**-0.475**	0.062	**0.482**	-0.066	**-0.255**	0.308			
ε	**0.092**	0.113	**0.105**	0.117	**0.118**	0.030			
Lat[int]	**-0.283**	0.156	0.137	0.043	**-0.222**	**0.240**	0.718		
ε	**0.094**	0.102	0.113	0.110	**0.110**	0.112	0.060		
Lat[time]	0.195	0.025	-0.182	-0.269	**0.343**	-0.201	**-0.642**	0.248	
ε	0.105	0.110	0.120	0.112	**0.110**	0.121	0.070	0.025	
Lat[rIIV]	0.119	0.156	0.007	0.099	0.069	-0.209	-0.210	**0.367**	0.124
ε	0.150	0.152	0.161	0.158	0.163	0.166	0.157	0.157	0.027

Predation

Cross-treatment difference

P_{MCMC}	< 0.1	< 0.05

	Act[int]	Act[time]	Act[rIIV]	WC[int]	WC[time]	WC[rIIV]	Lat[int]	Lat[time]	Lat[rIIV]
Act[int]	0.819								
ε	0.059								
Act[time]	**-0.236**	0.066							
ε	**0.094**	0.005							
Act[rIIV]	0.074	0.332	0.317						
ε	0.110	0.104	0.034						
WC[int]	0.055	-0.055	-0.188	0.985					
ε	0.101	0.105	0.112	0.082					
WC[time]	0.179	**0.260**	0.235	**-0.646**	0.379				
ε	0.106	**0.104**	0.120	**0.068**	0.035				
WC[rIIV]	-0.268	0.002	**0.344**	-0.149	0.082	0.293			
ε	0.106	0.117	**0.121**	0.117	0.127	0.031			
Lat[int]	-0.188	0.142	-0.202	**0.289**	**-0.309**	0.097	0.634		
ε	0.101	0.107	0.116	**0.102**	**0.109**	0.120	0.058		
Lat[time]	0.104	0.011	0.138	**-0.262**	**0.401**	0.048	**-0.625**	0.216	
ε	0.114	0.120	0.130	**0.113**	**0.114**	0.131	**0.079**	0.025	
Lat[rIIV]	0.209	0.135	0.092	0.131	-0.038	-0.035	**-0.259**	**0.380**	0.189
ε	0.120	0.125	0.140	0.129	0.138	0.141	**0.126**	**0.129**	0.026

Table 2: *Displayed are the best estimates with error estimates in parentheses of among-individual correlation coefficients for all pairs of intercepts (personality), slopes (temporal plasticity) and rIIV (predictability) across the three traits. On the diagonal is the standard*

deviation. Correlations in bold denote no overlap of the 95%CRI with 0, while highlighted cells denote a significant difference of between treatments.

Discussion

Predators induce profound developmental and evolutionary change in the phenotypes of their prey species and this is particularly true in guppies. Previous work has shown guppies from high predation populations are more social (Seghers 1974), less bold (Harris et al. 2010), higher in the water-column (Seghers 1973) and habituate slower (Brown et al. 2013) than the upstream low predation populations. Despite these strong and known effects of predators on guppies, we did not observe large differences between populations living under constant risk for 2.5yrs compared to those under predator-free conditions that were controlled for density. Fish from predator-exposed populations, exhibited no differences in activity rates and latency to feed, nor differed in acclimation rates to novel conditions than control populations. There was a subtle effect of predation history on water-column use – as predicted, predator exposed fish spent more time at the surface initially, and then decreased their use of surface areas over time. Further, as predicted there was greater among-individual variance in water-column use of predator exposed fish, with the effect also constrained to early trials.

Together, the results point to subtle effects of predation on the behaviours we measured, which contrasts with data from ecological comparisons and translocation experiments. There are however few comparisons for the effect of predation on trait variances in this species (but see Ioannou et al. 2017). We posit this contrast could be explained by a combination of three factors: 1) the standardisation of population density, 2) context dependence of behaviour and 3) the choice of predators.

1) Population density

Predators have a large impact on the ecological conditions of guppies, driving down population densities (Reznick and Endler 1982) and affecting size and age demographics (Travis et al. 2014). In contrast, low predation populations reach carrying capacity, and are therefore under greater intraspecific competition (and competition with *Rivulus hartii*) and reduced food availability when compared to high predation populations (Marshall et al. 2012; Travis et al. 2014; Zandonà et al. 2017). This may help explain the limited effects we saw in mean behaviour resulting from predator exposure. While it is intuitive and compelling to assume increased neophobia is due to increased benefit of being cautious in a high-risk environment, this could also occur due to decreases in costs associated with loss of foraging opportunity in a less resource-constrained environment (Brown et al. 2007). Consequently, as we were controlling densities and food availability, it is potentially unsurprising that we did not see differences in food motivation (latency to feed) and in the highly energetically costly behaviour (activity). By contrast, the traits where we did get a signal of an effect of predation was water-column use, which was likely the behaviour most directly tied to encounter rates with the benthic jaguar guapote.

2) Context dependence

There was strong evidence that context played an important role in behavioural trait expression. Behaviour is often measured under intensive handling protocols and novel conditions, leading to stress effects. If fish from contrasting predation regimes differ in stress coping styles (Koolhaas et al. 1999), this could exacerbate difference in population comparisons. In contrast, we tried to minimise handling time and performed all assays in home-tanks. Fish in our experiment were introduced to novel home-tank conditions, but were allowed to acclimate for 7 days before activity and water-column use assays begun. Supporting this explanation, in early trials predator exposed fish spent more time towards the surface, though with time and as fish continued to acclimate this difference between populations disappeared. Time also affected trait (co)variances, indicating the individual level expression of behaviour was highly context dependent.

Time of day effects could also explain the lack of differences between populations, the cichlids were most active at times associated with dawn and dusk, when lights were turned on and off. During this time, the cichlid was often observed out in the open and the majority of guppies occupied the predator refuge (D.J.M & P.A.B, *pers. obs.*). Predators are known to affect the diel patterns of guppy behaviour (Endler 1987) and behavioural assays taken at times associated with the increased activity of the predator may have resulted in larger effects. The data appears to indicate that activity and latency to feed during daytime hours were unlikely to have had large fitness consequences. However, water-column use may have been more important, given the observed differences in means, variances and covariances in water-column use.

3) Differences in predation

The final likely contributing factor to the lack of effects we found is the choice of predators. The most voracious natural guppy predator is the Pike cichlid (*Crenicichla frenata*). Pike cichlids are an active predator that preferentially preys on larger guppies (note sister species *C. saxatalis* used in citation) (Johansson et al. 2004), though due to quarantine legislation in Australia, we could not obtain *Crenicichla*. By contrast, Jaguar guapotes used here appeared to particularly prey on juveniles (fewer small fry and juveniles were seen in predator ponds), had a rounder body, and was likely ecologically closer to blue acara (*Aequidens pulcher*), which pose a more moderate risk to adult guppies (Deacon et al. 2018; Endler 1980). Therefore, juveniles were likely at greater risk and the predators limited the rate of recruitment, while larger females were relatively safe. These females likely continued to give birth to offspring only a couple generations removed from the founders. Further, female guppies store sperm which they can continue to use for prolonged periods of time (López-Sepulcre et al. 2013), also increasing the effective generation time. Consequently, while the cichlids were clearly an effective guppy predator (see Methods), and guppies can exhibit large evolutionary change in shorter periods than examined here (e.g. large colour pattern divergence was obseved within 14 months; Endler 1980), we may simply not have given sufficient time for the large phenotypic evolution observed in previous studies.

Predation effects on trait variances

While we did not see the evidence for strong directional selection that would erode trait variance (Levene 1953), this does not preclude the possibility that predation would promote trait variance. Predators could lead to niche specialisation (Ioannou et al. 2017) or diversifying selection through predators forming ‘search images’ (Clarke 1969). Similar to the effects on means, treatment differences in trait variances appeared transient and further point to the effects of predation history on behaviour being context dependent. As predicted, predation led to an inflation of among-individual variance in water-column use, although the reaction norms converged to similar levels of variance as the control. It is noteworthy that this inflation of variance occurred in the only trait to exhibit mean differences between treatments. It appears unlikely that the observed differences were due to selection induced by the predator as the effects were plastic and changed rapidly through time. In the other traits, variances were largely maintained, which indicates that stabilising selection or other mechanisms that would erode variance were absent.

At the within-individual level, treatments (and the interaction with time) did not affect rIIV in any trait, though some population differences were detected in latency to feed trials. Predictions of decreased predictability (increased rIIV) are based on repeated interactions at the individual level of predators are prey. While this is feasible with emergence of hermit crabs from a shell within one attack bout (Briffa 2013), or escape trajectories of cockroaches (Domenici et al. 2008), predictions on the individual level are unlikely in the large population sizes of guppies over the time periods these behavioural traits were observed. A predator trying to make predictions in such a situation is more likely to make them based on experience of the population – where we did find some effects on variance.

Predation effects on trait covariances

Predators did appear to affect the phenotypic integration of these behavioural traits. Previous work has demonstrated how predators may affect behavioural covariances (Adriaenssens and Johnsson 2013; Bell and Sih 2007), as the relative cost or benefit of a behaviour may be dependent on other aspects of the phenotype, leading to correlational selection (e.g. Calsbeek and Irschick 2007). In general, we observed evidence for a boldness syndrome in the control fish, with more active fish being higher in the water-column and (in early trials) fed quicker. By contrast, these effects were reduced in predator ponds and additionally, fish higher in the water-column were slower to begin feeding. Differences in these behavioural correlations appeared to centre on water-column use, a result likely driven by the benthic nature of the cichlid predator. This contradicted the *a priori* hypothesis of stronger trait correlations in guppies exposed to predators, though may be explained by the foraging strategy of the predators. Guppies in predation ponds were likely pushed towards the surface, away from where the predator resides. Predator fish appeared more willing to rest near the surface and results may indicate the surface was used as a refuge.

Temporal dependence of trait covariances

In addition to the population comparisons, we quantified multivariate behavioural plasticity. Although quantifying individual differences in behavioural plasticity has become common (Biro et al. 2010; Dingemanse et al. 2012; Martin and Réale 2008) few studies have assessed whether plasticity differences covary across multiple environmental gradients (Cornwell et al. 2018; Mitchell and Biro 2017; Saltz et al. 2017), or multiple behavioural traits (Stamps 2016). Through these cross-trait covariances in intercepts and slopes, we can assess how temporal plasticity shapes multivariate phenotypes (Brommer and Class 2015). What this analysis showed was "behavioural syndromes" were largely context dependent. Correlations of the same trait between the early trials and late trials were only moderate for all traits (r varied from 0.32 to 0.59), despite high intercept-specific repeatabilities. Further, in contrast to results on the movement behaviours of guppies which found stable behavioural covariances to contextual predation risk (Houslay et al. 2018), we found cross-trait covariances to be context dependent. In early trials, activity and water-column use were only weakly correlated, though in late trials the correlation was stronger. Between activity and latency to feed, a small negative correlation disappeared through time.

Further, no paper to our knowledge has examined whether behavioural predictability is correlated among individuals. Predictability is a measure of plasticity in response to endogenous factors or unaccounted for environmental stimuli (Stamps 2016; Stamps et al. 2012; Westneat et al. 2015). In all three traits, individuals differed in their residual variance and thus their predictability. These effects were present despite highly standardised conditions between observations, with minimal variation in temperature or water-chemistry and standardisation of feeding. This effect was small in the latency to feed data, and more pronounced in the other two behaviours. Interestingly, there were positive among-individual correlations in rIIV between activity and water column use in both treatments, indicating that animals which were predictable for one trait were also predictable for the other. This indicates a degree of domain generality to predictability, and is consistent with evidence for correlations between predictability and other forms of contextual plasticity (Mitchell and Biro 2017). Predictability in latency to feed trials did not correlate with predictability of the other two traits, though estimates were imprecise due to the low among-individual variance.

Taken together, the data shows strong integration of personality, plasticity and predictability. While the effects of predation history were small in this case, the integration of behavioural traits was highly context dependent. Over the last decade, large theories have gained a lot of traction purporting to predict broad correlations of behavioural traits across life-history continuums (Biro and Stamps 2008; Réale et al. 2010) or stress coping styles (Koolhaas et al. 1999), though available data fails to support this broad generality (Royauté et al. 2018). Understanding the stability of behavioural trait correlations to temporal or contextual change may prove highly informative in building predictions of under what conditions traits will covary.

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Data accessibility: Data and full analysis code can be found through Mitchell (2020).

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