

# Phylogenetic conservation of behavioural variation and behavioural syndromes

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## Abstract

Individuals frequently differ consistently from one another in their average behaviours (i.e. 'animal personality') and in correlated suites of consistent behavioural responses (i.e. 'behavioural syndromes'). However, understanding the evolutionary basis of this (co)variation has lagged behind demonstrations of its presence. This lag partially stems from comparative methods rarely being used in the field. Consequently, much of the research on animal personality has relied on 'adaptive stories' focused on single species and populations. Here, we used a comparative approach to examine the role of phylogeny in shaping patterns of average behaviours, behavioural variation and behavioural correlations. In comparing the behaviours and behavioural variation for five species of Gryllid crickets, we found that phylogeny shaped average behaviours and behavioural (co)variation. Despite differences among species, behavioural responses and variation were most similar among more closely related species. These results suggest that phylogenetic constraints play an important role in the expression of animal personalities and behavioural syndromes and emphasize the importance of examining evolutionary explanations within a comparative framework.

## KEYWORDS

behavioural syndrome, comparative method, field crickets, personality

## 1 | INTRODUCTION

Behavioural syndromes, correlations between behaviours at the among-individual level (Dingemanse et al., 2012), have been documented across taxa (Brommer & Class, 2017). Behavioural syndromes can conceptually be thought of as correlations between individual averages and stem from underlying genetic correlations and correlations due to developmental plasticity and other sources of permanent environmental covariance (Dingemanse & Dochtermann, 2014; Dingemanse et al., 2012). Among-individual variation in behaviour, often referred to as 'personality variation', has been found to be similarly ubiquitous (Bell et al., 2009). Similar to behavioural syndromes, this personality variation can be thought of as variation across individuals in their average behaviours and likewise stem from genetic and permanent environmental variation (Dingemanse & Dochtermann, 2013; Dochtermann et al., 2015). Attempts to infer whether general taxonomic patterns exist for

both personality variation and behavioural syndromes have generally been conducted via literature reviews and meta-analyses (Bell et al., 2009; Brommer & Class, 2017; Dochtermann, 2011; Dochtermann et al., 2015; Garamszegi et al., 2012, 2013). These synthesis efforts have shown that among-individual variation is common (average repeatability  $\sim 0.37$ ; Bell et al., 2009), that the magnitude of behavioural syndromes is generally weak (average  $r \sim 0.19$ ; Garamszegi et al., 2012, 2013) and that there is general alignment between nested patterns of correlations at the phenotypic, among-individual, within-individual and genetic levels (Brommer & Class, 2017; Dochtermann, 2011).

Although the observation that both among-individual variation and behavioural syndromes are common, we have poor understanding of the evolution of either. This gap in our understanding is partly because comparative approaches have rarely been used in studies of among-individual behavioural variation and behavioural syndromes (White et al., 2020). Comparative approaches allow for direct comparison

across species of behavioural (co)variation and are necessary for proper understanding of the importance of phylogeny in shaping 'personality' and behavioural syndromes (Royauté et al., 2020; White et al., 2020).

Direct assessment of evolutionary hypotheses can also be extended to the study of personality and behavioural syndromes: both among-individual variation and behavioural syndromes have clear connections to quantitative genetic parameters, specifically additive genetic variation and additive genetic covariances (Dingemanse & Dochtermann, 2014; Dochtermann & Roff, 2010). The mathematical relationships between among-individual (co)variances and additive genetic (co)variances (Boake, 1989; Dingemanse & Dochtermann, 2014; Dochtermann et al., 2015) allow for the extension of predictions from quantitative genetics to among-individual variation and behavioural syndromes.

One such prediction is that differences in the magnitude of variation present for a trait might be attributable to differences in selection between populations or species. Specifically, Mousseau and Roff (1987) argued that traits with low heritability might be indicative of strong selection having eroded genetic variation. Likewise, because among-individual variation represents the sum of additive genetic variation, dominance (and other epistatic) genetic variation and permanent environmental variation (e.g. irreversible and developmental plasticity), selection is expected to deplete this variation. Note, however, that drift is often also expected to reduce genetic and, therefore, among-individual variation.

Selection is likewise expected to shape additive genetic covariances and correlations, both by the loss of variation in single traits and changes to the magnitude and directions of covariances (Roff, 1997). For example, correlational selection is expected to produce genetic correlations (Armbruster & Schwaegerle, 1996; Phillips & Arnold, 1989). As in the case of among-individual variances, these effects on genetic correlations are expected to carry over to behavioural syndromes. In other words, behavioural syndromes are expected to reflect the effects of selection on genetic correlations. Therefore, if behavioural syndromes differ across populations, species or other groupings, then this suggests differences in genetic correlations and correlational selection (i.e. the 'adaptive' hypothesis; Bell, 2005). In contrast, if behavioural syndromes were conserved across groups, then this would suggest that either behavioural syndromes stem from pleiotropic effects (i.e. the 'constraints' hypothesis; Bell, 2005) or that selection is similar across groups.

Although these topics have been addressed for other types of traits, particularly morphological and chemical characteristics (Aguirre et al., 2014; Hine et al., 2014; McGlothlin et al., 2018), addressing them for behaviour remains important for several reasons. Firstly, considerable behavioural research assumes an adaptive framework for both among-individual variation and behavioural syndromes, thereby minimizing the importance of phylogeny and minimizing the potential role of phylogenetic constraints. Secondly, behaviours, life-history and physiological traits exhibit substantially lower heritability than morphological traits (Dochtermann et al., 2019; Mousseau & Roff, 1987; Stirling et al., 2002). Consequently, the role of phylogeny and selection in constraining and shaping morphology may not generalize to traits with lower heritability and, thus, greater plasticity. Failure to address alternative explanations, like phylogenetic constraints, can lead to the uncritical acceptance of adaptive arguments (Gould & Lewontin, 1979)

and the perpetuation of 'zombie ideas' (sensu Quiggin, 2012). For example, recent meta-analyses have cast doubt on general organizing frameworks for behaviour and behavioural correlations (Niemelä & Dingemanse, 2018; Royauté et al., 2018).

Here, we compared the behaviour of five closely related cricket species: *Gryllus integer*, *Gryllus assimilis*, *Gryllus lineaticeps*, *Gryllobates sigillatus* and *Acheta domesticus*. For each species, we measured exploratory behaviour and response to cues of predator presence. By working with the same behavioural assays in five closely related species, we were able to assess the importance of phylogeny for average behaviours and to evaluate predictions about trait (co)variation. Specifically, we addressed the following questions:

1. Does the average expression of behaviour differ among species? We predicted that species would differ but do so in a manner constrained by phylogeny. Put another way, more closely related species will have more similar average behaviours.
2. Do among-individual variances differ among species? We did not have species-level predictions but because selection and drift should both reduce among-individual variance, we predicted that among-individual variation would differ across species independent of phylogeny.
3. Do within-individual variances differ among species? Within-individual variation, typically disregarded as residual variation, includes phenotypic plasticity—specifically reversible plasticity or 'phenotypic flexibility' not captured by factors and covariates of a statistical model (Berdal & Dochtermann, 2019; Piersma & Drent, 2003; Piersma & Van Gils, 2011; Westneat et al., 2015; Whitman & Agrawal, 2009). Differences across groups in the magnitude of within-individual variation, therefore, are, in part, differences in the magnitude of plasticity. We did not have *a priori* expectations as to species differences or phylogenetic signals for within-individual variances.
4. Do behavioural syndromes differ among species? Because behavioural syndrome structure has been conserved at the genetic level across cricket populations of *G. integer* (Royauté et al., 2020), we predicted that syndromes would similarly be phylogenetically conserved and shared across species.

## 2 | METHODS

### 2.1 | Cricket acquisition, housing and rearing conditions

Data used in this study were originally collected for various studies investigating the effects of development on behavioural variation and the presence of behavioural constraints and behavioural syndromes (Royauté et al., 2019, 2020). *A. domesticus* males and females were obtained as nymphs (~1 mm in size) from a commercial supplier (Fluker's Cricket Farm) and were measured once mature. *G. integer* females were captured in Aguila, AZ; *G. lineaticeps* males and females were caught in Dunnigan, CA; and the *G. assimilis* males and

**TABLE 1** Number of individuals, by species, for which behaviour was assayed in a first, second and third repetition

Species	Behavioural assay	Repetition 1	Repetition 2	Repetition 3	Total trials
<i>Acheta domesticus</i>	Open field	281	263	225	769
	Antipredator	262	235	220	717
<i>Gryllus assimilis</i>	Open field	16	16	16	48
	Antipredator	16	16	15	47
<i>Gryllus integer</i>	Open field	92	91	74	257
	Antipredator	88	88	72	248
<i>Gryllus lineaticeps</i>	Open field	21	17	11	49
	Antipredator	21	13	11	45
<i>Gryllodes sigillatus</i>	Open field	50	50	49	149
	Antipredator	50	50	49	149
Total		896	837	743	2478

females were caught in Maricopa County, AZ. These species were all captured during the summer of 2017. *G. sigillatus* individuals were taken from an outbred population established by S. Sakaluk with crickets collected from California and currently maintained in Fargo, ND. For *G. lineaticeps* and *G. assimilis*, the same individuals that were caught in the field were measured, whereas laboratory-reared offspring of *G. integer* were measured. All species were reared under a 12:12 light:dark photoperiod at a temperature of 25–28°C. All individuals were housed in 0.71-L containers with transparent covers that included food, shelter and water-filled glass vials plugged with cotton balls. *A. domesticus* were exposed to a mixture of high- and low-quality diets described in Royauté et al. (2019), whereas all other species included in this study were fed ad libitum food (commercially purchased chicken feed).

## 2.2 | Behaviour trials

To measure exploratory behaviour and antipredator responses, we repeatedly recorded individuals' activity levels in an open field arena, followed by their responses to cues of predator presence created from diluted *Eublepharis macularius* excreta (see details below). *A. domesticus* were measured between March 2015 and October 2016, *G. lineaticeps* were measured from August 2017 to September 2017, *G. assimilis* were measured between September 2017 and October 2017, *G. integer* were measured between May 2018 and June 2018 and *G. sigillatus* were measured in May 2019. All trials were conducted in a plastic arena (60 cm × 60 cm and 15 cm high) with a Plexiglas lid. The arena was split into four 30-cm × 30-cm arenas separated by a divider, allowing up to four crickets to be tested at one time. Open field trials were always conducted first, followed by antipredator response trials either immediately after or on another day to minimize potential carryover effects from exposure to cues of predator presence. After each behavioural assay, arenas were thoroughly cleaned with 70% ethanol wipes to avoid accumulation of any chemical traces of conspecifics. Mass at the time of behavioural trials was recorded to the nearest

1 mg. All individuals were measured in each assay for a maximum of three repetitions, with some individuals measured fewer times due to escape or natural mortality (Table 1). In total, we conducted 2478 behavioural assays across a total of 460 individuals (Table 1).

By measuring behaviour in the same manner across species, we reduce the likelihood of naming fallacies—that is, jingle fallacies (where the same name is used for the different behaviours) and jangle fallacies (where different names are used for the same behaviour). The standardized protocols also allow us to assume similar measurement error across species.

## 2.3 | Open field behaviour

Individual crickets were left to rest for 30 s under a 5-cm-diameter cup after being introduced into the lower right section of the arena (Figure S1). After the 30 s, we allowed the individuals to move freely through the arena for 220 s. We measured each individual's exploratory propensity by digitally overlaying a 6 × 6 grid over the arena (Figure S1) and calculating the number of *unique zones* visited (UZ) by the cricket with Ethovision X (Noldus Information Technology). This behavioural protocol has previously been used with *A. domesticus* and *G. integer* to evaluate genetic and individual differences in activity and exploratory behaviours (Royauté & Dochtermann, 2017; Royauté et al., 2015, 2019, 2020).

## 2.4 | Predator cue response

To measure responses to cues of potential predator presence, we collected excreta from three adult leopard geckos, *Eublepharis macularius*, that were fed a mixed diet of *A. domesticus*, *G. sigillatus*, *G. lineaticeps*, *G. integer* and *G. assimilis*. Leopard geckos were housed according to the standards of the Institutional Animal Care and Use Committee of North Dakota State University (Protocol A14006, A17015 and A19067) and the Animal Behavior Society (2021). Collected excreta was frozen and then finely ground and diluted with

deionized water (1 ml H<sub>2</sub>O: 5 mg of excreta). This solution was then applied to 15-cm-diameter filter paper disks with a 5-cm-diameter central cut-out that allowed crickets to be left to rest unexposed to the predator cues (Royauté & Dochtermann, 2017; Royauté et al., 2019, 2020). Each predator cue disk was left to dry for a minimum of 2 h then stored at -23°C until needed for trials. Predator cue disks were allowed to warm to room temperature before use in antipredator trials and discarded after a single use. Between each trial, unused thawed cue disks were stored at 4°C for a maximum of 14 days. After 14 days, any unused disks were discarded.

We placed the predator cue disk at the bottom of a 15-cm-diameter arena and left the cricket to rest for a minimum of 30 s under a 5-cm-diameter cup in the nontreated central cut-out. We then removed the cup and allowed the cricket to move freely for 220 s and estimated the distance travelled in centimetre (AP distance) using Ethovision X (Figure S1). Previous studies with this protocol show that crickets had heightened activity levels in the presence of this diluted gecko excreta compared with water controls (Royauté & Dochtermann, 2017). Consistent with this, *G. sigillatus* crickets have been found to increase their activity after direct exposure to predators (Bucklaew & Dochtermann, 2020). Greater activity during these antipredator response assays, that is, greater AP distance, was therefore interpreted as a greater responsiveness to predator cues.

## 2.5 | Data analysis: Univariate models

To assess differences in behavioural responses between species for means and variances, we analysed behavioural data using separate univariate mixed-effects models for unique zones visited and AP distance (square root transformed). We included species, temperature (Celsius, mean centred), mass (using among- and within-individual centring (Van de Pol & Wright, 2009)) and sex as fixed effects. Individual ID was included as a random effect. We compared the fit of four univariate mixed models structured as follows:

1. Model 1:  $V_i = \& V_w = A$  A null model where the among- ( $V_i$ ) and within-individual ( $V_w$ ) variances were kept constant between species.
2. Model 2:  $V_i \neq \& V_w = A$  A model where the among-individual variance differed between species, but the within-individual variance was kept constant.
3. Model 3:  $V_i = \& V_w \neq$  The within-individual variance differs between species, but the among-individual variance was kept constant.
4. Model 4:  $V_i \neq \& V_w \neq$  Both the among- and within-individual variances were allowed to vary between species.

These models were specified using the `MCMCglmm` package for Bayesian mixed models (Hadfield, 2010) using Markov chain Monte Carlo (MCMC) with 1.3 million iterations, 300 000 iteration burn-in, a thinning interval of 1000 and an inverse-Wishart prior. AP distance

and unique zone models were fit with Gaussian and Poisson error distributions, respectively.

To determine whether species differed in average behaviour, Models 1 and 4 were run with and without species as a fixed effect and compared based on deviance information criterion (DIC) values. If species differ in average behaviour, models with species included as a fixed effect would be expected to have lower DIC values. Average behavioural differences among species reported in the Results section were then qualitatively assessed using posterior modal estimates for each species (Congdon, 2006).

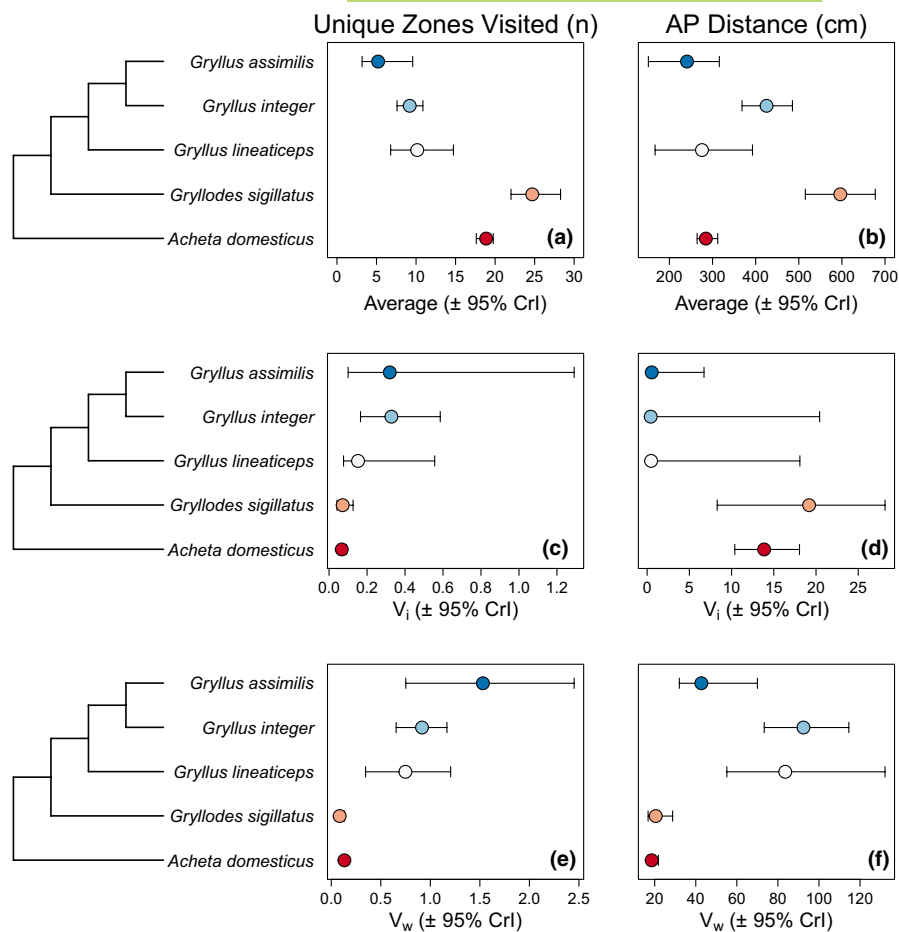
We then compared DIC values among Models 1 through 4 to determine whether either among- or within-individual variances differed among species following Royauté et al. (2019) and Royauté and Dochtermann (2021). The model with the lowest DIC value was considered the best model, and models with  $\Delta\text{DIC} > 5$  were considered to have a substantively poorer fit (Barnett et al., 2010). Models with  $\Delta\text{DIC} < 5$  were considered as having comparable support relative to the best model (Barnett et al., 2010). All models were specified with the same fixed effect structure as specified earlier to prevent biased estimates of variance components and repeatability (Nakagawa & Schielzeth, 2010b; Spiegelhalter et al., 2003; Westneat et al., 2011).

## 2.6 | Data analysis: Phylogenetic signal

As our primary questions were about differences in behavioural averages and variances, our results and discussion focus on the above model comparisons. However, we also calculated the variation in behaviour directly attributable to phylogeny. To do so, we fit mixed-effects models with the same fixed effects, prior structure and chain parameters as mentioned before but omitting species as a fixed effect. Species was instead incorporated as a random effect, along with individual ID, with the relationship among species modelled according to the current phylogeny (Figure 1; Gray et al., 2020; Yang et al., 2021). All nodes in our phylogeny had high support ( $\geq 95\%$ ) in prior phylogenetic analyses (Gray et al., 2020; Yang et al., 2021). Although Gray et al. (2020) provided divergence times, these were estimated with high uncertainty and unavailable across genera. Therefore, we did not include branch lengths in our analyses. From these models, we then estimated the strength of the phylogenetic signal as the proportion of variation attributable to the hierarchical pattern of relatedness among species (i.e.  $\lambda$ , Hadfield & Nakagawa, 2010; Nakagawa & Santos, 2012; Pagel, 1999). From the same models, we also estimated the proportion of variation attributable to among-individual differences (i.e.  $\tau$ , repeatability, Dingemanse & Dochtermann, 2013). We estimated both phylogenetic signal and repeatability as unadjusted values, that is, we included the variation attributable to fixed effects in the ratio denominator (Nakagawa & Schielzeth, 2010a).

Importantly, because we only had data for five species, our estimation of the phylogenetic signal must be interpreted with caution, despite high within-species replication (Table 1). As stated earlier,

**FIGURE 1** Species posterior modal values with 95% HPD credibility intervals. (a) Average unique zones visited. (b) Average AP distance in centimetres. (c) Among-individual variances in unique zones travelled. (d) Among-individual variances in AP distance. (e) Within-individual variances in unique zones travelled. (f) Within-individual variances in AP distance



our inferences are therefore primarily based on the model comparisons and qualitative comparison of values over the phylogeny.

## 2.7 | Data analysis: Bivariate models

Behavioural syndromes were estimated using bivariate mixed-effects models with unique zones travelled and AP distance as response variables, also using the `MCMCglmm` library (Hadfield, 2010), and analysed separately for each individual species. We fit models using temperature (Celsius, mean centred), mass (using among- and within-individual centring on subjects (Van de Pol & Wright, 2009)) and sex as fixed effects, and individual ID was fit as a random effect. These models were fit with 2.6 million iterations, a 600 000 burn-in period, a thinning interval of 2000 and a prior that was flat for correlations. Among-individual correlations were estimated for all species, whereas within-individual correlations were only assessed when individuals were measured for unique zones travelled and antipredator activity during the same testing period (Dingemanse & Dochtermann, 2013). Consequently, we were unable to assess within-individual covariation of *G. lineaticeps* and *G. assimilis* due to the fact that these species were not measured for each behaviour in immediate succession. Because model comparisons as used before for single traits could not be

conducted for correlations (due to software-imposed model limitations), differences in behavioural correlations across species were assessed based on whether 95% HPD intervals overlapped. Overlap of 95% intervals is an overconservative comparison metric (Royauté & Dochtermann, 2021), with an overlap of 83% intervals more closely approximating an alpha of 0.5 (Austin & Hux, 2002; MacGregor-Fors & Payton, 2013), but this did not affect our species comparison results here. All analyses were conducted in R 3.4.4 (R Core Team, 2018).

## 3 | RESULTS

### 3.1 | Differences in average behaviour among species

Species differed in average behaviours: the inclusion of species as a fixed effect substantially improved model fit for both behaviours (Table 2; Table S1). The monophyletic group of *G. assimilis*, *G. integer* and *G. lineaticeps* exhibited the lowest number of unique zones visited (Figure 1a), but differences in AP distance were less obviously associated with the phylogenetic structure (Figure 1b). Consistent with this, the phylogenetic signal was stronger for unique zones visited ( $\lambda$ : 0.27) than for AP distance ( $\lambda$ : 0.16; Table S2).

### 3.2 | Differences in variances among species

The best fit model for unique zones visited was Model 4, which allowed both among- and within-individual variances to vary across species. All other models were poorly supported ( $\Delta\text{DIC} > 8$ ; Table 3). This indicates that both among- and within-individual variances differed among species in open field trials. For AP distance, Models 3 and 4 fit comparably well (Table 3). Both of these models support differences among species in within-individual variances for AP distance. The difference between the models, therefore, suggests mixed support for species differences in among-individual variances for AP distance.

The monophyletic group of *G. assimilis*, *G. integer* and *G. lineaticeps* exhibited higher among-individual variation for unique zones visited and lower among-individual variation for AP distance (Figure 1c,d; Table S3). This monophyletic group also exhibited higher within-individual variation for both unique zones visited and AP distance than observed for *A. domesticus* and *G. sigillatus* (Figure 1e,f; Table S3).

### 3.3 | Differences in behavioural correlations among species

Among-individual behavioural correlations were of similar magnitude for *A. domesticus*, *G. assimilis*, *G. lineaticeps* and *G. sigillatus* (0.3:0.5; Figure 2a; Table S4), whereas the correlation for *G. integer* was estimated to be slightly higher (0.66; Figure 2a; Table S4). Importantly, the lower bounds of the HPD intervals for *G. assimilis*, *G. integer*, *G. lineaticeps* and *G. sigillatus* also overlapped with 0 (Figure 2; Table S3). This is perhaps unsurprising, given the small sample sizes for *G. assimilis* and *G. lineaticeps*.

Behavioural correlations at the within-individual level ranged from 0.1 to 0.35 for *A. domesticus*, *G. sigillatus* and *G. integer*, with *G. integer* having the lower bound of its HPD interval overlapping with 0 (Figure 2b). The overlapping of 0 indicates that behavioural plasticity might not be correlated in this species. Behavioural correlations at either level did not show obvious patterns relative to phylogeny and were not statistically different across species (Figure 2).

## 4 | DISCUSSION

Our results demonstrate that species differed in their exploratory behaviour and response to cues of predator presence at all levels

of variation but that behavioural variation and syndromes were conserved across species. These results suggest an important influence of phylogenetic constraints on how behaviours evolve.

Species differed from one another in their average behaviours (Table 2) and in a manner consistent with phylogenetic relationships. Specifically, the monophyletic group of *G. assimilis*, *G. integer* and *G. lineaticeps* were generally similar in average unique zones visited (Figure 1a). In contrast, although the average AP distance differed by species, it did not do so in a manner clearly concordant with phylogeny (Figure 1b). Consistent with this, the phylogenetic signal, the proportion of variation attributable to the hierarchical pattern of relatedness among species, was higher for unique zones visited than for AP distance (Table S2). Interestingly and relevant for future research, phylogeny explained considerably more variation in our measure of exploratory behaviour—unique zones visited—than did among-individual variation, that is, ‘animal personality’ ( $\tau = 0.15$  versus  $\lambda = 0.27$ ; Table S2). However, given that phylogenetic signal was estimated with only five species, this finding should be interpreted with caution. Further, although the patterns we detected are consistent with phylogenetic constraint, it is also possible that similarity among species in behaviours stems from niche similarity, rather than phylogenetic constraint on the observed behaviours.

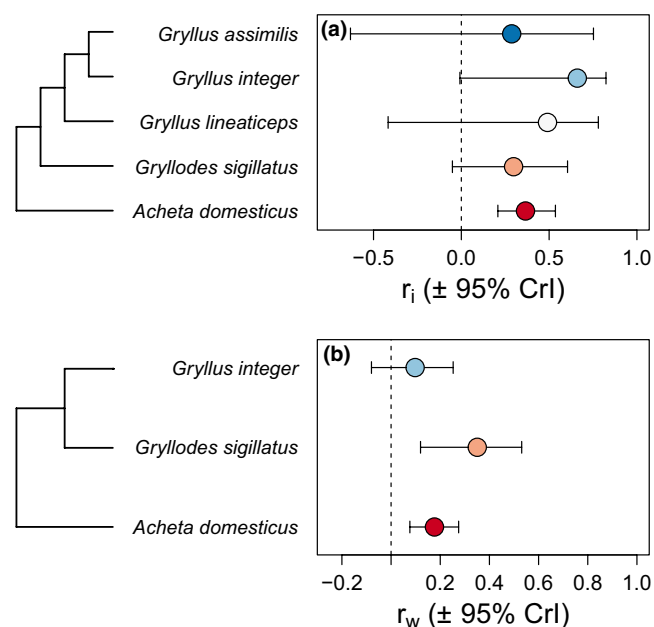
The species we examined also differed in among-individual variation in exploratory (unique zones visited) and predator response (AP distance) behaviours, again in a manner consistent with phylogenetic relationships (Figure 1c,d). Unfortunately, phylogenetic methods have been developed primarily with the goal of understanding differences in trait averages, rather than trait (co)variances. Our comparisons of ‘personality’ variation and syndromes among species are therefore based on the model comparison methods identifying the presence of species differences and subsequent qualitative comparisons of species-level estimates. Nonetheless, the concordance between patterns of the magnitude of among-individual variation and the currently described phylogeny suggests phylogenetic constraints on the magnitude of ‘personality’ variation. Of the five total species, the monophyly of *G. assimilis*, *G. integer* and *G. lineaticeps* exhibited the highest among-individual variation in unique zones visited and the lowest among-individual variation in the AP distance (Figure 1c,d). Although the expression of average behaviours and behavioural syndromes might be expected to exhibit a phylogenetic signal, we did not expect this to be the case for among-individual variances. One possible explanation

**TABLE 2** DIC values for statistical models with and without the inclusion of species as a fixed effect. The effect of species was evaluated in a model where variances did not (Model 1) or did (Model 4) differ by species. For both behaviors and three of four comparisons, the estimation of distinct species averages substantially improved model fit, as indicated by the lower DIC values for models with species included as a fixed effect. However, for unique zones visited and with variances fixed to be the same across species (Model 1), the exclusion of species led to a much better fit. Nonetheless, the estimation of species differences in both averages and variances (Model 4) did much better explaining the number of unique zones visited than did either version of Model 1

	Behaviour	DIC with species	DIC without species	DIC(without) – DIC(with)
Model 1 ( $V_i = \& V_w =$ )	AP distance	8025.51	8058.71	32.2
	Unique zones visited	8982.97	8456.17	–526.8
Model 4 ( $V_i \neq \& V_w \neq$ )	AP distance	7763.82	7780.94	17.12
	Unique zones visited	8338.21	8344.88	6.67

**TABLE 3** DIC and  $\Delta$ DIC values of model fit for AP distance and unique zones visited. Best ranked models, based on lowest DIC, are indicated in bold

Model (variance constraints)	Behaviour	DIC	$\Delta$ DIC
Model 1 ( $V_i = \& V_w =$ )	Unique zones visited	8982.97	644.76
Model 2 ( $V_i \neq \& V_w =$ )	Unique zones visited	8420.69	82.48
Model 3 ( $V_i = \& V_w \neq$ )	Unique zones visited	8346.44	8.23
<b>Model 4 (<math>V_i \neq \&amp; V_w \neq</math>)</b>	<b>Unique zones visited</b>	<b>8338.21</b>	<b>0</b>
Model 1 ( $V_i = \& V_w =$ )	AP distance	8025.51	263.31
Model 2 ( $V_i \neq \& V_w =$ )	AP distance	8010.04	247.84
<b>Model 3 (<math>V_i = \&amp; V_w \neq</math>)</b>	<b>AP distance</b>	<b>7762.20</b>	<b>0</b>
Model 4 ( $V_i \neq \& V_w \neq$ )	AP distance	7763.82	1.62



**FIGURE 2** Species posterior modal values with 95% HPD credibility intervals. (a) Among-individual behavioural correlations of unique zones visited and AP distance. (b) Within-individual differences of behavioural correlations of unique zones travelled and AP distance. Within-individual correlations for *Gryllus assimilis* and *Gryllus lineaticeps* were not calculated as behaviour trials were not performed in close succession

would be that bottlenecks at more basal phylogenetic nodes led to reduced genetic variation present in subsequent groupings. Although this could explain the lower among-individual variation in AP distance for *G. assimilis*, *G. integer* and *G. lineaticeps*, it does not explain that those same species exhibit higher within-individual variation for unique zones visited.

Differences observed in among-individual variation could also be attributable to selection differentially acting upon these species by reducing the additive genetic variation present in a population or species (Mousseau & Roff, 1987). Our results therefore suggest the possibility that exploratory behaviour, for which unique zones visited is a proxy, has been under stronger selection for *A. domesticus* and *G. sigillatus* than for the other species. Importantly, because we do not know the strength and direction of selection acting on these

phenotypes, the data presented here only suggest this possibility and cannot be used to distinguish between the effects of selection and drift for either behaviour.

Alternative explanations for the observed differences in among-individual variances stem from differences across source populations and sampling of these populations. For example, individual *A. domesticus* used in this study were from a captive population where inbreeding could have reduced genetic variation over generations. This potentially explains the low among-individual variation the species shows for unique zones visited (Figure 1c) but is contradicted by the high among-individual variation in the AP distance (Figure 1d). In contrast, *G. assimilis* and *G. lineaticeps* behaviour were measured for field-caught individuals. If individuals of these species experienced different developmental environments from one another, we would predict higher among-individual variation in behaviour because permanent environmental variation contributes, on average, 50% of the observed among-individual variation in behaviour present in populations (Dochtermann et al., 2015). This explanation is not, however, supported: although *G. assimilis* and *G. lineaticeps* indeed showed high relative among-individual variation in unique zones visited, the same was not the case for the AP distance (Figure 1c,d). Moreover, for both behaviours, *G. assimilis* and *G. lineaticeps* were very similar to *G. integer*, for which laboratory-reared individuals were measured. Another potential confound in our results is that species were measured at distinct times (*A. domesticus* first, *G. lineaticeps*, *G. assimilis* and *G. integer* second through fourth, respectively, and *G. sigillatus* last). However, there is no clear relationship between this sequence of sampling and behavioural averages or variance. To summarize, the conflicting patterns of among-individual variation observed between the AP distance and unique zones visited prevents clear interpretation.

Estimated within-individual variances include variation from a variety of sources, including plasticity in response to short-term environmental variation and measurement error (Berdal & Dochtermann, 2019; Dingemans et al., 2012). In comparing species, if we assume measurement error is similar among species, differences in within-individual variation will primarily represent differences in plasticity. This short-term plasticity, also referred to as phenotypic flexibility (Piersma & Van Gils, 2011), allows individuals to respond flexibly to an environment (Westneat et al., 2015). As was the case for among-individual variation and average unique zones visited, *G. assimilis*, *G.*

*integer* and *G. lineaticeps* were grouped together and exhibited similar magnitudes of within-individual variation (Figure 1e,f). For both behaviours, this group exhibited considerably higher within-individual variation than observed for *A. domesticus* and *G. sigillatus*, differences supported by our model comparison results (Table 3). In other words, the *Gryllus* genus exhibited greater behavioural plasticity.

One possible explanation for this pattern is that our sample of *G. assimilis*, *G. integer* and *G. lineaticeps* were of individuals either caught from the field or the direct offspring of field insemination and subsequently captured individuals. In contrast, the population of *G. sigillatus* we sampled had been in captivity for around 75 generations, and the population of *A. domesticus* was reared for production purposes for some undetermined but large number of generations. Consequently, the differences in within-individual variation could be attributable to exposure to a frequently changing environment (Relyea, 2001) in the case of *G. assimilis*, *G. integer* and *G. lineaticeps* and the loss of plasticity in *A. domesticus* and *G. sigillatus*. This possibility could be assessed for crickets via experimental evolution with populations experiencing different levels of environmental heterogeneity.

With regard to behavioural correlations, Bell (2005) proposed two hypotheses for the expression of behavioural syndromes within a population relevant to the species-level comparisons we performed. The first of these, the constraints hypothesis chiefly attributes behavioural syndromes to the presence of pleiotropy, with the expression of genes affecting multiple behaviours. This hypothesis can be extended to other mechanistic connections constraining independent trait expression. Secondly, the adaptive hypothesis states that behavioural syndromes are the adaptive outcome of correlated selection. Although pleiotropy and other mechanistic connections can evolve and be adaptive, syndromes attributable to the adaptive hypothesis are expected to respond more quickly to changes in selection (Roff, 1997). Consequently, phylogenetic similarity in behavioural syndromes provides indirect support for the constraints hypothesis. Due to among-individual correlations not substantively differing among species (Figure 2), our results are consistent with the constraints hypothesis, despite species differing in variances and average expressions of behaviours (Figure 1). Unfortunately, this conclusion is not strongly supported, given the large uncertainties around the estimates of among-individual correlations. Nonetheless, at least the direction of correlations is likely consistent across species.

Although a comparative approach has only rarely been used for examining behavioural variation, three particular studies are relevant to the interpretation of our results here. Firstly, Blankers et al. (2017) compared the phenotypic variances and (co)variances of seven calling traits of multiple cricket species (including *G. lineaticeps*, which was included in our study). These authors found that the phenotypic covariance matrices differed among cricket species. One of the major differences among species was in the magnitude of variation present in single traits (Blankers et al., 2017). This is consistent with our findings that variances of behaviours differed across species (Figure 1c–f). Unfortunately, these authors compared phenotypic (co)variances, which conflate among- and within-individual

(co)variation (Dingemanse et al., 2012). Secondly, White et al., (2020) compared the among-individual covariance matrices of seven species of fish. Comparable with our results, these authors detected differences in the magnitude of among-individual behavioural variability and also found overall phylogenetic signal and similarity in how variation was expressed across multiple behaviours (White et al., 2020). Finally, they compared the expression of additive genetic (co)variance (i.e. **G** matrices) in behaviour among four populations of *G. integer*. Similar to White et al. (2020) and our results presented here, they found differences in single trait variances and covariances, but the overall structure of trait covariance was generally conserved across populations—indicating support for the constraints hypothesis.

An additional area of research with which our results can be compared is comparative psychology. Although the operational definitions of animal personality and behavioural syndrome used by animal behaviourists have greatly diverged from the definition of personality used in comparative psychology, both areas examine patterns of behavioural (co)variation. Many of the same challenges in attempting comparative work appear in both fields. In particular, naming fallacies hinder broad descriptions (Carter et al., 2013; Gosling, 2001). Nonetheless, comparative psychology has found that similar patterns of trait correlations are observed in many species. Specifically, behavioural axes characterizing responses to novelty are common across taxa (Gosling, 2001). The frequency with which this reactivity (Koolhaas et al., 1997, 1999) or shy-bold (Sih et al., 2004a, 2004b; Smith & Blumstein, 2008) axis is observed across taxa is consistent with our finding of behavioural (co)variation being evolutionarily conserved.

Conserved trait correlations like those observed here constrain the divergence of populations and species (Schluter, 1996). Although the potential for such constraints has been speculated about for behaviours (Dochtermann & Dingemanse, 2013), prior demonstrations of such have primarily focused on morphological traits (McGlothlin et al., 2018; Szepeanacz & Houle, 2019) and chemical traits (Aguirre et al., 2014; Blows et al., 2004).

Jointly, our approach allowed us to determine whether there were differences in average behaviour, ‘personality’, behavioural plasticity and behavioural syndromes among species. Our results demonstrate phylogenetic conservation of behavioural averages, behavioural variation and behavioural syndromes. This finding is potentially surprising, given that behaviour is often assumed to be more flexible and labile than other types of traits (but see Zuk & Spencer, 2020) and suggests an important role for phylogenetic constraints as an alternative to the dominant adaptive explanations commonly employed when discussing animal personality and behavioural syndromes.

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## CONFLICTS OF INTEREST

The authors have no conflicts of interest.

## PEER REVIEW

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## OPEN RESEARCH BADGES



This article has earned Open Data and Open Materials badges. Data and materials are available at <https://osf.io/q23ud/>.

## DATA AVAILABILITY STATEMENT

All data and code are available at: <https://osf.io/q23ud/>; <https://doi.org/10.17605/OSF.IO/Q23UD>.

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