



Original Article

Behavioral syndromes vary among geographically distinct populations in a reptile

Marcus Michelangeli,[○] David. G. Chapple,[○] Celine. T. Goulet,[○] Michael G. Bertram[○] and Bob. B. M. Wong

School of Biological Sciences, Monash University, Victoria, 3800, Australia

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A key goal in the study of animal personalities is to determine their adaptive potential and importance for behavioral evolution. Behavioral syndromes are evolutionarily intriguing because they suggest that an adaptive change in one behavior requires a concomitant shift in another. Within species, behavioral syndromes might be evolutionarily constrained by intrinsic mechanisms that restrict behaviors from evolving independently. Alternatively, behavioral correlations might easily be decoupled over short evolutionary time scales due to variation in selective pressures between environments. In this regard, comparative studies that explore differences in diverse aspects of personality between geographically distinct populations can provide valuable insights into the evolutionary processes acting on different behavioral tendencies. Accordingly, we investigated how behavioral types and behavioral syndromes differed across four geographically distinct populations of the delicate skink, *Lampropholis delicata*. We found strong evidence of mean trait-level variation in activity, exploration, and boldness across populations, suggesting adaptation to local environmental conditions. Similarly, we found that within-population correlations involving boldness varied substantially between populations. However, we did find a consistent within- and among-population correlation between activity and exploration, suggesting that this behavioral syndrome is relatively stable and could explain behavioral divergence in activity and exploration between populations. We suggest that there may be thermal physiological mechanisms that could be limiting the adaptive potential of an activity-exploration correlation in the delicate skink. Broadly, we argue that some behavioral correlations may be more adaptive than others, and that this should be more regularly considered within the animal personality framework.

Key words: correlated evolution, geographic variation, lizard, local adaptation, repeatability.

INTRODUCTION

It has been well documented across a range of taxonomic groups that individuals within populations often show consistent differences in a range of behaviors [i.e., behavioral types: Sih et al. (2004) and Reale et al. (2010)] and that these consistent behaviors often correlate with functionally unrelated behaviors across time and context [i.e., behavioral syndromes: Sih et al. (2004) and Reale et al. (2010)]. Together, these phenomena are commonly referred to as “animal personalities” (Roche et al. 2016). A key goal in the study of animal personalities is to determine their adaptive potential and importance for behavioral evolution. At an individual-level, personalities are evolutionarily intriguing because they place a limit on behavioral plasticity and thus mediate an individual’s response to a given ecological situation with consequences for individual fitness (Sih et al. 2004). At a population- or species-level, animal personalities can affect higher-order ecological and evolutionary

processes, such as social networks and movement ecology (Spiegel et al. 2017), dispersal events (Cote et al. 2010), and biological invasions (Duckworth and Badyaev 2007). However, to understand the evolutionary potential of animal personalities, we must first determine to what extent multifarious personality traits are consistent across space and time.

Population-level characteristics are often shaped by their local biotic and abiotic conditions, but these environmental factors are rarely homogeneous between populations (Foster 1999). Indeed, there is some evidence that animal personalities are strongly influenced by both short- and long-term environmental effects, and that behavioral correlations are quite unstable and can be easily formed and broken down over relatively short evolutionary time scales [i.e., the “adaptive hypothesis”: Wilson (1998), Bell (2005), Bell and Sih (2007), and Dingemanse et al. (2007)]. For example, 3-spined sticklebacks, *Gasterosteus aculeatus*, bred under high predation risk have a bold-aggressive behavioral syndrome, whereas those bred in low predation risk lose this syndrome Bell and Sih 2007. In contrast, if two or more behaviors share a proximal association (e.g., physiological, hormonal, or genetic), then we might predict that behavioral

Address correspondence to M. Michelangeli. E-mail: marcus.michelangeli@monash.edu

correlates would remain rigid against strong environmental selection and thus be a consistent population- or species-level trait. Such behavioral syndromes would be evolutionarily constrained, as an intrinsic change in one behavioral trait requires an intrinsic change to another, and thus both behavioral traits cannot evolve independently [i.e., the “constraint hypothesis”: Pruitt et al. (2010) and Dochtermann and Dingemans (2013)]. In these circumstances, a shared behavioral syndrome can also hold explanatory power for personality variation between populations. For instance, Pruitt et al. (2010) found a consistent negative correlation between sociability and boldness both within and among 18 different populations of a spider, *Anelosimus studiosus*, separated by as much as 36° latitude, suggesting a lack of evolutionary independence and support for the constraint hypothesis. Based on this shared within- and among-population behavioral syndrome, the authors could predict that if population “A” is more social than population “B,” then population “A” must also be less bold than population “B” (i.e., because a positive shift in sociability corresponds to a negative shift in boldness).

Although comparisons of geographically distinct populations cannot unequivocally determine the evolutionary causations of personality without appropriate genetic- or environment-dependent data, such contrasts are still a vital first step towards identifying the adaptive or nonadaptive significance of animal personalities (Foster 1999, Herczeg et al. 2009). Most studies investigating animal personalities either 1) focus on multiple traits within 1 population or 2) focus on only 1 or 2 traits between multiple populations. Although such studies have provided tremendous insights into animal personality, neither approach addresses how adaptive or constrained different suites of behaviors might be amongst multiple populations. This is an important consideration because diverse aspects of animal personality may be less or more adaptive than others, and this can provide valuable insights into the evolutionary potential of different behavioral tendencies.

In the present study, we sought to compare personality traits among four populations of a widespread reptile, delicate skink, *Lampropholis delicata*. The delicate skink is a small, diurnal, group-living lizard species (adult snout-vent length [SVL] 34–55 mm) that is native, and abundant throughout south-eastern Australia. This species offers an ideal study system to examine geographical variation in animal personality. First, we know the phylogenetic history of the species (Chapple et al. 2011), providing pivotal information for the interpretation of comparative behavioral research on geographically distinct populations (Blomberg and Garland 2002). Second, we have previously found a behavioral syndrome between activity, exploration tendency, and sociability within the species (Michelangeli et al. 2016a), which is consistent between the sexes (Michelangeli et al. 2016b). Third, we recently demonstrated a robust link between thermal physiology and personality traits in the delicate skink. Briefly, “hot” thermal-type lizards perform optimally at higher body temperatures, have faster sprint speeds, are more active, explorative, social, and bold relative to “cold” thermal type lizards, which have the opposite set of characteristics (Goulet et al. 2017a, 2017b; Goulet et al. 2018; Michelangeli et al. 2018). In these studies, we suggest that differences in thermal physiological requirements could provide an intrinsic mechanism that maintains stable behavioral syndromes across geographically distinct populations, particularly in ectothermic organisms that rely on behavioral thermoregulation for ecological performance. This is because an individual’s specific thermal physiological demands (i.e., “hot” or “cold”) likely constrain them along a predictable behavioral continuum due to behavior’s dependence on inherently stable biomechanical processes that are

regulated by body temperature. If consistent differences in thermal physiology maintain consistent differences in behavior as predicted, we would expect to find that within-population behavioral syndromes are similar across populations of the delicate skink.

Accordingly, the aims of our study were to 1) test for potential mean trait-level differences in multiple behavioral types between populations of the delicate skink, 2) identify possible behavioral syndromes and determine whether they are consistent between populations, and 3) determine whether population differences in mean trait-level behavior are predicted by their within-population behavioral syndromes (sensu Pruitt et al. 2010).

METHODS

Ethical note

Research was conducted in accordance with appropriate collection and research permits (Queensland: WISP16338615, New South Wales: SL101600, Victoria: 1006866) and was approved by the Monash University Animal Welfare Committee (BSCI/2014/26).

Study sites

Delicate skinks were collected from 4 populations across eastern Australia: 29 lizards from Sydney (Sydney Park, 33°54S, 151°11E), 31 lizards from Coffs Harbour (Boambee Bay park, 30°21S, 153°05E), 30 lizards from Tenterfield (Bald Rock National Park, 28°51S, 152°03E), and 27 lizards from Brisbane (Ithaca Creek Parklands, 27°27S, 152°58E). We selected these sites because they are phylogeographically distinct (Chapple et al. 2011).

Animal collection and husbandry

Lizards were collected from all locations in November 2015, just after the species breeding season. Only adult (SVL > 34 mm), full-tailed (tail length > SVL) male lizards were retained in order to avoid the potential confounding influence of tail loss (Cromie and Chapple 2012) and gravidity (Shine 2003) on behavior. We used hand capture and mealworm fishing capture techniques as both methods have previously been shown not to retain any sampling bias towards particular behavioral types in delicate skinks (Michelangeli et al. 2016a).

Lizards were transported back to Monash University for behavioral experiments and, on arrival, individuals were given a minimally invasive unique permanent identification code using different color combinations of Visual Implant Elastomer (VIE, Northwest Marine Technology, WA). Focal lizards were housed in groups of 5 individuals within large plastic containers (300 × 230 × 370 mm). A basking area, consisting of a heat lamp over 2 terracotta tiles, was provided at one end of each housing container. This created a thermal gradient in the housing container (22–32 °C) allowing thermoregulation from 08:00 to 17:00 h. Small plastic pots were added to provide shelter. UV lighting was placed above the containers and was activated from 08:00 to 18:00 h. All housing containers were located in a temperature-controlled room with an ambient temperature of approximately 22–23 °C and room lighting from 07:00 to 21:00 h daily. Skinks were fed a diet of crickets, *Acheta domesticus*, dusted in a vitamin supplement (Reptivite™), 3 times per week, and water was made available ad libitum.

Behavioral experiments

We conducted a series of behavioral assays to examine behavioral variation and correlation within and among populations. Lizards

had been held in captivity for 2 weeks before behavioral assays commenced. Individuals were tested in each behavioral assay twice in order to assess behavioral repeatability (or consistency). Each retest was done 1 week apart to examine short-term repeatability and reduce any effects arising from potential developmental changes within individuals (Bell et al. 2009). An individual was therefore only ever exposed to 1 behavioral assay per week, for a total of 8 weeks (i.e., 4 behavioral assays, 2 trials per assay, and 1 trial per week). Assays were carried out in a fixed order (in the same order detailed below) where assays that could have the greatest influence on behavior were carried out last to reduce potential carry-over effects (Bell 2012). All behavioral assays were conducted between 09:00 and 15:00, in opaque-walled experimental arenas (550 × 320 × 240 mm) within temperature-controlled rooms which matched the lizard housing temperature (22–23 °C). The setup of the experimental arena was modified to accommodate the assay being conducted. Skinks were allowed to acclimate under transparent containers for 10 min prior to the start of each trial. All trials were recorded using JVC Everio GZ-E100 video cameras. Equipment was thoroughly washed between trials with hot water and scentless dishwashing detergent to prevent scent contamination. Since *Lampropholis* skinks are known to modify their behaviors after large meals (Shine 2003), we ensured that lizards were not fed in the 24 h prior to each behavioral trial.

Nondirected activity test

To measure activity levels, skinks were allowed to move freely in an experimental arena marked with 20 equal grid squares over a 20-min period. Activity was scored based on the number of transitions between grid squares made by the skink, and the mean time taken to transition across grid squares after the skink's initial transition. We took the latter measurement to control for those lizards that took a long time to initially move but were very active after their initial movement (sensu Chapple et al. 2011; Michelangeli et al. 2016a, 2016b; Michelangeli et al. 2017; Michelangeli et al. 2018).

Obstacle test

To measure an individual's propensity to explore a novel environment, skinks were placed into a test arena containing an obstacle in the form of a trapezium-shaped barrier, which divided the test arena into 2 compartments. Lizards commenced the trial in compartment 1 and could only reach compartment 2 by finding, and squeezing through, small gaps at either end of the barrier. This assay aimed to measure an individual's willingness to 1) approach a novel obstacle, 2) examine/explore the obstacle, and 3) cross the obstacle to explore an unknown environment. Over a 20-min trial, we recorded the time spent by lizards inspecting the barrier itself, the time lizards spent stationary, and whether the lizard reached compartment 2 over 20 min (sensu Chapple et al. 2011; Michelangeli et al. 2016a, 2016b, Chung et al. 2017).

Sociability test

We conducted a dichotomous choice experiment to measure the social behavior of skinks. Delicate skinks are often observed either basking in small groups (~2–10 individuals) or alone in the wild (our unpublished data). Thus, we offered individual lizards a choice between basking with a group of conspecifics and basking alone (sensu Michelangeli et al. 2016a, 2016b; Michelangeli et al. 2017). This was achieved by splitting the test arena into 3 zones: a social zone, an asocial zone, and an intermediate neutral zone. Both the social and asocial zones

were comprised of a basking site that was divided in half by a transparent Perspex™ barrier that spanned the length of the test arena. In the social zone, 3 stimulus lizards were placed behind the partition, whereas the asocial zone was left bare. Focal lizards could see, but not physically interact with the stimulus lizards. Stimulus lizards comprised individuals that were from the same population but were unfamiliar to the focal lizards (i.e., they were not housed together) and were caught during the collecting trip in November 2015. Stimulus lizards were not used for any other behavioral assay and no focal lizards were used as stimuli. Over a 20-min trial, we recorded the total amount of time spent by lizards basking in the social zone, as well as the mean amount of time a lizard spent within the social zone before transitioning into another zone.

Predator-response test

An individual's boldness is typically measured as their risk-taking response after a threatening situation. In reptiles, basking is considered to be a risky behavior as it exposes individuals to potential predators (Downes and Hofer 2004). We therefore recorded a lizard's reemergence time from a shelter site and their subsequent basking behavior after a simulated predatory attack, as measures of risk-taking. To achieve this, skinks were placed at the center of a test arena with a basking site on one end, and a shelter site on the other. The basking site was positioned under a 40-W heating lamp so that the temperature of the basking site (~35 °C) was substantially higher than the ambient temperature (~22–23 °C). After the acclimation period, an observer would simulate a predatory attack by prodding the lizard close to its tail with a rod until the lizard entered the shelter site (sensu Rodríguez-Prieto et al. 2011). We then allowed the lizard 30 min to reemerge from the shelter site, recording its time of reemergence. After reemergence, we then recorded the total time spent by the lizard basking over an additional 5-min period. Because we gave all lizards an additional 5 min to bask after reemergence from the shelter site, we treated both behavioral measures as independent behavioral traits.

Statistical analyses

Data were analyzed using R version 3.3.2 (R Core Development Team 2016). Data were checked for normality [Shapiro–Wilk test: Royston (1995)] and homogeneity of variance [Fligner–Killeen test: Conover et al. (1981)] where appropriate. Several variables required data transformations prior to analysis to approximate Gaussian error distributions (see Table 1 for specific transformations).

For each behavioral assay, we used principal component analysis (PCA) followed by varimax rotation to reduce related behavioral variables into single standardized personality scores (Table 1). All PCAs were implemented using a correlation matrix that standardized all variables (Tabachnick and Fidell 2013). Bartlett tests were significant, indicating that correlation matrices were significantly different from identity matrices. Principal components were retained based on the Kaiser–Guttman criterion (eigenvalue > 1; Jackson 1993). Because these PCAs combined data for both trial 1 and trial 2 (i.e., they did not consider repeated measures) and each population (i.e., they did not consider variation within populations), we also ran PCAs on the data for each trial and population separately. These separate trial and population PCAs produced very similar results to the combined data PCAs (Supplementary Tables S1 and S2). Due to the minimal difference, we used the 4 personality scores resulting from the combined data PCAs for the rest of the analysis (Table 1).

Table 1
Principal component scores on the behavioral variables for each behavioral assay

Behavioral assay	Principal component
1. Non-directed activity	PC1 (Activity score)
Behavior (transformation)	
Number of grid transitions	0.92
Mean transition time (log)	-0.92
Eigenvalue	1.69
% Variance explained	0.85
2. Obstacle Test	PC1 (Exploration score)
Behavior (transformation)	
Time spent inspecting barrier (sqrt)	0.89
Number of barrier passes	0.72
Time spent stationary	-0.90
Eigenvalue	2.11
% Variance explained	0.70
3. Sociability Test	PC1 (Sociability score)
Behavior (transformation)	
Time spent in social zone	0.91
Mean time in social zone (sqrt)	0.91
Eigenvalue	1.66
% Variance explained	0.83
4. Predator–response test	PC1 (Boldness score)
Behavior (transformation)	
Time to taken to reemerge (rank)	-0.80
Time spent basking (rank)	0.82
Eigenvalue	1.27
% Variance explained	0.63

Eigenvalue and explained variances are also provided for each component.

Behavioral repeatability

We used linear mixed-effects models (LMM, *lme4* package: Bates et al. 2015) with Gaussian error distributions to assess behavioral repeatability. Behavioral repeatability is calculated as the ratio of between-individual variance (BIV) to total phenotypic variance (BIV + within-individual variance [WIV]). Variance components were extracted from univariate mixed-effects models using restricted maximum likelihood with individual ID as a random factor. We ran separate models for each population and a model containing data from all populations. The model containing data from all populations included population as a fixed factor to consider variation between populations, and thus represents an adjusted repeatability estimate (Nakagawa and Schielzeth 2010). Confidence intervals were calculated by parametric bootstrapping using the package *rptR* (Stoffel et al. 2017).

Mean-trait level population differences

We compared LMM models with and without the fixed effects of population, trial number, population x trial number interaction, and SVL, to examine mean-trait population differences. Individual ID was assigned as a random factor in all models. *P* values were obtained from likelihood ratio tests (Bolker et al. 2009). After model selection, we used post hoc tests to determine to what extent populations differed from one another. Holm–Bonferroni correction method was applied to all *P* values resulting from multiple comparison post hoc tests.

Behavioral syndromes

To estimate within- and among-population correlations, we first calculated Pearson-product moment correlation coefficients between each of the personality scores. Holm–Bonferroni corrections were

Table 2
Effect size for each behavioral correlation estimated using Pearson product-moment correlation coefficients (*r*) within each population

	Exploration	Sociability	Boldness
Activity			
Sydney	0.24*	0.09	-0.34
Coffs Harbour	0.42	-0.01	0.29*
Tenterfield	0.33*	-0.04	-0.09
Brisbane	0.32*	0.08	0.08
Total	0.45	0.03	-0.07
Exploration			
Sydney	—	-0.01	-0.15
Coffs Harbour	—	0.16	0.25*
Tenterfield	—	-0.06	-0.37
Brisbane	—	-0.16	0.03
Total	—	-0.03	-0.13
Sociability			
Sydney	—	—	-0.15
Coffs Harbour	—	—	0.02
Tenterfield	—	—	-0.01
Brisbane	—	—	-0.01
Total	—	—	-0.01

Total refers to data for all populations combined.

Bold font indicates significant effect size after Bonferroni correction ($P < 0.008$).

*Indicates significant effect size without Bonferroni correction ($P < 0.05$).

Also see Table 5.

applied to account for multiple testing. We then used LMM models to assess syndrome similarity between populations. Within these models, we used one personality score as the response variable, and the other personality score as the covariate. Population x covariate interaction and trial x covariate interaction were fixed factors. Skink ID was incorporated as a random factor to consider the repeated measures. A significant interaction suggests that the magnitude and direction of the correlation differ between the levels of the main effect (i.e., population or trial). On the other hand, no interaction, but a significant covariate, suggests that the behavioral correlation is similar in magnitude and direction across population and trial. Sociability score was omitted from this part of the analysis due to its generally low effect size (Table 2).

RESULTS

Behavioral repeatability

All behaviors were repeatable (i.e., confidence intervals do not overlap zero) when data from all populations were pooled (i.e., species-level repeatability). When considering populations individually, repeatability estimates varied between populations and different behaviors (Table 3). However, most repeatability estimates would be considered relatively high ($r > 0.37$; see meta-analysis by Bell et al. 2009), although the uncertainty (i.e., confidence intervals) around these estimates is also quite large. Sociability, in general, was not repeatable within populations (Table 3).

Mean-trait level population differences

We found evidence of mean behavioral-type differences amongst populations (Table 4). Firstly, the Sydney population was significantly more active in the nondirected activity assay than the other 3 populations (Sydney–Coffs Harbour: $z = 2.75$, $P = 0.023$; Sydney–Tenterfield: $z = 5.31$, $P < 0.001$; Sydney–Brisbane:

Table 3 Repeatability (*r*) with associated confidence intervals (CIs) and variance components (between-individual variance: BIV, and within-individual variance: WIV) of behavioral traits measured in male delicate skinks (*L. delicata*) from four populations in Eastern Australia

Behavior	Sydney		Coffs Harbour		Tenterfield		Brisbane		Total	
	BIV	WIV	BIV	WIV	BIV	WIV	BIV	WIV	BIV	WIV
Activity	0.33	0.33	0.73	0.25	0.35	0.39	0.64	0.22	0.52	0.30
			0.50	(0.19, 0.72)	0.75	(0.55, 0.87)	0.48	(0.14, 0.72)	0.75	(0.51, 0.87)
Exploration	0.29	0.63	0.42	0.36	0.27	0.32	0.65	0.29	0.41	0.40
			0.32	(0.23, 0.74)	0.46	0.81	0.46	(0.15, 0.70)	0.69	(0.42, 0.85)
Sociability	0.21	0.45	0.13	0.51	0.46	0.81	0.22	0.97	0.26	0.75
			0.32	(0, 0.60)	0.36	(0, 0.63)	0.18	(0, 0.52)	0.18	0.25
Boldness	0.27	0.47	0.58	0.45	0.40	0.50	0.61	0.48	0.44	0.51
			0.37	(0.02, 0.63)	0.57	(0.27, 0.76)	0.45	(0.10, 0.68)	0.56	(0.20, 0.78)

Total refers to data for all populations pooled and represents an adjusted repeatability estimate controlling for between-population variance. Bold scores refer to significant repeatability estimates.

Table 4 Results from LMM model selection comparing behavioral traits

Behaviour	ΔAIC	χ ²	P value
<i>Activity</i>	–	–	–
Population x trial number	+3.63	2.371	0.499
Population	-25.29	31.291	<0.001
Trial number	+2.00	0.001	0.972
SVL	+1.72	0.275	0.599
<i>Exploration</i>	–	–	–
Population x trial number	+2.7	3.302	0.347
Population	-27.95	33.95	<0.001
Trial number	-5.43	7.423	0.006
SVL	+1.96	0.044	0.834
<i>Sociability</i>	–	–	–
Population x trial number	+3.95	2.059	0.562
Population	+2.56	3.440	0.329
Trial number	+1.99	0.011	0.915
SVL	+1.49	0.506	0.477
<i>Boldness</i>	–	–	–
Population x trial number	+5.75	0.246	0.970
Population	-6.80	12.750	0.005
Trial number	-12.42	14.365	<0.001
SVL	+1.94	0.056	0.813

Models containing the fixed effects (population, trial number, population x trial number interaction, and SVL) are compared with a model without the fixed effects. All models contained individual ID as a random factor. ΔAIC values refer to differences in AIC when specific fixed factors were included vs. excluded from the initial model. SVL = snout-vent length; AIC = Akaike information criterion; χ² = chi-square value. Bold refers to significant terms at *P* < 0.05.

z = 4.92, *P* < 0.001). Lizards from Coffs Harbour were more active than lizards from Tenterfield (*z* = 2.62, *P* = 0.026) and Brisbane (*z* = 2.29, *P* = 0.044). Tenterfield and Brisbane lizards did not differ in their level of activity (*z* = -0.25, *P* = 0.800).

Sydney lizards were also more explorative during the obstacle test (i.e., were more likely to explore and pass the barrier) than the other 3 populations (Sydney—Coffs Harbour: *z* = 3.54, *P* = 0.002; Sydney—Tenterfield: *z* = 6.22, *P* < 0.001; Sydney—Brisbane: *z* = 3.79, *P* < 0.001). Brisbane and Coffs Harbour lizards were also significantly more explorative than Tenterfield lizards (Brisbane—Tenterfield: *z* = 2.29, *P* = 0.044; Coffs Harbour—Tenterfield: *z* = 2.76, *P* = 0.018). Coffs Harbour and Brisbane lizards did not differ in their exploration score (*z* = 0.38, *P* = 0.707).

Finally, lizards from the Sydney population were less bold than lizards from Coffs Harbour (*z* = -3.50, *P* = 0.003) and Tenterfield (*z* = -2.73, *P* = 0.032), but not Brisbane lizards (*z* = -2.16, *P* = 0.123). There was no difference in boldness scores amongst the other populations (Coffs Harbour—Tenterfield: *z* = 0.76, *P* = 0.898; Tenterfield—Brisbane: *z* = 0.50, *P* = 0.898; Coffs Harbour—Brisbane: *z* = 1.24, *P* = 0.641).

We also found that lizards from all populations became more explorative and bolder between trial 1 and trial 2 (Table 4), suggesting potential habituation to the experimental procedure of both the obstacle test and predator-response test, respectively. We found no population differences in sociability (Table 4).

Behavioral syndromes

Overall, we found variation in behavioral syndromes between populations. First, we found a similar activity and exploration correlation within each population (Table 2). Exploration was a significant

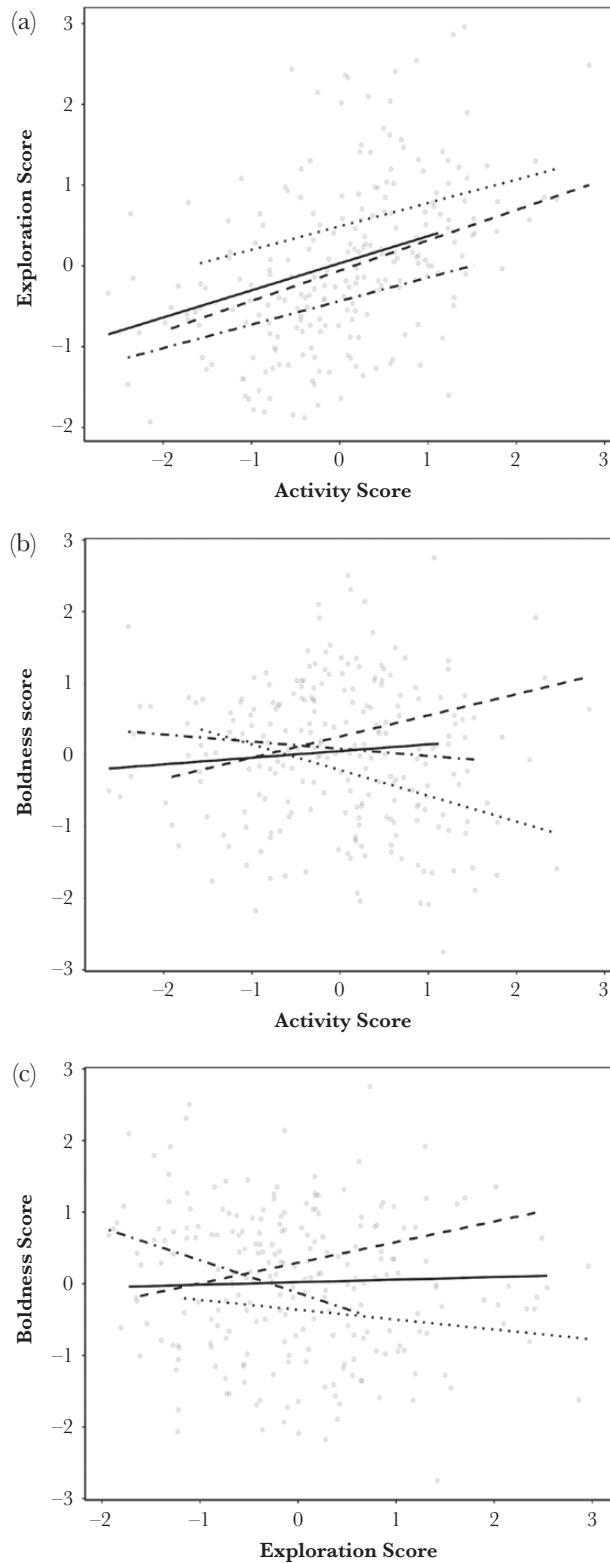


Figure 1

Within-population regression lines for relationships between (a) activity and exploration, (b) activity and boldness, and (c) exploration and boldness. Sydney = dotted line, Coffs Harbour = dashed line, Tenterfield = dotted-dashed line, and Brisbane = solid line.

covariate in the mixed-effects model containing activity as a response variable. Importantly, this within-population activity-exploration syndrome was consistent in magnitude and direction across populations

Table 5

Linear mixed effects models testing the behavioral relationships between traits of interest (i.e., traits that were found to have a significant effect size; Table 2) across populations and trial

Model	Term	df	χ^2	P value
Y: Activity ~ X: Exploration	Population	3	19.956	<0.001
	Exploration	1	18.062	<0.001
	Trial	1	0.727	0.494
	Population x exploration	3	1.794	0.616
	Trial x exploration	1	0.070	0.791
Y: Activity ~ X: Boldness	Population	3	30.673	<0.001
	Boldness	1	0.001	0.992
	Trial	1	0.001	0.971
	Population x boldness	3	9.535	0.023
	Trial x boldness	1	0.121	0.727
Y: Exploration ~ X: Boldness	Population	3	31.896	<0.001
	Boldness	1	0.324	0.569
	Trial	1	6.355	0.011
	Population x boldness	3	8.851	0.031
	Trial x boldness	1	0.030	0.863

Significant interaction terms suggest differences in the magnitude and direction of behavioral relationships (see Figure 1). Bold refers to significant terms in the full model.

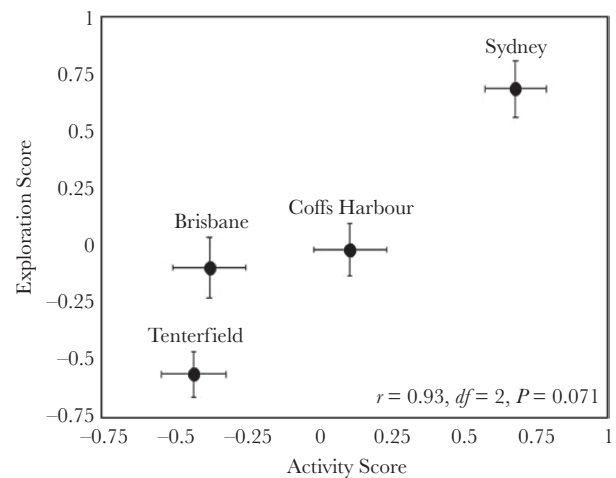


Figure 2

A positive correlation in mean-trait values for activity and exploration scores among 4 populations of the delicate skink.

(Figure 1a), as we found no interaction between the covariate and population in the mixed-effects model (Table 5). There is also suggestion of an among-population correlation in mean level activity and exploration, but this effect is marginally nonsignificant ($r = 0.93$, $df = 2$, $P = 0.071$, Figure 2). The activity-exploration correlation did not differ between trials (Table 5, also Supplementary Figure S1).

Second, activity and boldness were correlated within the Sydney and Coffs Harbour populations, but not in the Tenterfield or Brisbane populations (Table 2). However, the direction of the activity-boldness correlation differed between Sydney and Coffs Harbour, being negative in Sydney but positive in Coffs Harbour. In line with this result, we also found a significant interaction between population and the covariate (Table 5). This result suggests that the magnitude and direction of the activity-boldness relationship differ between populations (Figure 1b). There is also no suggestion of an among-population correlation ($r = -0.69$, $df = 2$, $P = 0.312$).

Third, exploration and boldness were significantly correlated in the Tenterfield and Coffs Harbour populations, but not in the Sydney or Brisbane populations. Again, the direction of this exploration–boldness correlation differed between the 2 populations, being positive in Coffs Harbour, but negative in Tenterfield. Indeed, we also found a significant interaction between population and the covariate (Table 5), suggesting population differences in the direction and magnitude of the exploration–boldness relationship (Figure 1c). There is also no suggestion of an among population correlation ($r = -0.79$, $df = 2$, $P = 0.208$).

DISCUSSION

We found markedly diverse personality traits across four native-range populations of the delicate skink. Briefly, the Sydney population was comprised of consistently more active and explorative behavioral types compared with the Coffs Harbour, Tenterfield, and Brisbane populations. Sydney lizards were also consistently less bold than lizards from Tenterfield and Coffs Harbour. Tenterfield lizards were consistently less explorative than all other populations. Importantly, we also found geographical variation in the magnitude and direction of different behavioral syndromes within populations. First, we found a common activity–exploration correlation within each population, and that this correlation was also in the same direction at the among-population level. This suggests that this syndrome is relatively stable and can help explain population-level variation in behavior (sensu Pruitt et al. 2010). Second, we found that the direction and magnitude of an activity–boldness correlation and exploration–boldness correlation varied greatly between populations. Taken together, our results suggest that variation in average behavioral types may be a product of adaptation to local environmental conditions, but when considering behavioral syndromes, some behavioral correlations are more evolutionarily stable and likely constrained by intrinsic factors, whereas other correlations hold greater adaptive potential.

The Sydney population was behaviorally distinct and was comprised of mainly active, explorative, and shy lizards, relative to the other populations. Conversely, lizards from Tenterfield were noticeably less explorative than all other populations, and less active than both Sydney and Coffs Harbour lizards. It is well recognized that divergence between populations, whether through behavior, physiology, or morphology, is often a result of adaptation to local ecological conditions, such as predation pressure (Michelangeli and Wong 2014), resource availability (Snekser et al. 2008), and population density (Nicolaus et al. 2016). The behavioral differences observed between Tenterfield lizards and the other populations (particularly Sydney lizards) could be explained by the fact that Tenterfield lizards were sourced from a relatively pristine environment (i.e., a national park: Bald Rock NP), whereas the other 3 populations were sourced from urbanized environments. Urbanized environments are often dramatically modified and thus expose their inhabitants to multiple novel selective pressures (e.g., human disturbance, pollution, and novel predators) not frequently encountered by inhabitants of natural environments, often requiring urban-dwellers to make drastic behavioral changes in order to persist and survive (Lowry et al. 2013; Sol et al. 2013). Several studies have documented diverse personalities between urban and natural populations (Sol et al. 2011; Bokony et al. 2012; Lapiedra et al. 2017). For instance, it was hypothesized that lower predation risk in urban environments

may allow urban common mynas, *Acridotheres tristis*, to be more explorative and thus more readily accept novel food resources than mynas from nonurban environments (Sol et al. 2011). However, although urbanization could explain the observed differences between the urban populations and Tenterfield lizards, it does not necessarily explain the personality differences between Sydney, Coffs Harbour, and Brisbane lizards. We suggest that these differences could be due to some unmeasured ecological factors (e.g., predation pressure, habitat availability, and competition) and/or due to the fact that populations might fall differently along the urban gradient (i.e., some populations may be more or less urbanized than others; Lowry et al. 2013). For example, previous work on the delicate skink has even found behavioral differences between 2 urbanized populations within suburban Sydney (Moule et al. 2016). Indeed, the results of our study are limited by the fact that we only tested four populations and did not measure any environment-dependent variables (e.g., level of urbanization); thus, we can only speculate as to reasons for the observed population differences. Future studies would benefit from adopting a replicated study design that measures multiple populations, and targets specific ecological factors of interest that could underlie population differences in personality (e.g., different levels of urbanization or thermal regimes). Such an approach would then allow for a more robust interpretation of the ecological and evolutionary factors underpinning consistent individual differences in behavior across populations (Dall and Griffith 2014).

We found evidence to suggest that some behavioral syndromes may be more stable and less adaptive than others. Most comparative studies on behavioral correlations have revealed remarkable population variation in behavioral syndromes, particularly syndromes consisting of traits related to boldness (Bell 2005; Bell and Sih 2007; Dingemanse et al. 2007; Brydges et al. 2008; Herczeg et al. 2009). These studies provide support that some syndromes develop under particular selective environments and can become decoupled over relatively short evolutionary time scales [i.e., the “adaptive hypothesis”; Wilson (1998)]. In this study, we also found evidence that syndromes which contained boldness varied greatly between populations, whereby correlations were either present or absent within populations, and if present, they differed in direction. Boldness is typically measured as the tendency to take risk under threatening situations (Reale et al. 2010). Thus, differences in boldness between populations are typically the result of population differences in the level of predation pressure (Bell 2005; Bell and Sih 2007; Dingemanse et al. 2007; Brydges et al. 2008; Herczeg et al. 2009). It is likely that these divergent correlations are a product of an interplay between predation pressure and other habitat-specific characteristics. For instance, Brydges et al. 2008 found in sticklebacks that boldness and activity were correlated in high-predation river populations, but not in high-predation pond populations, suggesting that predation pressure and habitat complexity interact to influence personality in multifarious ways.

In contrast to behaviors correlated with boldness, we found that activity and exploration were consistently correlated both at the within- and among-population level. Although the magnitude of the among-population correlation was not statistically significant, it had a large effect size (i.e., $r = 0.93$), and it was identical in sign and direction as the within-population correlations (see discussion by Sih and Bell 2008). Furthermore, we have previously found strong correlations between activity and exploration in delicate

skinks from Sydney (Michelangeli et al. 2016a; Moule et al. 2016; Michelangeli et al. 2018) and within both sexes (Michelangeli et al. 2016b). This among-population correlation between activity and exploration implies a lack of evolutionary independence between these traits (i.e., because a shift in one trait corresponds with a shift in the other), and that this result is suggestive of a species-level trait (Martins and Bhat 2014). Our study is one of the few to find empirical evidence that a behavioral correlation might be constrained by some intrinsic mechanism (e.g., genes, physiology, or hormones) across geographically distinct populations [but see Pruitt et al. (2010) and Alcalay et al. (2015)]. However, to test whether this activity–exploration syndrome is in fact evolutionarily constrained, we would need to investigate the genetics underlying these behaviors and correlations using appropriate pedigree information [e.g., test personality of F1 generation: Herzceg et al. (2009) and Dochtermann and Dingemans (2013)].

We contend that one possible underlying mechanism maintaining this consistent activity–exploration syndrome is thermal physiology. We recently found evidence that thermal physiology drives behavior in delicate skinks and that an individual's personality corresponds with their position on a thermal gradient [i.e., along a cold–hot axis: Goulet et al. (2017a), (2017b), Goulet et al. (2018), and Michelangeli et al. (2018)]. Briefly, individuals that prefer and perform optimally at high body temperatures tend to be faster sprinters, more active, explorative, and bold than individuals that prefer and perform optimally at lower body temperatures. We suggest that animals that need to behaviorally thermoregulate (i.e., ectotherms) in temporally variable environments are more likely to be constrained by their thermal physiological needs, particularly those behaviors that rely more heavily on locomotion (like activity and exploration), the mechanics of which are mediated by an individual's body temperature (Biro and Stamps 2010, Careau and Garland 2012). Indeed, various other studies have documented links between behavior, temperature, and physiology in ectothermic organisms (Stapley 2006, Rey et al. 2015, Cerqueira et al. 2016, Gilbert and Miles 2016). Thus, due to the inherent relationship between temperature, physiology, and behavior, even when traits related to thermal physiology are plastic or consistently vary between populations, we would expect a concomitant shift in personality. For example, a shift from a population largely composed of individuals with higher thermal physiological requirements (i.e., hot thermal types) to a population largely composed of individuals with lower thermal physiological requirements (i.e., cold thermal types) results in a corresponding shift towards an average behavioral profile that is less active and explorative [e.g., Gilbert and Miles (2016)]. Indeed, different thermal types (e.g., hot or cold) are likely linked to different life-history strategies [e.g., pace-of-life: Reale et al. (2010)] that are generated by genetic correlations and environmental effects (e.g., microclimates, early life experience, or incubation temperature). Detailed comparative studies that explore population differences in the covariation between thermal physiological traits, genetics, and personality are first needed to support these hypotheses.

To conclude, we found common and uncommon aspects of personality across four populations of the delicate skink. We found that populations differed in their frequency and composition of behavioral types and how boldness covaried with other behavioral traits. However, we did find a shared activity–exploration syndrome within and among populations. These results suggest that populations are modified by their environmental settings, but there are also likely intrinsic mechanisms that maintain some behavioral correlations across even geographically distinct populations. We

propose here that one such mechanism, particularly in ectotherms, could be thermal physiology in which individual differences in personality are inhibited by individual differences in thermal and metabolic requirements (Cerqueira et al. 2016, Goulet et al. 2017b, Michelangeli et al. 2018). We contend that some personality traits may be more adaptive than others and that this needs to be more regularly considered within the animal personality framework.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Michelangeli et al. (2018).

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