Testing the stability of behavioural coping style across stress contexts in the Trinidadian guppy

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Running title: Cross-context stability of coping styles

Summary

1. Within-populations, individuals can vary in stress response, a multivariate phenomenon comprising neuroendocrine, physiological and behavioural traits.

2. Verbal models of individual stress 'coping style' have proposed that the behavioural component of this variation can be described as a single axis, with each individual's coping style being consistent across time and stress contexts.

3. Focusing on this behavioural component of stress response, and combining repeated measures of multiple traits with a novel multivariate modelling framework, we test for the existence of coping style variation and assess its stability across contexts in the Trinidadian guppy (*Poecilia reticulata*).

4. Specifically, we test the following hypotheses: (i) there exists repeatable among-individual behavioural (co)variation ('personality') within a mild stress context consistent with a risk-averse—risk-prone continuum of behavioural coping style, (ii) there is population-level plasticity in behaviour as a function of stressor severity, (iii) there is among-individual variation in plasticity (i.e., IxE), and (iv) the presence of IxE reduces cross-context stability of behavioural coping style.

5. We found significant repeatable among-individual behavioural (co)variation in the mild stress context (open field trial), represented as an **I** matrix. However, **I** was not readily described by a simple risk-averse—risk-prone continuum as posited by the original coping style model. We also found strong evidence for

population-level changes in mean behaviour with increasing stressor severity (simulated avian and piscine predation risks).

6. Single-trait analyses did show the presence of individual-by-environment interactions (IxE), as among-individual cross-context correlations were significantly less than +1. However, multi-trait analysis revealed the consequences of this plasticity variation were minimal. Specifically, we found little evidence for changes in the structure of **I** between mild and moderate stress contexts overall, and only minor changes between the two moderate contexts (avian versus piscine predator).

7. We show that a multivariate approach to assessing changes in among-individual (co)variance across contexts can prevent the over-interpretation of statistically significant, but small, individual-by-environment effects. While behavioural flexibility enables populations (and individuals) to respond rapidly to changes in the environment, multivariate personality structure can be conserved strongly across such contexts.

Keywords

Coping styles, animal personality, individual plasticity, individual by environment interactions, behavioural syndromes, multi-response model, individual differences, *Poecilia reticulata*

Introduction

Coping with challenging environments and situations is a necessary part of life. In vertebrates, overcoming these challenges and maintaining organismal function involves a complex suite of neuroendocrine, physiological, and behavioural traits that together comprise the stress response (Wingfield 2003; Øverli *et al.* 2007; Romero, Dickens & Cyr 2009; McEwen & Wingfield 2010). Within populations there can exist consistent differences among individuals in their stress response, spanning a continuum of 'stress coping styles' (Koolhaas *et al.* 1999, 2007; Koolhaas 2008). We propose that recent advances in the fields of animal personality and individual plasticity variation can provide a useful framework for testing hypotheses about the structure of the behavioural component of coping style variation and the extent to which it is consistent across multiple stress contexts. Here we illustrate this framework empirically in a study of behavioural variation within and across stress contexts in the Trinidadian guppy, *Poecilia reticulata*.

The common verbal model of coping styles postulates that among-individual variation will span a continuum from 'reactive' to 'proactive', along which behavioural and physiological traits are predicted to both vary and covary in an integrated fashion (Koolhaas *et al.* 1999). To the extent that the nature of the stress response does differ among individuals, the behavioural components of coping style can be viewed as part of the broader phenomenon of animal 'personality' (Réale *et al.* 2010). While some have argued that personality predicts individual response to risks (Quinn *et al.* 2012), others have treated coping style as a personality trait in its own right (Réale *et al.* 2007; Carere, Caramaschi & Fawcett 2010). Although the distinction may be largely semantic, for current purposes we adopt the latter position, noting that the coping style model posits 'reactive—proactive' or 'risk-averse—risk-prone' behavioural variation among individuals analogous to a 'shy—bold' personality axis (see Boulton *et al.* 2015). This follows the common definition of boldness as an underlying axis of repeatable behavioural responses to perceived risk (Wilson *et al.* 1994). Empirically, individuals are most commonly placed along a shy—bold axis using data from repeated behavioural observations (ideally of multiple traits, e.g., Carter & Feeney 2012; Boulton *et al.* 2012; White *et al.* 2016).

In this study, we focus on characterising variation in stress-related behaviour in a captive population of the Trinidadian guppy (*P. reticulata*). We first characterise 'behavioural coping style' via a multivariate description of movement patterns using modified open field trials (OFTs), a technique used widely with small fishes, including guppies (e.g., Warren & Callaghan 1975; Burns 2008; Smith & Blumstein 2010; White *et al.* 2016). Since the OFT involves handling, transfer to a novel environment and isolation, we consider it a mild stressor for this shoaling species (Archard *et al.* 2012; Boulton *et al.* 2015). This enables us to test whether a single shy-bold type axis of among-individual behavioural variation provides an adequate model of repeatable behaviour across time within a single stress context.

However, the concept of a behavioural coping style is more compelling (and potentially more useful) if an individual's behavioural responses to stress are also consistent (and thus predictable) across stress contexts. Although personality studies emphasise the importance of among-individual differences in mean behaviour, there is a growing appreciation that this can exist alongside among-individual differences in behavioural plasticity (i.e., individual variation in the mean change in behaviour across contexts; Japyassú & Malange 2014). Critically, such individual variation in plasticity, also known as individual-by-environment interaction or IxE (Mathot *et al.* 2012; Dingemanse & Wolf 2013; Alonzo 2015; Stamps 2016), is expected to erode cross-context consistency in behaviour (and hence in behavioural coping styles; Figure 1). We therefore test for IxE and characterise the repeatable components of multivariate behaviour under two different moderate stressor contexts (visual cues of a fish predator, and both visual and disturbance cues of an avian predator strike), for comparison to the mild (OFT) context.

Guppies are a well-known model for behavioural studies, particularly in relation to environmental stressors associated with predation risk. The species is known to exhibit strong behavioural responses to perceived risk of attack from aquatic and aerial predators (Templeton & Shriner 2004), and previous research has shown guppy behaviours are repeatable under simple testing paradigms (Burns 2008). Personality variation has been linked to predation risk (Harris *et al.* 2010), and Endler (1995) found among-population variation in behaviour (as well as life history) associated with differences in predation regime. There is now evidence to suggest that such inter-individual behavioural differences have both developmental (Fischer, Ghalambor & Hoke 2016) and genetic origins (Bleakley, Martell & Brodie 2006). Indeed, prior work on the population used here has shown repeatable variation in OFT traits consistent with underlying personality variation (White *et al.* 2016) that is partly driven by heritable (genetic) effects (S.J. White, unpublished data).

Our primary goals are to test the hypotheses that (i) there exists repeatable among-individual behavioural (co)variation ('personality') within a given context (OFT), consistent with a risk-averse—risk-prone (or shy—bold) continuum of behavioural coping style, (ii) there is population-level plasticity in behaviour as a function of stressor severity (i.e., differences in population-level mean behaviour between the mild and moderate stress contexts), (iii) there exists among-individual variation in the nature of the plastic response to this change in stressor severity (i.e., IxE), and (iv) the existence of such IxE causes a lack of cross-context stability in behavioural coping style (manifest in significant changes across contexts in the overall among-individual behavioural variation and/or between-trait correlations). We use mixed effects models with repeated measures data to partition the among-individual effects from within-individual variation in each stress context. Since the use of single traits to infer personality axes can be problematic (Wilson *et al.* 2011; Carter & Feeney 2012; Carter *et al.* 2013) we employ a multi-trait (and thus a multivariate analytical) approach. While the use of 'reaction norm' models to study behavioural IxE has been strongly advocated in recent years (Dingemanse *et al.* 2010; Dingemanse & Dochtermann 2013), this is (at least in our view) not ideal for multi-trait analyses or for when individuals are assayed in more than two discrete environmental contexts, such that their relative positions on a continuous x-axis are unknown (Houslay & Wilson 2017). A secondary goal of our study is therefore to demonstrate a 'character state' approach to multivariate IxE that has broad applicability beyond the current investigation of behavioural coping style.

Methods

Husbandry

We used 128 sexually mature guppies (evenly split across sexes), sampled haphazardly from our captive population housed at the University of Exeter's Penryn Campus. This population is descended from wild fish collected in 2008 from the lower Aripo River, Trinidad. This site is viewed as 'high predation' under the high- versus low-predation paradigm used in the literature to characterise guppy populations (Seghers 1974a; b). We tagged fish for individual identification purposes using coloured elastomer (Northwest Marine Technology, http://www.nmt.us/products/vie/vie.shtml) after sedation by immersion in buffered MS222 (0.1g/L). Fish were housed in single-sex groups of 8 during the study, and fed to satiation twice daily (8-10am and 4-6pm) using commercial flake food and laboratory-prepared *Artemia salina* nauplii. The behavioural trials were carried out in 4 experimental 'blocks', each lasting 4 weeks. For analysis, we retained data only from those 105 individuals (51 males, 54 females) that completed at least 2 trials in each of the predator stimulus assays.

Behavioural assays

Individual behaviour was assessed in a 20x30x20cm tank, filled to a depth of 5cm with room-temperature water from the main supply (22˚C), and containing a small shelter. The tank was lit from below by placing on a light box, and screened with a cardboard casing to prevent external visual disturbance. We caught fish individually from their home tank using a dip net, examined them quickly for identification tags, and placed them immediately into the centre of the tank. After allowing 30s for acclimation, we filmed behaviour for 120s using a Sunkwang C160 video camera with 6-60mm manual focus lens suspended above the tank. At the end of this period we saved this 'pre-predator' recording (equivalent to the standard open field trial, OFT, as described in White et al. 2016, but for a shorter time period and with a refuge in the arena as described below), then applied a predator stimulus (see below) immediately and filmed behaviour for a further 120s. We then saved this second recording as 'post-predator'. At the end of the post-predator recording we returned the fish to its home tank.

We used two distinct types of predator stimulus: a simulated bird strike, and visual reveal of a piscivorous cichlid in an adjoining tank. Each guppy was exposed to both predator stimuli 4 times each over a period of 4 weeks, resulting in a total of 16 recordings per individual: 8 x pre-predator OFT, 4 x post-bird strike, 4 x post-cichlid reveal. To control for order effects, guppies were grouped by home tank to undergo either bird strike or cichlid reveal trials first. Predator types were then alternated, and were never carried out on consecutive days (resulting in gaps of 2 days between trials within weeks, and 4-5 days between the second trial of any given week and the first trial of the subsequent week). The water was replaced between each group of guppies, and individual order was randomised within groups. The bird strike consisted of swinging a counterweighted model heron head into the observation tank such that it struck the water, causing a physical disturbance to the tank, then removing the head immediately (as described in Boulton et al. 2015). By contrast, we revealed the cichlid predator by removing a visual divider between its tank and the observation tank; the cichlid was then visible for the duration of the 'post-predator' recording, but caused no physical disturbance to the observation tank.

We used the tracking software Viewer II (BiObserve) to extract behavioural data automatically from each recording. Note that we used a slightly different tank configuration for each of the two predator stimuli (Figure S1), but each comprised a shelter zone, an exposed zone, and one or more non-exposed zone(s). Within each predator treatment, these zone layouts were also used for the corresponding pre-predator behavioural trait definitions, such that changes from pre- to post-predator could be determined accurately. We used the following behaviours, characterised from the 120s videos, in our analyses: 'Area' (the percentage of the total tank area that the fish visited during a recording, determined using a 1cm x 1cm grid superimposed over the entire tank by the tracking software), 'Exposed' (duration spent in the exposed zone, in seconds), 'Freezings' (number of times the fish's speed dropped below the minimum velocity threshold of 4cm/s for at least 2.5 seconds), 'Shelter' (duration spent in the shelter zone, seconds), and 'Tracklength' (total distance travelled, cm). Behaviours were selected on the basis of their expected contribution to aspects of boldness and/or exploration, and that measurements were not autocorrelated. Our potential maximum number of behavioural measurements (given 5 behaviours measured in 128 fish in 16 total recordings) was 10240; due to mortalities during the period of data collection (note also that we removed the entire records of those individuals that failed to complete at least 2 trials of each assay type from the data set), our final total was 8150.

Control group

Since all fish experienced the mild stress stimulus (pre-predator OFT) before the moderate (post-predator) one, we used a separate control group to test for temporal changes in behaviour over the recording periods in the absence of predator stimuli. 32 untagged adult male guppies from the same stock population were recorded for a single replicate in the same manner as above, but no predator stimulus was applied: in the bird strike setup, we simply took 2 consecutive 120s recordings; for cichlid reveal, we removed the visual barrier to reveal an adjacent empty tank for the second recording. We used only males here as most of our mature females had entered a breeding experiment for a separate study at this time.

Statistical analyses

We analysed all data using linear mixed effect models in R version 3.3.2 (R Core Team 2016). Visual inspection of residuals from all models suggested all behaviours conformed to the assumption of residual normality. Behavioural measurements were scaled to standard deviation units (calculated from all observations – i.e., including pre-bird strike, pre-cichlid reveal, post-bird strike, and post-cichlid reveal) prior to analysis, enabling more meaningful comparison of effect sizes across traits and assisting multivariate model fitting (described below). In all models, continuous observed predictors fitted as fixed effects (e.g., time of day) were standardised by mean-centring and scaling, putting them on a common scale and aiding the interpretation of main effects (Gelman & Hill 2007;

Schielzeth 2010). Other continuous predictors were mean-centred only (e.g., order, replicate). We compared nested models using likelihood ratio tests (LRTs), in which we estimated $\chi^2_{n\mathrm{DF}}$ as twice the difference in model log likelihoods, with the number of degrees of freedom (n) equal to the number of additional parameters in the more complex model. When testing a single random effect, we assumed the test statistic to be asymptotically distributed as an equal mix of χ^2_0 and χ^2_1 (denoted as $\chi^2_{0,1}$; Visscher 2006). Except where explicitly noted below in relation to testing for population level mean response to stressor severity, fixed effects were used in our mixed models as statistical controls only; these are justified and described below in relation to models fitted, but estimates and their associated p-values are reported only in supplemental materials if not relevant to the biological hypotheses being tested (Tables S1, S2).

Among-individual behavioural (co)variation under mild stress

Using the observations from the pre-predator portion of all trials, we fitted a series of nested models in ASreml-R 3.0 (Butler 2009) to partition multivariate behavioural variation into a between-individual covariance matrix (subsequently denoted $\mathbf{I}_{\mathbf{pre}}$) and a corresponding within-individual (i.e., residual) component. Each model included trait-specific fixed effects to control for effects not directly relevant to hypotheses being tested. These included *sex*, the *order* that individuals were assayed within a single tank of water (to allow for possible effects of water-borne cues from previous fish), the *time* that the trial started (as seconds calculated from 9am each day) and *replicate* (i.e., cumulative total of trials experienced by an individual). Each model also included trait-specific fixed effects of tank and experimental block. Since the tank configuration differed slightly between the two predator contexts, we also included a trait-specific fixed effect of pre-predator context (i.e., pre-bird strike versus pre-cichlid reveal). Note that pooling data from the two trial types means that estimated $\mathbf{I_{pre}}$ will represent an average of variance-covariance structures from the two tank configurations if they differ. However, preliminary (univariate) models found no significant differences in among-individual variance (V_I) between pre-bird strike and pre-cichlid reveal trials for any trait, and among-individual correlations (r_I) across these configurations were not significantly different from +1 (all $P > 0.35$).

Our nested models featured different covariance specifications to test the expectation that there would be among-individual variance and covariance structure consistent with the presence of an axis of boldness variation. **Model 1A** has no random effects, such that all phenotypic variance (conditional on the fixed effects) is allocated to the residual component **R** (which can be considered 'within-individual' here). We specified **R** as a 'diagonal' matrix, where variances for each behavioural trait are estimated but all among-trait covariance terms are set to zero. **Model 1B** includes individual ID as a random effect, with among-individual component **I** also specified as a diagonal matrix. **Model 1C** allows among-trait covariance in **R** (i.e., estimating the off-diagonals in the residual covariance matrix). **Model 1D** extends **1C** by also allowing among-trait covariance in **I.** We then used likelihood ratio tests to provide global tests (i.e., across all traits) for i) among-individual behavioural variation (1A vs 1B), ii) among-trait covariation (1B vs 1C), and iii) significant contribution of individual differences to this among-trait covariation (1C versus 1D). Our final estimates of $\mathbf{I_{pre}}$ and $\mathbf{R_{pre}}$ are based on **Model 1D** (i.e., the fully unconstrained model). Note that since behaviours were scaled to standard deviation units (from all measurements across stages and contexts) prior to analysis, the among-individual variance (V_I) terms on the diagonal of $\mathbf{I_{pre}}$ can be viewed as analogous to repeatabilities (since repeatability = V_I/V_P, and the observed phenotypic variance V_P is 1). We also estimated the adjusted repeatability of each behaviour within-context (where V_P in this case is the sum of among-individual and residual variance from a context-specific model, having conditioned on fixed effects). We repeated these procedures using data from the post-bird strike (**Models 2A-2D**) and post-cichlid reveal (**Models 3A-3D**), such that models **2D** and **3D** yield estimates of $\mathbf{I_{post\text{-}bird}}$ and $\mathbf{I_{post\text{-}cichlid}}$. The inclusion of sex as a fixed effect in all models means that the among-individual (co)variance estimates (and comparisons thereof) are thus estimates of (co)variance around sex-specific means. We therefore assume homogeneity of **I** matrices across sexes, or – equivalently – we estimate **I** matrices that are interpretable as being averaged across any sex differences.

To aid the interpretation of covariance terms contained in $\mathbf{I_{pre}}$**,** we calculated the corresponding among-individual correlations r_{Ipre} (where for any pair of traits (x,y), $r_{Ipre(x,y)} = COV_{Ipre(x,y)} / (\sqrt{}(V_{Ipre(x)}) \times \sqrt{}(V_{Ipre(y)}))$. We also subjected $\mathbf{I_{pre}}$ to eigen decomposition to determine the proportion of among-individual variation captured by each principal component. We used this eigen decomposition to assess whether a single major axis of variation could indeed explain most of the among-individual variation (consistent with the simple proactive-reactive coping style model). We estimated uncertainty on the trait loadings associated with each principal component (eigen vector) using the parametric bootstrap approach as described by Boulton et al (2014).

Population-level response to increased stressor severity

To test for population-level (i.e., mean individual) plasticity in each behavioural trait as a function of stressor severity, we fitted univariate mixed models in the R package lme4 (Bates *et al.* 2015). We fitted separate models for each behaviour with each predator type, but using data from both the pre- and post-predator stages of the trial. A fixed effect of *stage* (i.e., pre- versus post-predator stimulus, coded as -0.5 and 0.5 respectively) was modelled to test for a change in behaviour with increased stressor severity. Additional fixed effects included the *time of day* at which the OFT started (in seconds, mean-centred and scaled), as well as *sex*, *order* and *replicate* (as described above). Random effects were tank, experimental block, and individual ID. For each combination of behaviour and predator type, we used a likelihood ratio test to compare this model (fitted using ML) to one without the *stage* predictor.

We also used data from the control group to check whether apparent effects of *stage* might be driven by a temporal confound (rather than the predator stimulus *per se*). We used similar univariate mixed models as for the data for testing stressor severity, but with fixed effects only of *stage* and *order* (as assay-specific controls were run from males selected from a single tank on a single day, such that *replicate*, *tank* and *block* were not required; we also omitted *time of day* as it was highly correlated with *order*). Individual ID was fitted as a random effect. For this smaller data set, some transformations were required in order that residuals met the assumptions of normality for all behaviours (namely, square-root transformation for duration exposed and number of freezings, and log+1 transformation for duration in the shelter zone, in the 'cichlid presence' setup only). We used a likelihood ratio test to compare the full model (fitted using ML) to one without the *stage* predictor to test whether mean fish behaviours changed across stages in the absence of the predator.

IxE: Among-individual variance in behavioural plasticity

Finally, we tested for among-individual variation in behavioural plasticity (IxE) to increased stressor severity: significant IxE would indicate that individuals differ in the magnitude of their behavioural change across stress contexts. While variation in behavioural plasticity is most commonly modelled using reaction norms (Dingemanse *et al.* 2010; Dingemanse & Dochtermann 2013), this framework is only applicable to more than two environments (here stress contexts) if they can be placed on a continuous axis (i.e., 'function-valued traits'; Stinchcombe & Kirkpatrick 2012). In our study, we make no assumption about the relative severity of the two higher stress (post-predator) contexts, rendering the reaction norm approach problematic (Brommer 2013). Furthermore, while linear reaction norms allow an intuitive separation of the context-dependent and -independent components of a trait (i.e., plasticity as slope, and mean phenotype as intercept), this interpretation does not scale readily to the multi-trait case, where interpreting covariances between intercept and slope terms for different behavioural traits quickly becomes unintuitive (e..g., the covariance between the intercept for area covered and the slope for shelter use). We instead use a character state approach, which can (given enough data) be extended to any number of discrete environments, thus enabling estimation – and therefore direct comparison – of among-individual variance in each context, in addition to all cross-context covariances.

For a behavioural trait expressed in a given stress context, let fish *j* have an expected individual deviation (from the population mean) of i_j. In the absence of IxE, this deviation – expressed relative to the context-specific mean – is independent of the 'environment' such that $i_{j(pre\text{-}predator)} = i_{j(post\text{-}bird)} = i_{j(post\text{-}cichlid)}$. It therefore follows that the variance in *i* (V_I, the among-individual variance in a given trait) is homogeneous across contexts. It also follows that the cross-context correlation of individual deviation must equal +1. Put simply, a lack of IxE means that among-individual variation remains the same across contexts, and that an individual's performance (relative to the phenotypic mean) in one context perfectly predicts its (relative) performance in another. Thus for each behaviour separately, starting with 'Area', we defined three context-specific response variables: pre-predator (pooled across assay types), post-bird strike, and post-cichlid reveal. We then used a series of bivariate models to estimate and test the three cross-context correlations of individual deviations: $r_{i(\text{pre, post-bird})}$, $r_{i(\text{pre, post-cichlid})}$, $r_{i(\text{post-bird, post-cichlid})}$. For each cross-context combination, we fit models with the following constraints: the cross-context correlation constrained to zero, correlation constrained to one, and unconstrained correlation (note that all correlation estimates were positive, so we did not create a model constrained to negative one). We used LRTs to test the unconstrained model against the zero model (i.e., is the correlation significantly different from zero, such that there is some level of positive correlation in individual performance across contexts?)

and the perfect correlation model (is the correlation significantly less than one, such that there does exist some statistically significant variation in individual performance across contexts, or IxE?). Fixed effects included context-specific means and effects of sex, replicate, order, and time, in addition to overall effects of tank and experimental block. A separate mean was also included for each assay type in the pooled pre-predator context. This process was repeated for the remaining behavioural variables (‘Exposed’, ‘Freezings’, ‘Shelter’ and ‘Tracklength’).

Extending the above to the multi-trait case, an absence of IxE means that $\mathbf{I}_{\mathbf{pre}} = \mathbf{I}_{\mathbf{post\text{-}bird}} = \mathbf{I}_{\mathbf{post\text{-}cichlid}}$. Similarity (or lack thereof) between matrices can be assessed in many ways (e.g. Roff et al. 2012; Melo et al. 2015), and here we used two complementary approaches (noting that all behavioural observations were scaled by their global standard deviation prior to analysis, putting each type of trait on a common scale but conserving any differences across contexts). First, we compared the traces (sum of diagonal elements) to determine simply where the total among-individual behavioural variance differed between contexts. Second, we calculated ‘difference matrices’ (**D**) between pairs of **I**, simply by subtracting one matrix from another (e.g., $\mathbf{D}_{\text{pre:post-bird}} = \mathbf{I}_{\text{post-bird}} - \mathbf{I}_{\text{pre}}$). Noting that if **I** matrices are identical then all elements of **D** will equal zero, we used parametric bootstrapping to estimate 95% confidence intervals around each element (and also on our trace comparisons). While this allows statistical inferences to be made, we caution that the confidence intervals estimated are necessarily approximate and based on assumed multivariate normality (see

Boulton et al. 2014; Houle and Meyer 2015 for discussion). We provide R code for this bootstrapping approach in Appendix S1.

Results

Among-individual behavioural (co)variation under mild stress

In the pooled 'pre-predator' mild stress context, comparison of models 1A-1D provided evidence of significant among-individual variance in multivariate phenotype, as well as covariance structure among traits driven in part by individual-level effects (Table 1). Table 2a shows the among-individual variance-covariance matrix $\mathbf{I}_{pre}$ estimated under Model 1D, in which the V_I estimates for each trait (analogous to behavioural repeatabilities over the full range of behaviours expressed in all contexts) are on the diagonal of the matrix. Table 3 shows the adjusted repeatabilities (i.e., repeatability calculated after controlling for confounding effects; Nakagawa & Schielzeth 2010) estimated within each context, which are low to moderate overall (ranging from 0.13 to 0.3). Overall, we find evidence for significant among-individual behavioural (co)variation (i.e., 'personality') under mild stress.

No single major axis of among-individual behavioural (co)variation

Examination of the between-trait correlations in $\mathbf{I}_{pre}$ (r_I; Table 2a, above-diagonals) indicates a number of significant pairwise relationships, both positive and negative (correlations where 95% confidence intervals do not cross zero are considered nominally significant). However, the results of our eigen analysis were not consistent with a single major axis of variation in $\mathbf{I}_{pre}$; rather, the first 2 eigen vectors of $\mathbf{I}_{\mathbf{pre}}$ both explained large amounts of among-individual variation ($EV1_{pre}$ = 49.7%, $EV2_{pre}$ = 39.8%), accounting for almost 90% altogether. We did not therefore find a single major axis of among-individual variation, as expected if observed behaviours are indicative of a single latent shy/bold (or reactive/proactive) axis as suggested by verbal models of behavioural coping styles.

For the first eigenvector $EV1_{pre}$, exposed duration and number of freezings loaded strongly in the same direction, with shelter duration loading heavily in the other (Fig. 2). Area covered and tracklength loaded in the same direction as exposed duration and number of freezings, but their estimates were close to zero (with large confidence intervals). $EV2_{pre}$ loaded strongly on area covered and tracklength in one direction, and number of freezings in the other. The first axis suggests a behavioural decision regarding shelter use, while the second suggests alternative strategies for those finding themselves outside of the shelter.

Predator stimuli induce population-level changes in behaviour

Consistent with our prediction of population-level plasticity in behaviour as a function of stressor severity, we found that both the bird strike and cichlid predator stimuli induced significant changes in the means of almost all behaviours (Fig. 3). Both the bird strike and the cichlid reveal caused individuals to – on average – cover less area of the tank, travel less distance, spend less time in the exposed zone, and spend more time in the shelter (all $P < 0.001$). These results indicate a shift towards more putatively ‘shy’ behavioural means in the higher-stress (post-predator) contexts than was observed in the lower stress (pre-predator) context. The mean number of freezings presents a single exception to this general shift: freezings increased significantly after the cichlid reveal (P = 0.002), but saw a non-significant decrease after the bird strike (P = 0.421).

In our control group, we found no significant effects of time stage for 9 of the 10 assay-specific behavioural traits (Table S3). Total tracklength was reduced after removal of the visual barrier (to show adjacent empty tank) in the 'cichlid reveal' assay setup (estimate = -71.25 ± 22.37, χ^2_1 = 8.8, P = 0.003). Given that this was the only behaviour affected significantly in this control context (where – unlike in the bird strike control – there was a physical change to the environment, the removal of the barrier), we therefore assume differences in the main experiment (as described above) are largely due to the predator stimuli.

Investigating IxE using trait-specific tests

Estimated cross-context among-individual correlations were significantly greater than zero for all behavioural traits and stress context pairs (Table 4). These cross-context correlations, and associated changes in among-individual variance across contexts, are illustrated in Fig. 4. For each behaviour in turn, we extracted individual BLUPs from trivariate models (with response variables being the behaviour in pooled pre, post-bird strike, and post-cichlid reveal contexts), and added these to the assay- and stage-specific population means (pre-bird strike, pre-cichlid presence, post-bird strike, and post-cichlid presence) so as to illustrate changes in average behaviour as well as in among-individual variation.

For all traits, an individual's behaviour relative to the population mean in one stress context (e.g., area covered in the OFT prior to predator presentation) is therefore strongly predictive of its relative behaviour in other stress contexts (e.g., area covered following a predator presentation). However, 8 of the 15 correlations were also significantly less than +1 (Table 3). Of these, 7 were between pre-predator and post-predator contexts, while the post-bird – post-cichlid correlation was only significantly less than +1 for a single behaviour ('Exposed'). Although this could reflect variation in power (sample sizes were larger for the pooled pre-predator behaviours), there is also a pattern of higher correlations between the two higher stress (post-predator) contexts (median across traits of 0.938) than between pre- and post-predator contexts (median 0.765). We conclude from the existence of correlations significantly less than +1 that individual-by-environment interactions are occurring and – equivalently – that there is among-individual variance in plasticity of behavioural response to stressor context. Notably, this IxE is largely occurring between the pre-predator and post-predator (i.e. mild and more severe) stress contexts and so is consistent with among-individual variance in behavioural plasticity as a response to a change in the level of stress.

Investigating IxE by examining conservation of I matrix structure across contexts

Extending to the multi-trait case, comparisons of Models 2A-D and 3A-D provided formal confirmation that fish in post-bird and post-cichlid contexts also exhibited significant among-individual (co)variation in behavioural traits assayed (Table 1). Similarly to $\mathbf{I}_{\mathbf{pre}}$, examination of between-trait correlations in $\mathbf{I}_{\mathbf{post\text{-}bird}}$ and $\mathbf{I}_{\mathbf{post\text{-}cichlid}}$ (r_I; Table 2b,c, above-diagonals) indicates a number of significant pairwise relationships among the observed traits, both positive and negative. However, despite the evidence for IxE when tested with trait-specific models, estimates of $\mathbf{I}_{\text{post-bird}}$ and $\mathbf{I}_{\text{post-cichlid}}$ were qualitatively very similar to that of $\mathbf{I}_{\text{pre}}$ (Table 2). Using difference matrices (**D**) to compare each pair of **I** matrices revealed no significant cross-context differences in the (co)variance structures for among-individual behavioural variation from $\mathbf{I}_{\text{pre}}$ to either $\mathbf{I}_{\text{post-bird}}$ or $\mathbf{I}_{\text{post-fish}}$ (all **D** matrix elements close to zero and non-significant; Table 5a,b). The **D** matrix showing differences from $\mathbf{I}_{\text{post-bird}}$ or $\mathbf{I}_{\text{post-fish}}$ did reveal some significant changes (Table 5c): an increase in the among-individual variance for area covered, a decrease in the among-individual variance for duration in the exposed zone, and a decrease in the among-individual correlation between the number of freezings and the duration in the exposed zone. The **D** matrix traces show no significant changes in total variance (across all traits) between **I** matrices (estimates and 95% confidence intervals: pre- to post-bird, -0.092 (-0.529, 0.324); pre- to post-fish, 0.004 (-0.387, 0.392); post-bird to post-fish, 0.097 (-0.372, 0.576)). On the basis of the lack of significant change in total among-individual behavioural variance, and no significant changes in any elements of the pre- to post-predator **I** matrices, we conclude that our multivariate approach shows little evidence of IxE.

Given the lack of significant differentiation between the three context-specific **I** matrices, we elected to fit one additional multivariate model post hoc, pooling all data (with all fixed and random effects as described earlier) to estimate an averaged (across all contexts) covariance matrix $\mathbf{I}_{\text{all}}$ that we subjected to eigen decomposition. Though obfuscating any IxE present (as suggested by single-trait models but not supported by multi-trait analyses), this allowed us to utilise data from all of the stress contexts at once, and thus generate a more precise estimate of the among-individual behavioural (co)variation structure first estimated above (as $\mathbf{I_{pre}}$) utilising solely the OFT stress context. That is, we estimated among-individual behavioural (co)variances by using up to 16 measurements of each behaviour per individual (8 x OFT, 4 x post-bird strike, 4 x post-cichlid reveal), and including fixed effects to control for environmental variables and – crucially – population-level plasticity in each trait across contexts. Similar to $\mathbf{I_{pre}}$, eigen decomposition of $\mathbf{I_{all}}$ showed no clear support for the idea of a single major axis of among-individual behavioural variation: together, the first two axes explained over 90% of the total among-individual variation ($EV1_{all}$ = 57.4%; $EV2_{all}$ = 34.2%). Trait loadings were equivalent to $\mathbf{I}_{pre}$ (see Fig. 2), and confidence intervals tightened around strongly-loading traits ($EV1_{all}$: exposed duration and number of freezings vs shelter duration; $EV2_{all}$: area covered and tracklength vs number of freezings; Fig. S2), lending support to statistical significance of the presence of 'alternative strategies' of behavioural stress coping styles which are consistent across stress contexts.

Discussion

We found significant repeatable among-individual (co)variation ('personality') in all behaviours, and within each stress context. We also found strong evidence for changes in mean behaviour (population-level behavioural plasticity) due to the predator stimuli. At the among-individual level, the majority of cross-context correlations were significantly different from a 'perfect' correlation, thus indicating the presence of individual-by-environment interactions (IxE). However, in contrast to the significant (albeit low) IxE found in these pairwise correlations, our multivariate analyses provided little evidence that individual variation in plasticity was causing instability of the **I** matrix across contexts. We found no evidence for changes in the structure of the among-individual covariance matrix (**I**) between pre- and post-predator contexts, and only minor changes between the two post-predator contexts. We also found no cross-context changes in the total among-individual variation in measured behaviours. Our investigation of the **I** matrix revealed no single major axis of behavioural variation (and we found that $\mathbf{I}_{pre}$ was qualitatively similar to the overall **I** matrix, $\mathbf{I}_{all}$, having pooled across all contexts and stages). Rather than the simple 'risk-prone—risk-averse' continuum as posited by the original coping styles model, our two axes indicate a more complex level of variation in individual strategies.

The strong evidence of behavioural change across different stress contexts that we found at the population level, with general shifts towards a 'more shy' behavioural mean, was expected: behaviour is often highly flexible, enabling individuals to react quickly in response to environmental changes (Komers 1997; Ghalambor, Angeloni & Carroll 2010). In the context of the stress literature, the adaptive response to stressors includes various processes (neuroendocrine, physiological and behavioural) that enable an individual to redirect behaviour and energy in order to establish homeostasis (Johnson *et al.* 1992). In this study, we found that our two moderate stress contexts induced similar amounts of population-level change (relative to the mild stressor of the pre-predator OFT) for several behaviours: the mean reduction in area covered, duration in the exposed zone, and distance travelled were equivalent in both bird strike and cichlid reveal.

One intriguing result is that the number of freezings increased significantly after the cichlid reveal, yet after the bird strike there was a marginally non-significant decrease. Our expectation of a tendency towards ‘more shy’ behaviours under greater stress had led us to predict an increase in the number of freezings in both post-predator contexts. However, this result might best be explained by the change in another behavioural variable: the mean increase in duration in the shelter post-bird strike was almost double that of post-cichlid reveal. We note that there is a significant negative correlation between variation in shelter use and in the number of freezings at both the among- and within-individual level for each stress context; also that the mean number of freezings per second out of the shelter increased across stages in both predator types (pre-bird = 0.028±0.002, post-bird = 0.032±0.002; pre-cichlid = 0.030±0.002, post-cichlid = 0.040±0.002). Taken together, these results provide a simpler explanation for the apparent increase in ‘bolder’ freezing behaviour (i.e., a decrease in the number of freezings) under increased stress: guppies increased their shelter use far more post-bird strike compared to post-cichlid reveal, with the result that individuals had fewer opportunities for freezing behaviour post-bird strike.

While population-level plasticity informs us about the average change in behaviour within said population, plasticity is itself the property of an individual (or, more specifically, a genotype; Via & Lande 1985; Falconer & Mackay 1996). Individuals can vary in the extent of their plasticity across different environments or contexts, and this phenomenon is known variously as individual variation in plasticity, individual differences in slopes (when using reaction norms), and individual-by-environment interactions (IxE). All of these mean the same thing: that individuals (or genotypes) do not change their phenotype (in this case, their behaviour) at the same rate with respect to changes in their environment. For behaviours related to coping styles, IxE would suggest that individuals do not maintain their position along the putative 'risk-prone – risk-averse' axis relative to others, and instead alter their relative performance as the environment (e.g., stressor severity) changes.

When testing each behavioural trait separately, we found evidence of statistically significant IxE across at least one pair of contexts for all five measured behaviours. Significant IxE was typically found between mild (pre-predator OFT) and moderate (post-predator) stress contexts: for all but duration in the exposed zone, the correlations across the two types of post-predator contexts were not significantly different from +1 (i.e., where r = +1 means that individual performance is perfectly correlated such that there is an absence of IxE in terms of rank order changes). The existence of IxE from pre- to post-predator contexts indicates some changes in the rank order of the relative performance of individuals across contexts, although all correlations were also significantly greater than zero – suggesting that relative performance is generally predictable across all contexts.

While we did find statistically significant IxE in our trait-specific tests, our second approach to analysing IxE (via examination of the **I** matrix) suggests that multivariate personality structure was largely conserved across each of the stress contexts – particularly between mild and moderate – thus indicating an apparent lack of IxE at the multivariate level. How might we reconcile these seemingly conflicting results? Rather than the reaction norm models (typically formulated as random regression mixed models) that are often used for the study of individual plasticity variation, we employed 'character state' models: the character state approach aids interpretation by estimating the among-individual variance in each context and the covariation between them (see Figure 1 and associated legend). This contrasts with reaction norm models in which (co)variances in intercepts and slopes are estimated, but on different scales such that their absolute and relative magnitudes are less easily interpreted (see Brommer 2013 for discussion). Here, our powerful study design enables us to detect statistically significant changes in variation and imperfect correlations across contexts in the univariate case, but our use of multivariate character state models better enables assessment of the magnitude of these changes. In this case, our univariate models demonstrate IxE effects that are statistically significant but small, ultimately producing only minor effects on the actual phenotypic values (and leading to the structure of the **I** matrix being largely conserved across stress contexts). As illustrated in Fig. 4, the rank order changes tend to be relatively minor, such that relative performance is fairly well conserved across all contexts. We can therefore infer, for example, that an individual that covers a relatively large area (compared to its peers) in a mild stress context would also cover a relatively large area in a higher stress context, having taken into account the expectation that all fish are likely to cover less area overall in the higher stress context.

Here we found that the structure of the **I** matrix between mild and moderate stress contexts was largely conserved, yet for the sake of interpretation it may be fruitful to consider how larger IxE across contexts would have been manifest in **I**. We might have expected, for example, that increased stressor severity would increase the amount of among-individual variation in behaviour (manifest as positive values on the diagonal of **D** matrices, and greater matrix traces in $\mathbf{I}_{\mathbf{post}}$). This would have meant that, in addition to the changes in mean behaviour across stress contexts (population-level behavioural plasticity), that individuals behave 'more differently' from one another (which would be seen as a 'fanning out' of the visualised reaction norms). Such a result would have been more consistent with the 'two-tier' model of stress coping styles described by Koolhaas *et al.* (2007), in which individuals differ not only in 'coping style' (i.e., where their response lies on a putative risk-prone—risk-averse continuum) but also in their 'responsiveness' (i.e., the magnitude of their response to the environmental stressor).

Here, not only did we find no difference in the amount of among-individual variation across contexts, but the covariance structure of the **I** matrix also showed few significant differences in their elements (and none between the mild and moderate stress contexts). The relationships between traits are therefore neither decoupled nor more tightly integrated under higher levels of stress. Accepting this conservation of **I** across contexts, our eigen decomposition of the post hoc matrix estimate based on all data (across contexts) best enables us to scrutinise the major axes of among-individual behavioural variation (see Houslay & Wilson 2017 for further discussion of this approach). While the behavioural component of 'coping styles' describes different ways in which individuals can attain successful environmental control (Koolhaas *et al.* 1999, 2007), the structure of **I** here does not really conform to expectations from verbal models in the literature. Specifically, behavioural coping style is typically portrayed as a single major axis of variation or even a simple bimodal distribution (although note that much of the work focusing on 'alternative response patterns' is informed by studies using artificial selection lines, which may lead to oversimplification of the true nature of the underlying behavioural variation; Réale *et al.* 2010). As noted previously, while the 'two-tier' model does embrace the idea of greater complexity in among-individual behavioural variation, it still implies the existence of a single axis denoting the type of behavioural response, while a second dimension shows variation in the magnitude of that response (Koolhaas *et al.* 2007, 2010).

In this study, rather than the single major axis posited by the verbal models of stress coping styles, we instead found two major axes of among-individual variation in behaviour. The first axis loaded strongly on increased shelter duration in one direction, while all other traits loaded in the other direction, indicating variation on a continuum from high use of the shelter (shyer, risk-averse individuals) to other behaviours (nominally bolder, more risk-prone individuals). The second axis loaded heavily on increased number of freezings in one direction, and greater area covered and tracklength (i.e., distance travelled) in the other direction. Increased duration in the exposed zone also loaded (non-significantly) in the same direction as the increased number of freezings, therefore indicating that increased area covered and distance travelled were not associated with time spent in the central exposed zone. Together, these two axes potentially correspond to multiple strategies for behavioural control of a stressful environment: individuals may seek refuge in the shelter, but otherwise may adopt a strategy of either freezing in place (typically in an exposed area) or actively trying to escape the situation. 'Freezing' vs 'active startle' have been demonstrated previously as alternative stress-response behaviours in guppies, using OFTs that did not include a shelter (Fischer *et al.* 2015). We note that freezing and hiding are both effectively passive, 'conservation-withdrawal' strategies, and might therefore be considered alternatives among more 'reactive' individuals (Øverli *et al.* 2007). Our results do raise the question, however, of whether simple additions to the testing environment can reveal complex behavioural (co)variation that might otherwise go unnoticed.

Overall, our results provide behavioural evidence in support of the concept of coping styles, but also highlight that the full range of their underlying variation might not be readily captured analytically by a simple, single-axis paradigm, even when considering behaviour alone. We have used this study to demonstrate how character state models – in comparison to a random regression approach – enable a better understanding of the magnitude of IxE and its consequences for among-individual variance in observed traits, by directly estimating changes in variance across contexts as well as testing specific hypotheses regarding the cross-context covariance. We also show that, even when behavioural flexibility enables populations (and individuals) to respond to environmental changes, personality structure can be strongly conserved. This stability of relative behaviour means that – while we do not know how selection on behavioural types might differ – the material upon which selection acts can show consistency across contexts.

Author Contributions Statement

M.V. and A.J.W. designed the experiment; T.M.H., M.V. and A.J.G collected the data; T.M.H. analysed the data; T.M.H., A.J.Y. and A.J.W. led the writing of the manuscript. All authors contributed critically to manuscript drafts and gave final approval for publication.

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Data Accessibility

All data will be uploaded to Dryad upon acceptance of this manuscript.

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Figures

Figure 1: Examples of how variation in plasticity might affect the stability of 'coping styles' across stress contexts. Each panel shows 'coping style' behavioural variation (i.e., differences among individuals in their average behaviour) in the 'mild stress' context (left hand side of x-axis), with identical population-level behavioural plasticity (the change in the mean behaviour across contexts). The four panels illustrate the outcome with no IxE (panel a) or three different forms of IxE (panels b-d): (a) coping styles are consistent across contexts (no IxE; $V_{mild} == V_{moderate}$, cross-context correlation $r = 1$); (b) increased stressor severity increases among individual behavioural variation (IxE), but rank order remains consistent ($V_{mild} < V_{moderate}$, $r = 1$); (c) among-individual variation exists within each context, but strong rank order changes (IxE) mean individual position cannot be predicted across contexts ($V_{mild} == V_{moderate}$, $r < 1$); (d) all individuals converge on a common behaviour (IxE), such that there is actually no among-individual variation in the moderate stress context ($V_{mild} > 0$, $V_{moderate} = 0$, $r = 0$).

Figure 2: Trait loadings on the first two eigenvectors (eigen one, left; eigen two, right), from I_{pre} (the I matrix for pooled pre-predator OFT behavioural variation). Lines represent 95% confidence intervals, calculated from 5000 bootstrapped replicates. Loadings are considered nominally significant if CIs do not cross zero (dashed vertical line). Arithmetic sign of loading denotes groups of behaviours that load in opposing directions (i.e., eigen one represents an axis where one extreme features individuals that spend more time in the exposed zone with a greater number of freezings and less time in the shelter; the other extreme those

that spend greater time in the shelter, with fewer freezings and less time in the exposed zone).

Figure 3: The estimated effect of predator stimulus (cichlid reveal, light grey; bird strike, dark grey) on average guppy behaviour. All behaviours (response variables) were mean-centred and scaled to 1 standard deviation for purposes of comparison. Effect sizes and confidence intervals (calculated as 1.96 times the standard error) were taken from linear mixed model analyses (see text for details). Effects are considered nominally significant if CIs do not cross zero (dashed vertical line). Both predator stimuli induced significant population-level plasticity in all behaviours (P = 0.002), except for the effect of bird strike on the number of freezings (P = 0.421).

Figure 4: Each line shows an individual's intercept deviation (after conditioning on main effects) across pre-predator, post-bird strike, and post-cichlid reveal stages ('pre' is shown twice to enable easier comparison of changes across all stages). Deviations are estimated by multivariate models with pooled pre-predator, post-fish and post-bird responses, with a separate model for each behaviour (see text for details). We use assay- and stage-specific means to show both individual- and population-level plasticity. We randomly selected eleven individuals (coloured lines) to illustrate reaction norms more clearly both within and across panels.

Tables

Table 1: Multivariate model comparisons showing tests of among-individual variation, among-trait covariance, and among-individual trait covariance within each context (pre-predator, post-bird strike and post-cichlid reveal). Models were fitted as described in main text and compared by likelihood ratio test.

Context	Comparison	Testing for	χ^2	DF	P
Pre-predator	1A vs 1B	Variance among individuals	394.9	5	<0.001
	1B vs 1C	Among trait covariance	1435.5	10	<0.001
	1C vs 1D	Among individual trait covariance	175.5	10	<0.001
Post-bird strike	1A vs 1B	Variance among individuals	88.5	5	<0.001
	1B vs 1C	Among trait covariance	1366.2	10	<0.001
	1C vs 1D	Among individual trait covariance	51.0	10	<0.001
Post-cichlid reveal	1A vs 1B	Variance among individuals	113.9	5	<0.001
	1B vs 1C	Among trait covariance	508.9	10	<0.001
	1C vs 1D	Among individual trait covariance	49.0	10	<0.001

Table 2: Among-individual (**I**) variance-covariance matrices estimated from a) pooled pre-predator data, b) post-bird strike data, and c) post-cichlid reveal data. Among-individual variances (V_I, analogous to repeatabilities over the full range of behavioural measurements) are given on the diagonals, with among-individual between-trait covariances (COV_I) below and the corresponding correlations (r_I) above. 95% confidence intervals in parentheses are based on 5000 bootstrapped **I** matrices.

	Area	**Exposed**	**Freezings**	**Shelter**	**Tracklength**
Area	0.18 (0.10,0.27)	0.30 (-0.05,0.62)	-0.14 (-0.47,0.16)	-0.52 (-0.75,-0.26)	0.57 (0.33,0.78)
Exposed	0.05 (-0.01,0.11)	0.15 (0.08,0.23)	0.83 (0.66,0.99)	-0.80 (-0.96,-0.64)	-0.03 (-0.36,0.31)
Freezings	-0.03 (-0.09,0.03)	0.16 (0.08,0.23)	0.24 (0.14,0.33)	-0.59 (-0.81,-0.38)	-0.37 (-0.63,-0.11)
Shelter	-0.09 (-0.14,-0.03)	-0.12 (-0.18,-0.06)	-0.11 (-0.17,-0.05)	0.15 (0.09,0.22)	-0.47 (-0.69,-0.22)
Tracklength	0.11 (0.04,0.18)	-0.01 (-0.05,0.06)	-0.08 (-0.14,-0.02)	-0.08 (-0.14,-0.03)	0.20 (0.12,0.28)

a) Pre-predator

	Area	**Exposed**	**Freezings**	**Shelter**	**Tracklength**
Area	0.09 (0.01,0.16)	0.41 (-0.13,0.82)	0.24 (-0.38,0.82)	-0.59 (-1.00,-0.07)	0.57 (0.11,0.90)
Exposed	0.06 (-0.02,0.15)	0.29 (0.13,0.44)	0.93 (0.79,1.10)	-0.87 (-1.06,-0.67)	0.07 (-0.44,0.44)
Freezings	0.03 (-0.04,0.09)	0.21 (0.09,0.32)	0.18 (0.07,0.28)	-0.64 (-0.91,-0.28)	-0.21 (-0.72,0.26)
Shelter	-0.07 (-0.14,0.01)	-0.18 (-0.30,-0.07)	-0.11 (-0.20,-0.01)	0.16 (0.05,0.27)	-0.50 (-0.85,-0.08)
Tracklength	0.06 (0.00,0.12)	0.01 (-0.06,0.08)	-0.03 (-0.09,0.03)	-0.07 (-0.14,0.00)	0.12 (0.05,0.19)

b) Post-bird strike

	Area	**Exposed**	**Freezings**	**Shelter**	**Tracklength**
Area	0.25 (0.13,0.37)	0.52 (-0.01,0.95)	0.12 (-0.27,0.51)	-0.59 (-0.91,-0.26)	0.66 (0.40,0.91)
Exposed	0.06 (0.00,0.12)	0.06 (0.01,0.12)	0.48 (-0.04,0.97)	-0.81 (-1.37,-0.37)	0.56 (0.06,1.14)
Freezings	0.03 (-0.07,0.12)	0.06 (0.00,0.13)	0.28 (0.14,0.42)	-0.72 (-1.04,-0.43)	-0.22 (-0.63,0.20)
Shelter	-0.12 (-0.20,-0.03)	-0.08 (-0.14,-0.02)	-0.15 (-0.26,-0.06)	0.16 (0.06,0.27)	-0.45 (-0.81,-0.04)
Tracklength	0.14 (0.05,0.22)	0.06 (0.00,0.11)	-0.05 (-0.13,0.04)	-0.08 (-0.15,0.01)	0.17 (0.08,0.28)

c) Post-cichlid reveal

Table 3: Adjusted repeatabilities (estimate and SE) for each behaviour, calculated within each context.

Behaviour	**Pre-predator**	**Post-bird strike**	**Post-cichlid reveal**
Area	0.20 (0.04)	0.14 (0.05)	0.30 (0.06)
Exposed	0.17 (0.04)	0.26 (0.06)	0.13 (0.05)
Freezings	0.27 (0.04)	0.21 (0.06)	0.27 (0.06)
Shelter	0.27 (0.04)	0.17 (0.05)	0.18 (0.06)
Tracklength	0.27 (0.04)	0.22 (0.06)	0.23 (0.06)

Table 4: Cross-context among-individual correlations for each behaviour, with tests of whether they are significantly different from 0 (i.e., positive correlation) and +1 (i.e., not perfect correlation). All correlations are significantly greater than 0. Correlations in bold are both significantly different from 0 and +1, indicating significant individual-by-environment interactions (IxE).

Behaviour	Contexts		Correlation	SE	Compare to 0		Compare to 1	
					χ^2_1	*P*	χ^2_1	*P*
Area	pre	post-bird	0.76	0.15	16.1	<0.001	2.4	0.060
	pre	post-cichlid	**0.68**	0.11	21.7	<0.001	12.9	<0.001
	post-bird	post-cichlid	0.96	0.16	26.4	<0.001	-0.3	0.500
Exposed	pre	post-bird	**0.77**	0.11	19.4	<0.001	4.3	0.019
	pre	post-cichlid	**0.42**	0.18	4.3	0.019	7.0	0.004
	post-bird	post-cichlid	**0.57**	0.20	5.0	0.013	4.4	0.018
Freezings	pre	post-bird	**0.83**	0.08	36.8	<0.001	4.7	0.015
	pre	post-cichlid	0.91	0.08	49.3	<0.001	0.6	0.220
	post-bird	post-cichlid	0.94	0.11	38.9	<0.001	-0.1	0.500
Shelter	pre	post-bird	0.92	0.10	33.4	<0.001	0.5	0.237
	pre	post-cichlid	**0.78**	0.09	32.0	<0.001	9.2	0.001
	post-bird	post-cichlid	0.94	0.14	25.3	<0.001	-0.4	0.500
Tracklength	pre	post-bird	**0.74**	0.10	25.6	<0.001	7.3	0.003
	pre	post-cichlid	**0.69**	0.11	22.0	<0.001	11.5	<0.001
	post-bird	post-cichlid	0.85	0.13	21.4	<0.001	1.4	0.115

Table 5: Difference (**D**) variance-covariance matrices for comparisons of (a) $\mathbf{I}_{\mathbf{pre}}$ to $\mathbf{I}_{\mathbf{post\text{-}bird}}$; (b) pre-predator to post-cichlid reveal; (c) post-bird strike to post-cichlid reveal. Differences in variances appear on the diagonals, and differences in covariances off-diagonal; 95% confidence intervals are taken from differences across 5000 bootstrapped replicate pairs for each **D** matrix. Bold values indicate elements where 95% confidence intervals do not span zero.

(a)

	Area	Exposed	Freezings	Shelter	Tracklength
Area	-0.10 (-0.20,0.02)				
Exposed	0.01 (-0.09,0.11)	0.13 (-0.04,0.30)			
Freezings	0.06 (-0.03,0.15)	0.05 (-0.09,0.19)	-0.06 (-0.20,0.08)		
Shelter	0.02 (-0.08,0.11)	-0.06 (-0.20,0.06)	0.01 (-0.11,0.12)	0.00 (-0.13,0.13)	
Tracklength	-0.05 (-0.14,0.04)	0.02 (-0.08,0.11)	0.05 (-0.04,0.14)	0.01 (-0.08,0.10)	-0.08 (-0.18,0.03)

(b)

	Area	Exposed	Freezings	Shelter	Tracklength
Area	0.06 (-0.08,0.21)				
Exposed	0.01 (-0.07,0.10)	-0.09 (-0.18,0.00)			
Freezings	0.06 (-0.05,0.17)	-0.09 (-0.19,0.01)	0.05 (-0.12,0.23)		
Shelter	-0.03 (-0.14,0.07)	0.04 (-0.04,0.13)	-0.04 (-0.16,0.08)	0.01 (-0.12,0.14)	
Tracklength	0.03 (-0.09,0.13)	0.06 (-0.01,0.14)	0.03 (-0.08,0.13)	0.01 (-0.09,0.10)	-0.02 (-0.15,0.10)

(c)

	Area	Exposed	Freezings	Shelter	Tracklength
Area	**0.16 (0.03,0.30)**				
Exposed	0.00 (-0.10,0.10)	**-0.22 (-0.39,-0.06)**			
Freezings	0.00 (-0.12,0.11)	**-0.15 (-0.28,-0.02)**	0.10 (-0.08,0.27)		
Shelter	-0.05 (-0.17,0.06)	0.10 (-0.03,0.23)	-0.05 (-0.19,0.09)	0.01 (-0.15,0.16)	
Tracklength	0.08 (-0.03,0.18)	0.05 (-0.04,0.14)	-0.02 (-0.12,0.09)	-0.01 (-0.11,0.11)	0.05 (-0.06,0.18)

Supporting Information

Figure S1: Tank configurations for (a) bird strike, and (b) cichlid reveal assays.

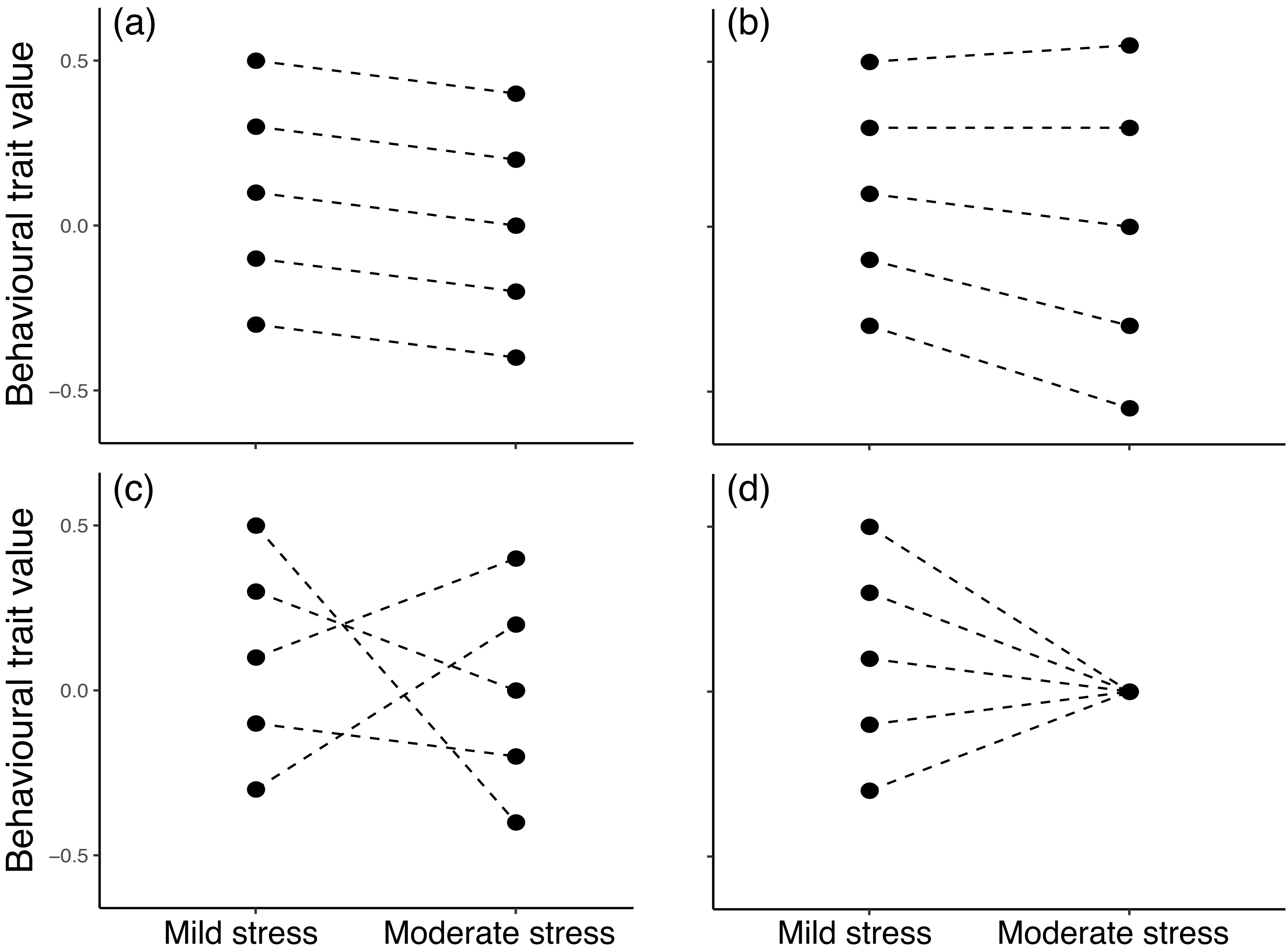
Figure S2: Trait loadings on the first two eigenvectors from $\mathbf{I}_{all}$ (the $\mathbf{I}$ matrix for behavioural variation pooled across all contexts and assay types).

Table S1: Conditional Wald *F*-tests for fixed effects in multivariate mixed-effects models.

Table S2: Fixed effects summaries from multivariate mixed-effects models.

Table S3: Effects of 'stage' (pre- to post-) in the control group, where no predator stimulus was applied.

Appendix S1: Annotated R code for multivariate mixed effects-models and the parametric bootstrapping procedure used.


(a)
(b)
(c)
(d)
Behavioural trait value
Behavioural trait value
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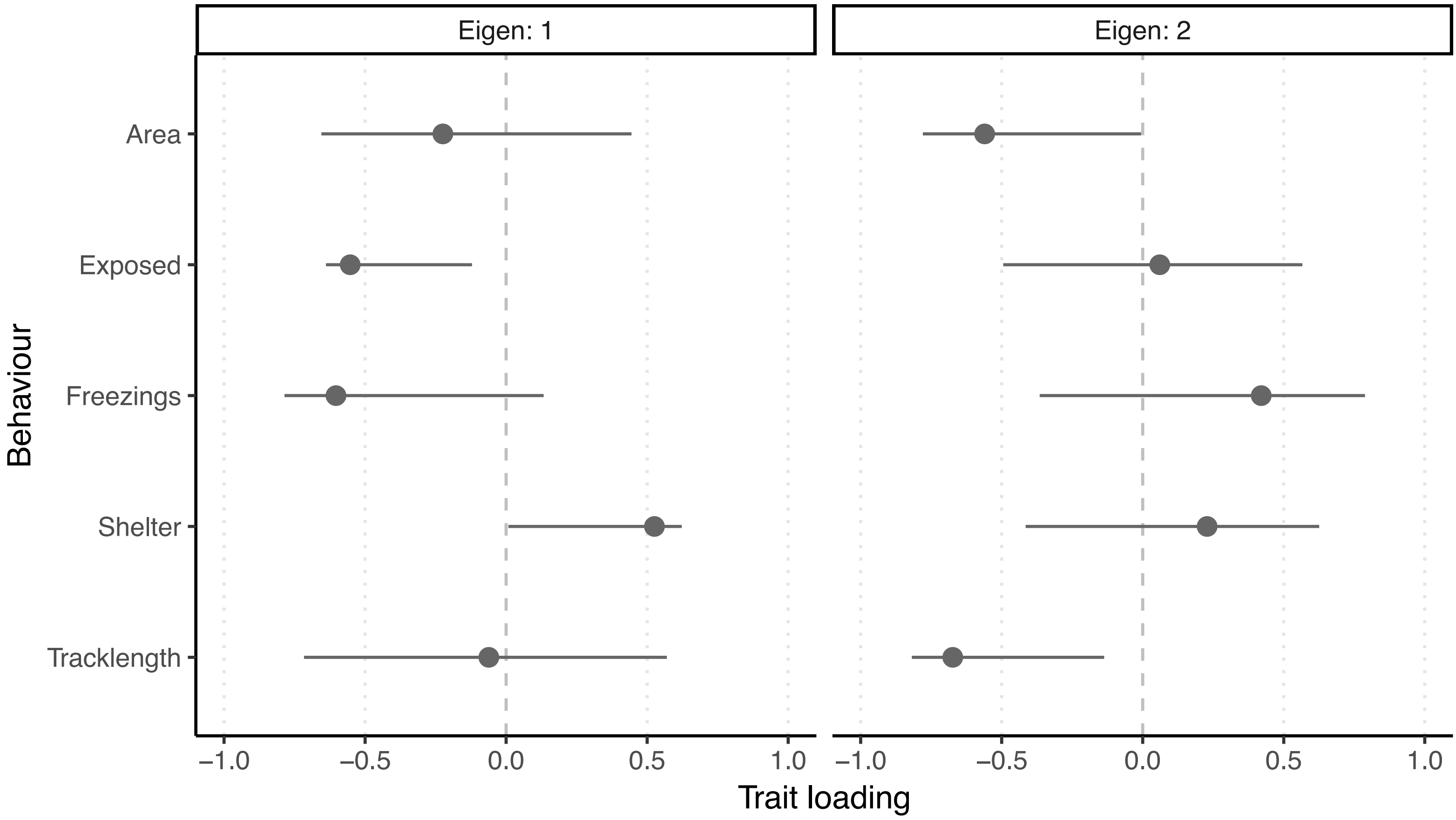
0.0
−0.5
0.5
0.0
−0.5
Mild stress
Moderate stress
Mild stress
Moderate stress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Eigen: 2
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Exposed
Freezings
Shelter
Tracklength
Behaviour
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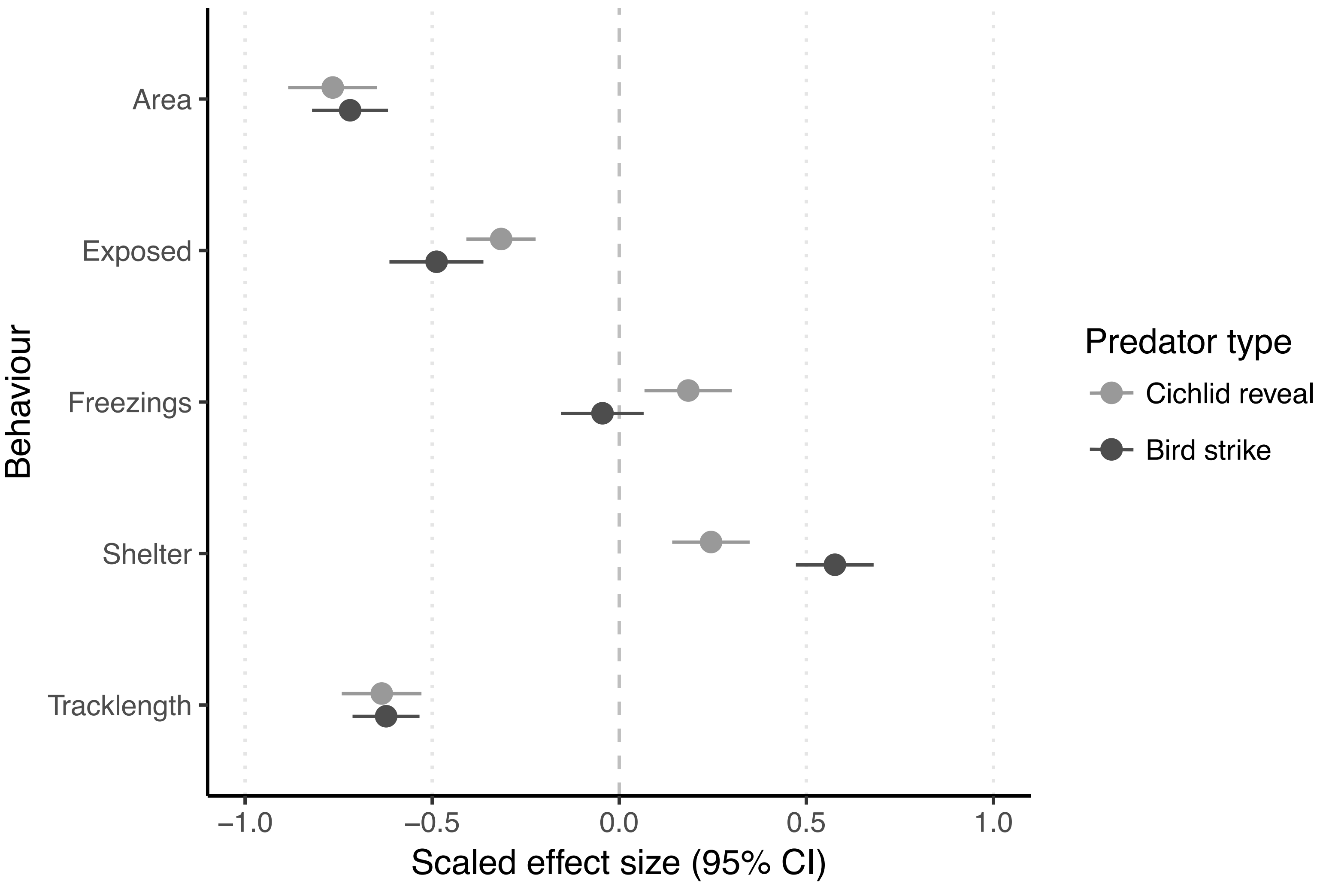
−0.5
0.0
0.5
1.0
Trait loading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Exposed
Freezings
Shelter
Tracklength
Behaviour
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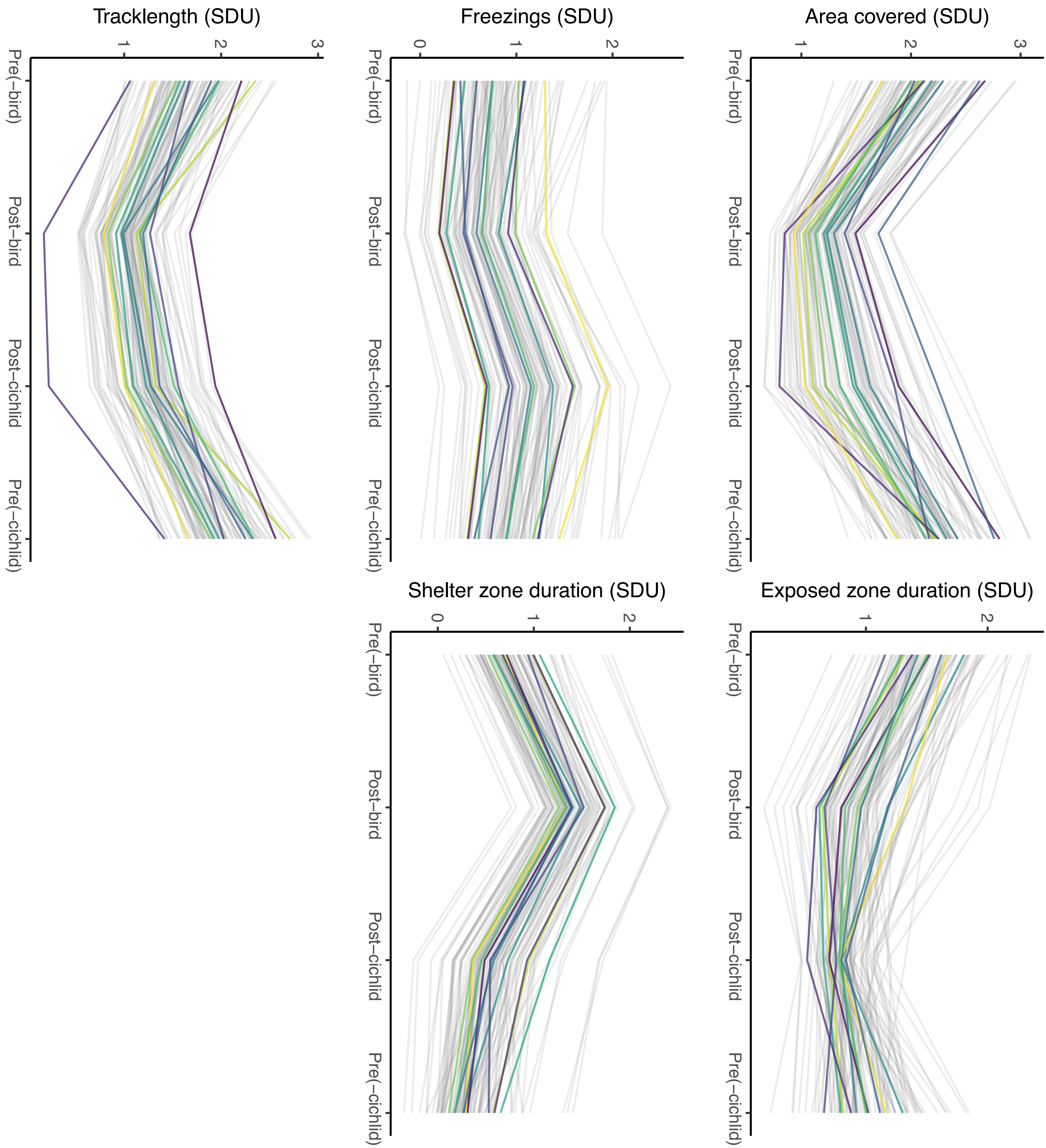
0.0
0.5
1.0
Scaled effect size (95% CI)
Predator type
Cichlid reveal
Bird strike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Exposed zone duration (SDU)
Freezings (SDU)
Shelter zone duration (SDU)
Tracklength (SDU)
Pre(−bird)
Post−bird
Post−cichlid
Pre(−cichlid)
0
1
2
3

Title: Testing the stability of behavioural coping style across stress contexts in the Trinidadian guppy

Running headline: Cross-context stability of coping styles

Key words: Coping styles, animal personality, individual plasticity, individual by environment interactions, behavioural syndromes, multi-response model, individual differences, *Poecilia reticulata.*

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Supporting Information

Contents

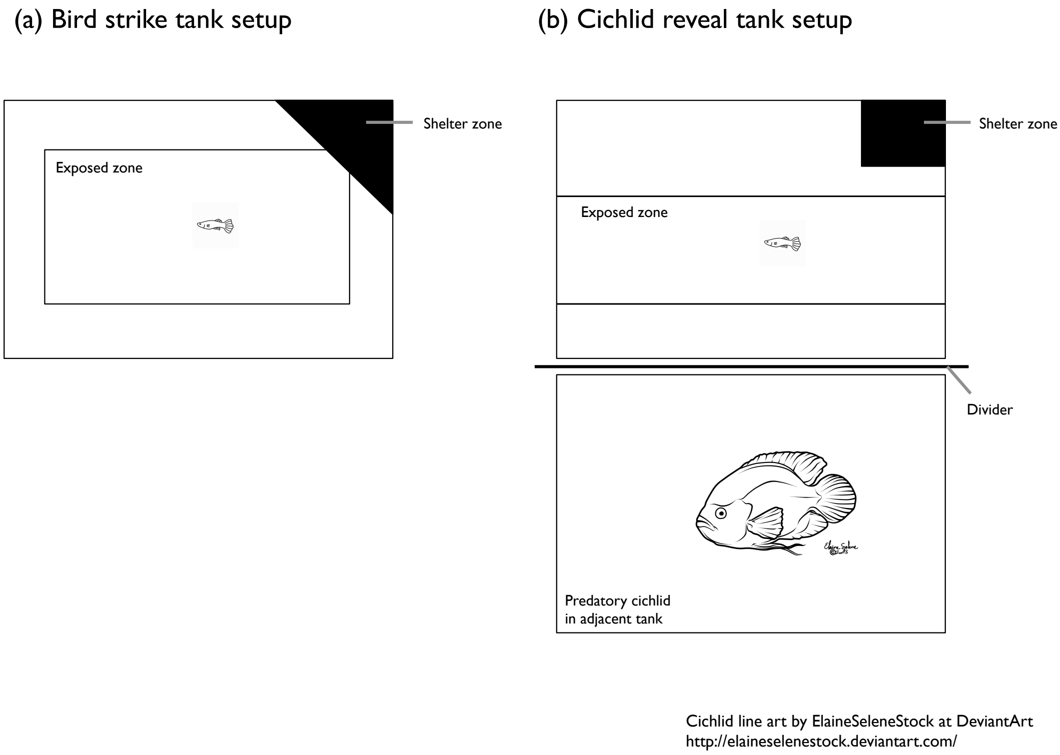

Figure S1: Tank configurations for (a) bird strike, and (b) cichlid reveal assays.

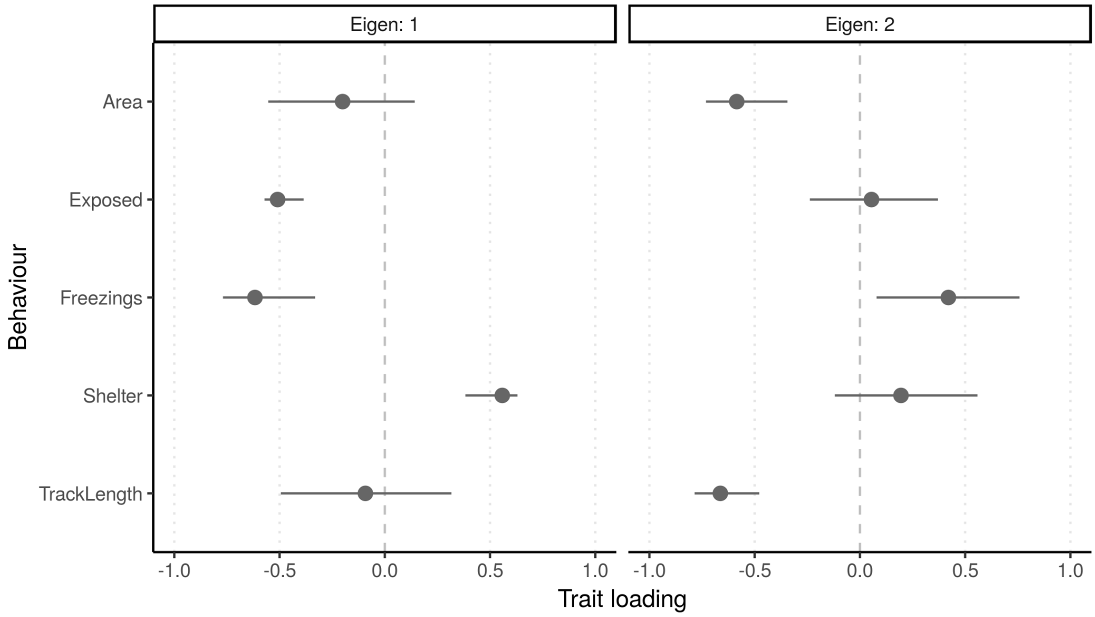

Figure S2: Trait loadings on the first two eigenvectors from $\mathbf{I}_{all}$ (the **I** matrix for behavioural variation pooled across all contexts and assay types).

Table S1: Conditional Wald *F*-tests for fixed effects in multivariate mixed-effects models.

Context	Parameter	df	F	P
Pooled pre	trait	5,82.3	4910	<0.001
	trait:Assay	5,703.5	60.3	<0.001
	trait:Sex (Male)	5,97.1	11.9	<0.001
	trait:Replicate	5,715.0	7.5	<0.001
	trait:Order	5,742.8	2.5	0.03
	trait:Time	5,778.4	0.8	0.52
	trait:Block	10,179.5	7.8	<0.001
	trait:Tank	70,263.8	1.1	0.25
Post-bird	trait	5,82.4	3039	<0.001
	trait:Sex (Male)	5,122.8	10.2	<0.001
	trait:Replicate	5,304.5	4.5	<0.001
	trait:Order	5,378.4	1.8	0.11
	trait:Time	5,351.1	0.08	0.99
	trait:Block	10,189.8	2.4	0.01
	trait:Tank	70,276.5	0.91	0.68
Post-fish	trait	5,81.8	925.7	<0.001
	trait:Sex (Male)	5,88.9	11.8	<0.001
	trait:Replicate	5,303.4	7.9	<0.001
	trait:Order	5,365.3	1.9	0.09
	trait:Time	5,373.0	1.5	0.2
	trait:Block	10,167.0	6.6	<0.001
	trait:Tank	70,267.5	1.1	0.28

Table S2: Fixed effects estimates, standard errors and z-ratios from multivariate mixed models for observations at: (a) pooled pre-stimulus; (b) post-bird strike; (c) post-cichlid reveal; (d) all stages and configurations. These values are taken from models corresponding to 1D, 2D, 3D, and the full unstructured model.

(a)

	solution	std error	z ratio
trait_Area:Block_Tank_GRIM_1_Q10b	0	NA	NA
trait_Area:Block_Tank_GRIM_1_Q11a	-0.261291754	0.275812438	-0.94735305
trait_Area:Block_Tank_GRIM_1_Q12b	-0.594794205	0.283453371	-2.098384655
trait_Area:Block_Tank_GRIM_1_Q9a	-0.035571016	0.284646973	-0.124965376
trait_Area:Block_Tank_GRIM_2_R10a	0	NA	NA
trait_Area:Block_Tank_GRIM_2_R11a	-0.022549669	0.296814403	-0.075972287
trait_Area:Block_Tank_GRIM_2_R12a	-0.197067157	0.309401073	-0.63693107
trait_Area:Block_Tank_GRIM_2_R9a	0.576791343	0.311745817	1.850197537
trait_Area:Block_Tank_SMV_1	0	NA	NA
trait_Area:Block_Tank_SMV_2	0.370487114	0.319778461	1.158574322
trait_Area:Block_Tank_SMV_3	0.387965377	0.360392976	1.07650649
trait_Area:Block_Tank_SMV_4	0.129653696	0.355944521	0.364252539
trait_Area:Block_Tank_SMV_5	0.26405794	0.332018204	0.795311633
trait_Area:Block_Tank_SMV_6	0.117834258	0.360264016	0.327077512
trait_Area:Block_Tank_TMH_P10a	0	NA	NA
trait_Area:Block_Tank_TMH_P10b	0.068429208	0.317754286	0.215352589
trait_Area:Block_Tank_TMH_P9a	0.083906114	0.332463853	0.252376653
trait_Area:Block_Tank_TMH_P9b	0.109357246	0.307701194	0.355400785
trait_Exposed:Block_Tank_GRIM_1_Q10b	0	NA	NA
trait_Exposed:Block_Tank_GRIM_1_Q11a	-0.267134621	0.259654703	-1.028807172
trait_Exposed:Block_Tank_GRIM_1_Q12b	-0.733354927	0.266725397	-2.74947544
trait_Exposed:Block_Tank_GRIM_1_Q9a	-0.307379293	0.267963115	-1.147095536
trait_Exposed:Block_Tank_GRIM_2_R10a	0	NA	NA
trait_Exposed:Block_Tank_GRIM_2_R11a	0.695118118	0.27944738	2.487474091
trait_Exposed:Block_Tank_GRIM_2_R12a	0.089780452	0.291349139	0.308154172
trait_Exposed:Block_Tank_GRIM_2_R9a	0.546524321	0.293792779	1.860237418
trait_Exposed:Block_Tank_SMV_1	0	NA	NA
trait_Exposed:Block_Tank_SMV_2	-0.1227487	0.300876141	-0.407970866
trait_Exposed:Block_Tank_SMV_3	-0.363576803	0.3395619	-1.070723198
trait_Exposed:Block_Tank_SMV_4	0.054766928	0.335000276	0.163483231
trait_Exposed:Block_Tank_SMV_5	-0.146656695	0.312199984	-0.469752409
trait_Exposed:Block_Tank_SMV_6	0.082006204	0.339452509	0.241583731
trait_Exposed:Block_Tank_TMH_P10a	0	NA	NA
trait_Exposed:Block_Tank_TMH_P10b	-0.205667701	0.298779634	-0.688359169
trait_Exposed:Block_Tank_TMH_P9a	-0.129831421	0.312675405	-0.415227481
trait_Exposed:Block_Tank_TMH_P9b	0.137628566	0.28937012	0.475614297
trait_Freezings:Block_Tank_GRIM_1_Q10b	0	NA	NA
trait_Freezings:Block_Tank_GRIM_1_Q11a	-0.025380374	0.294782562	-0.086098628

trait_Freezings:Block_Tank_GRIM_1_Q12b	-0.56535985	0.303296964	-1.864047179
trait_Freezings:Block_Tank_GRIM_1_Q9a	-0.229269629	0.304276399	-0.753491329
trait_Freezings:Block_Tank_GRIM_2_R10a	0	NA	NA
trait_Freezings:Block_Tank_GRIM_2_R11a	0.318249257	0.317148827	1.003469759
trait_Freezings:Block_Tank_GRIM_2_R12a	-0.028986392	0.330265882	-0.087766837
trait_Freezings:Block_Tank_GRIM_2_R9a	-0.147905986	0.332191333	-0.445243363
trait_Freezings:Block_Tank_SMV_1	0	NA	NA
trait_Freezings:Block_Tank_SMV_2	-0.399253036	0.342487827	-1.165743727
trait_Freezings:Block_Tank_SMV_3	-0.493097965	0.384458168	-1.282578981
trait_Freezings:Block_Tank_SMV_4	-0.149904439	0.380803154	-0.393653354
trait_Freezings:Block_Tank_SMV_5	-0.186599038	0.356096916	-0.524011947
trait_Freezings:Block_Tank_SMV_6	0.372285223	0.384347401	0.96861647
trait_Freezings:Block_Tank_TMH_P10a	0	NA	NA
trait_Freezings:Block_Tank_TMH_P10b	-0.002047864	0.340831063	-0.006008443
trait_Freezings:Block_Tank_TMH_P9a	-0.065253938	0.35646069	-0.183060683
trait_Freezings:Block_Tank_TMH_P9b	0.259503843	0.329936699	0.786526154
trait_Shelter:Block_Tank_GRIM_1_Q10b	0	NA	NA
trait_Shelter:Block_Tank_GRIM_1_Q11a	0.316695378	0.237519838	1.333342852
trait_Shelter:Block_Tank_GRIM_1_Q12b	0.919750265	0.244376931	3.763654204
trait_Shelter:Block_Tank_GRIM_1_Q9a	0.166302743	0.245166393	0.678326018
trait_Shelter:Block_Tank_GRIM_2_R10a	0	NA	NA
trait_Shelter:Block_Tank_GRIM_2_R11a	-0.334468549	0.255544041	-1.308848945
trait_Shelter:Block_Tank_GRIM_2_R12a	-0.095069569	0.2661341	-0.357224305
trait_Shelter:Block_Tank_GRIM_2_R9a	-0.339406957	0.267682304	-1.267946933
trait_Shelter:Block_Tank_SMV_1	0	NA	NA
trait_Shelter:Block_Tank_SMV_2	-0.051756963	0.275928805	-0.187573613
trait_Shelter:Block_Tank_SMV_3	-0.091788544	0.309774828	-0.296307302
trait_Shelter:Block_Tank_SMV_4	0.245114563	0.306815841	0.798898003
trait_Shelter:Block_Tank_SMV_5	-0.018855119	0.286892578	-0.065721878
trait_Shelter:Block_Tank_SMV_6	0.260264511	0.309679358	0.84043222
trait_Shelter:Block_Tank_TMH_P10a	0	NA	NA
trait_Shelter:Block_Tank_TMH_P10b	0.187780846	0.274592229	0.68385346
trait_Shelter:Block_Tank_TMH_P9a	0.074925274	0.287182471	0.260897795
trait_Shelter:Block_Tank_TMH_P9b	-0.048616536	0.265815134	-0.182896041
trait_TrackLen:Block_Tank_GRIM_1_Q10b	0	NA	NA
trait_TrackLen:Block_Tank_GRIM_1_Q11a	-0.367429957	0.268844533	-1.366700497
trait_TrackLen:Block_Tank_GRIM_1_Q12b	-0.455054586	0.276616287	-1.645075171
trait_TrackLen:Block_Tank_GRIM_1_Q9a	-0.023609471	0.277500394	-0.085079055
trait_TrackLen:Block_Tank_GRIM_2_R10a	0	NA	NA
trait_TrackLen:Block_Tank_GRIM_2_R11a	-0.13189995	0.289243929	-0.456016312
trait_TrackLen:Block_Tank_GRIM_2_R12a	-0.246638879	0.301225372	-0.818785209
trait_TrackLen:Block_Tank_GRIM_2_R9a	0.20861597	0.302958134	0.688596696
trait_TrackLen:Block_Tank_SMV_1	0	NA	NA
trait_TrackLen:Block_Tank_SMV_2	0.541257548	0.312334263	1.732943236
trait_TrackLen:Block_Tank_SMV_3	0.752068447	0.350605139	2.14505825
trait_TrackLen:Block_Tank_SMV_4	-0.009159756	0.347287716	-0.026375123

trait_TrackLen:Block_Tank_SMV_5	0.264745161	0.324760487	0.815201269
trait_TrackLen:Block_Tank_SMV_6	-0.258557958	0.350496296	-0.737690985
trait_TrackLen:Block_Tank_TMH_P10a	0	NA	NA
trait_TrackLen:Block_Tank_TMH_P10b	-0.142886785	0.310837278	-0.459683556
trait_TrackLen:Block_Tank_TMH_P9a	0.088554459	0.32508415	0.272404727
trait_TrackLen:Block_Tank_TMH_P9b	-0.258208438	0.300898083	-0.858125898
trait_Area:Block_GRIM_1	0	NA	NA
trait_Area:Block_GRIM_2	-0.26086403	0.298540483	-0.873797841
trait_Area:Block_SMV	0	NA	NA
trait_Area:Block_TMH	0.441793878	0.349615483	1.263656501
trait_Exposed:Block_GRIM_1	0	NA	NA
trait_Exposed:Block_GRIM_2	-0.40513937	0.281144113	-1.441038069
trait_Exposed:Block_SMV	0	NA	NA
trait_Exposed:Block_TMH	-0.486000142	0.330709111	-1.46956986
trait_Freezings:Block_GRIM_1	0	NA	NA
trait_Freezings:Block_GRIM_2	0.026676874	0.318575939	0.083737881
trait_Freezings:Block_SMV	0	NA	NA
trait_Freezings:Block_TMH	-1.038667021	0.370560695	-2.802960582
trait_Shelter:Block_GRIM_1	0	NA	NA
trait_Shelter:Block_GRIM_2	0.114245573	0.256718281	0.445023128
trait_Shelter:Block_SMV	0	NA	NA
trait_Shelter:Block_TMH	-0.445004027	0.298474842	-1.490926417
trait_TrackLen:Block_GRIM_1	0	NA	NA
trait_TrackLen:Block_GRIM_2	0.005383185	0.290565975	0.018526549
trait_TrackLen:Block_SMV	0	NA	NA
trait_TrackLen:Block_TMH	1.399961366	0.337710862	4.145443704
trait_Area:scale(preTimeNum)	-0.030408546	0.051904549	-0.585855127
trait_Exposed:scale(preTimeNum)	0.000942463	0.051686102	0.018234363
trait_Freezings:scale(preTimeNum)	0.014968137	0.048586917	0.308069286
trait_Shelter:scale(preTimeNum)	0.063562343	0.039027172	1.628668958
trait_TrackLen:scale(preTimeNum)	-0.072099017	0.04390274	-1.642244133
trait_Area:scale(Order, scale = FALSE)	-0.017683917	0.016537342	-1.069332454
trait_Exposed:scale(Order, scale = FALSE)	-0.049057679	0.016189711	-3.030176273
trait_Freezings:scale(Order, scale = FALSE)	-0.028913464	0.015500936	-1.865272146
trait_Shelter:scale(Order, scale = FALSE)	0.007047184	0.012537977	0.562067092
trait_TrackLen:scale(Order, scale = FALSE)	0.015822409	0.014129299	1.119829768
trait_Area:scale(Replicate, scale = FALSE)	0.016234624	0.027564572	0.588967029
trait_Exposed:scale(Replicate, scale = FALSE)	0.12392161	0.027420989	4.519224587
trait_Freezings:scale(Replicate, scale = FALSE)	0.104656808	0.025805816	4.05555116
trait_Shelter:scale(Replicate, scale = FALSE)	-0.041152008	0.020737065	-1.984466409
trait_TrackLen:scale(Replicate, scale = FALSE)	-0.073747902	0.023330253	-3.161041632
trait_Area:SexM	-0.594997131	0.323562187	-1.838895751
trait_Exposed:SexM	0.437992922	0.305878031	1.431920168
trait_Freezings:SexM	0.494136448	0.342989529	1.440675025
trait_Shelter:SexM	-0.007941277	0.276313573	-0.028740089
trait_TrackLen:SexM	-0.613189234	0.312650072	-1.96126369

trait_Area:Assay_Bird	0	NA	NA
trait_Area:Assay_Fish	0.129535488	0.060525499	2.140180415
trait_Exposed:Assay_Bird	0	NA	NA
trait_Exposed:Assay_Fish	-0.509592218	0.060287881	-8.45264765
trait_Freezings:Assay_Bird	0	NA	NA
trait_Freezings:Assay_Fish	0.142913633	0.056656207	2.522470892
trait_Shelter:Assay_Bird	0	NA	NA
trait_Shelter:Assay_Fish	-0.405937012	0.045503333	-8.921039053
trait_TrackLen:Assay_Bird	0	NA	NA
trait_TrackLen:Assay_Fish	0.350720464	0.051186412	6.851827481
trait_Area	2.052341031	0.20523178	10.00011321
trait_Exposed	1.459497782	0.193547908	7.540757225
trait_Freezings	0.792955002	0.218413891	3.630515438
trait_Shelter	0.764275323	0.175992156	4.342666962
trait_TrackLen	1.596969926	0.19917387	8.017969062

(b)

	solution	std error	z ratio
trait_Area:Block_Tank_GRIM_1_Q10b	0	NA	NA
trait_Area:Block_Tank_GRIM_1_Q11a	-0.558058828	0.260180825	-2.144888379
trait_Area:Block_Tank_GRIM_1_Q12b	-0.520926375	0.254139382	-2.049766433
trait_Area:Block_Tank_GRIM_1_Q9a	-0.019016556	0.265584174	-0.071602744
trait_Area:Block_Tank_GRIM_2_R10a	0	NA	NA
trait_Area:Block_Tank_GRIM_2_R11a	-0.043537765	0.270638231	-0.160870714
trait_Area:Block_Tank_GRIM_2_R12a	-0.289622216	0.278457264	-1.040095747
trait_Area:Block_Tank_GRIM_2_R9a	0.337722555	0.286987983	1.176782912
trait_Area:Block_Tank_SMV_1	0	NA	NA
trait_Area:Block_Tank_SMV_2	-0.018882291	0.293153496	-0.064410936
trait_Area:Block_Tank_SMV_3	0.018563459	0.332035224	0.055908101
trait_Area:Block_Tank_SMV_4	-0.272375187	0.32411146	-0.840375058
trait_Area:Block_Tank_SMV_5	-0.124640108	0.298249309	-0.417905774
trait_Area:Block_Tank_SMV_6	-0.35152807	0.331333105	-1.06095064
trait_Area:Block_Tank_TMH_P10a	0	NA	NA
trait_Area:Block_Tank_TMH_P10b	-0.437657745	0.287342592	-1.52312173
trait_Area:Block_Tank_TMH_P9a	-0.169425063	0.303241478	-0.558713352
trait_Area:Block_Tank_TMH_P9b	-0.043696247	0.278374483	-0.156969298
trait_Exposed:Block_Tank_GRIM_1_Q10b	0	NA	NA
trait_Exposed:Block_Tank_GRIM_1_Q11a	-0.400328427	0.381292659	-1.049924297
trait_Exposed:Block_Tank_GRIM_1_Q12b	-0.703547771	0.378618719	-1.858195952
trait_Exposed:Block_Tank_GRIM_1_Q9a	-0.307996461	0.390511088	-0.788700937
trait_Exposed:Block_Tank_GRIM_2_R10a	0	NA	NA
trait_Exposed:Block_Tank_GRIM_2_R11a	0.668400586	0.400431721	1.669199895
trait_Exposed:Block_Tank_GRIM_2_R12a	-0.009514311	0.413136734	-0.023029449
trait_Exposed:Block_Tank_GRIM_2_R9a	0.36093216	0.422082662	0.855121976
trait_Exposed:Block_Tank_SMV_1	0	NA	NA

trait_Exposed:Block_Tank_SMV_2	-0.332002179	0.434336984	-0.764388461
trait_Exposed:Block_Tank_SMV_3	-0.411169412	0.489308025	-0.840307926
trait_Exposed:Block_Tank_SMV_4	-0.103232596	0.480513391	-0.214838124
trait_Exposed:Block_Tank_SMV_5	-0.001460196	0.445397518	-0.00327841
trait_Exposed:Block_Tank_SMV_6	0.314957962	0.488592098	0.644623528
trait_Exposed:Block_Tank_TMH_P10a	0	NA	NA
trait_Exposed:Block_Tank_TMH_P10b	-0.250786673	0.428215265	-0.585655611
trait_Exposed:Block_Tank_TMH_P9a	-0.074083087	0.450480116	-0.164453622
trait_Exposed:Block_Tank_TMH_P9b	0.471974404	0.414625478	1.138315006
trait_Freezings:Block_Tank_GRIM_1_Q10b	0	NA	NA
trait_Freezings:Block_Tank_GRIM_1_Q11a	-0.24909158	0.321224782	-0.775443222
trait_Freezings:Block_Tank_GRIM_1_Q12b	-0.537759046	0.317287919	-1.694861399
trait_Freezings:Block_Tank_GRIM_1_Q9a	-0.127560379	0.328637187	-0.388149559
trait_Freezings:Block_Tank_GRIM_2_R10a	0	NA	NA
trait_Freezings:Block_Tank_GRIM_2_R11a	0.438291927	0.336303463	1.303263201
trait_Freezings:Block_Tank_GRIM_2_R12a	0.04387408	0.346642385	0.12656871
trait_Freezings:Block_Tank_GRIM_2_R9a	0.176421885	0.355128945	0.496782611
trait_Freezings:Block_Tank_SMV_1	0	NA	NA
trait_Freezings:Block_Tank_SMV_2	-0.391205836	0.364630277	-1.072883576
trait_Freezings:Block_Tank_SMV_3	-0.413039416	0.411322766	-1.004173485
trait_Freezings:Block_Tank_SMV_4	-0.110772457	0.403310694	-0.274657871
trait_Freezings:Block_Tank_SMV_5	0.30277586	0.372989031	0.811755401
trait_Freezings:Block_Tank_SMV_6	0.111092874	0.410626513	0.270544816
trait_Freezings:Block_Tank_TMH_P10a	0	NA	NA
trait_Freezings:Block_Tank_TMH_P10b	-0.233656532	0.358856796	-0.651113577
trait_Freezings:Block_Tank_TMH_P9a	-0.28442918	0.377897086	-0.752663067
trait_Freezings:Block_Tank_TMH_P9b	0.238853734	0.347524545	0.687300327
trait_Shelter:Block_Tank_GRIM_1_Q10b	0	NA	NA
trait_Shelter:Block_Tank_GRIM_1_Q11a	0.743798752	0.326979519	2.274756395
trait_Shelter:Block_Tank_GRIM_1_Q12b	1.080357881	0.321029329	3.365293402
trait_Shelter:Block_Tank_GRIM_1_Q9a	0.219316284	0.334115606	0.65640838
trait_Shelter:Block_Tank_GRIM_2_R10a	0	NA	NA
trait_Shelter:Block_Tank_GRIM_2_R11a	-0.339039105	0.341130167	-0.993870195
trait_Shelter:Block_Tank_GRIM_2_R12a	-0.203667779	0.351268533	-0.579806501
trait_Shelter:Block_Tank_GRIM_2_R9a	-0.449366345	0.361029645	-1.244679906
trait_Shelter:Block_Tank_SMV_1	0	NA	NA
trait_Shelter:Block_Tank_SMV_2	0.486925531	0.369676135	1.317167881
trait_Shelter:Block_Tank_SMV_3	0.410938895	0.417877579	0.983395415
trait_Shelter:Block_Tank_SMV_4	0.401935664	0.408796138	0.98321786
trait_Shelter:Block_Tank_SMV_5	-0.038484692	0.377051566	-0.102067451
trait_Shelter:Block_Tank_SMV_6	0.337390648	0.417072137	0.808950343
trait_Shelter:Block_Tank_TMH_P10a	0	NA	NA
trait_Shelter:Block_Tank_TMH_P10b	0.54889126	0.363038521	1.51193669
trait_Shelter:Block_Tank_TMH_P9a	0.454010252	0.382744581	1.186196421
trait_Shelter:Block_Tank_TMH_P9b	-0.029622783	0.351644988	-0.084240596
trait_TrackLen:Block_Tank_GRIM_1_Q10b	0	NA	NA

trait_TrackLen:Block_Tank_GRIM_1_Q11a	-0.619883377	0.258790557	-2.395309098
trait_TrackLen:Block_Tank_GRIM_1_Q12b	-0.515497835	0.255974855	-2.013861229
trait_TrackLen:Block_Tank_GRIM_1_Q9a	-0.078907167	0.264836074	-0.297947202
trait_TrackLen:Block_Tank_GRIM_2_R10a	0	NA	NA
trait_TrackLen:Block_Tank_GRIM_2_R11a	-0.094187579	0.271160718	-0.347349644
trait_TrackLen:Block_Tank_GRIM_2_R12a	-0.048752248	0.279577763	-0.17437813
trait_TrackLen:Block_Tank_GRIM_2_R9a	0.274697009	0.286222073	0.959733839
trait_TrackLen:Block_Tank_SMV_1	0	NA	NA
trait_TrackLen:Block_Tank_SMV_2	-0.069336569	0.29402745	-0.235816654
trait_TrackLen:Block_Tank_SMV_3	-0.016895188	0.331632198	-0.050945561
trait_TrackLen:Block_Tank_SMV_4	-0.271561486	0.325236956	-0.834965033
trait_TrackLen:Block_Tank_SMV_5	-0.103863684	0.300958121	-0.345110088
trait_TrackLen:Block_Tank_SMV_6	-0.41105915	0.331094201	-1.241517215
trait_TrackLen:Block_Tank_TMH_P10a	0	NA	NA
trait_TrackLen:Block_Tank_TMH_P10b	-0.481010271	0.289492596	-1.661563293
trait_TrackLen:Block_Tank_TMH_P9a	-0.43916702	0.30477107	-1.440973449
trait_TrackLen:Block_Tank_TMH_P9b	-0.286588544	0.280340241	-1.022288283
trait_Area:Block_GRIM_1	0	NA	NA
trait_Area:Block_GRIM_2	-0.283839133	0.268566105	-1.056868783
trait_Area:Block_SMV	0	NA	NA
trait_Area:Block_TMH	0.608358743	0.360038478	1.689704797
trait_Exposed:Block_GRIM_1	0	NA	NA
trait_Exposed:Block_GRIM_2	-0.262895283	0.398398049	-0.659880951
trait_Exposed:Block_SMV	0	NA	NA
trait_Exposed:Block_TMH	-0.026904142	0.510843701	-0.052666093
trait_Freezings:Block_GRIM_1	0	NA	NA
trait_Freezings:Block_GRIM_2	-0.065391413	0.334278499	-0.195619559
trait_Freezings:Block_SMV	0	NA	NA
trait_Freezings:Block_TMH	-0.062705328	0.435036914	-0.144137948
trait_Shelter:Block_GRIM_1	0	NA	NA
trait_Shelter:Block_GRIM_2	0.467341257	0.33876278	1.379553143
trait_Shelter:Block_SMV	0	NA	NA
trait_Shelter:Block_TMH	-0.777593933	0.448101698	-1.735306821
trait_TrackLen:Block_GRIM_1	0	NA	NA
trait_TrackLen:Block_GRIM_2	-0.317189993	0.26961137	-1.176471129
trait_TrackLen:Block_SMV	0	NA	NA
trait_TrackLen:Block_TMH	1.139021275	0.349492683	3.259070452
trait_Area:scale(preTimeNum)	0.01535016	0.107023724	0.143427642
trait_Exposed:scale(preTimeNum)	0.001692853	0.132789025	0.012748438
trait_Freezings:scale(preTimeNum)	-0.009086295	0.118830619	-0.076464254
trait_Shelter:scale(preTimeNum)	0.001832597	0.128490489	0.014262511
trait_TrackLen:scale(preTimeNum)	-0.022357865	0.094302624	-0.237086348
trait_Area:scale(Order, scale = FALSE)	0.005736583	0.020111297	0.285241826
trait_Exposed:scale(Order, scale = FALSE)	-0.046456438	0.025465755	-1.82427099
trait_Freezings:scale(Order, scale = FALSE)	-0.011155984	0.0224677	-0.496534316
trait_Shelter:scale(Order, scale = FALSE)	0.016620899	0.024165841	0.68778483

trait_TrackLen:scale(Order, scale = FALSE)	0.014926214	0.017948563	0.8316105
trait_Area:scale(Replicate, scale = FALSE)	-0.029996607	0.033191212	-0.903751508
trait_Exposed:scale(Replicate, scale = FALSE)	0.038839129	0.041174999	0.943269708
trait_Freezings:scale(Replicate, scale = FALSE)	0.12969127	0.036855107	3.518949806
trait_Shelter:scale(Replicate, scale = FALSE)	-0.069288669	0.039851624	-1.738666149
trait_TrackLen:scale(Replicate, scale = FALSE)	-0.047295152	0.02924357	-1.61728377
trait_Area:SexM	0.020535053	0.347652764	0.059067712
trait_Exposed:SexM	0.380983184	0.488676438	0.779622578
trait_Freezings:SexM	0.284126434	0.417453952	0.680617426
trait_Shelter:SexM	-0.142755581	0.431474513	-0.330855187
trait_TrackLen:SexM	-0.19167768	0.335115192	-0.571975501
trait_Area	1.175443146	0.194025363	6.058193243
trait_Exposed	0.86995043	0.282751832	3.076727824
trait_Freezings	0.638552221	0.238623021	2.6759875
trait_Shelter	1.266464511	0.243403128	5.203156266
trait_TrackLen	1.052989007	0.192164941	5.479610384

(c)

	solution	std error	z ratio
trait_Area:Block_Tank_GRIM_1_Q10b	0	NA	NA
trait_Area:Block_Tank_GRIM_1_Q11a	-0.382994011	0.326343262	-1.173592516
trait_Area:Block_Tank_GRIM_1_Q12b	-0.489551559	0.337161283	-1.451980355
trait_Area:Block_Tank_GRIM_1_Q9a	0.108506337	0.336857696	0.322113279
trait_Area:Block_Tank_GRIM_2_R10a	0	NA	NA
trait_Area:Block_Tank_GRIM_2_R11a	-0.209452297	0.352587403	-0.59404362
trait_Area:Block_Tank_GRIM_2_R12a	-0.144365097	0.369848112	-0.390336173
trait_Area:Block_Tank_GRIM_2_R9a	0.712791471	0.372406963	1.914012199
trait_Area:Block_Tank_SMV_1	0	NA	NA
trait_Area:Block_Tank_SMV_2	-0.25138173	0.384531689	-0.653734755
trait_Area:Block_Tank_SMV_3	0.2977268	0.425998747	0.698891259
trait_Area:Block_Tank_SMV_4	-0.442395875	0.429109202	-1.030963385
trait_Area:Block_Tank_SMV_5	0.116759305	0.392164241	0.297730627
trait_Area:Block_Tank_SMV_6	0.116216965	0.425058648	0.273413952
trait_Area:Block_Tank_TMH_P10a	0	NA	NA
trait_Area:Block_Tank_TMH_P10b	-0.351563228	0.375513814	-0.936219161
trait_Area:Block_Tank_TMH_P9a	-0.163707173	0.39236372	-0.417233207
trait_Area:Block_Tank_TMH_P9b	-0.139765755	0.363667944	-0.384322449
trait_Exposed:Block_Tank_GRIM_1_Q10b	0	NA	NA
trait_Exposed:Block_Tank_GRIM_1_Q11a	-0.290884357	0.21410366	-1.358614592
trait_Exposed:Block_Tank_GRIM_1_Q12b	-0.575470682	0.221395358	-2.599289735
trait_Exposed:Block_Tank_GRIM_1_Q9a	-0.18307461	0.220964048	-0.828526683
trait_Exposed:Block_Tank_GRIM_2_R10a	0	NA	NA
trait_Exposed:Block_Tank_GRIM_2_R11a	-0.083556607	0.231935917	-0.360257299
trait_Exposed:Block_Tank_GRIM_2_R12a	0.275319936	0.244492694	1.126086557
trait_Exposed:Block_Tank_GRIM_2_R9a	0.316981967	0.247247188	1.28204478

trait_Exposed:Block_Tank_SMV_1	0	NA	NA
trait_Exposed:Block_Tank_SMV_2	-0.176314391	0.25412805	-0.69380138
trait_Exposed:Block_Tank_SMV_3	-0.103625951	0.280621472	-0.369273065
trait_Exposed:Block_Tank_SMV_4	-0.280369085	0.284309674	-0.986139802
trait_Exposed:Block_Tank_SMV_5	-0.035892086	0.255169385	-0.140659846
trait_Exposed:Block_Tank_SMV_6	0.123160661	0.280069593	0.439750206
trait_Exposed:Block_Tank_TMH_P10a	0	NA	NA
trait_Exposed:Block_Tank_TMH_P10b	0.232107641	0.244351884	0.949890941
trait_Exposed:Block_Tank_TMH_P9a	0.148247919	0.255385998	0.580485698
trait_Exposed:Block_Tank_TMH_P9b	-0.101369614	0.236843717	-0.428002123
trait_Freezings:Block_Tank_GRIM_1_Q10b	0	NA	NA
trait_Freezings:Block_Tank_GRIM_1_Q11a	-0.400117315	0.361477211	-1.106894993
trait_Freezings:Block_Tank_GRIM_1_Q12b	-0.724305746	0.373509401	-1.939190136
trait_Freezings:Block_Tank_GRIM_1_Q9a	0.17083584	0.373112896	0.457866351
trait_Freezings:Block_Tank_GRIM_2_R10a	0	NA	NA
trait_Freezings:Block_Tank_GRIM_2_R11a	0.016963716	0.390712428	0.043417396
trait_Freezings:Block_Tank_GRIM_2_R12a	0.07738651	0.410167316	0.188670592
trait_Freezings:Block_Tank_GRIM_2_R9a	0.254843387	0.413290507	0.616620471
trait_Freezings:Block_Tank_SMV_1	0	NA	NA
trait_Freezings:Block_Tank_SMV_2	-0.155604726	0.426413739	-0.364914897
trait_Freezings:Block_Tank_SMV_3	-0.06584416	0.472167887	-0.139450738
trait_Freezings:Block_Tank_SMV_4	-0.126282287	0.476048781	-0.265271737
trait_Freezings:Block_Tank_SMV_5	0.143275872	0.433812306	0.33027157
trait_Freezings:Block_Tank_SMV_6	0.511534679	0.471137344	1.085744284
trait_Freezings:Block_Tank_TMH_P10a	0	NA	NA
trait_Freezings:Block_Tank_TMH_P10b	0.165225025	0.415397993	0.39775114
trait_Freezings:Block_Tank_TMH_P9a	-0.135610898	0.434055949	-0.31242723
trait_Freezings:Block_Tank_TMH_P9b	0.298109006	0.402347534	0.740924152
trait_Shelter:Block_Tank_GRIM_1_Q10b	0	NA	NA
trait_Shelter:Block_Tank_GRIM_1_Q11a	0.489350937	0.311162439	1.572654266
trait_Shelter:Block_Tank_GRIM_1_Q12b	0.747597511	0.321661116	2.324177444
trait_Shelter:Block_Tank_GRIM_1_Q9a	-0.078062071	0.321151933	-0.243068975
trait_Shelter:Block_Tank_GRIM_2_R10a	0	NA	NA
trait_Shelter:Block_Tank_GRIM_2_R11a	-0.484832995	0.336767927	-1.439664993
trait_Shelter:Block_Tank_GRIM_2_R12a	-0.126659394	0.35439551	-0.357395593
trait_Shelter:Block_Tank_GRIM_2_R9a	-0.549100434	0.357856937	-1.534413274
trait_Shelter:Block_Tank_SMV_1	0	NA	NA
trait_Shelter:Block_Tank_SMV_2	0.600369528	0.36839566	1.629686755
trait_Shelter:Block_Tank_SMV_3	-0.265103523	0.407259079	-0.650945643
trait_Shelter:Block_Tank_SMV_4	0.683963965	0.411788268	1.6609603
trait_Shelter:Block_Tank_SMV_5	0.444880941	0.371918427	1.196178811
trait_Shelter:Block_Tank_SMV_6	0.071405707	0.406423315	0.175692939
trait_Shelter:Block_Tank_TMH_P10a	0	NA	NA
trait_Shelter:Block_Tank_TMH_P10b	0.063200673	0.356143104	0.177458646
trait_Shelter:Block_Tank_TMH_P9a	-0.043243158	0.372189578	-0.116185839
trait_Shelter:Block_Tank_TMH_P9b	-0.053659817	0.345097295	-0.155491849

trait_TrackLen:Block_Tank_GRIM_1_Q10b	0	NA	NA
trait_TrackLen:Block_Tank_GRIM_1_Q11a	-0.304819365	0.297173211	-1.02572962
trait_TrackLen:Block_Tank_GRIM_1_Q12b	-0.391683183	0.307108896	-1.275388592
trait_TrackLen:Block_Tank_GRIM_1_Q9a	-0.049246794	0.306727997	-0.160555262
trait_TrackLen:Block_Tank_GRIM_2_R10a	0	NA	NA
trait_TrackLen:Block_Tank_GRIM_2_R11a	-0.227943077	0.321366652	-0.709292875
trait_TrackLen:Block_Tank_GRIM_2_R12a	-0.088515356	0.33768569	-0.262123504
trait_TrackLen:Block_Tank_GRIM_2_R9a	0.413771933	0.340525926	1.215096712
trait_TrackLen:Block_Tank_SMV_1	0	NA	NA
trait_TrackLen:Block_Tank_SMV_2	0.07172328	0.35100213	0.20433859
trait_TrackLen:Block_Tank_SMV_3	0.830134491	0.38846679	2.13695099
trait_TrackLen:Block_Tank_SMV_4	-0.391234986	0.392060998	-0.997893153
trait_TrackLen:Block_Tank_SMV_5	0.003481612	0.356085665	0.009777456
trait_TrackLen:Block_Tank_SMV_6	-0.317219727	0.387621625	-0.818374691
trait_TrackLen:Block_Tank_TMH_P10a	0	NA	NA
trait_TrackLen:Block_Tank_TMH_P10b	-0.048866502	0.340974914	-0.143314069
trait_TrackLen:Block_Tank_TMH_P9a	0.390314208	0.356307506	1.095442003
trait_TrackLen:Block_Tank_TMH_P9b	-0.182850463	0.330314318	-0.553565052
trait_Area:Block_GRIM_1	0	NA	NA
trait_Area:Block_GRIM_2	-0.393422092	0.356403577	-1.103866844
trait_Area:Block_SMV	0	NA	NA
trait_Area:Block_TMH	0.825952278	0.415794525	1.986443373
trait_Exposed:Block_GRIM_1	0	NA	NA
trait_Exposed:Block_GRIM_2	-0.35662529	0.235613498	-1.513602972
trait_Exposed:Block_SMV	0	NA	NA
trait_Exposed:Block_TMH	0.189149312	0.280866974	0.673448036
trait_Freezings:Block_GRIM_1	0	NA	NA
trait_Freezings:Block_GRIM_2	-0.086546509	0.395259161	-0.218961424
trait_Freezings:Block_SMV	0	NA	NA
trait_Freezings:Block_TMH	-0.348715359	0.462719199	-0.75362198
trait_Shelter:Block_GRIM_1	0	NA	NA
trait_Shelter:Block_GRIM_2	0.370258205	0.341520843	1.084145265
trait_Shelter:Block_SMV	0	NA	NA
trait_Shelter:Block_TMH	-0.38955457	0.404137475	-0.96391598
trait_TrackLen:Block_GRIM_1	0	NA	NA
trait_TrackLen:Block_GRIM_2	-0.145026413	0.325413551	-0.445668021
trait_TrackLen:Block_SMV	0	NA	NA
trait_TrackLen:Block_TMH	1.482151104	0.382417175	3.875744081
trait_Area:scale(preTimeNum)	0.009396772	0.059277476	0.158521805
trait_Exposed:scale(preTimeNum)	0.048782362	0.050345292	0.968955785
trait_Freezings:scale(preTimeNum)	-0.010781717	0.069061195	-0.156118316
trait_Shelter:scale(preTimeNum)	0.016690542	0.067831164	0.24606008
trait_TrackLen:scale(preTimeNum)	-0.109382543	0.059821361	-1.828486374
trait_Area:scale(Order, scale = FALSE)	0.007067797	0.021394606	0.330354162
trait_Exposed:scale(Order, scale = FALSE)	-0.006535431	0.017311058	-0.377529268
trait_Freezings:scale(Order, scale = FALSE)	-0.038900161	0.024665519	-1.577106954

trait_Shelter:scale(Order, scale = FALSE)	0.036241736	0.023609921	1.535021507
trait_TrackLen:scale(Order, scale = FALSE)	0.029923146	0.021172128	1.413327296
trait_Area:scale(Replicate, scale = FALSE)	-0.005105541	0.033940513	-0.150426148
trait_Exposed:scale(Replicate, scale = FALSE)	0.0703098	0.028798206	2.441464616
trait_Freezings:scale(Replicate, scale = FALSE)	0.213229851	0.039533576	5.393639275
trait_Shelter:scale(Replicate, scale = FALSE)	-0.075530574	0.038809628	-1.94618134
trait_TrackLen:scale(Replicate, scale = FALSE)	-0.093428349	0.034237535	-2.728828099
trait_Area:SexM	-0.58708839	0.3804024	-1.543335136
trait_Exposed:SexM	-0.315357566	0.254412273	-1.239553276
trait_Freezings:SexM	-0.203943488	0.422652627	-0.482532167
trait_Shelter:SexM	-0.034750514	0.367306643	-0.094608998
trait_TrackLen:SexM	-0.27830016	0.34868365	-0.798145138
trait_Area	1.476743637	0.241152885	6.123682223
trait_Exposed	0.861256719	0.159065896	5.414464954
trait_Freezings	1.28596682	0.267347565	4.810093627
trait_Shelter	0.534378093	0.230743958	2.315892024
trait_TrackLen	1.168066865	0.220013736	5.309063356

(d)

	solution	std error	z ratio
trait_Area:Assay_Bird:StageBin	0	NA	NA
trait_Area:Assay_Fish:StageBin	-0.046416417	0.08146533	-0.569768968
trait_Exposed:Assay_Bird:StageBin	0	NA	NA
trait_Exposed:Assay_Fish:StageBin	0.172559573	0.084847578	2.033759556
trait_Freezings:Assay_Bird:StageBin	0	NA	NA
trait_Freezings:Assay_Fish:StageBin	0.229381489	0.082465069	2.78155942
trait_Shelter:Assay_Bird:StageBin	0	NA	NA
trait_Shelter:Assay_Fish:StageBin	-0.330943241	0.075931466	-4.358446623
trait_TrackLen:Assay_Bird:StageBin	0	NA	NA
trait_TrackLen:Assay_Fish:StageBin	-0.011829921	0.072523743	-0.163117909
trait_Area:Block_Tank_GRIM_1_Q10b	0	NA	NA
trait_Area:Block_Tank_GRIM_1_Q11a	-0.370171501	0.230307218	-1.607294396
trait_Area:Block_Tank_GRIM_1_Q12b	-0.535262109	0.237081834	-2.25771034
trait_Area:Block_Tank_GRIM_1_Q9a	-0.004893664	0.237739337	-0.020584158
trait_Area:Block_Tank_GRIM_2_R10a	0	NA	NA
trait_Area:Block_Tank_GRIM_2_R11a	-0.080991898	0.247755787	-0.326902145
trait_Area:Block_Tank_GRIM_2_R12a	-0.200440205	0.257908728	-0.777174958
trait_Area:Block_Tank_GRIM_2_R9a	0.52318694	0.25919645	2.018495775
trait_Area:Block_Tank_SMV_1	0	NA	NA
trait_Area:Block_Tank_SMV_2	0.140058569	0.267800672	0.522995585
trait_Area:Block_Tank_SMV_3	0.30996092	0.300104334	1.032843863
trait_Area:Block_Tank_SMV_4	-0.082605208	0.297631739	-0.277541662
trait_Area:Block_Tank_SMV_5	0.137421263	0.278622745	0.493216242
trait_Area:Block_Tank_SMV_6	0.027587722	0.300019807	0.091953002
trait_Area:Block_Tank_TMH_P10a	0	NA	NA

trait_Area:Block_Tank_TMH_P10b	-0.156867024	0.266688282	-0.588203662
trait_Area:Block_Tank_TMH_P9a	-0.030561796	0.278861816	-0.109594766
trait_Area:Block_Tank_TMH_P9b	0.022932225	0.25812358	0.088842038
trait_Exposed:Block_Tank_GRIM_1_Q10b	0	NA	NA
trait_Exposed:Block_Tank_GRIM_1_Q11a	-0.30840162	0.22075588	-1.397025621
trait_Exposed:Block_Tank_GRIM_1_Q12b	-0.678986828	0.227146161	-2.989206711
trait_Exposed:Block_Tank_GRIM_1_Q9a	-0.281090199	0.227872081	-1.233543828
trait_Exposed:Block_Tank_GRIM_2_R10a	0	NA	NA
trait_Exposed:Block_Tank_GRIM_2_R11a	0.477307696	0.237499025	2.009724866
trait_Exposed:Block_Tank_GRIM_2_R12a	0.097132176	0.247276583	0.392807821
trait_Exposed:Block_Tank_GRIM_2_R9a	0.4191034	0.248711042	1.685101704
trait_Exposed:Block_Tank_SMV_1	0	NA	NA
trait_Exposed:Block_Tank_SMV_2	-0.164601983	0.256550012	-0.641598033
trait_Exposed:Block_Tank_SMV_3	-0.300555191	0.287897647	-1.04396543
trait_Exposed:Block_Tank_SMV_4	-0.043235368	0.2852102	-0.151591241
trait_Exposed:Block_Tank_SMV_5	-0.089032363	0.266756828	-0.333758515
trait_Exposed:Block_Tank_SMV_6	0.139062762	0.287826979	0.483147069
trait_Exposed:Block_Tank_TMH_P10a	0	NA	NA
trait_Exposed:Block_Tank_TMH_P10b	-0.107722937	0.255323957	-0.421906892
trait_Exposed:Block_Tank_TMH_P9a	-0.041568459	0.267032161	-0.15566836
trait_Exposed:Block_Tank_TMH_P9b	0.167423437	0.247160127	0.677388536
trait_Freezings:Block_Tank_GRIM_1_Q10b	0	NA	NA
trait_Freezings:Block_Tank_GRIM_1_Q11a	-0.181030612	0.276997104	-0.653546947
trait_Freezings:Block_Tank_GRIM_1_Q12b	-0.595383514	0.285418444	-2.086002246
trait_Freezings:Block_Tank_GRIM_1_Q9a	-0.111608398	0.285978397	-0.390268632
trait_Freezings:Block_Tank_GRIM_2_R10a	0	NA	NA
trait_Freezings:Block_Tank_GRIM_2_R11a	0.255085267	0.297918697	0.856224433
trait_Freezings:Block_Tank_GRIM_2_R12a	-0.003113741	0.309849001	-0.010049221
trait_Freezings:Block_Tank_GRIM_2_R9a	0.008350157	0.31094709	0.026853948
trait_Freezings:Block_Tank_SMV_1	0	NA	NA
trait_Freezings:Block_Tank_SMV_2	-0.326259587	0.322672624	-1.011116416
trait_Freezings:Block_Tank_SMV_3	-0.365241819	0.360384546	-1.013478027
trait_Freezings:Block_Tank_SMV_4	-0.129173777	0.358277806	-0.360540828
trait_Freezings:Block_Tank_SMV_5	0.025822341	0.33609775	0.076829852
trait_Freezings:Block_Tank_SMV_6	0.341674395	0.360311207	0.94827579
trait_Freezings:Block_Tank_TMH_P10a	0	NA	NA
trait_Freezings:Block_Tank_TMH_P10b	-0.016078545	0.321727353	-0.049975685
trait_Freezings:Block_Tank_TMH_P9a	-0.133337706	0.336300842	-0.396483413
trait_Freezings:Block_Tank_TMH_P9b	0.267518957	0.31130967	0.859333913
trait_Shelter:Block_Tank_GRIM_1_Q10b	0	NA	NA
trait_Shelter:Block_Tank_GRIM_1_Q11a	0.480091895	0.236535375	2.029683276
trait_Shelter:Block_Tank_GRIM_1_Q12b	0.914428538	0.243632578	3.753309786
trait_Shelter:Block_Tank_GRIM_1_Q9a	0.13402476	0.244189666	0.548855167
trait_Shelter:Block_Tank_GRIM_2_R10a	0	NA	NA
trait_Shelter:Block_Tank_GRIM_2_R11a	-0.351065594	0.254423345	-1.379848199
trait_Shelter:Block_Tank_GRIM_2_R12a	-0.124987627	0.264711364	-0.4721657

trait_Shelter:Block_Tank_GRIM_2_R9a	-0.386999693	0.265802387	-1.45596771
trait_Shelter:Block_Tank_SMV_1	0	NA	NA
trait_Shelter:Block_Tank_SMV_2	0.234624596	0.275334587	0.852143565
trait_Shelter:Block_Tank_SMV_3	-0.029568839	0.307932827	-0.096023665
trait_Shelter:Block_Tank_SMV_4	0.386620912	0.305834967	1.264148819
trait_Shelter:Block_Tank_SMV_5	0.085015136	0.286658779	0.296572588
trait_Shelter:Block_Tank_SMV_6	0.232741534	0.307859045	0.756000311
trait_Shelter:Block_Tank_TMH_P10a	0	NA	NA
trait_Shelter:Block_Tank_TMH_P10b	0.242572872	0.274393163	0.884033953
trait_Shelter:Block_Tank_TMH_P9a	0.13115582	0.286860401	0.457211312
trait_Shelter:Block_Tank_TMH_P9b	-0.052430041	0.265537225	-0.197448928
trait_TrackLen:Block_Tank_GRIM_1_Q10b	0	NA	NA
trait_TrackLen:Block_Tank_GRIM_1_Q11a	-0.429858596	0.2253746	-1.907307195
trait_TrackLen:Block_Tank_GRIM_1_Q12b	-0.458035469	0.232131569	-1.973171816
trait_TrackLen:Block_Tank_GRIM_1_Q9a	-0.058702933	0.232666292	-0.252305277
trait_TrackLen:Block_Tank_GRIM_2_R10a	0	NA	NA
trait_TrackLen:Block_Tank_GRIM_2_R11a	-0.151020979	0.242420226	-0.62297186
trait_TrackLen:Block_Tank_GRIM_2_R12a	-0.144306136	0.252232949	-0.572114531
trait_TrackLen:Block_Tank_GRIM_2_R9a	0.263394201	0.25327898	1.03993707
trait_TrackLen:Block_Tank_SMV_1	0	NA	NA
trait_TrackLen:Block_Tank_SMV_2	0.264502005	0.262325999	1.008295046
trait_TrackLen:Block_Tank_SMV_3	0.61411161	0.29341183	2.093002214
trait_TrackLen:Block_Tank_SMV_4	-0.173259197	0.291395319	-0.594584696
trait_TrackLen:Block_Tank_SMV_5	0.108504481	0.273108702	0.397294117
trait_TrackLen:Block_Tank_SMV_6	-0.308224113	0.29333927	-1.050742757
trait_TrackLen:Block_Tank_TMH_P10a	0	NA	NA
trait_TrackLen:Block_Tank_TMH_P10b	-0.196051834	0.261422132	-0.749943521
trait_TrackLen:Block_Tank_TMH_P9a	0.04160908	0.273301431	0.15224611
trait_TrackLen:Block_Tank_TMH_P9b	-0.237149299	0.252986243	-0.937399978
trait_Area:Block_GRIM_1	0	NA	NA
trait_Area:Block_GRIM_2	-0.292587225	0.24875001	-1.176230002
trait_Area:Block_SMV	0	NA	NA
trait_Area:Block_TMH	0.650991021	0.288235428	2.258539228
trait_Exposed:Block_GRIM_1	0	NA	NA
trait_Exposed:Block_GRIM_2	-0.34091809	0.238514966	-1.429336262
trait_Exposed:Block_SMV	0	NA	NA
trait_Exposed:Block_TMH	-0.168360424	0.277609526	-0.606464866
trait_Freezings:Block_GRIM_1	0	NA	NA
trait_Freezings:Block_GRIM_2	-0.010152278	0.298767611	-0.033980518
trait_Freezings:Block_SMV	0	NA	NA
trait_Freezings:Block_TMH	-0.590584396	0.344303989	-1.715299314
trait_Shelter:Block_GRIM_1	0	NA	NA
trait_Shelter:Block_GRIM_2	0.252327233	0.255271717	0.988465296
trait_Shelter:Block_SMV	0	NA	NA
trait_Shelter:Block_TMH	-0.56677235	0.294800423	-1.922562879
trait_TrackLen:Block_GRIM_1	0	NA	NA

trait_TrackLen:Block_GRIM_2	-0.117916181	0.243240487	-0.484772015
trait_TrackLen:Block_SMV	0	NA	NA
trait_TrackLen:Block_TMH	1.386988094	0.280904319	4.937581951
trait_Area:scale(preTimeNum)	-0.041753733	0.034979416	-1.193665811
trait_Exposed:scale(preTimeNum)	-0.002208688	0.036409713	-0.060662052
trait_Freezings:scale(preTimeNum)	-0.01176336	0.035408424	-0.332219248
trait_Shelter:scale(preTimeNum)	0.060897541	0.032604636	1.867757101
trait_TrackLen:scale(preTimeNum)	-0.085670861	0.031143259	-2.75086367
trait_Area:scale(Order, scale = FALSE)	-0.009459663	0.011297924	-0.837292107
trait_Exposed:scale(Order, scale = FALSE)	-0.036987964	0.011469254	-3.224966752
trait_Freezings:scale(Order, scale = FALSE)	-0.027452271	0.011436254	-2.400459973
trait_Shelter:scale(Order, scale = FALSE)	0.016517544	0.01055033	1.565595062
trait_TrackLen:scale(Order, scale = FALSE)	0.018053867	0.010102288	1.787106761
trait_Area:scale(Replicate, scale = FALSE)	-0.002999472	0.018598139	-0.161278052
trait_Exposed:scale(Replicate, scale = FALSE)	0.090050019	0.019328975	4.658809868
trait_Freezings:scale(Replicate, scale = FALSE)	0.137218633	0.018826736	7.288498217
trait_Shelter:scale(Replicate, scale = FALSE)	-0.056668022	0.017337819	-3.268463072
trait_TrackLen:scale(Replicate, scale = FALSE)	-0.072424478	0.016563329	-4.372579834
trait_Area:SexM	-0.496415978	0.266866898	-1.86016318
trait_Exposed:SexM	0.210461181	0.256874036	0.819316675
trait_Freezings:SexM	0.23963484	0.318776117	0.751733982
trait_Shelter:SexM	-0.000204822	0.272953053	-0.000750392
trait_TrackLen:SexM	-0.461565141	0.260098505	-1.774578219
trait_Area:StageBin	-0.719645712	0.057498568	-12.51588924
trait_Exposed:StageBin	-0.488632902	0.059885774	-8.159415377
trait_Freezings:StageBin	-0.04518896	0.058204188	-0.776386735
trait_Shelter:StageBin	0.575984723	0.053592744	10.74743849
trait_TrackLen:StageBin	-0.623339068	0.051187559	-12.17755014
trait_Area:Assay_Bird	0	NA	NA
trait_Area:Assay_Fish	0.105279933	0.04079309	2.580827603
trait_Exposed:Assay_Bird	0	NA	NA
trait_Exposed:Assay_Fish	-0.42175376	0.042478817	-9.928566532
trait_Freezings:Assay_Bird	0	NA	NA
trait_Freezings:Assay_Fish	0.260098332	0.041293726	6.298737344
trait_Shelter:Assay_Bird	0	NA	NA
trait_Shelter:Assay_Fish	-0.571147784	0.038022606	-15.02126862
trait_TrackLen:Assay_Bird	0	NA	NA
trait_TrackLen:Assay_Fish	0.344231401	0.03631688	9.478551149
trait_Area	1.672313366	0.170307953	9.819349789
trait_Exposed	1.247229705	0.163531987	7.626824114
trait_Freezings	0.788474294	0.204096363	3.863245194
trait_Shelter	1.005075444	0.174537197	5.758517161
trait_TrackLen	1.282569611	0.166315671	7.711658222

Table S3: Effects of 'stage' (pre- to post-) in the control group, where no predator stimulus was applied.

Tank configuration	Behaviour	Effect size	SE	Chisq	P
Bird strike	Area	-1.15	2.2	0.28	0.6
Bird strike	Exposed	-0.38	3.55	0.01	0.91
Bird strike	Freezings	0.19	0.53	0.13	0.72
Bird strike	Shelter	-0.45	0.33	2.6	0.11
Bird strike	Tracklength	3.23	2.19	0.5	0.48
Cichlid reveal	Area	1.32	3.02	0.2	0.66
Cichlid reveal	Exposed	-0.26	0.55	0.24	0.63
Cichlid reveal	Freezings	0.07	0.21	0.13	0.72
Cichlid reveal	Shelter	0.38	0.29	1.77	0.18
Cichlid reveal	Tracklength	-71.25	22.37	8.81	0.003

Appendix S1: ASReml-R code

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Overview

Below, we provide code to accompany our 2017 Functional Ecology paper, "Testing the stability of behavioural coping style across stress contexts in the Trinidadian guppy". Here we focus on using multivariate mixed models to partition among-individual (co)variation in 5 behavioural traits (measured simultaneously in an open field trial, or OFT). We will demonstrate how to:

- Specify a multivariate mixed model
- Extract the among-individual covariance matrix, known as **I**
- Subject **I** to eigenvector decomposition
- Use bootstrapping methods to estimate 95% confidence intervals around various parameters of interest for **I**
- Compare **I** matrices

Note that we use the `R` interface for `ASReml`, which is commercial software available from VSNi. Similar results can be achieved using the free `R` package `MCMCglmm`, although this requires knowledge of working in a Bayesian framework. We have provided tutorials for multivariate mixed models in both `ASReml-R` and `MCMCglmm` at https://tomhouslay.com/tutorials/, which are associated with an earlier paper *(Houslay & Wilson 2017 Behavioural Ecology)*.

Initialising

Load libraries

Note that you must have the following libraries installed and loaded before running this code.

```
library(asreml)
library(nadiv)
library(mvtnorm)
library(coda)

library(knitr)
library(tidyverse)
```

Data loading / wrangling

The data associated with this paper is available via Dryad.

```
df_oft <- read_csv("Houslayetal_FuncEcol_2017.csv")
```

The data frame comprises the following variables:

- **ID** for each individual
- **Block**
- **Block__Tank**, denoting distinct tanks used over the course of the experiment
- **Assay** indicates tank setup / predator stimulus type
- **Stage**, pre- or post-stimulus
- **StageBin**, as Stage but on a numeric scale

- **preTimeNum**, giving the time (in seconds, from 9am) that the trial began
- **Replicate**, ranging from 1-4
- **Order**, the order in which individuals were assayed within a tank
- **SexM**, numeric variable where 0==Female and 1==Male
- **Mass**, in grams, measured at the end of each trial
- **Area**, calculated as the percent of 1cm x 1cm grid squares entered by the individual during the trial
- **Exposed**, the time (in seconds) the individual spent in the central exposed zone during the trial
- **Freezings**, the number of times the individual 'froze' during the trial
- **Shelter**, the time (in seconds) the individual spent in the shelter during the trial
- **TrackLen**, the total distance travelled (in cm) by the individual during the trial.

We provided the data in raw measurements, but for ease of fitting (and interpreting) multivariate mixed models, we will standardise each behavioural trait by its overall standard deviation (across all setups and contexts). By doing so, we put traits onto similar scales (where 1 unit == 1 standard deviation), but retain any differences in both variation and mean values across contexts.

First, we calculate the global standard deviation for each behaviour:

```
df_stdev <- df_oft %>%
  select(Area, Exposed, Freezings, Shelter, TrackLen) %>%
  gather(Behaviour, Value,
         Area:TrackLen) %>%
  group_by(Behaviour) %>%
  summarise(sdu = sd(Value))

df_stdev
```

```
## # A tibble: 5 x 2
##   Behaviour        sdu
##       <chr>      <dbl>
## 1      Area  13.166626
## 2   Exposed  30.425689
## 3 Freezings   3.516881
## 4   Shelter  42.768470
## 5  TrackLen 157.317042
```

We then divide each observation by the relevant standard deviation:

```
df_oft_sdu <- df_oft %>%  # new data frame will be original after we...
  gather(Behaviour, Value,
         Area:TrackLen) %>%  # convert to 'long' format
  left_join(., df_stdev,
            by = "Behaviour") %>% # join the SD data frame to this by the 'Behaviour' variable
  mutate(Value = Value/sdu) %>% # divide value by its standard deviation
  select(-sdu) %>% # remove the standard deviation variable (no longer needed)
  spread(Behaviour, Value) # return data to the 'wide' format required for multivariate models
```

We also need to create subsets of the data, corresponding to:

- pre-stimulus (both bird strike and cichlid reveal setups)
- post-bird strike
- post-cichlid reveal

```
df_pre <- df_oft_sdu %>%
  filter(Stage == "pre")

df_postbird <- df_oft_sdu %>%
  filter(Stage == "post", Assay == "Bird")
```

```r
df_postfish <- df_oft_sdu %>%
  filter(Stage == "post", Assay == "Fish")
```

Model the data

Below, we show the code for the final models in each sequence of context-specific models described in the main text (i.e., 1D, 2D, 3D). These models estimate fully unstructured covariance matrices at both the among-individual and residual levels.

```r
# Model 1D
asr_1D <- asreml(cbind(Area,
                       Exposed,
                       Freezings,
                       Shelter,
                       TrackLen) ~
                   trait +
                   trait:(Assay +
                            SexM +
                            scale(Replicate, scale=FALSE) +
                            scale(Order, scale=FALSE) +
                            scale(preTimeNum) +
                            Block +
                            Block_Tank),
                 random =~ ID:us(trait,
                                 init = c(1,
                                          0.1,1,
                                          0.1,0.1,1,
                                          0.1,0.1,0.1,1,
                                          0.1,0.1,0.1,0.1,1)),
                 rcov =~ units:us(trait,
                                  init = rep(0.1,15)),
                 data = df_pre,
                 maxiter = 500)

# Diagnostic plots
hist(residuals(asr_1D))
plot(residuals(asr_1D))
plot(residuals(asr_1D) ~ asr_1D$fitted.values)
qqnorm(resid(asr_1D), main="Q-Q plot for residuals")
```

The variance component summary provides variances and covariances at both the among-individual ('ID:trait!') and residual ('R!') levels, which you can see using the following command (hidden here as it takes up a lot of space!):

```r
summary(asr_1D)$varcomp
```

We can repeat these models to partition the among-individual (co)variance in both post-bird strike (2D) and post-cichlid reveal (3D) contexts. Note that we do not need the fixed effect of 'Assay' in these models, as we used that in the pooled pre-stimulus model to allow observations from different setups to have separate means.

```r
# Model 2D
asr_2D <- asreml(cbind(Area,
                       Exposed,
```

```
                       Freezings,
                       Shelter,
                       TrackLen) ~
                   trait +
                   trait:(SexM +
                            scale(Replicate, scale=FALSE) +
                            scale(Order, scale=FALSE) +
                            scale(preTimeNum) +
                            Block +
                            Block_Tank),
                 random =~ ID:us(trait,
                                 init = c(1,
                                          0.1,1,
                                          0.1,0.1,1,
                                          0.1,0.1,0.1,1,
                                          0.1,0.1,0.1,0.1,1)),
                 rcov =~ units:us(trait,
                                  init = rep(0.1,15)),
                 data = df_postbird,
                 maxiter = 500)

# Model 3D
asr_3D <- asreml(cbind(Area,
                       Exposed,
                       Freezings,
                       Shelter,
                       TrackLen) ~
                   trait +
                   trait:(SexM +
                            scale(Replicate, scale=FALSE) +
                            scale(Order, scale=FALSE) +
                            scale(preTimeNum) +
                            Block +
                            Block_Tank),
                 random =~ ID:us(trait,
                                 init = c(1,
                                          0.1,1,
                                          0.1,0.1,1,
                                          0.1,0.1,0.1,1,
                                          0.1,0.1,0.1,0.1,1)),
                 rcov =~ units:us(trait,
                                  init = rep(0.1,15)),
                 data = df_postfish,
                 maxiter = 500)
```

Extracting the I matrix

We first define a custom function for reshaping a vector into a full covariance matrix:

```
vecToMat <- function(X, n) {
  S <- diag(n)
  S[upper.tri(S, diag=TRUE)] <- X
  S <- S + t(S) - diag(diag(S))
```

```
  return(S)
}
```

. . . and then extract the among-individual (co)variance estimates from the model summary and create our matrix:

```
# Extract variance components from the model
modpre_df <- data_frame(Var = row.names(summary(asr_1D)$varcomp),
                        Num = summary(asr_1D)$varcomp$component)

# Subset for those where the variable name begins 'ID'
modpre_I_df <- modpre_df %>%
  filter(substring(Var, 1, 2) == "ID")

# Get list of trait names from the model
traitNames <- asr_1D$G.param$ID$trait$levels

# Reform values into covariance matrix
modpre_I_mat <- vecToMat(modpre_I_df$Num, length(traitNames))  ## Second value is number of traits

# Set row and column names
colnames(modpre_I_mat) <- traitNames
rownames(modpre_I_mat) <- traitNames

# Show matrix
kable(modpre_I_mat, digits = 3)
```

	Area	Exposed	Freezings	Shelter	TrackLen
Area	0.182	0.049	-0.030	-0.087	0.109
Exposed	0.049	0.151	0.155	-0.122	-0.005
Freezings	-0.030	0.155	0.235	-0.112	-0.080
Shelter	-0.087	-0.122	-0.112	0.153	-0.081
TrackLen	0.109	-0.005	-0.080	-0.081	0.197

```
# Can also quickly show correlation matrix
kable(cov2cor(modpre_I_mat), digits = 3)
```

	Area	Exposed	Freezings	Shelter	TrackLen
Area	1.000	0.297	-0.144	-0.519	0.574
Exposed	0.297	1.000	0.825	-0.802	-0.026
Freezings	-0.144	0.825	1.000	-0.591	-0.373
Shelter	-0.519	-0.802	-0.591	1.000	-0.465
TrackLen	0.574	-0.026	-0.373	-0.465	1.000

Eigen decomposition

Eigen decomposition is similar to applying a principal components analysis, but here we have isolated the among-individual (co)variance matrix first. As noted in Houslay & Wilson (2017), this enables us to investigate the major axis of among-individual variation (whereas studies that use univariate mixed models on PCA scores from multivariate data are asking whether the major axis of observed behavioural (co)variation is repeatable, where that (co)variation includes both among- and within-individual trait variation).

The output of eigen decomposition is a set of eigenvectors, each of which is associated with:

- An eigenvalue, or the amount of variation associated with that vector
- A 'loading' for each trait, where:
- the value shows how heavily the trait loads
- the sign indicates groupings of traits that load in the same direction

```
# Perform eigen decomposition on pre-stimulus I
I_poolpre_eigen <- eigen(modpre_I_mat)

# View results
I_poolpre_eigen
```

```
## eigen() decomposition
## $values
## [1] 0.455916340 0.365275333 0.079500062 0.013376777 0.004059684
##
## $vectors
##             [,1]        [,2]       [,3]        [,4]       [,5]
## [1,] -0.22423490 -0.56032955  0.7415386 -0.23068443 0.18070633
## [2,] -0.55275677  0.06053543  0.1287940  0.82082935 0.02113501
## [3,] -0.60320962  0.42031140 -0.1228185 -0.43102929 0.50853304
## [4,]  0.52589282  0.22835634  0.2407339  0.28070360 0.73112434
## [5,] -0.06126631 -0.67346713 -0.6004127  0.09188642 0.41683316
```

```
I_poolpre_eigenVals <- I_poolpre_eigen$values
I_poolpre_eigenVecs <- I_poolpre_eigen$vectors

# View proportion of total variation explained by EVs 1 and 2
I_poolpre_eigenVals[1]/sum(I_poolpre_eigenVals)
```

```
## [1] 0.4965715
```

```
I_poolpre_eigenVals[2]/sum(I_poolpre_eigenVals)
```

```
## [1] 0.3978479
```

```
# Associate trait names with the eigen vectors
rownames(I_poolpre_eigenVecs) <- traitNames
I_poolpre_eigenVecs
```

```
##                  [,1]        [,2]       [,3]        [,4]       [,5]
## Area      -0.22423490 -0.56032955  0.7415386 -0.23068443 0.18070633
## Exposed   -0.55275677  0.06053543  0.1287940  0.82082935 0.02113501
## Freezings -0.60320962  0.42031140 -0.1228185 -0.43102929 0.50853304
## Shelter    0.52589282  0.22835634  0.2407339  0.28070360 0.73112434
## TrackLen  -0.06126631 -0.67346713 -0.6004127  0.09188642 0.41683316
```

These steps can be repeated for models 2D and 3D to investigate **I** matrices for post-bird strike and post-cichlid reveal.

Bootstrapping procedure

In our paper, we use a bootstrapping algorithm to put 95% confidence intervals on various estimates (including the trait loadings from the eigenvector decomposition). More importantly, it also enables us to put these confidence intervals on the 'difference matrices' we use to compare context-specific **I** matrices. Note that, while estimates from the models above should match our results in the paper, there are likely to be small differences in the bootstrapped CIs (as these are calculated from random draws from a specified distribution).

We need the estimates of our three covariance matrices, and for each of these we also need the sampling covariances. Together, these will allow us to specify a multivariate normal distribution from which we can take sample random draws.

```
# Pooled pre

# Get average information matrix
modpre_ai <- as.numeric(asr_1D$ai)

# Find the sampling (co)-variances
modpre_VC <- aiFun(asr_1D, modpre_ai)

# Subset for I (the section of the ai matrix concerned with ID - numbers hard-coded here)
modpre_I_VC <- modpre_VC[1:15,1:15]

# Get estimates of covariances
modpre_I_ests <- modpre_I_df$Num

# Eigenvectors 1 and 2
modpre_I_PC1 <- eigen(modpre_I_mat)$vectors[,1]
modpre_I_PC2 <- eigen(modpre_I_mat)$vectors[,2]



# Post-bird strike

# Extract variance components from the model
modbird_df <- data_frame(Var = row.names(summary(asr_2D)$varcomp),
                        Num = summary(asr_2D)$varcomp$component)

# Subset for those where the variable name begins 'ID'
modbird_I_df <- modbird_df %>%
  filter(substring(Var, 1, 2) == "ID")

# Get list of trait names from the model
traitNames <- asr_2D$G.param$ID$trait$levels

# Reform values into covariance matrix
modbird_I_mat <- vecToMat(modbird_I_df$Num, length(traitNames))  ## Second value is number of traits

# Get average information matrix
modbird_ai <- as.numeric(asr_2D$ai)

# Find the sampling (co)-variances
modbird_VC <- aiFun(asr_2D, modbird_ai)

# Subset for I (the section of the ai matrix concerned with ID - numbers hard-coded here)
modbird_I_VC <- modbird_VC[1:15,1:15]

# Get estimates of covariances
modbird_I_ests <- modbird_I_df$Num
```

```
# Eigenvectors 1 and 2
modbird_I_PC1 <- eigen(modbird_I_mat)$vectors[,1]
modbird_I_PC2 <- eigen(modbird_I_mat)$vectors[,2]



# Post-fish reveal

# Extract variance components from the model
modfish_df <- data_frame(Var = row.names(summary(asr_3D)$varcomp),
                        Num = summary(asr_3D)$varcomp$component)

# Subset for those where the variable name begins 'ID'
modfish_I_df <- modfish_df %>%
  filter(substring(Var, 1, 2) == "ID")

# Get list of trait names from the model
traitNames <- asr_3D$G.param$ID$trait$levels

# Reform values into covariance matrix
modfish_I_mat <- vecToMat(modfish_I_df$Num, length(traitNames))  ## Second value is number of traits

# Get average information matrix
modfish_ai <- as.numeric(asr_3D$ai)

# Find the sampling (co)-variances
modfish_VC <- aiFun(asr_3D, modfish_ai)

# Subset for I (the section of the ai matrix concerned with ID - numbers hard-coded here)
modfish_I_VC <- modfish_VC[1:15,1:15]

# Get estimates of covariances
modfish_I_ests <- modfish_I_df$Num

# Eigenvectors 1 and 2
modfish_I_PC1 <- eigen(modfish_I_mat)$vectors[,1]
modfish_I_PC2 <- eigen(modfish_I_mat)$vectors[,2]
```

We also need to set up a number of empty vectors that can be populated within the bootstrapping algorithm:

```
# Set the number of iterations for the bootstrap
N <- 5000

# I matrices
boot_I_pre <- numeric()
boot_I_postbird <- numeric()
boot_I_postfish <- numeric()

# I correlation
boot_I_pre_cor <- numeric()
boot_I_postbird_cor <- numeric()
boot_I_postfish_cor <- numeric()

## Eigen analysis
```

```
boot_loading_pre_1 <- numeric()
boot_loading_postbird_1 <- numeric()
boot_loading_postfish_1 <- numeric()

boot_loading_pre_2 <- numeric()
boot_loading_postbird_2 <- numeric()
boot_loading_postfish_2 <- numeric()
```

Next we perform the bootstrap algorithm. For 5000 replicates, we sample a matrix draw from each of the pre-stimulus, post-bird strike, and post-cichlid reveal multivariate normal distributions. We store these covariance matrix draws, along with correlation matrix versions and trait loadings for the first 2 eigenvectors.

```
for (i in 1:N)
{

  ## Sample from multivariate normal for each I matrix
  draw_I_pre <- rmvnorm(1, modpre_I_ests, modpre_I_VC)
  draw_I_postbird <- rmvnorm(1, modbird_I_ests, modbird_I_VC)
  draw_I_postfish <- rmvnorm(1, modfish_I_ests, modfish_I_VC)

  ## Store I sample
  boot_I_pre <- rbind(boot_I_pre, draw_I_pre)
  boot_I_postbird <- rbind(boot_I_postbird, draw_I_postbird)
  boot_I_postfish <- rbind(boot_I_postfish, draw_I_postfish)

  ## Convert samples to matrix form (to get correlations easily)
  draw_I_pre_mat <- vecToMat(draw_I_pre, 5)
  draw_I_postbird_mat <- vecToMat(draw_I_postbird, 5)
  draw_I_postfish_mat <- vecToMat(draw_I_postfish, 5)

  ## Calculate and store bootstrapped correlations

  # ..calculate
  draw_I_pre_cormat <- cov2cor(draw_I_pre_mat)
  draw_I_pre_cor <- draw_I_pre_cormat[upper.tri(draw_I_pre_cormat, diag=TRUE)]
  draw_I_postbird_cormat <- cov2cor(draw_I_postbird_mat)
  draw_I_postbird_cor <- draw_I_postbird_cormat[upper.tri(draw_I_postbird_cormat, diag=TRUE)]
  draw_I_postfish_cormat <- cov2cor(draw_I_postfish_mat)
  draw_I_postfish_cor <- draw_I_postfish_cormat[upper.tri(draw_I_postfish_cormat, diag=TRUE)]

  # ..store
  boot_I_pre_cor <- rbind(boot_I_pre_cor, draw_I_pre_cor)
  boot_I_postbird_cor <- rbind(boot_I_postbird_cor, draw_I_postbird_cor)
  boot_I_postfish_cor <- rbind(boot_I_postfish_cor, draw_I_postfish_cor)


  ## Eigenvector decomposition
  eigen_pre <- eigen(draw_I_pre_mat)
  eigen_postbird <- eigen(draw_I_postbird_mat)
  eigen_postfish <- eigen(draw_I_postfish_mat)


  ## Get trait loadings for eigens 1 and 2 (PC1-2)
  draw_I_pre_PC1 <- eigen_pre$vectors[,1]
```

```
draw_I_postbird_PC1 <- eigen_postbird$vectors[,1]
draw_I_postfish_PC1 <- eigen_postfish$vectors[,1]

draw_I_pre_PC2 <- eigen_pre$vectors[,2]
draw_I_postbird_PC2 <- eigen_postbird$vectors[,2]
draw_I_postfish_PC2 <- eigen_postfish$vectors[,2]

##
# Draws aren't necessarily done in the same 'space' as original eigen decomp of I matrix
# - ie, the sign is just used to group traits that load in the same direction, but
#        the sign itself is assigned arbitrarily
# - to make sure we are putting everything in the same space,
#     if angle between draw and mean is >90 then flip signs on all loadings
##

## Pre (pooled)

## PC 1
theta_pre_PC1 <- acos(sum(modpre_I_PC1*draw_I_pre_PC1) /
                     (sqrt(sum(modpre_I_PC1 * modpre_I_PC1)) *
                        sqrt(sum(draw_I_pre_PC1 * draw_I_pre_PC1))))
### convert to degrees
theta_pre_deg1 <- (180/pi)*theta_pre_PC1

#if statement flips signs of trait loadings on this draw if angle >90
if (theta_pre_deg1 > 90) {
  draw_I_pre_PC1 <- draw_I_pre_PC1*-1
} else {
  draw_I_pre_PC1 < -draw_I_pre_PC1
}

## PC 2
theta_pre_PC2 <- acos(sum(modpre_I_PC2*draw_I_pre_PC2) /
                     (sqrt(sum(modpre_I_PC2 * modpre_I_PC2)) *
                        sqrt(sum(draw_I_pre_PC2 * draw_I_pre_PC2))))
### convert to degrees
theta_pre_deg2 <- (180/pi)*theta_pre_PC2

#if statement flips signs of trait loadings on this draw if angle >90
if (theta_pre_deg2 > 90) {
  draw_I_pre_PC2 <- draw_I_pre_PC2*-1
} else {
  draw_I_pre_PC2 < -draw_I_pre_PC2
}

## Store trait loadings
boot_loading_pre_1 <- rbind(boot_loading_pre_1, draw_I_pre_PC1)
boot_loading_pre_2 <- rbind(boot_loading_pre_2, draw_I_pre_PC2)




## Postbird
```

```
## PC 1
theta_postbird_PC1 <- acos(sum(modbird_I_PC1*draw_I_postbird_PC1) /
                     (sqrt(sum(modbird_I_PC1 * modbird_I_PC1)) *
                        sqrt(sum(draw_I_postbird_PC1 * draw_I_postbird_PC1))))
### convert to degrees
theta_postbird_deg1 <- (180/pi)*theta_postbird_PC1

#if statement flips signs of trait loadings on this draw if angle >90
if (theta_postbird_deg1 > 90) {
  draw_I_postbird_PC1 <- draw_I_postbird_PC1*-1
} else {
  draw_I_postbird_PC1 <- draw_I_postbird_PC1
}

## PC 2
theta_postbird_PC2 <- acos(sum(modbird_I_PC1*draw_I_postbird_PC2) /
                     (sqrt(sum(modbird_I_PC2 * modbird_I_PC2)) *
                        sqrt(sum(draw_I_postbird_PC2 * draw_I_postbird_PC2))))
### convert to degrees
theta_postbird_deg2 <- (180/pi)*theta_postbird_PC2

#if statement flips signs of trait loadings on this draw if angle >90
if (theta_postbird_deg2 > 90) {
  draw_I_postbird_PC2 <- draw_I_postbird_PC2*-1
} else {
  draw_I_postbird_PC2 <- draw_I_postbird_PC2
}

## Store trait loadings
boot_loading_postbird_1 <- rbind(boot_loading_postbird_1, draw_I_postbird_PC1)
boot_loading_postbird_2 <- rbind(boot_loading_postbird_2, draw_I_postbird_PC2)



## Postfish

## PC 1
theta_postfish_PC1 <- acos(sum(modfish_I_PC1*draw_I_postfish_PC1) /
                     (sqrt(sum(modfish_I_PC1 * modfish_I_PC1)) *
                        sqrt(sum(draw_I_postfish_PC1 * draw_I_postfish_PC1))))
### convert to degrees
theta_postfish_deg1 <- (180/pi)*theta_postfish_PC1

#if statement flips signs of trait loadings on this draw if angle >90
if (theta_postfish_deg1 > 90) {
  draw_I_postfish_PC1 <- draw_I_postfish_PC1*-1
} else {
  draw_I_postfish_PC1 <- draw_I_postfish_PC1
}

## PC 2
theta_postfish_PC2 <- acos(sum(modfish_I_PC1*draw_I_postfish_PC2) /
                     (sqrt(sum(modfish_I_PC2 * modfish_I_PC2)) *
```

```
                        sqrt(sum(draw_I_postfish_PC2 * draw_I_postfish_PC2))))
  ### convert to degrees
  theta_postfish_deg2 <- (180/pi)*theta_postfish_PC2

  #if statement flips signs of trait loadings on this draw if angle >90
  if (theta_postfish_deg2 > 90) {
    draw_I_postfish_PC2 <- draw_I_postfish_PC2*-1
  } else {
    draw_I_postfish_PC2 <- draw_I_postfish_PC2
  }

  ## Store trait loadings
  boot_loading_postfish_1 <- rbind(boot_loading_postfish_1, draw_I_postfish_PC1)
  boot_loading_postfish_2 <- rbind(boot_loading_postfish_2, draw_I_postfish_PC2)


}
```

Confidence intervals on I matrices

Here we demonstrate how to find the 95% confidence intervals on variance, covariance and correlation estimates for the pre-stimulus **I** matrix (and output this in a readable format):

```
## Get upper and lower bounds of I matrix estimates

modpre_I_mat_lower <- vecToMat(as.numeric(HPDinterval(as.mcmc(boot_I_pre), prob=0.95)[,'lower']),5)
modpre_I_mat_upper <- vecToMat(as.numeric(HPDinterval(as.mcmc(boot_I_pre), prob=0.95)[,'upper']),5)


modpre_I_mat_cor_lower <- vecToMat(c(HPDinterval(as.mcmc(boot_I_pre_cor[,1]), prob=0.95)[,'lower'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,2]), prob=0.95)[,'lower'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,3]), prob=0.95)[,'lower'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,4]), prob=0.95)[,'lower'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,5]), prob=0.95)[,'lower'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,6]), prob=0.95)[,'lower'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,7]), prob=0.95)[,'lower'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,8]), prob=0.95)[,'lower'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,9]), prob=0.95)[,'lower'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,10]), prob=0.95)[,'lower'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,11]), prob=0.95)[,'lower'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,12]), prob=0.95)[,'lower'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,13]), prob=0.95)[,'lower'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,14]), prob=0.95)[,'lower'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,15]), prob=0.95)[,'lower']),
         5)

modpre_I_mat_cor_upper <- vecToMat(c(HPDinterval(as.mcmc(boot_I_pre_cor[,1]), prob=0.95)[,'lower'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,2]), prob=0.95)[,'upper'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,3]), prob=0.95)[,'upper'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,4]), prob=0.95)[,'upper'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,5]), prob=0.95)[,'upper'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,6]), prob=0.95)[,'upper'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,7]), prob=0.95)[,'upper'],
```

```
           HPDinterval(as.mcmc(boot_I_pre_cor[,8]), prob=0.95)[,'upper'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,9]), prob=0.95)[,'upper'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,10]), prob=0.95)[,'upper'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,11]), prob=0.95)[,'upper'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,12]), prob=0.95)[,'upper'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,13]), prob=0.95)[,'upper'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,14]), prob=0.95)[,'upper'],
           HPDinterval(as.mcmc(boot_I_pre_cor[,15]), prob=0.95)[,'upper']),
         5)



modpre_I_mat_cor <- cov2cor(modpre_I_mat)

I_error_pre <- matrix(NA, 5, 5)

for(i in 1:5){
  for(j in 1:5){
    if(j > i){
      I_error_pre[i,j] <- paste(round(modpre_I_mat_cor[i,j],digits=2),
                                " (",
                                round(modpre_I_mat_cor_lower[i,j],digits=2),
                                ",",
                                round(modpre_I_mat_cor_upper[i,j],digits=2),
                                ")",
                                sep = "")
    } else {
      I_error_pre[i,j] <- paste(round(modpre_I_mat[i,j],digits=2),
                                " (",
                                round(modpre_I_mat_lower[i,j],digits=2),
                                ",",
                                round(modpre_I_mat_upper[i,j],digits=2),
                                ")",
                                sep = "")
    }
  }
}

colnames(I_error_pre) <- traitNames
rownames(I_error_pre) <- traitNames

kable(I_error_pre)
```

	Area	Exposed	Freezings	Shelter	TrackLen
Area	0.18 (0.1,0.26)	0.3 (-0.06,0.61)	-0.14 (-0.44,0.2)	-0.52 (-0.76,-0.27)	0.57 (0.34,0.78)
Exposed	0.05 (-0.01,0.11)	0.15 (0.08,0.22)	0.82 (0.67,1)	-0.8 (-0.96,-0.65)	-0.03 (-0.35,0.32)
Freezings	-0.03 (-0.09,0.03)	0.16 (0.08,0.22)	0.24 (0.14,0.34)	-0.59 (-0.8,-0.38)	-0.37 (-0.62,-0.1)
Shelter	-0.09 (-0.14,-0.03)	-0.12 (-0.18,-0.07)	-0.11 (-0.17,-0.05)	0.15 (0.09,0.21)	-0.47 (-0.69,-0.23)
TrackLen	0.11 (0.05,0.17)	0 (-0.06,0.05)	-0.08 (-0.15,-0.02)	-0.08 (-0.14,-0.03)	0.2 (0.12,0.28)

Confidence intervals on trait loadings for eigen decomposition

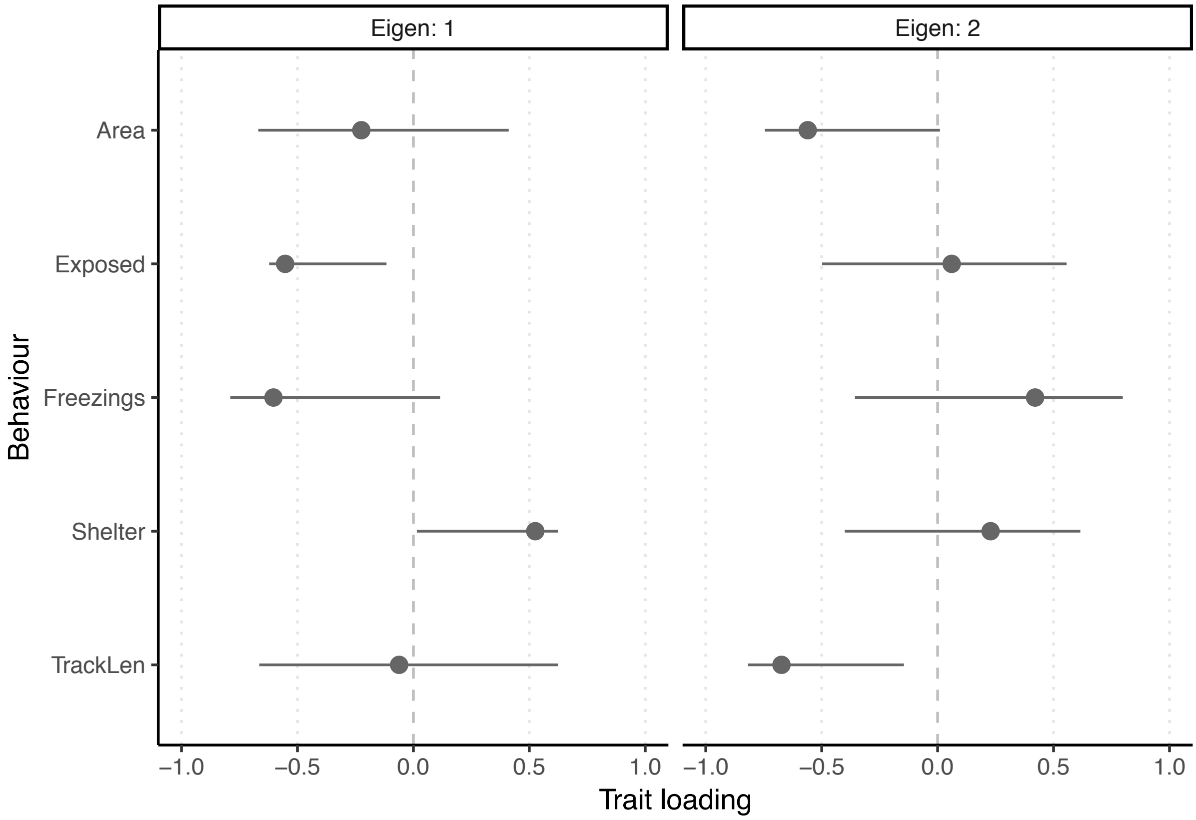
```
df_vis_eigen_poolpre <- data.frame(Eigen = 1:2,
                                   as.data.frame(rbind(I_poolpre_eigenVecs[,1],
                                                       I_poolpre_eigenVecs[,2]))) %>%
  gather(., Trait, Value, Area:TrackLen)

df_vis_eigen_poolpre$lower <- c(HPDinterval(as.mcmc(boot_loading_pre_1[,1]), 0.95)[,"lower"],
                                HPDinterval(as.mcmc(boot_loading_pre_2[,1]), 0.95)[,"lower"],
                                HPDinterval(as.mcmc(boot_loading_pre_1[,2]), 0.95)[,"lower"],
                                HPDinterval(as.mcmc(boot_loading_pre_2[,2]), 0.95)[,"lower"],
                                HPDinterval(as.mcmc(boot_loading_pre_1[,3]), 0.95)[,"lower"],
                                HPDinterval(as.mcmc(boot_loading_pre_2[,3]), 0.95)[,"lower"],
                                HPDinterval(as.mcmc(boot_loading_pre_1[,4]), 0.95)[,"lower"],
                                HPDinterval(as.mcmc(boot_loading_pre_2[,4]), 0.95)[,"lower"],
                                HPDinterval(as.mcmc(boot_loading_pre_1[,5]), 0.95)[,"lower"],
                                HPDinterval(as.mcmc(boot_loading_pre_2[,5]), 0.95)[,"lower"])


df_vis_eigen_poolpre$upper <- c(HPDinterval(as.mcmc(boot_loading_pre_1[,1]), 0.95)[,"upper"],
                                HPDinterval(as.mcmc(boot_loading_pre_2[,1]), 0.95)[,"upper"],
                                HPDinterval(as.mcmc(boot_loading_pre_1[,2]), 0.95)[,"upper"],
                                HPDinterval(as.mcmc(boot_loading_pre_2[,2]), 0.95)[,"upper"],
                                HPDinterval(as.mcmc(boot_loading_pre_1[,3]), 0.95)[,"upper"],
                                HPDinterval(as.mcmc(boot_loading_pre_2[,3]), 0.95)[,"upper"],
                                HPDinterval(as.mcmc(boot_loading_pre_1[,4]), 0.95)[,"upper"],
                                HPDinterval(as.mcmc(boot_loading_pre_2[,4]), 0.95)[,"upper"],
                                HPDinterval(as.mcmc(boot_loading_pre_1[,5]), 0.95)[,"upper"],
                                HPDinterval(as.mcmc(boot_loading_pre_2[,5]), 0.95)[,"upper"])


ggplot(df_vis_eigen_poolpre, aes(x = Trait, y = Value)) +
  geom_hline(yintercept = 0,
             linetype = 2,
             colour = 'grey75') +
  geom_hline(yintercept = -0.5,
             linetype = 3,
             colour = 'grey90') +
  geom_hline(yintercept = 0.5,
             linetype = 3,
             colour = 'grey90') +
    geom_hline(yintercept = -1,
             linetype = 3,
             colour = 'grey90') +
  geom_hline(yintercept = 1,
             linetype = 3,
             colour = 'grey90') +
  geom_pointrange(aes(ymin = lower,
                      ymax = upper),
                  colour = "grey40") +
  labs(x = "Behaviour",
       y = "Trait loading") +
  scale_x_discrete(limits = rev(traitNames)) +
```

```
  ylim(c(-1,1)) +
  coord_flip() +
  facet_grid(. ~ Eigen, labeller = label_both) +
  theme_classic()
```



Difference matrix

Here, we show how to demonstrate the difference between the (pooled) pre-stimulus **I** matrix and the post-bird strike **I** matrix. The estimates of the differences are given by simply subtracting I_{pre} from $I_{post\text{-}bird}$; the confidence intervals are estimated by subtracting the set of pre-stimulus bootstrap draws from those of post-bird strike and then finding the 95% confidence limits of the resultant distribution.

```
# Get difference in estimates from respective I matrices
I_diff_mat_pre_postbird <- modbird_I_mat - modpre_I_mat

# Subtract one set of bootstrap draws from the other
I_bootdiff_pre_postbird <- boot_I_postbird - boot_I_pre

# Get upper and lower confidence intervals from this set of difference values
I_diff_mat_pre_postbird_lower <- vecToMat(as.numeric(HPDinterval(as.mcmc(I_bootdiff_pre_postbird),
                                                        prob=0.95)[,'lower']),5)
I_diff_mat_pre_postbird_upper <- vecToMat(as.numeric(HPDinterval(as.mcmc(I_bootdiff_pre_postbird),
                                                        prob=0.95)[,'upper']),5)


## Reform into readable matrix
```

```
I_diff_error_pre_postbird <- matrix(NA, 5, 5)

for(i in 1:5){
  for(j in 1:5){
    I_diff_error_pre_postbird[i,j] <- paste(round(I_diff_mat_pre_postbird[i,j],digits=2),
                                              " (",
                                              round(I_diff_mat_pre_postbird_lower[i,j],digits=2),
                                              ",",
                                              round(I_diff_mat_pre_postbird_upper[i,j],digits=2),
                                            ")",
                                            sep = "")
  }
}

# Associate trait names
colnames(I_diff_error_pre_postbird) <- traitNames
rownames(I_diff_error_pre_postbird) <- traitNames

# Print matrix
kable(I_diff_error_pre_postbird)
```

	Area	Exposed	Freezings	Shelter	TrackLen
Area	-0.1 (-0.2,0.01)	0.01 (-0.09,0.11)	0.06 (-0.03,0.15)	0.02 (-0.07,0.11)	-0.05 (-0.14,0.03)
Exposed	0.01 (-0.09,0.11)	0.13 (-0.03,0.3)	0.05 (-0.08,0.19)	-0.06 (-0.2,0.06)	0.02 (-0.07,0.1)
Freezings	0.06 (-0.03,0.15)	0.05 (-0.08,0.19)	-0.06 (-0.21,0.08)	0.01 (-0.11,0.12)	0.05 (-0.04,0.14)
Shelter	0.02 (-0.07,0.11)	-0.06 (-0.2,0.06)	0.01 (-0.11,0.12)	0 (-0.12,0.13)	0.01 (-0.08,0.1)
TrackLen	-0.05 (-0.14,0.03)	0.02 (-0.07,0.1)	0.05 (-0.04,0.14)	0.01 (-0.08,0.1)	-0.08 (-0.18,0.03)