Title: Avoiding the misuse of BLUP in behavioral ecology

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Running title: Avoiding misuse of BLUP

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Lay summary: Research of causes and consequences of animal personality promises exciting insights, yet widely-used tests can lead to spurious results: when predictions of individual-level random effects are used in secondary analyses, their error is not carried forward, leading to increased likelihood of ‘false positive’ errors. We demonstrate how alternative approaches enable behavioural ecologists to test hypotheses about the causes and consequences of individual behavioural variation while accounting for the uncertainty inherent in the random effects.

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Abstract: Having recognized that variation around the population-level ‘Golden Mean’ of labile traits contains biologically meaningful information, behavioral ecologists have focused increasingly on exploring the causes and consequences of individual variation in behavior. These are exciting new directions for the field, assisted in no small part by the adoption of mixed-effects modeling techniques that enable the partitioning of among- and within-individual behavioral variation. It has become commonplace to extract predictions of individual random effects from such models for use in subsequent analyses (for example, between a personality trait and other individual traits such as cognition, physiology, or fitness-related measures). However, these predictions are made with large amounts of error that is not carried forward, rendering further tests susceptible to spurious P-values from these individual-level point
estimates. We briefly summarize the problems with such statistical methods that are used regularly by behavioral ecologists, and highlight the robust solutions that exist within the mixed model framework, providing tutorials to aid in their implementation.
Characterizing individual variation in behavior is an exciting research area in behavioral ecology, with great interest in the fields of ‘animal personality’ and individual differences in behavioral plasticity (Réale, Dingemanse, et al. 2010; Japyassú and Malange 2014). This research is predicated on exploring previously ignored phenotypic variation: behavioral ecologists have escaped the ‘tyranny of the Golden Mean’ in labile traits (Bennett 1987; Wilson 1998; Williams 2008), and are increasingly finding meaningful biology in what was formerly considered residual variation (Cleasby and Nakagawa 2011; Stamps et al. 2012; Brommer 2013a). Progress in these fields has been boosted by the adoption of mixed-effects modeling techniques, particularly the use of quantitative genetics-style approaches for partitioning phenotypic variation into its ‘between-individual’ and ‘within-individual’ components (Nussey et al. 2007; Smiseth et al. 2008; van de Pol and Wright 2009; Dingemanse et al. 2012; Dingemanse and Dochtermann 2013; Royle et al. 2014; Allegue et al. 2016). Behavioral ecologists are also increasingly interested in extending these analyses of individual behavioral variation for new avenues and purposes (Sih et al. 2004; Dall et al. 2012; Japyassú and Malange 2014; Roche et al. 2016; Stamps and Biro 2016). These typically involve exploration of the causes and consequences of individual variation in behavior (and/or behavioral plasticity), by testing for their association with variation in other individual traits (e.g., physiological, cognitive, social, or fitness-related) or environmental variables. However, the use of anticonservative methods has become pervasive in this field. Here we highlight not only the problems with a widely-used approach in the study of individual behavioral variation, but also the straightforward statistical solutions to these problems that should thereby hasten progress.
Specifically, it has become common practice to extract predictions of individual random effects from fitted mixed models and to use these in subsequent analyses, such as correlation tests or linear regression models (Table 1). Problems arise from this approach because individual point estimates from random effects in mixed models (sometimes known as conditional modes, or best linear unbiased predictors, BLUPs) are predicted with large amounts of error. Their use in secondary analyses can therefore lead to highly anticonservative tests of biological hypotheses, because the error inherent in their prediction is excluded from these further tests (Hadfield et al. 2010). We stress that BLUP is an incredibly useful technique that should not be dismissed in any way as inherently ‘bad’ (Robinson 1991). Indeed, it is entirely appropriate to use individual-level predictions to say something about individuals (or genotypes, or specific levels of some other random effect). For example, scrutiny of BLUPs could be used to identify which individuals are the ‘boldest’, or to select individuals for groups to be used in further experimental study. However, when the objective is to say something about population-level processes or relationships then analyzing sets of model predictions while ignoring their associated error is not statistically correct. This has been recognized in other fields (notably ecological and evolutionary quantitative genetics), but less so in behavioral ecology, where these improper analyses persist. As detailed by Hadfield et al. (2010), such analyses can therefore result in spuriously narrow confidence intervals and/or spuriously low P-values that are interpreted as indicators of biological significance. While the qualitative conclusions of individual papers employing these methods may prove robust in many cases,
failure to properly account for uncertainty will increase Type I errors (false positives) across the field. In short, published P-values are systematically anticonservative and should not be taken at face value.

Recent examples of publications (mis-)using BLUPs include tests of associations between personality (and/or individual variation in behavioral plasticity) and a wide range of traits, including physiology, cognition, social networks, niche specialization, and fitness (Table 1). In many cases, authors have explicitly acknowledged the potential for problems as outlined by Hadfield et al. (2010). Nonetheless, use of these ‘stats on stats’ approaches that are known to be inappropriate for hypothesis testing (see Brommer 2013b for further discussion) continues unabated. This is presumably because researchers are not aware of how to implement more robust analytical strategies, and/or because of a misconception that problems are restricted to quantitative genetic models. On the latter point we note that predictions from mixed models in which random effects are assumed to covary between individuals (through e.g., genetic relatedness, spatial/temporal autocorrelation, or social processes) cannot be treated as independent ‘data points’. However, this in no way justifies ignoring uncertainty when random effects are predicted from a model that assumes no among-individual covariance.

Fortunately, the mixed-effects model framework does offer a way to test hypotheses such as those listed above while fully accounting for the uncertainty inherent in the random effects. An overreliance on the (otherwise excellent) lme4 package for mixed models in R (Bates et al. 2015) may have held many
behavioral ecologists in the ‘Flatland’ of univariate modeling (Walsh 2007). In
the majority of cases, questions that are multivariate in nature are best answered
using a multivariate framework. That is, a modeling framework containing
multiple response variables, enabling (i) testing of how explanatory variables
(‘fixed effects’) predict these responses, as in standard univariate models, and
(ii) the simultaneous estimation of the variance of each response and the
covariance between them, at group levels specified within the random effects
structure. It is relatively straightforward to rephrase these multivariate
questions in terms of variances and covariances (or derived correlations and
regressions), and to fit multivariate models accordingly (some examples include
Careau et al. 2015; Niemelä et al. 2015; Petelle et al. 2015; Sanderson et al. 2015;
Santostefano et al. 2016; Vallon et al. 2016; White et al. 2016). For instance, we
might hypothesize a behavioral syndrome in which positive correlations are
predicted between the (repeatable) tendencies of individuals to exhibit three
behaviors. Having assayed each of these behaviors on multiple occasions for a
set of individuals, the correct approach would be to estimate – and test the
significance of – those among-individual correlations directly in a trivariate
mixed model incorporating all of the behavioral data. This method yields
correlation estimates with valid measures of uncertainty (SE or CI). This is not
the case when generating individual-level random effect predictions from three
separate univariate models (one for each behavior) and then testing whether
they are correlated. In the latter approach, uncertainty will be underestimated
and thus Type I error is more likely to occur (Figure 1).
On a pragmatic point, we note that it is not required that each variable of interest be a repeated measure in these models – for example, it is perfectly feasible to test for the existence of an among-individual correlation between a personality trait (with repeated measures) and some other variable with only one observation per individual, such as an estimate of its lifetime reproductive success. In the supplementary material, we provide worked examples of how to set up multivariate statistical models to address these (and several similar) questions using the R packages ASReml-R (Butler 2009) and MCMCglmm (Hadfield 2010). These examples provide users with the tools to test their hypotheses in a multivariate framework, incorporating all of their data and avoiding potentially spurious results.

We also note that multivariate mixed models may often provide a more appropriate route to testing hypotheses about multivariate phenotypes in other contexts. For instance, one approach to exploring behavioral syndromes has been to reduce the dimensionality of observed behaviors by performing principal components analysis (PCA) on multivariate data, and then to use univariate mixed models to calculate repeatability on individual scores for each component (e.g., Edenbrow & Croft 2013; Le Galliard et al. 2013; Brent et al. 2014; Patrick & Weimerskirch 2014; Sussman et al. 2014; Rangassamy et al. 2015). This allows us to ask whether, for instance, the major axis of observed behavioral (co)variation is repeatable. This is a valid question but in many cases perhaps not the most pertinent one, since the first principal component of observed variation includes both among- and within-individual trait variation. For studies of individual differences in behavior, the more relevant question
might be better focused at the among-individual level – that is, what does the major axis of among-individual variation look like? If so, then isolating the among-individual (co)variance matrix (sometimes denoted $I$; Wilson et al. 2011) by applying a multivariate mixed model to a set of traits is the proper first step. Principal components (or eigen vectors) of $I$ can then be examined directly. This strategy is probably more appropriate for testing models such as ‘pace of life syndrome’ or stress coping styles that posit trait correlations at the among-individual level – i.e., that these correlations are due to consistent differences among individuals, and not because of some temporary aspect of environmental variation (Koolhaas et al. 2007; Carere et al. 2010; Coppens et al. 2010; Réale, Garant, et al. 2010; Carter et al. 2013). The value of partitioning individual (co)variances has been discussed in more detail by Brommer (2013a), and illustrations exist in the literature of the use of multivariate mixed models for studying pace of life syndrome (White et al. 2016) and stress coping styles (Boulton et al. 2015).

We fully acknowledge that multivariate mixed models are data hungry. However, a failure of these multivariate models to converge to sensible and/or precise solutions does not mean that we can retreat to the relative comfort of previous methods: in fact, this is likely to indicate a lack of power to answer the question at hand (see Martin et al. 2011; Wolak, Fairbairn & Paulsen 2012). In cases where logistical constraints prevent there being enough measurements to partition out the among-individual behavioral (co)variation, a preferable method may sometimes be to work with observed phenotypic (co)variance while acknowledging this and the assumptions that underpin conclusions drawn.
Indeed, much of behavioral ecology is predicated on the 'phenotypic gambit', the assumption that phenotypic patterns of trait (co)variation (denoted $P$) provide a workable proxy for patterns of genetic (co)variance ($G$). If $P$ can be used (with caveats) in place of $G$ where estimation of genetic parameters is not feasible, then it can also be used (with caveats) in place of $I$ where partitioning of among-from within-individual covariation is not feasible.

To conclude, we absolutely wish to encourage more studies that further our understanding of the causes and consequences of individual differences in behavior. However, we also make a plea to the community to avoid inappropriate methods of analysis that lead to spurious precision and increased Type I errors. This field depends upon embracing the power of previously ignored phenotypic variation, and it is flourishing because of the exciting questions we can now address – but we must ensure that we use the right tools when doing so.

REFERENCES


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Gibelli J, Dubois F. 2016. Does personality affect the ability of individuals to track and respond to changing conditions? Behav. Ecol. 0:arw137.


Behav. 103:7–15.


FIGURE LEGENDS

Figure 1: Taken from a worked example provided in the Supplementary Information, (a) shows a scatterplot of individual-level estimates (BLUPs) of two personality traits, extracted from separate univariate models. Bars around each point show the standard error of the estimate for both traits, which is ignored by subsequent analyses of these BLUPs. Testing a correlation using only BLUPs and ignoring their error results in an anticonservative test, as illustrated in (b). The correlation test using BLUPs produces narrow confidence intervals, and a correspondingly small P-value of 0.0019, indicating statistical significance (‘BLUP’ on x-axis). However, testing the correlation directly in a bivariate model using REML and retaining all data returns larger (approximate) confidence intervals which straddle zero (95% CI approximated as $r +/\pm 1.96SE$) and a P-value (based on a likelihood ratio test) of 0.12, such that the correlation is not statistically significant (‘Bivariate ASReml’ on x-axis). Using the same data, Bayesian 95% credible intervals also cross zero, which indicates a lack of statistical significance (‘Bivariate MCMCglmm’).
Table 1: Examples in the behavioural literature of questions regarding individual variation in behaviour (‘personality’) and behavioural plasticity, using best linear unbiased predictors (BLUPs) in secondary analyses rather than multivariate models. All were published after the publication of Hadfield et al (2010).
<table>
<thead>
<tr>
<th>Test</th>
<th>Species</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Behavioural syndromes</td>
<td>Taeniopygia guttata</td>
<td>Wuerz and Krüger 2015</td>
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<tr>
<td></td>
<td>Latrodectus hesperus</td>
<td>Montiglio and DiRienzo 2016</td>
</tr>
<tr>
<td>Personality across life stages</td>
<td>Tamiasciurus hudsonicus</td>
<td>Kelley et al. 2015</td>
</tr>
<tr>
<td></td>
<td>Pomacentrus wardi, P. amboinensis</td>
<td>Beckmann and Biro 2013</td>
</tr>
<tr>
<td>Personality &amp; hormones</td>
<td>Tamias striatus</td>
<td>Montiglio et al. 2012</td>
</tr>
<tr>
<td></td>
<td>Canis latrans</td>
<td>Schell et al. 2016</td>
</tr>
<tr>
<td>Personality &amp; physiology</td>
<td>Cavia aperea</td>
<td>Guenther and Trillmich 2015</td>
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<tr>
<td></td>
<td>C. aperea</td>
<td>Finkemeier et al. 2016</td>
</tr>
<tr>
<td>Personality &amp; telomere length</td>
<td>Salmo trutta</td>
<td>Adriaenssens et al. 2016</td>
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<td>Personality &amp; cognition</td>
<td>C. aperea</td>
<td>Guenther et al. 2014</td>
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<tr>
<td></td>
<td>C. aperea, C. porcellus</td>
<td>Brust and Guenther 2015</td>
</tr>
<tr>
<td>Personality &amp; social network attributes</td>
<td>Anguilla anguilla</td>
<td>Jeffroy et al. 2014</td>
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<td>Personality &amp; local density</td>
<td>Marmota flaviventris</td>
<td>Fuong et al. 2015</td>
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<tr>
<td>Personality &amp; social niche specialisation</td>
<td>T. hudsonicus</td>
<td>Shonfield et al. 2012</td>
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<td>Personality &amp; group-size preference</td>
<td>Suricata suricatta</td>
<td>Carter et al. 2014</td>
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<td>Personality &amp; predation risk</td>
<td>Perca fluviatilis</td>
<td>Hellström et al. 2016</td>
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<td>Personality &amp; mating behaviour</td>
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<td>Magnhagen et al. 2012</td>
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<td>Aquarius remigis</td>
<td>Heynen et al. 2016</td>
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<td>Personality &amp; survival</td>
<td>Gerris buenoi</td>
<td>Wey et al. 2014; Wey et al. 2015</td>
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<td>T. striatus</td>
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<td>Personality &amp; fitness-related traits</td>
<td>S. trutta</td>
<td>Bergeron et al. 2013</td>
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<td>Personality &amp; individual variation in behavioural plasticity</td>
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<td>Adriaenssens and Johnsson 2011</td>
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<td>Personality, behavioural plasticity &amp; reproductive success</td>
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<td>Personality, behavioural plasticity &amp; fitness</td>
<td>A. remigis</td>
<td>Betini and Norris 2012</td>
</tr>
<tr>
<td></td>
<td>Tenagogerris euphrosyne</td>
<td>Montiglio et al. 2016a; Montiglio et al. 2016b</td>
</tr>
</tbody>
</table>

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FIGURES

Figure 1

(a)

(b)

Exploration, Bodiness Correlation +/- 95% CI

BLUP, Bivariate ASReml Method, Bivariate MCMCgmm
Avoiding the misuse of BLUP in behavioral ecology: Multivariate modelling for individual variation (ASReml-R tutorial)

T.M. Houslay & A.J. Wilson, Behavioral Ecology
January 2017

Introduction

Overview

This tutorial accompanies our paper, “Avoiding the misuse of BLUP in behavioral ecology”. Below, we provide worked examples of multivariate statistical methods for directly testing hypotheses about associations between individual variation in behaviour and other traits. Below, we will:

- Test the correlation between two personality traits (behaviours measured repeatedly on individuals);
- Test for an association between these personality traits and a measure of fitness (one value per individual).

In this version, we illustrate these models using the R interface for ASReml, which is commercial software available from VSNi. We have provided a separate tutorial for the free R package MCMCglmm, but note that MCMCglmm uses Bayesian methods while ASReml uses maximum likelihood (and is therefore likely to be more familiar to users of the R package lme4).

Aims

Please note that we do assume readers are familiar with the general principles of specifying univariate mixed effects models, and using diagnostic plots to check that the fitted model does not violate assumptions of the linear model. Readers unfamiliar with using univariate mixed effects models for modelling a single behavioural trait might prefer to start with (for example) Dingemanse & Dochtermann’s 2013 paper, ‘Quantifying individual variation in behaviour: mixed effects modelling approaches’.

We also use various methods for manipulating and visualising data frames using the tidyverse package (including tidyr, dplyr, ggplot2 etc) — more details on their use can be found at http://r4ds.had.co.nz/.

In our tutorial, we aim to teach the following:

- How to phrase questions of interest in terms of variances and covariances (or derived correlations or regressions);
- How to incorporate more advanced model structures, such as:
  - Fixed effects that apply only to a subset of the response traits;
  - Traits which are measured a different number of times (e.g., repeated measures of behaviour and a single value of breeding success);
- Hypothesis testing using likelihood ratio tests.
Packages required

There are several packages that you must have installed in R prior to starting this tutorial:

- `asreml` (note that this should be provided by the vendor, VSNi)
- `lme4`
- `nadin`
- `tidyverse`
- `broom`

‘Study system’

For this tutorial, we have collected data on a population of wild haggis (*Haggis scoticus*) that roam the Highlands of Scotland.

![A male haggis in the wild](http://www.ewood-art.co.uk/)

Figure 1: A male haggis in the wild (thanks to Emma Wood, http://www.ewood-art.co.uk/)

We tag all haggis individually when they emerge from their burrows as juveniles in their first spring. Here, we concentrate on male haggis, which are solitary and territorial. Previous work has identified behaviours that can be measured repeatedly, and used to represent the personality traits **boldness** and **exploration**. We also have the ability to collect a single measure of mating success (as a fitness proxy) for each male at the end of the season.

**Behavioural syndromes**

One type of ‘behavioural syndrome’ is a correlation between personality traits. Since personality can be viewed (under most definitions) as the repeatable (among-individual) component of behaviour, evidence
for the presence of a behavioural syndrome is provided by covariance among behaviours that arises from among-individual differences.

Here we have repeatedly measured behaviours that represent **boldness** and **exploration**. We observed each behaviour 4 times per individual. We also measured their body size on the day of behavioural assay so as to control for general size effects in our statistical models.

**Load libraries and inspect data**

```r
library(lme4)
library(asreml)
library(tidyverse)
library(broom)
library(nadiv)

df_syndrome <- read_csv("syndrome.csv")
```

This data frame has 6 variables:

- Individual **ID**
- The repeat number for each behavioural test, **assay_rep**
- **boldness**, measured 4 times per individual
- **exploration**, measured 4 times per individual
- **fitness**, our measure of mating success, with a single value for each individual
- Individual **body_size**, as measured on the day of testing.

**Univariate models**

We first use the R package **lme4** to determine the proportion of phenotypic variation (adjusted for fixed effects) that is due to differences among individuals, separately for each behaviour. We assume readers have knowledge of these ‘univariate’ models and their use in behavioural studies — if not, there are various other publications that go into them in greater detail (e.g., Dingemanse & Dochtermann (2013)).

**Boldness**

Our model includes fixed effects of the assay repeat number (centred) and individual body size (centred and scaled to standard deviation units), as we wish to control for any systematic effects of these variables on individual behaviour. Please be aware that controlling variables are at your discretion — for example, while we want to characterise among-individual variance in boldness after controlling for size effects in this study, others may wish to characterise among-individual variance in boldness in the absence of such control. Indeed, using the techniques shown later in this tutorial, it would be entirely possible to characterise both among-individual variance in boldness and in size, and the among-individual covariance between these measurements.

```r
lmer_b <- lmer(boldness ~ scale(assay_rep, scale=False) +
                 scale(body_size) +
                 (1|ID),
                 data = df_syndrome)
plot(lmer_b)
qqnorm(residuals(lmer_b))
hist(residuals(lmer_b))
summary(lmer_b)
```
Having examined diagnostic plots of the model fit, we can check the model summary. We are interested in the random effects section of the lme4 model output (specifically the variance component — note that the standard deviation here is simply the square root of the variance). Evidence for ‘animal personality’ (or ‘consistent among-individual differences in behaviour’) in the literature is largely taken from the repeatability of behavioural traits: we can compute this repeatability (also known as the intraclass correlation coefficient) by dividing the variance in the trait due to differences among individuals ($V_{ID}$) by the total phenotypic variance after accounting for the fixed effects ($V_{ID} + V_{residual}$). This can be done quickly and automatically through the use of the R package broom:

```r
rep_bold <- tidy(lmer_b, effects = "ran_pars", scales = "vcov") %>%
  select(group, estimate) %>%
  spread(group, estimate) %>%
  mutate(repeatability = ID/(ID + Residual))
```

So we can see that 37.3% of the phenotypic variation in boldness (having controlled for body size and assay repeat number) is due to differences among individuals.
Exploration

\[
\text{lmer_e} \leftarrow \text{lmer(} \text{exploration} \sim \text{scale(} \text{assay_rep}, \text{scale=FALSE}) + \text{scale(body_size)} + (1|\text{ID}), \text{data = df_syndrome})
\]

\[
\text{rep_expl} \leftarrow \text{tidy(lmer_e, effects = "ran_pars", scales = "vcov") } \%\% \\
\text{select(group, estimate)} \%\% \\
\text{spread(group, estimate)} \%\% \\
\text{mutate(repeatability = ID/(ID + Residual))}
\]

<table>
<thead>
<tr>
<th>ID</th>
<th>Residual</th>
<th>repeatability</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.362</td>
<td>0.909</td>
<td>0.285</td>
</tr>
</tbody>
</table>

Both of our traits of interest are repeatable at the among-individual level — the remaining question is characterising the association between these personality traits. Are individuals that are consistently bolder than average also more exploratory than average (and vice versa)?

Correlation using BLUPs

In our paper, we advise against the use of BLUPs due to their potential for spurious results due to anticonservative hypothesis tests and/or confidence intervals.

Here we will run through this method, purely so that we can then contrast the results with those that we get having (correctly) estimated the among-individual correlation between these behaviours directly from a multivariate model (in this case, bivariate).

We create two data frames of individual predictions extracted from model fits, one for each of our univariate \text{lme4} models for boldness and exploration. We then join these (by individual ID) to create a single data frame:

\[
\text{df_BLUPS_B} \leftarrow \text{data_frame(ID = row.names(ranef(lmer_b)$ID),} \\
\text{BLUP_B = ranef(lmer_b)$ID[, "(Intercept)"])}
\]

\[
\text{df_BLUPS_E} \leftarrow \text{data_frame(ID = row.names(ranef(lmer_e)$ID),} \\
\text{BLUP_E = ranef(lmer_e)$ID[, "(Intercept)"])}
\]

\[
\text{df_BLUPS_EB} \leftarrow \text{left_join(df_BLUPS_E,} \\
\text{df_BLUPS_B,} \\
\text{by = "ID")}
\]

We can plot these to see what our expectation of a correlation might be:
..and then simply perform a correlation test of these two traits using the `cor.test` function:

```r
cor.test(df_BLUPS_EB$BLUP_E, df_BLUPS_EB$BLUP_B)
```

```
## Pearson's product-moment correlation
## data: df_BLUPS_EB$BLUP_E and df_BLUPS_EB$BLUP_B
## t = 3.2131, df = 78, p-value = 0.00191
## alternative hypothesis: true correlation is not equal to 0
## 95 percent confidence interval:
## 0.1320924 0.5223645
## sample estimates:
## cor
## 0.3418867
```

As you can see, we get a positive correlation with a very small p-value ($P = 0.0019$), indicating that these traits are involved in a behavioural syndrome. While the correlation itself is fairly weak ($r = 0.34$), it appears to be highly significant, and suggests that individuals that are bolder than average also tend to be more exploratory than average.

However, as discussed in our paper (and in greater detail by Hadfield *et al*), using BLUPs in this way leads to anticonservative significance tests. This is because the error inherent in their prediction is not carried forward from the `lmer` models to the subsequent analysis (in this case, a correlation test). To illustrate this point quickly, below we plot the individual estimates along with their associated standard errors:
We now go on to estimate the correlation between these behaviours directly in a multivariate model, using ASreml.

**Bivariate models**

The correct approach for testing the hypothesised behavioural syndrome uses both response variables in a two-trait (‘bivariate’) mixed model. This model estimates the among-individual variance for each response variable (and the covariance between them). Separate (co)variances are also fitted for the residual variation. The bivariate model also allows for fixed effects to be fitted on both response variables.

We set up our model using the `asreml` function call, with our bivariate response variable being `exploration` and `boldness` bound together using `cbind`. You will also note that we `scale` our response variables, meaning that each is centred at their mean value and standardised to units of 1 standard deviation. This is not essential, but simply makes it easier for the model to be fit. Scaling the response variables also aids our understanding of the output, as both boldness and exploration are now on the same scale.

```r
asr_E_B_us <- asreml(cbind(scale(exploration), scale(boldness)) ~ trait + 
                      trait:scale(assay_rep, scale = FALSE) + 
                      trait:scale(body_size), 
                      random = ID:us(trait, init = c(1, 0.1, 1)), 
                      rcov =~ units:us(trait, init = c(0.1, 0.1, 0.1)), 
                      data = df_syndrome, 
                      maxiter = 100)
```
On the right hand side of our model formula, we use the \texttt{trait} keyword to specify that this is a multivariate model — \texttt{trait} itself tells the model to give us the intercept for each trait. We then interact \texttt{trait} with our fixed effects, \texttt{assay\_rep} and \texttt{body\_size}, so that we get estimates for the effect of these variables on each of our behaviours.

Our random effects structure starts with the \texttt{random} effects, where we tell the model to fit an ‘unstructured’ (us) covariance matrix for the grouping variable \texttt{ID}. This means that we want to calculate the variance in exploration due to differences among individuals, the variance in boldness due to differences among individuals, and the \texttt{covariance} between these variances.

Next, we set a structure for the residual variation (\texttt{rcoev}), which is also sometimes known as the ‘within-individual variation’. As we have repeated measures for both traits at the individual level, we also set an unstructured covariance matrix, which finds the residual variance for each trait and also allows the residuals to covary across the two traits.

Finally, we provide the name of the data frame, and a maximum number of iterations for \texttt{ASReml} to attempt to fit the model.

After the model has been fit by \texttt{ASReml}, we can check the fit using the same type of model diagnostic plots as we use for \texttt{lme4}:

\begin{verbatim}
plot(residuals(asr_E_B_us)-fitted(asr_E_B_us))
qqnorm(residuals(asr_E_B_us))
hist(residuals(asr_E_B_us))
\end{verbatim}

The \texttt{summary} part of the \texttt{ASReml} model fit contains a large amount of information, so it is best to look only at certain parts of it at a single time. While we are not particularly interested in the fixed effects for current purposes, you can inspect these using the following code to check whether there were any large effects of assay repeat or body size on either trait:

\begin{verbatim}
summary(asr_E_B_us, all=T)$coef.fixed
\end{verbatim}

We can see that there is a separate intercept for both personality traits (no surprise that these are very close to zero, given that we mean-centred and scaled each trait before fitting the model), and an estimate of the effect of assay repeat and body size on both traits. None of these appear to be large effects, so let’s move on to the more interesting parts — the random effects estimates:

\begin{verbatim}
summary(asr_E_B_us)$varcomp
\end{verbatim}

\begin{verbatim}
## gamma component std.error
## ID:trait!trait.exploration:exploration 0.2863101 0.2863101 0.07637361
## ID:trait!trait.boldness:exploration 0.0883864 0.0883864 0.06067166
## ID:trait!trait.boldness:boldness 0.3733306 0.3733306 0.08607573
## R!variance 1.0000000 1.0000000 NA
## R!trait.exploration:exploration 0.7184419 0.7184419 0.06572786
## R!trait.boldness:exploration 0.3263211 0.3263211 0.04829180
## R!trait.boldness:boldness 0.6274169 0.6274169 0.05740290
## z.ratio constraint
## ID:trait!trait.exploration:exploration 3.748810 Positive
## ID:trait!trait.boldness:exploration 1.456799 Positive
## ID:trait!trait.boldness:boldness 4.337234 Positive
## R!variance NA Fixed
## R!trait.exploration:exploration 10.930554 Positive
## R!trait.boldness:exploration 6.757279 Positive
## R!trait.boldness:boldness 10.930055 Positive
\end{verbatim}

Multivariate modelling for individual variation
In the above summary table, we have the among-individual (co)variances listed first (starting with ID), then the residual (or within-individual) (co)variances (starting with R). You will notice that the variance estimates here are actually close to the lme4 repeatability estimates, because our response variables were scaled to phenotypic standard deviations. We can also find the ‘adjusted repeatability’ (i.e., the repeatability conditional on the fixed effects) for each trait by dividing its among-individual variance estimate by the sum of its among-individual and residual variances.

Here, we use the pin function from the nadiv package (Wolak 2012) to estimate the repeatability and its standard error for each trait, conditional on the effects of assay repeat and body size. For this function, we provide the name of the model object, followed by a name that we want to give the estimate being returned, and a formula for the calculation. Each ‘V’ term in the formula refers to a variance component, using its position in the model summary shown above.

```r
nadiv:::pin(asr_E_B_us, prop_expl ~ V1/(V1+V5))
nadiv:::pin(asr_E_B_us, prop_bold ~ V3/(V3+V7))
```

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>prop_expl</td>
<td>0.284956</td>
<td>0.06113612</td>
</tr>
<tr>
<td>prop_bold</td>
<td>0.3730518</td>
<td>0.06124283</td>
</tr>
</tbody>
</table>

We can also use this function to calculate the estimate and standard error of the correlation from our model (co)variances. We do this by specifying the formula for the correlation:

```r
nadiv:::pin(asr_E_B_us, cor ~ V2/(sqrt(V1)*sqrt(V3)))
```

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>cor</td>
<td>0.2703462</td>
<td>0.1594158</td>
</tr>
</tbody>
</table>

In this case, the estimate is similar (here, slightly lower) than our correlation estimate using BLUPs. However, if we consider confidence intervals as +/- 1.96SE around the estimate, the lower bound of the confidence interval would actually be -0.042. With confidence intervals straddling zero, we would conclude that this correlation is likely non-significant. As the use of standard errors in this way is only approximate, we should also test our hypothesis formally using likelihood ratio tests.

**Hypothesis testing**

We can now test the statistical significance of this correlation directly, by fitting a second model without the among-individual covariance between our two behavioural traits, and then using a likelihood ratio test to determine whether the model with the covariance produces a better fit.

Here, we use the idh structure for our random effects. This stands for ‘identity matrix’ (i.e., with 0s on the off-diagonals) with heterogeneous variances (i.e., the variance components for our two response traits are allowed to be different from one another). The rest of the model is identical to the us version.

```r
asr_E_B_idh <- asreml(cbind(scale(exploration),
                        scale(boldness)) ~ trait +
                        trait:scale(assay_rep, scale = FALSE) +
                        trait:scale(body_size),
                        random = ~ ID:idh(trait, init = c(1,1)),
                        rcov = ~ units:us(trait, init = c(0.1, 0.1, 0.1)),
                        data = df_syndrome,
                        maxiter = 100)
```

Multivariate modelling for individual variation
The likelihood ratio test is calculated as twice the difference between model log-likelihoods, on a single degree of freedom (the covariance term):

\[
\text{pchisq}(2 \times (\text{asr_E_B_us$loglik - asr_E_B_idh$loglik}), 1, \text{lower.tail} = \text{FALSE})
\]

## [1] 0.1170403

In sharp contrast to the highly-significant P-value given by a correlation test using BLUPs, here we find no evidence for a behavioural syndrome between exploration and boldness.

To better understand why BLUPs produce an anticonservative p-value in comparison to multivariate models, we should plot the correlation estimates and their confidence intervals. The confidence intervals are taken directly from the `cor.test` function for BLUPs, and for ASReml they are calculated as 1.96 times the standard error from the `pin` function.

### Comparison of methods for testing behavioural syndromes

*Correlation between individual variation in both exploration and boldness*

Here we can clearly see that the BLUPs method - having failed to carry through the error around the predictions of individual-level estimates - is anticonservative, with small confidence intervals and a correspondingly small P-value (\(P = 0.0019\)). Testing the syndrome directly in a bivariate model that retains all the data, by comparison, enables us to capture the true uncertainty about the estimate of the correlation. This is reflected in the larger confidence intervals and, in this case, the non-significant P-value (\(P = 0.117\)).

### Adding further traits

As part of our data collection, we also have a single value of mating success for each individual (which we will use as a proxy for fitness). We are interested in whether our personality traits are associated with variation...
in this fitness-related measure. While our test above showed that the correlation between the measured personality traits was not significant, there did appear to be some relationship — so we shall incorporate both personality traits and fitness into a single trivariate model for hypothesis testing.

In this case, because the new response variable to be added to our model is fitness, we are not going to mean-centre and scale by phenotypic standard deviations, but instead divide by the mean fitness value (such that we are investigating among-individual covariance between personality traits and relative fitness). We create this new variable, rel_fitness, as follows:

```r
df_syndrome <- df_syndrome %>%
  mutate(rel_fitness = fitness/mean(fitness, na.rm=TRUE))
```

Note that we will refer to this relative fitness trait simply as ‘fitness’ below for simplicity’s sake.

**Setting up the model**

Below, we will set up our main model, which will allow for heterogeneous among-individual variances in our 3 traits (boldness, exploration, fitness), and will estimate the associations between them. Note, however, that we will use the corgh structure instead of us in the random effects. These structures fit the same model, but on a correlation rather than covariance scale. Note in this case we are just using corgh because it makes it easier in ASReml to specify some constraints that we require and (as we will see later, we can always backcalculate the covariances from the estimated correlations if we want them).

First, we set up starting values from the model, which we also use to set some constraints. We set constraints in ASReml by specifying some starting values in a numeric vector, then giving each value a ‘name’ that corresponds to how ASReml should treat the corresponding part of the random effects matrix during model fitting:

- U: Unconstrained (can take any value, positive or negative)
- P: Positive (must be a positive value)
- F: Fixed (remains fixed at the given value)

An important point: while the starting values (init) for the us structure were provided in the form of the lower triangle of a covariance matrix, for corgh we provide the correlations first, and then the variances.

For the random effects, we set generic starting values — the 3 correlations have starting values close to 0 and are unconstrained, while the variance components have starting values of unit variance (and are constrained to be positive values):

```r
init_E_B_fit_cor <- c(0.1,
  0.1,0.1,
  1,1,1)
names(init_E_B_fit_cor) <- c("U", "U", "U",
  "P", "P", "P")
```

For the residuals (or ‘within-individual’ variance), we must bear in mind that we have only a single fitness value per individual — therefore, that trait has no within-individual variance, and **within-individual correlations involving fitness must be set to zero as they cannot be estimated**. We set the starting value for both correlations to 0 below, and denote them as fixed at those values using ‘F’. The variance component is slightly trickier — variances have to be positive, therefore we simply fix the within-individual variance at a very small positive number (here, 1e-08 — i.e., so small as to be effectively 0):
Adding further traits

ASReml-R tutorial

BEHAVIOURAL SYNDROMES

init_E_B_fit_res <- c(0.1,
0.0,
0.1, 0.1, 1e-08)

names(init_E_B_fit_res) <- c("U",
"F", "F",
"P", "P", "F")

Now, we can fit our model with these starting values and constraints. Again, we `cbind` our response variables on the left-hand side of the formula, and use `trait` to denote a multivariate model. Remember that we have created the ‘relative fitness’ variable by essentially scaling by its mean, so this does not need to be scaled as the behavioural traits are.

We can also use the `at` keyword to specify that fixed effects are estimated only for certain traits — here, we test for an effect of assay repeat only on exploration and boldness (because these were measured repeatedly), while we test for the effect of body size on all of our traits.

Fit the model as follows (and be sure to use visual diagnostic checks of the residuals):

```r
asr_E_B_fit_cor <- asreml(cbind(scale(exploration),
scale(boldness),
rel_fitness) ~
trait +
at(trait,1):assay_rep +
at(trait,2):assay_rep +
trait:scale(body_size),
random =- ID:corgh(trait, init = init_E_B_fit_cor),
rcov =- units:corgh(trait, init = init_E_B_fit_res),
data = df_syndrome, 
maxiter = 500)
```

We can take a quick look at the fixed effects:

```r
summary(asr_E_B_fit_cor, all=T)$coef.fixed
```

Below, we specify that we want to look at the variance components using `$varcomp`. In the interests of space, we will request only the `component` (i.e., the variance estimate) and its `std.error`:

```r
summary(asr_E_B_fit_cor)$varcomp[,c("component","std.error")]
```

```
## component std.error
## ID:trait!trait.boldness:!trait.exploration.cor 0.27031497 0.159419988
## ID:trait!trait.rel_fitness:!trait.exploration.cor 0.23386699 0.138687881
## ID:trait!trait.rel_fitness:!trait.boldness.cor 0.66168293 0.087961997
## ID:trait!trait.exploration 0.28630613 0.076372770
## ID:trait!trait.boldness 0.37322016 0.086051330
## ID:trait!trait.rel_fitness 0.05659086 0.009060437
## R!variance 1.00000000 NA
## R!trait.boldness:!trait.exploration.cor 0.48603894 0.049410253
## R!trait.rel_fitness:!trait.exploration.cor 0.00000000 NA
## R!trait.rel_fitness:!trait.boldness.cor 0.00000000 NA
## R!trait.exploration 0.71844420 0.065728071
## R!trait.boldness 0.62744922 0.057405898
## R!trait.rel_fitness 0.00000001 NA
```
Here we can see that the fit provides us with estimates and standard errors of:

- 3 among-individual correlations;
- 3 among-individual variance components;
- 3 within-individual correlations;
- 3 within-individual variance components.

You can see from the estimates that our constraints have worked in the model: within-individual correlations featuring fitness are at 0, and the residual fitness variance is a very small positive number (such that all the variation is at the among-individual level).

A quick sanity check also tells us that the correlation between boldness and exploration (the first variance component in our summary table above, \( r = 0.27 \) SE 0.159) estimated in this model is the same as in our earlier bivariate model.

From a first glance at the correlation estimates and their associated standard errors, it appears likely that there is a significant among-individual correlation between relative fitness and boldness (\( r = 0.662 \) SE 0.088), but not between relative fitness and exploration (\( r = 0.234 \) SE 0.139).

**Hypothesis testing**

We can again use likelihood ratio tests for hypothesis testing with these models. We first test for an association between relative fitness and our bivariate personality phenotype (defined by the two traits). We do this by fixing both correlations with fitness (\( r_{\text{boldness,fitness}} \) and \( r_{\text{exploration,fitness}} \)) to 0. We then use a likelihood ratio test to analytically compare our main model (with all correlations estimated) to this second model (no correlation between fitness and boldness/exploration), which tests whether allowing those correlations provides a statistically significant improvement in the model fit. Note this is not testing the significance of each trait-fitness correlation separately, it is testing whether there is any significant fitness-phenotype correlation overall.

We set the correlations to 0 as follows:

```r
init_E_B_fit_cor_FEB0 <- c(0.1, 0, 1, 1, 1)
names(init_E_B_fit_cor_FEB0) <- c("U", "F", "F", "P", "P")
asr_E_B_fit_cor_FEB0 <- asreml(cbind(scale(exploration),
  scale(boldness),
  rel_fitness) ~ trait +
  at(trait,1):assay_rep +
  at(trait,2):assay_rep +
  trait:scale(body_size),
  random =- ID:corgh(trait, init = init_E_B_fit_cor_FEB0),
  rcov =- units:corgh(trait, init = init_E_B_fit_res),
  data = df_syndrome,
  maxiter = 800)
```

We then test the difference in model fits using a likelihood ratio test with 2 degrees of freedom:
Here we find evidence of significant correlation structure — based on the estimates and SEs from the model summary, it’s a fairly safe bet that this is being driven by the fitness-boldness association. If tests of each of the specific trait-fitness correlations are needed, we advise using pairwise models (but note of course that multiple testing issues might require consideration if you want to statistically test every pairwise correlation estimate and you have a lot of traits). We will fit the two bivariate trait-fitness models below for completeness, and they should confirm our suspicions about which personality trait is driving the correlation between the bivariate behavioural phenotype and fitness.

As with tests of the earlier bivariate models for behavioural syndromes, we fit models with both us and idh structures (or corgh with setting the correlation to 0) for hypothesis testing using likelihood ratio tests. In this case, we also have to set the residual variation in fitness to a very small (near-zero) positive number, and we do not fit a residual covariance. Here we demonstrate for boldness and fitness:

```r
init_fitbiv_res <- c(0.1, 1e-08)
names(init_fitbiv_res) <- c("P", "F")
asr_B_fit_us <- asreml(cbind(scale(boldness),
                      rel_fitness) ~ trait +
                      at(trait,1):assay_rep +
                      trait:scale(body_size),
                      random =~ ID:us(trait, init = c(1, 0.1, 1)),
                      rcov =~ units:idh(trait, init = init_fitbiv_res),
                      data = df_syndrome,
                      maxiter = 800)
asr_B_fit_idh <- asreml(cbind(scale(boldness),
                          rel_fitness) ~ trait +
                          at(trait,1):assay_rep +
                          trait:scale(body_size),
                          random =~ ID:idh(trait, init = c(1, 1)),
                          rcov =~ units:idh(trait, init = init_fitbiv_res),
                          data = df_syndrome,
                          maxiter = 800)
```

We can now run the same test for exploration and fitness:

```r
## [1] 8.164003e-08
```

As we had anticipated from the estimate and standard error of the correlations in our trivariate model, the association between individual variation in boldness and relative fitness is significant, while there is no evidence for a significant association between individual variation in exploration and fitness.
A slight digression: converting correlations back to covariances can be useful

While we set up the trivariate model to output results in terms of correlation matrices, we could have fit the model on a covariance scale using \texttt{us}. While correlations are intuitive, sometimes having the answers on the covariance scale is useful. For instance, in the current example, the trait-fitness correlations could be used to infer selection — but if we wanted to express the strength of that selection, the normal way to do so is through selection differentials. These are the trait – (relative) fitness covariances, and/or selection gradients (the partial regressions of relative fitness on traits which can be calculated from variance and covariance terms).

Since a correlation is simply the covariance rescaled by the product of the squared variances, we can retrieve the covariance terms by simply rearranging as follows:

$$\text{COV}_{T_1,T_2} = r_{T_1,T_2} \times \sqrt{V_{T_1}} \times \sqrt{V_{T_2}}$$

Again, the \texttt{pin} function comes to our rescue. As an example, we can get the covariance between exploration and boldness from our trivariate model (with \texttt{corgh} correlation-structure) as follows:

\begin{verbatim}
nadiv:::pin(asr_E_B_fit_cor, cov_E_B ~ V1*sqrt(V4)*sqrt(V5))
\end{verbatim}

<table>
<thead>
<tr>
<th>## Estimate</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>cov_E_B</td>
<td>0.08836249 0.06066255</td>
</tr>
</tbody>
</table>

We might want to present our final results as a matrix with variances on the diagonals, covariances below and correlations above (with standard errors in parentheses):

<table>
<thead>
<tr>
<th></th>
<th>Exploration</th>
<th>Boldness</th>
<th>Fitness</th>
</tr>
</thead>
<tbody>
<tr>
<td>Exploration</td>
<td>0.29 (0.08)</td>
<td>0.27 (0.16)</td>
<td>0.23 (0.14)</td>
</tr>
<tr>
<td>Boldness</td>
<td>0.09 (0.06)</td>
<td>0.37 (0.09)</td>
<td>0.66 (0.09)</td>
</tr>
<tr>
<td>Fitness</td>
<td>0.03 (0.02)</td>
<td>0.1 (0.02)</td>
<td>0.06 (0.01)</td>
</tr>
</tbody>
</table>

Conclusions

To conclude, then: we found that the correlation between boldness and exploration tends to be positive among male haggis. This correlation is not statistically significant, and thus does not provide strong evidence for a behavioural syndrome. However, inappropriate analysis of BLUP extracted from univariate models would lead to a different (erroneous) conclusion. We also found no statistically significant association between among-individual variation in exploration and fitness. However, we did find a statistically significant positive association between among-individual variation in boldness and our fitness proxy, indicating that bolder male haggis had greater mating success (see figure below).

Note: below, we use BLUPs from our trivariate model to construct a figure that illustrates the association between boldness and fitness. Unlike its use in secondary statistical analyses, this is an appropriate use of BLUPs — i.e., just for illustrative purposes!
Further tutorials

We will continue to develop tutorials for multivariate modelling of individual (co)variation, which will cover some of the more advanced issues discussed in our paper. Please visit tomhouslay.com for more information.
Avoiding the misuse of BLUP in behavioral ecology: Multivariate modelling for individual variation
(MCMCglmm tutorial)

T.M. Houslay & A.J. Wilson, Behavioral Ecology
January 2017

Introduction

Overview

This tutorial accompanies our paper, “Avoiding the misuse of BLUP in behavioral ecology”. Below, we provide worked examples of multivariate statistical methods for directly testing hypotheses about associations between individual variation in behaviour and other traits. Below, we will:

- Test the correlation between two personality traits (behaviours measured repeatedly on individuals);
- Test for an association between these personality traits and a measure of fitness (one value per individual).

In this version of the tutorial, we illustrate these models using the R package MCMCglmm, developed by Jarrod Hadfield. Visit the CRAN page for MCMCglmm here for links and citation info: https://cran.r-project.org/web/packages/MCMCglmm/index.html.

MCMCglmm fits generalised linear mixed modes (GLMMs) in a Bayesian framework, using Markov chain Monte Carlo techniques. We have also provided a separate tutorial for the R interface for ASReml, which fits GLMMs using maximum likelihood (and so is likely more familiar to lme4 users) but is commercially licensed software.

Aims

Please note that we do assume readers are familiar with the general principles of specifying mixed effects models, and in particular with the use of MCMCglmm for univariate mixed effects models. Readers unfamiliar with using univariate mixed effects models for modelling a single behavioural trait might prefer to start with Dingemanse & Dochtermann’s 2013 paper, ‘Quantifying individual variation in behaviour: mixed effects modelling approaches’. Readers unfamiliar with MCMCglmm should look at Jarrod Hadfield’s excellent course notes, available at the MCMCglmm CRAN page: https://cran.r-project.org/web/packages/MCMCglmm/index.html.

We also use various methods for manipulating and visualising data frames using the tidyverse package (including tidyr, dplyr, ggplot2 etc) — more details on their use can be found at http://r4ds.had.co.nz/.

In our tutorial, we aim to teach the following:

- How to phrase questions of interest in terms of variances and covariances (or derived correlations or regressions);
- How to incorporate more advanced model structures, such as:
  - Fixed effects that apply only to a subset of the response traits;
  - Traits which are measured a different number of times (e.g., repeated measures of behaviour and a single value of breeding success);
- Interpreting MCMC credible intervals.
Packages required

There are several packages that you must have installed in R prior to starting this tutorial:

- MCMCglmm
- lme4
- nadi
- tidyverse
- broom

‘Study system’

For this tutorial, we have collected data on populations of wild haggis that roam the Highlands of Scotland.

![Figure 1](http://www.ewood-art.co.uk/)  

Figure 1: A male haggis in the wild (thanks to Emma Wood, http://www.ewood-art.co.uk/)

We tag all haggis individually when they emerge from their burrows as juveniles in their first spring. Here, we concentrate on male haggis, which are solitary and territorial. Previous work has identified behaviours that can be measured repeatedly, and used to represent three personality traits: **boldness**, **exploration**, and **aggression**. We also have the ability to collect a single measure of mating success (as a fitness proxy) for each male at the end of the season.

Behavioural syndromes

One type of ‘behavioural syndrome’ is a correlation between personality traits. Since personality can be viewed (under most definitions) as the repeatable (among-individual) component of behaviour, evidence for the presence of a behavioural syndrome is provided by covariance among behaviours that arises from among-individual differences.
Here we have repeatedly measured behaviours that represent **boldness** and **exploration**. We observed each behaviour 4 times per individual. We also measured their body size on the day of behavioural assay to control for general size effects. in our statistical models.

**Load libraries and inspect data**

```r
library(lme4)
library(MCMCglmm)
library(tidyverse)
library(broom)
library(nadiv)

df_syndrome <- read_csv("syndrome.csv")
```

This data frame has 6 variables:

- Individual **ID**
- The repeat number for each behavioural test, **assay_rep**
- **boldness**, measured 4 times per individual
- **exploration**, measured 4 times per individual
- **fitness**, our measure of mating success, with a single value for each individual
- Individual **body_size**, as measured on the day of testing.

**Univariate models**

We first use the R package **lme4** to determine the proportion of phenotypic variation (adjusted for fixed effects) that is due to differences among individuals, separately for each behaviour. We assume readers have knowledge of these ‘univariate’ models and their use in behavioural studies — if not, there are various other publications that go into them in greater detail (e.g., Dingemanse & Dochtermann (2013)).

**Boldness**

Our model includes fixed effects of the assay repeat number (centred) and individual body size (centred and scaled to standard deviation units), as we wish to control for any systematic effects of these variables on individual behaviour. Please be aware that controlling variables are at your discretion — for example, while we want to characterise among-individual variance in boldness after controlling for size effects in this study, others may wish to characterise among-individual variance in boldness without such control. Indeed, using the techniques shown later in this tutorial, it would be entirely possible to characterise both among-individual variance in boldness and in size, and the among-individual covariance between these measurements.

```r
lmer_b <- lmer(boldness ~ scale(assay_rep, scale=FALSE) +
               scale(body_size) +
               (1|ID),
               data = df_syndrome)
plot(lmer_b)
qqnorm(residuals(lmer_b))
hist(residuals(lmer_b))
summary(lmer_b)
```
## Linear mixed model fit by REML ['lmerMod']

Formula: boldness ~ scale(assay_rep, scale = FALSE) + scale(body_size) +
         (1 | ID)

Data: df_syndrome

REML criterion at convergence: 1061.4

Scaled residuals:
     Min   1Q Median   3Q   Max
-2.3645 -0.6496 -0.1154 0.6463 2.6894

Random effects:
   Groups   Name   Variance Std.Dev.
   ID (Intercept) 0.6951  0.8337
   Residual       1.1682  1.0808
   Number of obs: 320, groups: ID, 80

Fixed effects:
   Estimate Std. Error   t value
   (Intercept) 20.09133   0.11108 180.87
   scale(assay_rep, scale = FALSE) -0.04805   0.05404  -0.89
   scale(body_size)  0.14128   0.10893   1.30

Correlation of Fixed Effects:
           (Intr) s(_s=F)
 scale(_s=F) 0.000
 scl(bdy_sz) 0.000 -0.002

Having examined diagnostic plots of the model fit, we can check the model summary. We are interested in the random effects section of the lme4 model output (specifically the variance component — note that the standard deviation here is simply the square root of the variance). Evidence for ‘animal personality’ (or ‘consistent among-individual differences in behaviour’) in the literature is largely taken from the repeatability of behavioral traits: we can compute this repeatability (also known as the intraclass correlation coefficient) by dividing the variance in the trait due to differences among individuals (V_{ID}) by the total phenotypic variance after accounting for the fixed effects (V_{ID} + V_{residual}). This can be done quickly and automatically through the use of the R package broom:

```r
rep_bold <- tidy(lmer_b, effects = "ran_pars", scales = "vcov") %>%
  select(group, estimate) %>%
  spread(group, estimate) %>%
  mutate(repeatability = ID/(ID + Residual))
```

<table>
<thead>
<tr>
<th>ID</th>
<th>Residual</th>
<th>repeatability</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.695</td>
<td>1.168</td>
<td>0.373</td>
</tr>
</tbody>
</table>

So we can see that 37.3% of the phenotypic variation in boldness (having controlled for body size and assay repeat number) is due to differences among individuals.

Let’s do the same for our other behavioural trait, exploration:
Exploration

\texttt{\textcolor{red}{lmer_e <- lmer(\texttt{exploration} - \texttt{scale(assay_rep, scale=FALSE)} +
  \texttt{scale(body_size)} +
  \texttt{(1|ID)},
  \texttt{data = df_syndrome})}}

\texttt{\textcolor{red}{rep_expl <- tidy(lmer_e, effects = "ran_pars", scales = "vcov") %>%
  select(group, estimate) %>%
  spread(group, estimate) %>%
  mutate(repeatability = ID/(ID + Residual))}}

\begin{tabular}{ccc}
\hline
ID & Residual & repeatability \\
\hline
0.362 & 0.909 & 0.285 \\
\hline
\end{tabular}

Both of our traits of interest are repeatable at the among-individual level — the remaining question is characterising the association between these personality traits. Are individuals that are consistently bolder than average also more exploratory than average (and vice versa)?

\textbf{Correlation using BLUPs}

In our paper, we advise against the use of BLUPs due to their potential for spurious results due to anticonservative hypothesis tests and/or confidence intervals.

Here we will run through this method, purely so that we can then contrast the results with those that we get having (correctly) estimated the among-individual correlation between these behaviours directly from a multivariate model (in this case, bivariate).

We create two data frames of individual predictions extracted from model fits, one for each of our univariate \textit{lme4} models for boldness and exploration. We then join these (by individual ID) to create a single data frame:

\texttt{\textcolor{red}{df_BLUPS_B <- data_frame(ID = row.names(ranef(lmer_b)$ID),
  BLUP_B = ranef(lmer_b)$ID[,"(Intercept)"])}}

\texttt{\textcolor{red}{df_BLUPS_E <- data_frame(ID = row.names(ranef(lmer_e)$ID),
  BLUP_E = ranef(lmer_e)$ID[,"(Intercept)"])}}

\texttt{\textcolor{red}{df_BLUPS_EB <- left_join(df_BLUPS_E,
  df_BLUPS_B,
  by = "ID")}}

We can plot these to see what our expectation of a correlation might be:
Correlation using BLUPs

Exploration (BLUP)

and then simply perform a correlation test of these two traits using the cor.test function:

```r
cor.test(df_BLUPS_EB$BLUP_E, df_BLUPS_EB$BLUP_B)
```

As you can see, we get a positive correlation with a very small p-value \((P = 0.0019)\), indicating that these traits are involved in a behavioural syndrome. While the correlation itself is fairly weak \((r = 0.34)\), it appears to be highly significant, and suggests that individuals that are bolder than average also tend to be more exploratory than average.

However, as discussed in our paper (and in greater detail by Hadfield et al), using BLUPs in this way leads to anticonservative significance tests. This is because the error inherent in their prediction is not carried forward from the \texttt{lmer} models to the subsequent analysis (in this case, a correlation test). To illustrate this point quickly, below we plot the individual estimates along with their associated standard errors:
We now go on to estimate the correlation between these behaviours directly in a multivariate model, using MCMCglmm.

Bivariate models

The correct approach for testing the hypothesised behavioural syndrome uses both response variables in a two-trait (‘bivariate’) mixed model. This model estimates the among-individual variance for each response variable (and the covariance between them). Separate (co)variances are also fitted for the residual variation. The bivariate model also allows for fixed effects to be fitted on both response variables.

First, we need to create a ‘prior’ for our model. We recommend reading up on the use of priors; briefly, we use a parameter-expanded prior here that should be uninformative for our model. One of the model diagnostic steps that should be used later is to check that the model is robust to multiple prior specifications.

```r
prior_E_B_1px = list(R = list(V = diag(2), nu = 0.002),
                  G = list(G1 = list(V = diag(2), nu = 2,
                                 alpha.mu = rep(0,2),
                                 alpha.V = diag(25^2,2,2))))
```

We set up our model using the `MCMCglmm` function call, with our bivariate response variable being **exploration** and **boldness** bound together using `cbind`. You will also note that we **scale** our response variables, meaning that each is centred at their mean value and standardised to units of 1 phenotypic standard deviation. This simply makes it easier for the model to be fit, and for us to understand the output, as both boldness and exploration are now on the same scale.
mcmc_E_B_us <- MCMCglmm(cbind(scale(exploration), scale(boldness)) ~ trait-1 +
       trait:scale(assay_rep, scale = FALSE) +
       trait:scale(body_size),
    random = us(trait):ID,
    rcov = us(trait):units,
    family = c("gaussian","gaussian"),
    prior = prior_E_B_1px,
    nitt=420000,
    burnin=20000,
    thin=100,
    verbose = TRUE,
    data = as.data.frame(df_syndrome))

On the right hand side of our model formula, we use the **trait** keyword to specify that this is a multivariate model — **trait-1** effectively tells the model to give us a distinct intercept for each trait. We then interact **trait** with our fixed effects, **assay_rep** and **body_size**, so that we get estimates for the effect of these variables on each of our behaviours.

Our random effects structure starts with the **random** effects, where we tell the model to fit an ‘unstructured’ (us) covariance matrix for the grouping variable **ID**. This means that we want to calculate the variance in exploration due to differences among individuals, the variance in boldness due to differences among individuals, and the **covariance** between these variances.

Next, we set a structure for the residual variation (**rcov**), which is also sometimes known as the ‘within-individual variation’. As we have repeated measures for both traits at the individual level, we also set an unstructured covariance matrix, which finds the residual variance for each trait and also allows these variances to covary.

We then provide the name of the object we set up as the model prior, and values for the total number of iterations (**nitt**), the ‘burn-in’ of initial iterations to be discarded as the model starts to converge (**burnin**), and the number of iterations to discard in between successive stored samples (**thin**, which helps to reduce autocorrelation in sampling).

Finally, we provide the name of the data frame — we enclose this in the **as.data.frame** function as MCMCglmm does not work with the **tbl_df** format used in the tidyverse group of packages.

After the model has been fit by MCMCglmm (which will take some time!), we can check some model diagnostics using plots of the MCMC samples. Here we show just the plots for our variance components (these plots are also available for fixed effects, using Sol):

```
plot(mcmc_E_B_us$VCV)
```

For current purposes these should look fine, assuming you have used our simulated data and the settings above. Note however that for any real analysis various other tests (e.g. of autocorrelation, robustness to different priors, and good model convergence using the geweke.diag and gelman.diag diagnostic functions) should be used before accepting final results.

The summary part of the MCMCglmm model fit contains a large amount of information. Some general information at the start of the summary includes the model **DIC**. The **G-structure** then contains information about the random effects (co)variances, the **R-structure** the residual (co)variances, and the **Location effects** holds the fixed effects results information.

Each of these sections provides the mean of the posterior distribution returned by MCMCglmm, in addition to the lower and upper bounds of the 95% credible intervals. The effective sample size is also provided, and – for the fixed effects only – a pMCMC value.
## Iterations = 20001:419901
## Thinning interval = 100
## Sample size = 4000
##
## DIC: 1596.616
##
## G-structure: ~us(trait):ID
##
## | post.mean | l-95% CI | u-95% CI | eff.samp |
## |-----------|---------|---------|----------|
## | traitexploration:traitexploration.ID | 0.29234 | 0.14609 | 0.4538  | 4000   |
## | traitboldness:traitexploration.ID  | 0.08287 | -0.03125 | 0.2079  | 4000   |
## | traitexploration:traitboldness.ID  | 0.08287 | -0.03125 | 0.2079  | 4000   |
## | traitboldness:traitboldness.ID    | 0.38889 | 0.22405 | 0.5735  | 4000   |
##
## R-structure: ~us(trait):units
##
## | post.mean | l-95% CI | u-95% CI |
## |-----------|---------|---------|
## | traitexploration:traitexploration.units | 0.7340  | 0.5996  | 0.8697  |
## | traitboldness:traitexploration.units  | 0.3338  | 0.2390  | 0.4353  |
## | traitexploration:traitboldness.units  | 0.3338  | 0.2390  | 0.4353  |
## | traitboldness:traitboldness.units    | 0.6391  | 0.5287  | 0.7614  |
##
## | eff.samp |
## |---------|
## | 4000    |
## | 3365    |
## | 3365    |
## | 3685    |
##
## Location effects: cbind(scale(exploration), scale(boldness)) ~ trait - 1 + trait:scale(assay_rep, scale = FALSE) + trait:scale(body_size)
##
## | post.mean | l-95% CI | u-95% CI | eff.samp | pMCMC |
## |-----------|---------|---------|----------|-------|
## | traitexploration | 0.0002371 | -0.1503944 | 4000   | 0.992 |
## | traitboldness   | -0.0013789 | -0.1529724 | 4000   | 0.992 |
## | traitexploration:scale(assay_rep, scale = FALSE) | -0.0226367 | -0.1030113 | 3779  | 0.349 |
## | traitboldness:scale(assay_rep, scale = FALSE)    | -0.0355084 | -0.1083371 | 4000   | 0.184 |
## | traitexploration:scale(body_size) | 0.0714747 | -0.0887465 | 3779  | 0.349 |
## | traitboldness:scale(body_size)    | 0.1047925 | -0.0543119 | 4000   | 0.184 |
## | traitboldness:scale(body_size)  | 0.1047925 | -0.0543119 | 4000   | 0.184 |
##
Note that you will **not** have exactly the same results as we have, because of the way that the MCMC process works — if you run it again yourself, you will get slightly different answers again. However, they should be very similar.

From the fixed effects, we can see that there is a separate intercept for both personality traits (no surprise that these are very close to zero, given that we mean-centred and scaled each trait before fitting the model),
and an estimate of the effect of assay repeat and body size on both traits. None of these appear to be large effects, so let’s move on to the more interesting parts — the random effects estimates.

In the **G-structure**, we have the among-individual (co)variances. These are given such that they can be reformed into a matrix, which is why $V_{\text{boldness}}$ and $V_{\text{exploration}}$ are shown once each, while the among-individual covariance between them (COV$_{\text{boldness,exploration}}$) is shown twice.

You will notice that the variance estimates here are actually close to the **lme4** repeatability estimates, which is because we scaled our response variables to phenotypic standard deviations. We can also find the ‘adjusted repeatability’ (i.e., the repeatability conditional on the fixed effects) for each trait by dividing its among-individual variance estimate by the sum of its among-individual and residual variances. To do this, we can create a new posterior distribution of (for example) ‘proportion of exploration variance explained by differences among individuals’. We do this by referencing the different variance components by their name as shown in the summary (note that sometimes different versions display these with or without the ‘trait’ prefix, so check how yours has displayed).

```r
mcmc_prop_E <- mcmc_E_B_us$VCV[,"traitexploration:traitexploration.ID"]/(
mcmc_E_B_us$VCV[,"traitexploration:traitexploration.ID"] +
mcmc_E_B_us$VCV[,"traitexploration:traitexploration.units"]
)
```

![Trace and density plots](image)

We can interrogate this new distribution for its mean and 95% CIs:

```r
mean(mcmc_prop_E)
```

```r
## [1] 0.2824676
```
Note that, while it is often claimed that Bayesian 95% credible intervals that do not cross zero can be used to indicate statistical significance in the classical (Frequentist) sense, this does not hold for variance components here as they are constrained to be positive in MCMCglmm. As such, a lower bound of the credible interval close to zero might actually indicate low confidence in a non-zero proportion of the phenotypic variance in exploration being explained by differences among individuals.

Let’s do the same for boldness:

```r
mcmc_prop_B <- mcmc_E_B_us$VCV[, "traitboldness:traitboldness.ID"]/
               (mcmc_E_B_us$VCV[, "traitboldness:traitboldness.ID"] + 
                mcmc_E_B_us$VCV[, "traitboldness:traitboldness.units"])
mean(mcmc_prop_B)
```

```text
## [1] 0.3751389
```

```r
HPDinterval(mcmc_prop_B)
```

```text
## lower upper
## var1 0.2602269 0.4977966
## attr("Probability")
## [1] 0.95
```

We can also use this process to estimate the mean and credible intervals of the correlation from our model (co)variances. We create a posterior distribution of the among-individual correlation by dividing the corresponding covariance between boldness and exploration by the product of the square root of their variances (i.e., standardising the covariance to a scale from -1 to 1):

```r
mcmc_cor_EB <- mcmc_E_B_us$VCV[, "traitboldness:traitexploration.ID"]/
               (sqrt(mcmc_E_B_us$VCV[, "traitboldness:traitboldness.ID"])*
                sqrt(mcmc_E_B_us$VCV[, "traitexploration:traitexploration.ID"]))
plot(mcmc_cor_EB)
```

```text Multivariate modelling for individual variation 11
```
In this case, because the correlation can take on either positive or negative then we can use the credible interval to assess statistical significance. Here the 95% credible interval spans zero, and since the model fit is good, we should conclude that there is no evidence of a statistically significant correlation.

To better demonstrate that BLUPs produce anticonservative hypothesis tests, we can plot the correlation estimates and their confidence/credible intervals from the two approaches that we have taken. The CI are taken directly from the `cor.test` function for the BLUPs, and for `MCMCglmm` they are taken from the posterior distribution of correlation samples (using the `HPDinterval` function).
Here we can clearly see that the BLUPs method - having failed to carry through the error around the predictions of individual-level estimates - is anticonservative, with small confidence intervals (and a correspondingly small P-value, \( P = 0.0019 \)). Testing the syndrome directly in a bivariate model that retains all the data, by comparison, enables us to capture the true uncertainty about the estimate of the correlation. This is reflected in the larger CI which, in this case, cross zero and thus indicate a lack of support for a statistically significant behavioural syndrome.

### Adding further traits

As part of our data collection, we also have a single value of mating success for each individual (which we will use as a proxy for fitness). We are interested in how our personality traits correlate with variation in this fitness-related measure. While our test above showed that the correlation between the measured personality traits was not significant, there did appear to be some relationship — so we shall incorporate both personality traits and fitness into a single trivariate model for hypothesis testing.

In this case, because the new response variable to be added to our model is fitness, we are not going to mean-centre and scale by phenotypic standard deviations, but instead divide by the mean fitness value (such that we are investigating among-individual covariance between personality traits and relative fitness). We create this new variable, `rel_fitness`, as follows:

```r
df_syndrome <- df_syndrome %>%
  mutate(rel_fitness = fitness/mean(fitness, na.rm=TRUE))
```

Note that we will refer to this relative fitness trait simply as ‘fitness’ below for simplicity’s sake.

### Setting up the model
Below, we will set up our main model, which will allow for heterogeneous among-individual variances in our 3 traits (boldness, exploration, fitness), and will estimate the covariance between them.

First, we set up a prior, which we specify in a similar way as the bivariate model. However, for the residuals (or ‘within-individual’ variance), we must bear in mind that we have only a single fitness value per individual — therefore, that trait has no within-individual variance, and within-individual correlations involving fitness must be 0. We can set the variance component to a particular value using the fix command, although as variances have to be positive we fix the within-individual variance in fitness to a small positive number (here, 0.0001):

```
prior_E_B_fit_1px = list(R = list(V = diag(c(1,1,0.0001),3,3), nu = 1.002, fix = 3),
                       G = list(G1 = list(V = diag(3), nu = 3,
                                   alpha.mu = rep(0,3),
                                   alpha.V = diag(25^2,3,3)))))
```

Now, we can fit our model with these starting values and constraints. Again, we `cbind` our response variables on the left-hand side of the formula, and use `trait` to denote a multivariate model. We can also use the `at.level` keyword to specify that fixed effects are estimated only for certain traits — here, we test for an effect of assay repeat only on exploration and boldness (because these were measured repeatedly), while we test for the effect of body size on all of our traits.

Note that in the model specification below, we set the argument `pr = TRUE`. This saves the posterior distribution of the individual random effects (analogous to the BLUP from the REML analysis) so we can visualise them later, but does take up more memory (over 8Mb compared to <1Mb for a model run without saving these values).

Fit the model as follows (and be sure to use diagnostic checks). Note that I have increased the number of iterations (and both the burnin and thinning interval), so once it’s underway, that’s a good time to go and make a cup of tea... (the run will likely take over 20 minutes).

```
mcmc_E_B_fit <- MCMCglmm(cbind(scale(exploration),
                           scale(boldness),
                           rel_fitness) ~
                           trait-1 +
                           at.level(trait,1):scale(assay_rep, scale = FALSE) +
                           at.level(trait,2):scale(assay_rep, scale = FALSE) +
                           trait:scale(body_size),
                           random = - us(trait):ID,
                           rcov = - us(trait):units,
                           family = c("gaussian","gaussian","gaussian"),
                           prior = prior_E_B_fit_1px,
                           nitt=750000,
                           burnin=500000,
                           thin=175,
                           verbose = TRUE,
                           pr = TRUE,
                           data = as.data.frame(df_syndrome))
```

Take a look at the model summary:

```
summary(mcmc_E_B_fit)
```

As before, we get (co)variance estimates, credible intervals, and effective sample sizes for the among-individual and residual variance terms. Note that our constraint on the residual (‘within-individual’) variance term for our fitness measure: the `rel_fitness:rel_fitness.units` estimate is at 0.0001, with an effective sample
size of 0. You should also note that the within-individual covariance terms involving the fitness trait are very close to 0, with very small effective sample sizes, so the model has effectively not fit these covariances (which is what we wanted).

A quick sanity check also tells us that the correlation between boldness and exploration estimated in this model is the same as in our earlier bivariate model:

```r
mcmc_E_B_fit_cor_EB <- mcmc_E_B_fit$VCV[, "traitboldness:traitexploration.ID"]/
  (sqrt(mcmc_E_B_fit$VCV[, "traitboldness:traitboldness.ID"])*
   sqrt(mcmc_E_B_fit$VCV[, "traitexploration:traitexploration.ID"]))
mean(mcmc_E_B_fit_cor_EB)
HPDinterval(mcmc_E_B_fit_cor_EB)
## [1] 0.2374761
## lower upper
## var1 -0.08700906 0.5379599
## attr("Probability")
## [1] 0.95
```

As before, we can use our posterior distributions to estimate the among-individual correlations between each of our traits of interest, and assess statistical significance using their 95% credible intervals from our MCMCglmm model:

```r
mcmc_E_B_fit_cor_Efit <- mcmc_E_B_fit$VCV[, "traitrel_fitness:traitexploration.ID"]/
  (sqrt(mcmc_E_B_fit$VCV[, "traitrel_fitness:traitrel_fitness.ID"])*
   sqrt(mcmc_E_B_fit$VCV[, "traitexploration:traitexploration.ID"]))
mcmc_E_B_fit_cor_Bfit <- mcmc_E_B_fit$VCV[, "traitrel_fitness:traitboldness.ID"]/
  (sqrt(mcmc_E_B_fit$VCV[, "traitrel_fitness:traitrel_fitness.ID"])*
   sqrt(mcmc_E_B_fit$VCV[, "traitboldness:traitboldness.ID"]))

df_mcmc_cors <- data_frame(Traits = c("Exploration, Boldness", "Exploration, Fitness", "Boldness, Fitness"),
                            Estimate = c(mean(mcmc_E_B_fit_cor_EB),
                                         mean(mcmc_E_B_fit_cor_Efit),
                                         mean(mcmc_E_B_fit_cor_Bfit)),
                            Lower = c(HPDinterval(mcmc_E_B_fit_cor_EB)["lower"],
                                      HPDinterval(mcmc_E_B_fit_cor_Efit)["lower"],
                                      HPDinterval(mcmc_E_B_fit_cor_Bfit)["lower"]),
                            Upper = c(HPDinterval(mcmc_E_B_fit_cor_EB)["upper"],
                                      HPDinterval(mcmc_E_B_fit_cor_Efit)["upper"],
                                      HPDinterval(mcmc_E_B_fit_cor_Bfit)["upper"]))
```

```r
ggplot(df_mcmc_cors, aes(x = Traits, y = Estimate)) +
  geom_pointrange(aes(ymin = Lower, ymax = Upper)) +
  geom_hline(yintercept = 0, linetype = "dotted",
  ```
We might want to present our final results as a matrix with variances on the diagonals, covariances below and correlations above (with the lower and upper bounds of 95% CIs in parentheses):

<table>
<thead>
<tr>
<th></th>
<th>Exploration</th>
<th>Boldness</th>
<th>Fitness</th>
</tr>
</thead>
<tbody>
<tr>
<td>Exploration</td>
<td>0.29</td>
<td>0.24</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>(0.13, 0.45)</td>
<td>(-0.09, 0.54)</td>
<td>(-0.06, 0.46)</td>
</tr>
<tr>
<td>Boldness</td>
<td>0.08</td>
<td>0.39</td>
<td>0.62</td>
</tr>
<tr>
<td></td>
<td>(-0.04, 0.21)</td>
<td>(0.22, 0.57)</td>
<td>(0.44, 0.79)</td>
</tr>
<tr>
<td>Fitness</td>
<td>0.03</td>
<td>0.09</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td>(-0.01, 0.07)</td>
<td>(0.05, 0.14)</td>
<td>(0.04, 0.08)</td>
</tr>
</tbody>
</table>
Conclusions

To conclude, then: we found that the correlation between boldness and exploration tends to be positive among male haggis, but this correlation is not statistically significant and thus does not provide strong evidence for a behavioural syndrome. However, inappropriate analysis of BLUP extracted from univariate models would lead to a different (erroneous) conclusion. We also found no statistically significant association between among-individual variation in exploration and fitness. However, we did find a statistically significant positive association between among-individual variation in boldness and our fitness proxy, indicating that bolder male haggis had greater mating success (see figure below).

Note: below, we use posterior modes of random effects (BLUPs from the MCMCglmm model) from our trivariate model to construct a figure that illustrates the association between boldness and fitness. Unlike its use in secondary statistical analyses, this is an appropriate use of BLUPs — i.e., just for illustrative purposes!

```r
df_bf_coefs <- data_frame(Trait = attr(colMeans(mcmc_E_B_fit$Sol), "names"),
                           Value = colMeans(mcmc_E_B_fit$Sol)) %>%
          separate(Trait, c("Trait","Type","ID"), sep = ".", fill = "right") %>%
          filter(Trait == "ID") %>%
          filter(Trait %in% c("traitboldness", "traitrel_fitness")) %>%
          select(-Type) %>%
          spread(Trait, Value)

  # Find the regression line -
  # the covariance of boldness, relative fitness divided by
  # the square root of the variance in boldness
B_fit_slope <- mcmc_E_B_fit$VCV[,"traitrel_fitness:traitboldness.ID"]/
               mcmc_E_B_fit$VCV[,"traitboldness:traitboldness.ID"]

  ggplot(df_bf_coefs, aes(x = traitboldness, y = traitrel_fitness, group = ID)) +
  geom_point(alpha = 0.7) +
  geom_abline(intercept = 0, slope = mean(B_fit_slope)) +
  labs(x = "Boldness (BLUP)",
       y = "Relative fitness (BLUP)") +
  theme_classic()
```
Further tutorials

We will continue to develop tutorials for multivariate modelling of individual (co)variation, which will cover some of the more advanced issues discussed in our paper. Please visit tomhouslay.com for more information.
<table>
<thead>
<tr>
<th>ID</th>
<th>assay_rep</th>
<th>boldness</th>
<th>exploration</th>
<th>fitness</th>
<th>body_size</th>
</tr>
</thead>
<tbody>
<tr>
<td>S_1</td>
<td>1</td>
<td>18.5745096</td>
<td>39.7364776</td>
<td>39</td>
<td>21.7179479</td>
</tr>
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<tr>
<td>S_1</td>
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<td>40.2904165</td>
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<td>20.777609</td>
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