



## Original Article

# Population differences in the effect of context on personality in an invasive lizard

Jack A. Brand,<sup>a,○</sup> Annalise C. Naimo,<sup>a</sup> Marcus Michelangeli,<sup>a,b,○</sup> Jake M. Martin,<sup>a,○</sup> Andrew Sih,<sup>b,○</sup> Bob B.M. Wong,<sup>a,†,○</sup> and David G. Chapple<sup>a,†,○</sup>

<sup>a</sup>School of Biological Sciences, Monash University, Melbourne, Victoria 3800, Australia and

<sup>b</sup>Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA

Received 16 February 2021; revised 19 July 2021; editorial decision 17 August 2021; accepted 3 September 2021.

Within populations, individuals often differ consistently in their average level of behavior (i.e., animal personality), as well as their response to environmental change (i.e., behavioral plasticity). Thus, changes in environmental conditions might be expected to mediate the structure of animal personality traits. However, it is currently not well understood how personality traits change in response to environmental conditions, and whether this effect is consistent across multiple populations within the same species. Accordingly, we investigated variation in personality traits across two ecological contexts in the invasive delicate skink (*Lampropholis delicata*). Specifically, lizards from three different populations were repeatedly measured for individual activity in group behavioral assays under differing levels of food availability. We found that environmental context had a clear effect on the structure of lizard personality, where activity rates were not repeatable in the absence of food, but were repeatable in the presence of food resources. The difference in repeatability of activity rates across contexts appeared to be largely driven by an increase in among-individual variance when tested in the presence of food resources. However, this was only true for one of the populations tested, with food context having no effect on the expression of personality traits in the other two populations. Our results highlight the important role of environmental context in mediating the structure of animal personality traits and suggest that this effect may vary among populations.

**Keywords:** behavioral plasticity, behavioral syndrome, behavioral type, environmental change, repeatability

## INTRODUCTION

Individuals often show repeatable differences in their average level of behavior (i.e., personality or behavioral type; Dingemanse et al. 2002; Sih et al. 2004; Bell et al. 2009). For example, previous research in Trinidadian guppies (*Poecilia reticulata*) found stable individual differences in risk-taking behavior, with some individuals being consistently more risk-averse than their conspecifics (Harris et al. 2010; Brown and Irving 2014). Similar evidence for personality traits has now been found in a wide variety of taxa (see Réale et al. 2007; Wolf and Weissing 2012; Payne et al. 2021), suggesting that consistent among-individual variation in behavior may be widespread throughout the animal kingdom. Further, many of these behaviors have been shown to be heritable (e.g., Dingemanse et al. 2002; Dochtermann et al. 2015), can affect survival (Smith and Blumstein 2008; Moirón et al. 2019) and reproductive success (Schuett et al. 2010; Munson et al. 2020) and, therefore, have significant consequences for species ecology and evolution (Réale et al. 2007; Sih et al. 2012; Wolf and Weissing 2012).

Behavioral traits are also often correlated with one another, either over time or across multiple contexts (i.e., behavioral syndromes; Sih et al. 2004). For instance, previous research in the fishing spider (*Dolomedes triton*) found that individuals which were bolder when foraging were also bolder during courtship, suggesting that some spiders were consistently more risk-prone than their conspecifics across separate ecological contexts (Johnson and Sih 2007). When considering the same behavioral trait measured across multiple contexts, the existence of behavioral syndromes suggests that organisms are limited in how they modulate their behavior in response to environmental change (Sih et al. 2004; Johnson and Sih 2007). This may be especially true in cases where behavioral syndromes have an underlying genetic basis (Dochtermann and Dingemanse 2013; Royauté et al. 2020). For example, Royauté et al. (2020) reported that there was a genetically conserved behavioral syndrome between risk-taking behavior and activity in both the presence and absence of a predator cue among multiple populations of the field cricket (*Gryllus integer*). These syndromes may, therefore, act as evolutionary constraints by preventing behavioral traits from reaching local optima in response to novel selection pressures (Dochtermann and Dingemanse 2013). Taken together, this research suggests that personality traits and behavioral syndromes

<sup>†</sup>These authors contributed equally to this work.

Address correspondence to J.A. Brand. E-mail: [jack.brand@monash.edu](mailto:jack.brand@monash.edu).

may constrain situation-specific plasticity and evolutionary adaptations by limiting how both individuals and populations behaviorally respond to changing environmental conditions.

However, the existence of personality traits and behavioral syndromes does not preclude individuals from altering their behavior in response to environmental change (e.g., Dingemanse et al. 2010; Mitchell and Biro 2017; Urszán et al. 2018; Cornwell et al. 2019; Jolles et al. 2019). Indeed, previous meta-analyses have shown that whilst behavioral traits are often repeatable, the majority of measured behavioral variation exists within-individuals (i.e., behavioral plasticity; Bell et al. 2009). For example, wild great tits (*Parus major*) significantly reduced their foraging behavior in the presence of increased predation risk (Quinn et al. 2012), but individuals also differed in their responsiveness. Specifically, while the majority of birds decreased their foraging behavior when the threat of predation was highest, others were relatively unresponsive, or even increased their feeding behavior (Quinn et al. 2012). These individual differences in behavioral plasticity suggest that the structure of personality traits or of behavioral syndromes may vary in response to differing environmental conditions (Bell and Sih 2007; Biro et al. 2010; Cornwell et al. 2019; Mitchell and Houslay 2021). For example, Klueen and Brommer (2013) reported that while neophobia in blue tits (*Cyanistes caeruleus*) was repeatable when measured in winter, the behavior was not repeatable during the breeding season. The authors found that this decrease in repeatability during the breeding season was driven by a reduction in variation between individuals (Klueen and Brommer 2013), further suggesting that environmental conditions may mediate the structure of personality traits within species. With this in mind, understanding how the expression of personality traits varies when measured under differing environmental conditions is an important topic of study. Further, whether the effect of context on personality traits is similar across multiple populations within the same species is not clear. Therefore, research repeatedly measuring behavioral traits from multiple populations under differing environmental conditions is needed to gain a greater appreciation of how personality traits vary within species.

Here we investigated average-level behavioral traits, as well as both behavioral repeatability (both among- and within-individual behavioral variation) and behavioral syndromes, across multiple contexts in three independent populations of the delicate skink (*Lampropholis delicata*), established on separate islands in Hawaii. The delicate skink is a small, social lizard species, and is the only Australian lizard to have established and invaded overseas, where it is known as the plague or rainbow skink (Chapple et al. 2013). The invasive population in Hawaii is thought to have been introduced onto the island of O'ahu around 1900 via unintentional release from shipping cargo (Chapple et al. 2013). However, after World War II, the species rapidly spread across much of the Hawaiian archipelago (Chapple et al. 2013). Previous research has shown that all Hawaiian delicate skinks share a common mitochondrial haplotype, suggesting that invasive Hawaiian populations are descended from the original founder population on the island of O'ahu (Chapple et al. 2013). We capitalized on the well-studied invasion history of the delicate skink in Hawaii to investigate how environmental context may influence behavioral variation across three separate populations that share common, recent ancestry. More specifically, we repeatedly measured activity rates of skinks while in both the presence and absence of food resources. Further, much of the current research investigating behavioral differences between individuals and populations typically measures the behavior of a

single individual in isolation from their conspecifics—even in social species (see Webster and Ward 2011). However, the presence of conspecifics can exert a strong influence on both average-level behavioral traits and individual level behavioral variation (King et al. 2015; Jolles et al. 2016; Guayasamin et al. 2017; Jäger et al. 2019; Munson et al. 2021). We, therefore, measured skinks when within social groups to understand context-specific variation in behavior when tested in a more ecologically realistic setting.

Previous research in delicate skinks has found that activity rates are repeatable when measured in social isolation (Michelangeli et al. 2017, 2019) and consistent across varying social conditions (Littlewood et al. 2021). However, whether activity levels are repeatable when within social groups, and how this variation shifts in response to changing environmental conditions (i.e., food resources) has not been studied. We predicted that activity rates would be repeatable, but that repeatability estimates, patterns of among and within-individual behavioral variation, and behavioral syndromes might all differ between the no-food and food conditions. We also investigated whether this variation differed among populations, but had no directional predictions for possible population differences. In addition, we predicted that individual differences in activity would be positively correlated to the amount of food consumed. Further, based on previous research finding differences in average-level activity across multiple native range populations of the delicate skink (Michelangeli et al. 2019), we hypothesized that there would be differences in average levels of activity across the invasive Hawaiian populations. Specifically, as previous evidence has suggested that invasion may select for increased activity rates (e.g., Mueller et al. 2017; Pizzatto et al. 2017), we predicted that the two more recently established populations (see Methods) would be more active when compared with the longer established founder population.

## METHODS

### Animal collection and husbandry

We used lizards caught from both the original invasive population on O'ahu (Tantalus;  $n = 35$ ), and from two separate populations located on the islands of Hawai'i (Volcano;  $n = 36$ ) and Kaua'i (Kokee;  $n = 36$ ) that represent secondary invasive populations (i.e., spread within the Hawaiian Islands) established in the 1960s (Chapple et al. 2013). Skinks were caught using hand capture and mealworm fishing. These methods have been previously shown to not retain any bias toward specific behavioral types (Michelangeli, Wong, et al. 2016). After capture, each lizard was given an identification code using unique color combinations of Visual Implant Elastomer (Northwest Marine Technology, Shaw Island, WA, USA) and measured for snout-vent length (SVL; from the tip of the snout to the cloaca) using digital calipers. Previous studies have shown significant effects of reproductive state (Shine 2003) and tail loss (Cromie and Chapple 2012; Michelangeli et al. 2020) on *Lampropholis* behavior. Therefore, to avoid these confounding effects, we collected and used only adult male skinks (SVL range: 32–44 mm; Miller et al. 2017) with full tails (SVL > tail length).

All skinks were transported to animal facilities at The University of California, Davis. Lizards from each population were split into three groups of 12 individuals each (i.e., three groups per population; nine groups total), with the exception of one group from the Tantalus population which had 11 skinks. Each group was housed communally in a plastic enclosure (400 × 300 × 370 mm) within a temperature-controlled

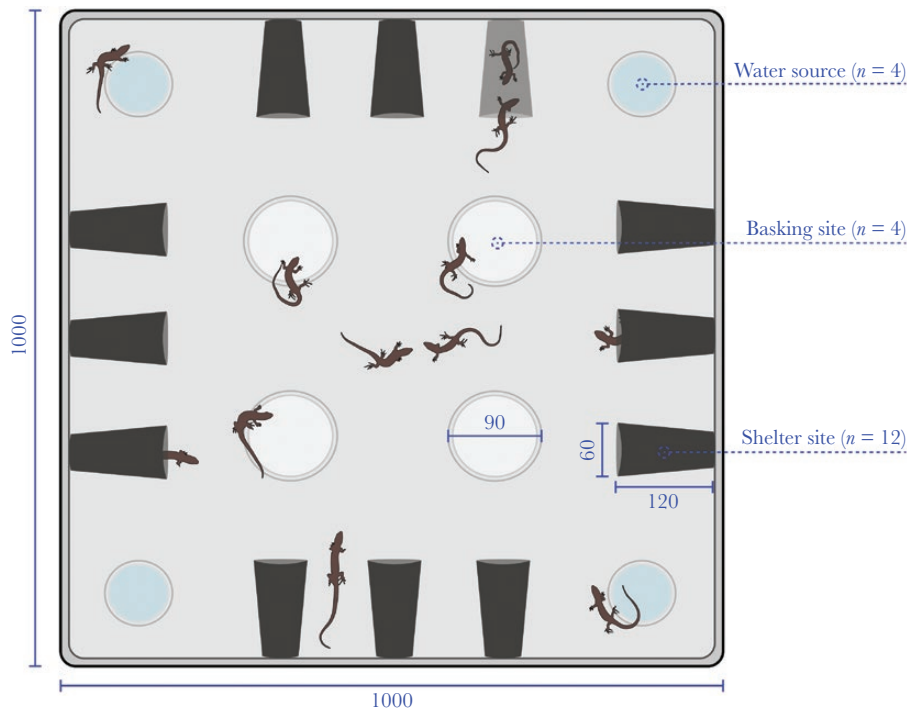
room (13:11 h light:dark cycle) maintained at  $22.5 \pm 0.5$  °C. Enclosures were furnished with small plastic pots and newspaper for shelter, with a terracotta basking tile heated with commercial heat-tape between 0800 and 1700 h placed at one end of the enclosure to create a thermal gradient (22–32 °C) that allowed animals to thermoregulate. During husbandry, all lizards were provided with UV lighting between 0800 and 1800 h. Lizards were fed communally within their housing groups with each skink receiving three small (1 cm) crickets (*Acheta domesticus*) dusted in a vitamin supplement (Reptivite™), three times a week. Water was available ad libitum. All animals were acclimated to their social group and these standardized laboratory conditions for approximately 4 weeks before the start of behavioral trials.

### Group behavioral assay

Experiments were carried out over 3 days to investigate population differences in behavioral variation in activity both in the presence and absence of food resources. Assays were conducted in nine large (100 × 100 × 30 cm) arenas fitted with 12 shelter sites (120 × 60 mm), four basking sites (90 mm diameter) maintained at  $29.5 \pm 0.5$  °C using individual heat packs, and four water sources (Figure 1). All assays were performed in a temperature-controlled room maintained at  $22.5 \pm 0.5$  °C, with trials video-recorded from above (JVC Everio GZ-E100) for later analysis. Each lizard was dorsally painted with a unique color combination of nontoxic paint that allowed the tracking of individual identity from recordings throughout the course of behavioral trials. Individual delicate skinks were tested within their housing groups (i.e., groups of 12 skinks with all lizards from the same population) as this more accurately reflects ecological conditions throughout the species invasive

range, where they are observed in densities of up to 20 skinks per m<sup>2</sup> (A.C. Naimo, personal observation; Michelangeli et al. 2017).

To begin the assay, each group of 12 skinks was initially confined to a clear acclimation container (260 × 140 mm) located in the center of the arena for 10 min. After acclimation, all 12 skinks within each group were simultaneously released into the center of the arena and allowed to freely explore. The behavior of each lizard was recorded over the following 20 min trial. After this initial behavioral observation period, skinks remained in their respective arenas for 4 h. At the 4 h mark, 12 crickets (*Acheta domesticus*) were introduced into the center of the arena, and lizard behavior was again recorded over the following 20 min trial. This experimental design allowed us to measure each individual's behavior in both the presence and absence of food resources. Following this second 20 min trial, lizards were kept in their respective arenas overnight. The next morning, all animals were recaptured and repainted with their unique color combinations to maintain individual identities, before being reintroduced into the acclimation containers to undergo a second day of trials. This process was repeated for 3 days so that each lizard was scored for a total of six trials (i.e., three trials under no-food conditions and three trials under food-present conditions). Behavioral observations in the absence of food were always performed first to eliminate the possibility that any crickets would survive during initial food trials and be present during the subsequent no-food trials. During the behavioral observations we recorded the cumulative number of times that an individual moved from one area to another (i.e., 12 shelters, four basking sites, and a central neutral zone) as a measure of activity. We also recorded the number of food items eaten by each skink to determine whether there were any associations between activity and foraging rates. Videos were scored blind to experimental population using the key-logging software BORIS (Friard and Gamba 2016).



**Figure 1**

Experimental arenas for lizard behavioral trials. Skinks were dorsally painted with a unique color combination to allow the tracking of individual identity across trials. During trials we recorded activity and foraging rates. All measurements are in mm. Lizards not to scale.

## Statistical analysis

Data were analyzed using R version 4.0.3 (R Core Team 2019). Observations were excluded from analysis where a positive individual ID could not be accurately obtained from experimental videos. This resulted in a total of 543 observations included in the analysis. Activity data (i.e., total number of areas entered) were  $\log_e$  transformed to approximate a Gaussian error distribution and continuous covariates (i.e., SVL) were mean centered prior to analysis to aid interpretation of model covariates. We report posterior means with 89% credibility intervals (CrI) as suggested by McElreath (2020), from Bayesian generalized linear mixed-effects models (*brms* package; Bürkner 2017). Inference was based on nonoverlapping CrIs with zero. Models were run for 5000 iterations (500 warmup) on 4 chains, using relatively uninformative, default priors and a thinning interval of 2 (total post-warmup samples = 9000). Model convergence was checked using trace plots, with all Rhat = 1.

We first investigated population differences in activity in both the presence and absence of food resources as well as foraging rates using a multivariate generalized linear mixed-effects model (see Supplementary Table S1 for model output). We fitted activity scored in the presence or absence of food, as well as the number of food items eaten as three separate dependent variables. We assumed a Gaussian error structure for activity variables, while the number of food items eaten was modeled using a zero-inflated Poisson distribution. Both activity in the presence and absence of food were scaled (mean = 0, SD = 1) prior to analysis to aid in model fitting. Each model contained population (Kokee, Tantalus, Volcano), experimental day (1–3), and SVL as fixed effects. Further, five observers took part in scoring behavioral videos and, therefore, observer ID was included as a fixed effect to statistically account for any differences between observers (see Supplementary Table S1 for model output). In addition, both individual ID and group ID were included as random intercepts in the model. We used this model to compare populations in average-level activity in both the presence and absence of food, as well as foraging rates with the *hypothesis* function in the *brms* package (Bürkner 2017). Further, we allowed variance components (i.e., among-individual variance [ $V_A$ ]; among-group variance [ $V_{A-GROUP}$ ]; within-individual variance [ $V_W$ ]) to vary among populations for activity. These estimates of  $V_A$ ,  $V_{A-GROUP}$ , and  $V_W$  were used to calculate the short-term adjusted repeatability ( $R$ ) of activity in both contexts for each population. Adjusted repeatability was calculated as the proportion of total behavioral variation that was due to among-individual differences (i.e.,  $R = \frac{V_A}{V_A + V_{A-GROUP} + V_W}$ ), after accounting for fixed-effects. To statistically compare variance estimates and repeatability between populations, we calculated the effect size of the magnitude difference in variance and repeatability amongst populations ( $\Delta V_A$ ,  $\Delta V_{A-GROUP}$ ,  $\Delta V_W$ ,  $\Delta R$ ) for activity in both the presence and absence of food (Royauté et al. 2015).

Second, within the multivariate model we also allowed correlations between each of the measured behaviors (i.e., activity in the presence or absence of food and foraging rates) to vary among individuals within each population. In other words, we investigated if populations differed in 1) their activity behavioral syndrome (i.e., activity in the presence versus absence of food) across the foraging contexts, and 2) their relationship between activity in either context and foraging rates. These among-individual correlations were calculated using the same Bayesian multivariate model as described directly above.

Finally, we investigated how populations changed their activity across the food conditions. As activity in the presence and absence of food were independently transformed, scaled, and included as separate response variables in the Bayesian multivariate model described above, this precluded an analysis of how population behavior changed across the food conditions. Therefore, we ran a separate Bayesian univariate generalized linear mixed effects model (*brms* package; Bürkner 2017) to investigate this further. The food treatment variable was centered (i.e., no food = -1; food = 1) prior to analysis. We fitted the total number of areas entered as the dependent variable, while population, food treatment (presence vs. absence of food), experimental day, SVL, observer ID, and a population  $\times$  food treatment interaction were modeled as fixed-effects. We also included individual ID and Group ID as random intercepts. We used the *hypothesis* function in the *brms* package (Bürkner 2017) to calculate whether the population-level slopes were different from 0 (i.e., populations changed their behavior in response to the food treatment).

## Ethical note

All lizards were collected and transported under permits issued by the State of Hawaii Department of Land and Natural Resources (Special Use Permit: K2019-4044cc; Transport Permit: EX-19-18). Research was conducted in accordance with relevant animal ethics guidelines and was approved by the Institutional Animal Care and Use Committee at The University of California, Davis (Protocol number: 211194). The Visual Implant Elastomer tagging procedure was performed quickly (< 1 min) by experienced personnel, in line with previously published research (e.g., Michelangeli et al. 2019, 2020). Skinks were closely monitored following the procedure and no adverse effects were observed. Finally, as delicate skinks are an invasive species, they could not be returned to the wild following experiments. Therefore, after the completion of experiments, all lizards were humanely killed via a subcutaneous injection of Euthasol (100 mg/kg). This procedure was performed by trained veterinarians and is a recommended method by which to humanely kill reptiles according to the American Veterinary Medical Association.

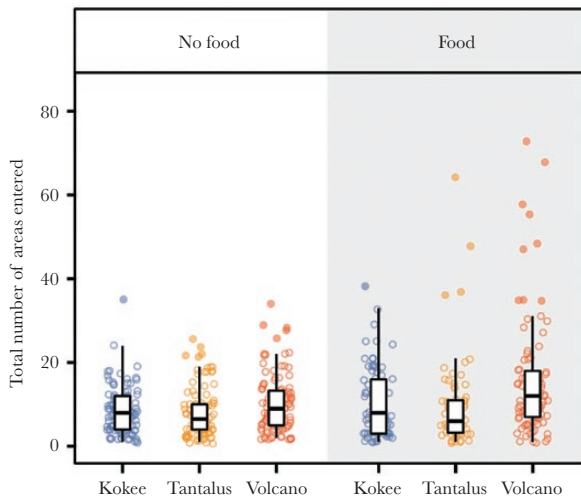
## RESULTS

### Population-level effects

We found no differences among populations in the average lizard activity levels, either in the presence or absence of food (i.e., all CrI's included zero; Figure 2; Supplementary Table S1). Intriguingly, however, we found several interactive effects of population, food availability, trial day, or lizard size on patterns of activity. Lizards from both the Tantalus (slope estimate [89% CrI] = 0.107 [0.005, 0.209]) and Volcano (0.092 [0.003, 0.182]) populations increased their activity in response to food availability. In contrast, Kokee lizards did not alter their behavior across the foraging conditions (i.e., slope was not different from 0; -0.036 [-0.129, 0.058]). In trials conducted with no food present, skinks substantially decreased their activity across experimental days (mean of posterior distribution [89% CrI] = -0.38 [-0.50, -0.26]), and smaller skinks were more active than larger conspecifics (-0.13 [-0.23, -0.02]). In contrast, in the trials with food present, neither experimental day (-0.02 [-0.13, 0.09]) nor SVL (0.01 [-0.11, 0.14]) affected activity levels. Finally, there were no effects of population, experimental day, or SVL on the number of food items consumed (i.e., all CrI's included 0; Supplementary Table S1).

### Population differences in variance and repeatability

There was no evidence that activity levels were repeatable in any of the populations during trials without food available (Table 1). Similarly, activity levels were also not repeatable during trials with food available in both the Kokee and Tantalus populations (Table 1). In contrast, lizards from the Volcano population demonstrated repeatability in their activity in the presence of food (Table 1). Indeed, population contrasts of the magnitude difference in repeatability found that the Volcano population was substantially more repeatable in their activity than the Tantalus population during trials where food was available ( $\Delta R$  [89% CrI] = 0.287 [0.052, 0.529]). Population contrasts also showed that during trials with food available, the Volcano population exhibited both higher among-individual variation ( $\Delta V_A$  [89% CrI] = 0.317 [0.035, 0.623]) and lower within-individual variation ( $\Delta V_W$  [89% CrI] = -0.364 [-0.713, -0.022]) relative to the Tantalus population. A similar pattern was observed when comparing the Volcano and Kokee



**Figure 2** Activity rates (i.e., total number of areas entered) in the Kokee ( $n = 36$ ), Tantalus ( $n = 35$ ), and Volcano ( $n = 36$ ) populations measured in both the presence (i.e., Food) and absence (i.e., No Food) of food resources. Filled dots above boxplot whiskers represent outliers. Statistical comparisons were performed only within each context. There were no significant differences between populations in activity in either context.

**Table 1**

**Adjusted repeatability (R) and variance components (among-individual variance [ $V_A$ ]; among-group variance [ $V_{A-GROUP}$ ]; within-individual variance [ $V_W$ ])  $\pm$  89% credibility intervals (CrI) for activity scored in both the presence and absence of food for each population**

	Activity (no food)				Activity (food)			
	R (89% CrI)	$V_A$ (89% CrI)	$V_{A-GROUP}$ (89% CrI)	$V_W$ (89% CrI)	R (89% CrI)	$V_A$ (89% CrI)	$V_{A-GROUP}$ (89% CrI)	$V_W$ (89% CrI)
Kokee	0.098 (0, 0.234)	0.106 (0, 0.239)	0.801 (0, 1.703)	0.641 (0.434, 0.825)	0.122 (0, 0.263)	0.145 (0, 0.298)	0.770 (0, 1.495)	0.739 (0.507, 0.951)
Tantalus	0.119 (0, 0.283)	0.191 (0, 0.420)	1.472 (0, 2.947)	0.840 (0.531, 1.128)	0.056 (0, 0.143)	0.080 (0, 0.198)	1.049 (0, 1.896)	0.915 (0.608, 1.188)
Volcano	0.162 (0, 0.296)	0.149 (0, 0.267)	0.525 (0, 0.775)	0.591 (0.420, 0.747)	<b>0.343</b> <b>(0.122, 0.558)</b>	0.397 (0.148, 0.629)	0.586 (0, 0.887)	0.551 (0.387, 0.713)

Repeatable estimates are indicated in bold.

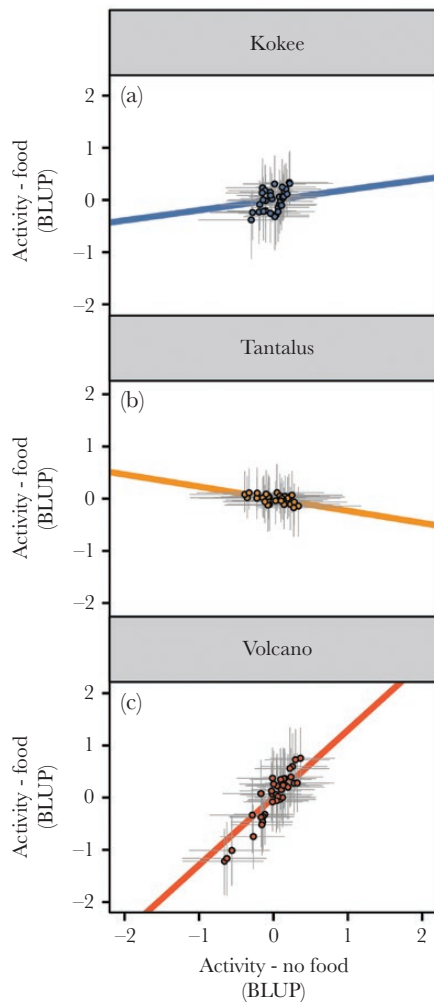
populations, where the Volcano population demonstrated a marginally higher repeatability ( $\Delta R$  [89% CrI] = 0.221 [-0.041, 0.491]) and among-individual variance ( $\Delta V_A$  [89% CrI] = 0.252 [-0.065, 0.569]) during trials when food was available. There were no clear differences in repeatability and variance components in the other population contrasts (Supplementary Tables S2 and S3). Further, there was limited evidence for changes in repeatability and variance components within each population across the foraging conditions (Supplementary Table S4). While there was an increase in repeatability ( $\Delta R$  [89% CrI] = 0.181 [-0.079, 0.432]) and among-individual variation ( $\Delta V_A$  [89% CrI] = 0.247 [-0.031, 0.515]) during trials with food available in the Volcano population, there was substantial uncertainty around these estimates with CrI's including zero (Supplementary Table S4).

### Behavioral syndromes and predictors of foraging success

In the Volcano population, we detected a significant among-individual correlation between activity levels across food contexts. Skinks that were more active in the absence of food were also the most active in the presence of food (cor [89% CrI] = 0.69 [0.29, 0.95]; Figure 3c). Skinks in the Volcano population that were more active during trials where food was available also ate more food items (0.68 [0.23, 0.95]). In contrast, there were no among-individual correlations (i.e., no behavioral syndromes) between activity levels recorded in the presence and absence of food in either the Kokee (0.17 [-0.62, 0.82]; Figure 3a) or Tantalus (-0.16 [-0.85, 0.67]; Figure 3b) populations, most probably due to the limited amount of among-individual variation in activity rates within these populations. We also found no relationship between activity scored in the absence of food resources and subsequent feeding rates in either the Kokee (0.26 [-0.51, 0.84]), Tantalus (0.13 [-0.68, 0.81]), or Volcano (0.42 [-0.20, 0.89]) populations. Similarly, there was no evident correlation between activity levels during trials with food available and the number of food items eaten in either the Kokee (0.54 [-0.17, 0.94]) or Tantalus (0.01 [-0.76, 0.78]) populations.

### DISCUSSION

We found evidence that the expression of personality traits is context specific in the invasive delicate skink. However, this effect varied among populations. More specifically, activity rates were not repeatable in any of the populations when measured in the absence of food resources. However, only skinks from the Volcano population



**Figure 3**

Behavioral syndromes between activity scored in either the presence or absence of food for the (a) Kokee, (b) Tantalus, and (c) Volcano populations. Data represent Best Linear Unbiased Predictors (BLUPs) from the Bayesian multivariate generalized linear mixed-effects model, where error bars (i.e., gray lines) denote 89% credibility intervals (CrIs).

demonstrated short-term repeatability in their activity when food resources were present. This was driven primarily by an increase in among-individual variance in Volcano lizards in the presence of food. Interestingly, while populations differed in their repeatability across the foraging contexts, there were no population differences in average activity levels when scored in either the presence or absence of food resources. We also found evidence for a behavioral syndrome in skinks from the Volcano population, where lizards that were more active during trials without food, were also more active in the presence of food resources. However, there was no evidence for behavioral syndromes in either the Kokee or Tantalus populations. Taken together, these results suggest that context can exert a strong effect on personality traits, and that this effect may vary among populations.

We found that lizards from both the Tantalus and Volcano, but not Kokee, populations increased their activity in the presence of food resources. However, despite this potential difference in how populations responded to increased food availability, analysis of average activity levels within each context found no population differences when measured either in the presence or absence of food

resources. This result was surprising and contrary to predictions considering prior research has found clear differences in activity levels among multiple populations of delicate skinks across their native geographical range (Michelangeli et al. 2019) and within smaller urbanized regions (Moule et al. 2016). Similarly, invasion has been suggested to select for increased activity levels (Chapple et al. 2012; Mueller et al. 2017). For example, increasingly active and exploratory individuals may be more likely to disperse or become ensnared within transport vectors, resulting in newly established populations being more active and exploratory than longer-established conspecifics (Chapple et al. 2012; Myles-Gonzalez et al. 2015; Thorlacius et al. 2015; Gruber et al. 2017). In contrast, we found no difference in activity between the original founder (Tantalus) and more recently established (Kokee and Volcano) populations. However, even the most recently established populations of delicate skink in Hawaii have been established for approximately 60+ years. Thus, any potential selection on activity rates during the initial spread of the delicate skink across the Hawaiian islands may have subsided as the species became established and was subjected to predation-induced, density-dependent, and/or spatiotemporally fluctuating natural selection (e.g., Le Cœur et al. 2015; Le Galliard et al. 2015; Lapiedra et al. 2018; Mouchet et al. 2021).

However, despite finding no population differences in average levels of activity across the foraging conditions, we did find that populations differed in their among- and within-individual variance in activity in response to increased food availability. Indeed, evidence for personality in activity rates (i.e., repeatability) was only found in the Volcano population during trials where food was available. This was primarily due to an increase in among-individual variation in lizards from the Volcano population in the presence of food resources. Further, Volcano lizards were also less behaviorally variable (i.e., decreased  $V_W$ ) than skinks from the Tantalus population when measured in the presence of food resources. However, there was limited evidence that Volcano lizards altered their within-individual behavioral variation across the foraging conditions. Previous research has also reported significant effects of context on the expression of personality traits in a variety of species (Biro et al. 2010; Klueen and Brommer 2013; Jolles et al. 2016). Indeed, Biro et al. (2010) found that while activity rates and boldness were both repeatable in juvenile speckled damselfish (*Pomacentrus bankanensis*), fish differed in how they modified their behavior in response to temperature variation. These differences in behavioral plasticity changed the rank order of individuals across temperatures, therefore altering their personality (Biro et al. 2010). Similar results were found in the salt marsh periwinkle (*Littoraria irrorata*) where tidal shifts were associated with changes in residual, within-individual variation in risk-taking behavior, resulting in differences in behavioral repeatability at either high or low tide (Cornwell et al. 2019). Taken together, these results highlight the importance of environmental context in shaping the structure of animal personality traits.

It is not clear why there was an effect of context on the repeatability of activity levels in only one of our study populations (i.e., Volcano). We surmise that this may have been due to associations between activity and foraging success in the dynamic group foraging assay. Indeed, we found among-individual correlations between activity during trials where food was available, and the number of food items eaten in the Volcano population, with more active individuals eating more food items. However, there were no relationships between these traits in either the Tantalus or Kokee populations. Importantly, however, there were no general population differences in the number of food

items eaten, meaning that lizards from both the Tantalus and Kokee populations still consumed the food items when available. Such an association between activity and foraging success in the Volcano population may have resulted in more active lizards consistently monopolizing food resources, potentially suppressing the behavior of their less active conspecifics (i.e., via interference or exploitative competition; e.g., Damas-Moreira et al. 2020). Indeed, previous research in delicate skinks reported a positive relationship between aggression and dispersal, and suggested that this may be due to interference competition, whereby dominant individuals force their less aggressive counterparts into hiding, thus reducing their dispersal rates (Michelangeli et al. 2017). These group dynamics where dominant skinks are consistently more active and monopolize resources (thereby suppressing the activity of their conspecifics via either interference or exploitative competition) may explain the increased among-individual variation in the presence of food resources. However, why this was only evident in one of the populations, and why activity rates were not associated with foraging success more broadly across the populations, requires further study. Further, whether these patterns are solely driven by group dynamics or are an interaction between heritable, intraindividual variation in behavior and the social environment is not clear and will be an important topic for future research.

The population differences in context-dependent personality is surprising, considering that we found no average level differences in activity, and that the three invasive populations share a common recent evolutionary history (having only diverged in the last 60 years; Chapple et al. 2013). Further, the recency of invasion also does not explain the population differences in behavioral variation as both the Volcano and Kokee populations were independently established during a similar period after WWII. Together, these results suggest that potential founder effects during the invasion of the Volcano population or local ecological differences between the Hawaiian Islands may be driving differences in how populations respond to changes in resource availability (e.g., Pintor et al. 2008; Gruber et al. 2018).

Interestingly, we found that while activity rates decreased over time during trials without food, there was no change in activity over time during trials where food was available. Locomotion and increased activity levels consume valuable energetic resources, and therefore, lizards may have reduced their activity over time during trials without food available due to a combination of habituation and the absence of any energetic benefits to gain from high activity rates. However, this is not the case during trials where food was available, as lizards had to search out and pursue live crickets in order to feed. Similarly, we found a difference in the relationship between body size and activity across the two contexts. More specifically, while there was no effect of body size on activity during trials with food, smaller lizards demonstrated increased activity rates in the absence of food resources. Previous research has not reported any relationship between SVL and activity rates in delicate skinks (Michelangeli, Chapple, et al. 2016; Michelangeli et al. 2019). However, the context-specific effect of SVL on activity in the present study may have again been due to group dynamics during behavioral assays. Indeed, prior work has found that larger lizards are more dominant (Riley et al. 2017) and competitively superior to smaller conspecifics (Sacchi et al. 2009). During trials without food available, larger lizards may have competitively excluded and displaced smaller conspecifics from valuable sheltering and/or basking sites, forcing smaller individuals to actively search for unoccupied

areas within the experimental arenas. In contrast, the addition of food resources may have ameliorated this effect, as dominant individuals left sheltering/basking sites to actively pursue live food items. Taken together, this research suggests that although variation in body size does not predict activity rates when measured during individual trials, this is not true when lizards are measured under more ecologically realistic settings where smaller lizards may increase their activity due to potential displacement from larger, more dominant conspecifics.

In summary, we found that the expression of personality in activity rates was context-specific in the invasive delicate skink when measured in a dynamic group foraging assay. More specifically, activity rates were only significantly repeatable in the presence, but not absence, of food resources. However, this was only true for one of the three populations, partially driven by an increase in among-individual variation in the presence of food resources. We suggest that this may have been caused by changes in group dynamics under high resource conditions, highlighting the benefit of using more ecologically realistic assay settings in animal behavior research. Together, these results suggest that context can play an important role in shaping animal personality traits, and that this effect can differ among closely related populations.

## SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

## FUNDING

This work was supported by funding from The Australian Research Council (DP170100684 to D.G.C., B.B.M.W., and A.S.); The Australasian Society for the Study of Animal Behaviour (to J.A.B.); The Holsworth Wildlife Research Endowment (to J.A.B.); and The Ecological Society of Australia (to J.A.B.); as well as Australian Government Research Training Program Scholarships awarded to J.A.B. and A.C.N.

We would like to thank two anonymous reviewers for constructive feedback on earlier versions of this manuscript. J.A.B., A.C.N., A.S., B.B.M.W., and D.G.C. conceived the ideas and designed the study. Skinks were collected by A.C.N., M.M., and A.S. Experiments were carried out by A.C.N. and M.M., while J.A.B., A.C.N., and J.M.M. extracted and collated experimental data, which was analyzed by J.A.B. with input from all co-authors. J.A.B. led the writing of the manuscript. All authors contributed critically to manuscript preparation and gave final approval for publication.

Conflict of interest: We have no competing interests.

Data availability: Analyses reported in this article can be reproduced using the data provided by Brand et al. (2021).

**Handling editor:** Mark Briffa

## REFERENCES

- Bell AM, Hankison SJ, Laskowski KL. 2009. The repeatability of behaviour: a meta-analysis. *Anim Behav*. 77:771–783.
- Bell AM, Sih A. 2007. Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecol Lett*. 10:828–834.
- Biro PA, Beckmann C, Stamps JA. 2010. Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proc Biol Sci*. 277:71–77.
- Brand JA, Naimo AC, Michelangeli M, Martin JM, Sih A, Wong BBM, Chapple DG. 2021. Data and statistical code from: population differences in the effect of context on personality in an invasive lizard. *Behav Ecol*. doi:10.5061/dryad.bcc2fqzcx
- Brown C, Irving E. 2014. Individual personality traits influence group exploration in a feral guppy population. *Behav Ecol*. 25:95–101.

- Bürkner PC. 2017. brms: an R package for Bayesian multilevel models using Stan. *J Stat Softw.* 80:1–28.
- Chapple DG, Miller KA, Kraus F, Thompson MB. 2013. Divergent introduction histories among invasive populations of the delicate skink (*Lampropholis delicata*): has the importance of genetic admixture in the success of biological invasions been overemphasized? *Divers Distrib.* 19:134–146.
- Chapple DG, Simmonds SM, Wong BB. 2012. Can behavioral and personality traits influence the success of unintentional species introductions? *Trends Ecol Evol.* 27:57–64.
- Cornwell TO, McCarthy ID, Snyder CRA, Biro PA. 2019. The influence of environmental gradients on individual behaviour: individual plasticity is consistent across risk and temperature gradients. *J Anim Ecol.* 88:511–520.
- Cromie GL, Chapple DG. 2012. Impact of tail loss on the behaviour and locomotor performance of two sympatric *Lampropholis* skink species. *PLoS One.* 7:e34732.
- Damas-Moreira I, Riley JL, Carretero MA, Harris DJ, Whiting MJ. 2020. Getting ahead: exploitative competition by an invasive lizard. *Behav Ecol Sociobiol.* 74:117.
- Dingemanse NJ, Both C, Drent PJ, Van Oers K, Van Noordwijk AJ. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Anim Behav.* 64:929–938.
- Dingemanse NJ, Kazem AJN, Réale D, Wright J. 2010. Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol Evol.* 25:81–89.
- Dochtermann NA, Dingemanse NJ. 2013. Behavioral syndromes as evolutionary constraints. *Behav Ecol.* 24:806–811.
- Dochtermann NA, Schwab T, Sih A. 2015. The contribution of additive genetic variation to personality variation: heritability of personality. *Proc Biol Sci.* 282:20142201.
- Friard O, Gamba M. 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol Evol.* 7:1325–1330.
- Gruber J, Brown G, Whiting MJ, Shine R. 2017. Is the behavioural divergence between range-core and range-edge populations of cane toads (*Rhinella marina*) due to evolutionary change or developmental plasticity? *R Soc Open Sci.* 4:170789.
- Gruber J, Brown G, Whiting MJ, Shine R. 2018. Behavioural divergence during biological invasions: a study of cane toads (*Rhinella marina*) from contrasting environments in Hawai'i. *R Soc Open Sci.* 5:180197.
- Guayasamin OL, Couzin ID, Miller NY. 2017. Behavioural plasticity across social contexts is regulated by the directionality of inter-individual differences. *Behav Processes.* 141:196–204.
- Harris S, Ramnarine IW, Smith HG, Pettersson LB. 2010. Picking personalities apart: estimating the influence of predation, sex and body size on boldness in the guppy *Poecilia reticulata*. *Oikos.* 119:1711–1718.
- Jäger HY, Han CS, Dingemanse NJ. 2019. Social experiences shape behavioral individuality and within-individual stability. *Behav Ecol.* 30:1012–1019.
- Johnson JC, Sih A. 2007. Fear, food, sex and parental care: a syndrome of boldness in the fishing spider, *Dolomedes triton*. *Anim Behav.* 74:1131–1138.
- Jolles JW, Aaron Taylor B, Manica A. 2016. Recent social conditions affect boldness repeatability in individual sticklebacks. *Anim Behav.* 112:139–145.
- Jolles JW, Briggs HD, Araya-Ajoy YG, Boogert NJ. 2019. Personality, plasticity and predictability in sticklebacks: bold fish are less plastic and more predictable than shy fish. *Anim Behav.* 154:193–202.
- King AJ, Williams IJ, Mettke-Hofmann C. 2015. The effects of social conformity on Gouldian finch personality. *Anim Behav.* 99:25–31.
- Kluen E, Brommer JE. 2013. Context-specific repeatability of personality traits in a wild bird: a reaction-norm perspective. *Behav Ecol.* 24:650–658.
- Lapiedra O, Schoener TW, Leal M, Losos JB, Kolbe JJ. 2018. Predator-driven natural selection on risk-taking behavior in anole lizards. *Science.* 360:1017–1020.
- Le Cœur C, Thibault M, Pisanu B, Thibault S, Chapuis J-L, Baudry E. 2015. Temporally fluctuating selection on a personality trait in a wild rodent population. *Behav Ecol.* 26:1285–1291.
- Le Galliard JF, Paquet M, Mugabo M. 2015. An experimental test of density-dependent selection on temperament traits of activity, boldness and sociability. *J Evol Biol.* 28:1144–1155.
- Littlewood D, Goulet CT, Chapple DG. 2021. Behavioural phenotype modulates group size effects in a lizard. *Anim Behav.* 175:181–192.
- McElreath R. 2020. Statistical rethinking: a Bayesian course with examples in R and Stan. 2nd ed. Boca Raton, FL: CRC Press.
- Michelangeli M, Chapple DG, Goulet CT, Bertram MG, Wong BBM. 2019. Behavioral syndromes vary among geographically distinct populations in a reptile. *Behav Ecol.* 30:393–401.
- Michelangeli M, Chapple DG, Wong BBM. 2016. Are behavioural syndromes sex specific? Personality in a widespread lizard species. *Behav Ecol Sociobiol.* 70:1911–1919.
- Michelangeli M, Melki-Wegner B, Laskowski K, Wong BBM, Chapple DG. 2020. Impacts of caudal autotomy on personality. *Anim Behav.* 162:67–78.
- Michelangeli M, Smith CR, Wong BBM, Chapple DG. 2017. Aggression mediates dispersal tendency in an invasive lizard. *Anim Behav.* 133:29–34.
- Michelangeli M, Wong BBM, Chapple DG. 2016. It's a trap: sampling bias due to animal personality is not always inevitable. *Behav Ecol.* 27:62–67.
- Miller KA, Duran A, Melville J, Thompson MB, Chapple DG. 2017. Sex-specific shifts in morphology and colour pattern polymorphism during range expansion of an invasive lizard. *J Biogeogr.* 44:2778–2788.
- Mitchell DJ, Biro PA. 2017. Is behavioural plasticity consistent across different environmental gradients and through time? *Proc R Soc B Biol Sci.* 284:20170893.
- Mitchell DJ, Houslay TM. 2021. Context-dependent trait covariances: how plasticity shapes behavioral syndromes. *Behav Ecol.* 32:25–29.
- Moirón M, Laskowski KL, Niemelä PT. 2019. Individual differences in behaviour explain variation in survival: a meta-analysis. *Ecol Lett.* 23:399–408.
- Mouchet A, Cole EF, Matthysen E, Nicolaus M, Quinn JL, Roth AM, Tinbergen JM, van Oers K, van Overveld T, Dingemanse NJ. 2021. Heterogeneous selection on exploration behavior within and among West European populations of a passerine bird. *Proc Natl Acad Sci USA.* 118:e2024994118.
- Moule H, Michelangeli M, Thompson MB, Chapple DG. 2016. The influence of urbanization on the behaviour of an Australian lizard and the presence of an activity-exploratory behavioural syndrome. *J Zool.* 298:103–111.
- Mueller JC, Edelaar P, Baños-Villalba A, Carrete M, Potti J, Blas J, Tella JL, Kempnaers B. 2017. Selection on a behaviour-related gene during the first stages of the biological invasion pathway. *Mol Ecol.* 26:6110–6121.
- Munson AA, Jones C, Schraft H, Sih A. 2020. You're just my type: mate choice and behavioral types. *Trends Ecol Evol.* 35:823–833.
- Munson AA, Michelangeli M, Sih A. 2021. Stable social groups foster conformity and among-group differences. *Anim Behav.* 174:197–206.
- Myles-Gonzalez E, Burness G, Yavno S, Rooke A, Fox MG. 2015. To boldly go where no goby has gone before: boldness, dispersal tendency, and metabolism at the invasion front. *Behav Ecol.* 26:1083–1090.
- Payne E, Sinn DL, Spiegel O, Leu ST, Gardner MG, Godfrey SS, Wohlfeil C, Sih A. 2021. Consistent after all: behavioural repeatability in a long-lived lizard across a 6-year field study. *Anim Behav.* 174:263–277.
- Pintor LM, Sih A, Bauer ML. 2008. Differences in aggression, activity and boldness between native and introduced populations of an invasive crayfish. *Oikos.* 117:1629–1636.
- Pizzatto L, Both C, Brown G, Shine R. 2017. The accelerating invasion: dispersal rates of cane toads at an invasion front compared to an already-colonized location. *Evol Ecol.* 31:533–545.
- Quinn JL, Cole EF, Bates J, Payne RW, Cresswell W. 2012. Personality predicts individual responsiveness to the risks of starvation and predation. *Proc Biol Sci.* 279:1919–1926.
- R Core Team. 2019. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. <https://www.r-project.org/>
- Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007. Integrating animal temperament within ecology and evolution. *Biol Rev Camb Philos Soc.* 82:291–318.
- Riley JL, Noble DWA, Byrne RW, Whiting MJ. 2017. Early social environment influences the behaviour of a family-living lizard. *R Soc Open Sci.* 4:161082.
- Royauté R, Buddle CM, Vincent C. 2015. Under the influence: sublethal exposure to an insecticide affects personality expression in a jumping spider. *Funct Ecol.* 29:962–970.
- Royauté R, Hedrick A, Dochtermann NA. 2020. Behavioural syndromes shape evolutionary trajectories via conserved genetic architecture. *Proc Biol Sci.* 287:20200183.



- Sacchi R, Pupin F, Gentilli A, Rubolini D, Scali S, Fasola M, Galeotti P. 2009. Male-male combats in a polymorphic lizard: residency and size, but not color, affect fighting rules and contest outcome. *Aggress Behav*. 35:274–283.
- Schuett W, Tregenza T, Dall SR. 2010. Sexual selection and animal personality. *Biol Rev Camb Philos Soc*. 85:217–246.
- Shine R. 2003. Locomotor speeds of gravid lizards: placing “costs of reproduction” within an ecological context. *Funct Ecol*. 17:526–533.
- Sih A, Bell A, Johnson JC. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evol*. 19:372–378.
- Sih A, Cote J, Evans M, Fogarty S, Pruitt J. 2012. Ecological implications of behavioural syndromes. *Ecol Lett*. 15:278–289.
- Smith BR, Blumstein DT. 2008. Fitness consequences of personality: a meta-analysis. *Behav Ecol*. 19:448–455.
- Thorlacius M, Hellström G, Brodin T. 2015. Behavioral dependent dispersal in the invasive round goby *Neogobius melanostomus* depends on population age. *Curr Zool*. 61:529–542.
- Urszán TJ, Garamszegi LZ, Nagy G, Hettyey A, Török J, Herczeg G. 2018. Experience during development triggers between-individual variation in behavioural plasticity. *J Anim Ecol*. 87:1264–1273.
- Webster MM, Ward AJ. 2011. Personality and social context. *Biol Rev Camb Philos Soc*. 86:759–773.
- Wolf M, Weissing FJ. 2012. Animal personalities: consequences for ecology and evolution. *Trends Ecol Evol*. 27:452–461.