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ORIGINAL PAPER

Temporal repeatability of behaviour in a lizard: implications for behavioural syndrome studies

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Abstract

It is well established that, across taxa, individuals within populations exhibit consistent differences in their behaviour across time and/or contexts. Further, the functional coupling of traits may result in the formation of a behavioural syndrome. Despite extensive evidence on the existence of consistent among-individual differences in behaviour and behavioural syndromes in the animal realm, these findings are predominately based upon short-term assessments, leading to questions regarding their stability over longer periods. Understanding if these estimates are temporally stable would allow predictions of individual behaviour to be made using short-term repeated measures. Here, we used 57 adult male delicate skinks (*Lampropholis delicata*) to evaluate the stability of behavioural variation observed both among (animal personality and behavioural plasticity) and within individuals (behavioural predictability), as well as behavioural syndromes, across short (four weeks) and long (five months) timeframes. To do so, we repeatedly assayed activity, exploration, and boldness five times per each individual. Overall, our study revealed complex patterns of behavioural variation and trait (co)variation over time. Activity was always repeatable across time intervals, whereas behavioural differences among individuals in exploration and boldness were not consistent. Yet a behavioural syndrome between activity and exploration was detected at both shorter and longer temporal scales, suggesting that syndrome structure in these traits does not vary as a function of time. Our findings indicate that, at least for some traits (e.g. activity) and studies, short-term measures may be adequate in serving as a proxy for long-term variation in individual behaviour, and to reveal the existence of behavioural syndromes at the population level.

Keywords Animal personality · Behavioural individuality · Behavioural plasticity · Boldness · Exploration · Reptile

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Introduction

It has now become widely accepted that most species of animals, beyond humans, exhibit what some refer to as personality (Bell et al. 2009; Boulton et al. 2014; Moiron et al. 2020a, b). By definition, individuals differing in their personality traits behave differently from one another, and these differences among individuals are consistently maintained through time and/or across contexts (Sih et al. 2004; Bell et al. 2009). However, individuals often differ from each other also in how they adjust their behaviour across environmental conditions (i.e., behavioural plasticity; Dingemanse et al. 2010), and in the predictability of their own behaviour over time (behavioural predictability; Westneat et al. 2015). These behavioural differences are evolutionary important and, for instance, an individual's personality (i.e., shy versus bold) is likely to influence its survival and reproductive success (Smith and Blumstein 2008; Debeffe et al. 2015; Moiron et al. 2020a, b).

Consistency in the behavioural expression of animals can also extend beyond a single trait and apply to correlations among multiple traits as well. This functional coupling of behavioural traits is commonly referred to as behavioural syndromes (Sih et al. 2004; Sih and Bell 2008). Some have argued that, because of the tight link among behavioural traits, syndromes may impose developmental or evolutionary constraints on the expression of optimal behaviour (Bell and Stamps 2004; Dochtermann and Dingemanse 2013; Wuez and Kruger 2015). Under this perspective, the traits structured into a syndrome are not free to vary independently as the shared proximate mechanisms (i.e., hormonal, physiologic, or genetic) underpinning their correlation are difficult to uncouple (Bell 2005; Adriaenssens and Johnsson 2013, Royaute et al. 2020). Thus, it is predicted that behavioural adjustments in one behaviour will result in similar directional changes in each of the associated traits. In this vein, few studies have found that syndrome structure remains stable across varying selective environments (Bell and Stamps 2004; van Oers et al. 2005; Nakayama and Miyatake 2010; Michelangeli et al. 2019, Royaute et al. 2020).

Despite the large body of literature on both consistent among-individual variation in behaviour, as well as behavioural syndromes, their stability over ecologically-relevant periods has been challenged (David et al. 2012; Mowles et al 2012; Biro 2012; Brommer and Class 2015; Polverino et al. 2021; Thys et al. 2017). Time has been shown to have the potential to affect the consistency in an individual's behavioural expression, whereby the level of among-individual variation tends to decrease, and even become negligible, over increasing temporal scales (Bell et al. 2009; Polverino et al. 2016a; Rohrer and Ferkin 2020); but see (Carlson and Tetzlaff 2020) in which behavioural differences among eastern box turtles (*Terrapene carolina*) were found to be consistent across multiple years both in the wild and in captivity. The decrease in behavioural difference over time is thought to depend upon individuals progressing through different ontogenetic stages (Debeffe et al. 2015; Wuez and Kruger 2015; Stamps and Krishnan 2017; Mitchell et al. 2020). However, several longitudinal studies indicate that personality estimates can also increase with animals' age, revealing that behavioural differences are often more consistent later in life (Debeffe et al. 2015; Polverino et al. 2016a, 2016b; Sakai 2018; Rohrer and Ferkin 2020). If behavioural differences among individuals increase over a lifetime, behavioural syndromes might also be more pronounced in groups of older than young individuals (Polverino 2020).

Temporal autocorrelation can also affect estimates of behavioural repeatability, whereby consecutive observations of the same individuals over short periods of time (e.g. hours, days) are more likely to be correlated than measurements taken over longer bouts (e.g.

weeks, months; Mitchell et al. 2020; often referred to as ‘pseudo-repeatability’, Niemelä and Dingemanse 2017). This is because internal states are relatively stable over short periods of time (e.g., metabolic rate or energy levels), and individual variation in behaviour is typically state-dependent (Sih et al. 2015). As more time elapses, individuals have a greater opportunity to experience shifts in ecological conditions which may affect long-term consistency in states and, in turn, behavioural traits. This was demonstrated by Horvath et al. (2017) when they tested the effects of resource fluctuations on the consistency of behavioural differences among European green lizards, (*Lacerta viridis*). The authors found that shifts in the availability of food and basking opportunities altered substantially the expression of activity and boldness behaviour among individuals, albeit in the short-term. Boldness behaviour was shown to only be consistent when thermoregulatory opportunities were low, with repeatability estimates increasing in small lizards under low food conditions. By contrast, individual differences in activity levels remained unchanged between treatments, suggesting that ecological factors are less likely to affect individual variation in activity than boldness behaviour.

Likewise, just as with single behavioural traits, evidence also suggests that developmental processes and fluctuations in ecological conditions occurring over time may influence the associations among traits comprising a syndrome (Bell and Sih 2007; Kanda et al. 2012; Adriaenssens and Johnsson 2013; Wuez and Kruger 2015; Dhellemmes et al. 2020). For instance, in juvenile lemon sharks (*Negaprion brevirostris*) a behavioural syndrome was only found in areas where there was a high abundance of predatory sharks (Dhellemmes et al. 2020). Under this scenario, behavioural trait should be free to evolve independently in response to variation in the selective environment (Bell 2005). It is possible that either the constituent traits making up the syndrome (e.g., activity and exploration) or the direction of their relationship (e.g., more active and explorative, or more active and less explorative) were favoured under some environmental situations (i.e., high predation) and ontogenetic stages, but not others (i.e., low predation; Polverino et al. 2018). Temporal shifts over evolutionary time seemingly have the capacity to not only alter the structural consistency of syndromes in terms of magnitude and sign of behavioural correlations, but even alter the development of syndromes altogether. However, it should be noted that the aforementioned studies either assessed the effects of age and ecological conditions on syndrome stability over relatively short timeframes (Bell and Sih 2007; Kanda et al. 2012; Adriaenssens and Johnsson 2013; but see Wuez and Kruger 2015) or across populations (Brommer and Class 2015; Dhellemmes et al. 2020; Mitchell and Houslay 2021).

Thus, given that temporal factors have the potential to play a critical role when measuring consistent among-individual (co)variation in behavioural traits, at least over smaller time scales, more studies conducting long-term repeated measures within populations are greatly needed to better assess the consistency of individual behavioural expression and correlations among traits. Understanding whether these phenomena are stable over long temporal scales would allow predictions on the future behaviour of individuals to be made using short-term assessments, and will assist our understanding of the ecological and evolutionary relevance of their relationship with other biological traits and fitness. This is not only crucial for moving forward in the field, but also in light of the fact that behavioural estimates derived from data collected over short time intervals predominate the literature. Determining the predictive power of short-term estimates would, therefore, provide some level of validation of previous works as well as allow researchers to overcome the logistical challenges of performing behavioural studies over longer, ecologically relevant timeframes.

Here, we used 57 adult male delicate skinks (*Lampropholis delicata*) to evaluate the stability of consistent among-individual differences in behaviour, as well as syndrome structures, across short (four weeks) and long (five months) timeframes. Consistent among-individual variation in behavioural traits as well as their correlation has already been extensively studied in this species, where individuals were found to exhibit a well-characterized activity-exploration syndrome (Michelangeli et al. 2016a,b, 2018, 2019, 2020; Moule et al. 2016; Goulet et al. 2017a,b; Chung et al. 2017), which has been linked to its success as an invasive species (Chapple et al. 2011, 2012, 2022; Chapple and Wong 2016; Hamilton et al. 2020) and urban adapter (Moule et al. 2016; Kang et al. 2018; Walsh et al. 2018). Despite the extent of this research, measurements were limited to two datapoints per individual taken over short time frames [three days to two weeks (Michelangeli et al. 2016a, b, 2018, 2019, 2020; Moule et al. 2016; Goulet et al. 2017a,b; Chung et al. 2017)]. Thus, the primary aim of the present study was to establish whether short-term behavioural assessments are predictive of longer-term variation and trait correlation in individual behavioural tendencies. We predict that among-individual differences in mean behaviour (personality) and behavioural adjustments (plasticity) measured over short time periods should be higher than over longer periods. The opposite should be true for the within-individual residual variance (behavioural predictability), which can be attributed to stochasticity and measurement errors. We repeatedly assayed two behavioural traits known to be linked at the individual level (activity and exploration), and one that has been found to be repeatable, but independent of known syndromes in this species (boldness). Behaviours were measured in adult individuals at five time points with intervals ranging from two to 20 weeks. As a short-lived species (~3–5 years), this longer time period represents a considerable portion of an individual's lifespan and is, therefore, an ecologically relevant timeframe within which to assess behavioural stability (Chapple et al. 2014).

Materials and methods

Animal husbandry

The delicate skink is a small (~35–55 mm adult, snout-vent-length SVL) diurnal lizard occurring among leaf litter and debris in a wide variety of natural and urban habitats throughout its native (eastern Australia: Queensland to Tasmania) and introduced ranges (Lord Howe Island, New Zealand, and Hawaii; Chapple et al. 2013a,b, 2014, 2016a; b; Moule et al. 2015; Tingley et al. 2016; Miller et al. 2017). Fifty-seven adult male delicate skinks collected in 2013 from Sydney, New South Wales, Australia (27°38 S, 153°05 E), were used in this study. Lizards were captured with a combination of methods not to bias certain behavioural types and obtain a sample size representative of the behavioural variation observed in the wild; namely, hand capture, pitfall trapping, and mealworm fishing (for detailed capture methodology see Michelangeli et al. 2016b). The lizards were previously used in other studies using the same, or similar, behavioural assays (Michelangeli et al. 2016b; Moule et al. 2016). Only males were used to avoid the potentially confounding effects of gravidity (Shine 2003). Each individual was marked with a unique Visible Implant Elastomer (Northwest Marine Technology) colour code. As a gregarious species (e.g. Hamilton et al. 2020; Littlewood et al. 2021), lizards were housed in groups of six individuals within a temperature-controlled animal housing facility at Monash University (Clayton, Victoria, Australia). The room was maintained at 20 °C with a 14 h light: 10 h dark cycle (0600–2000 h). Housing containers (300 × 230 × 370 mm) were equipped with shelter and basking sites and placed on heat tape, providing a thermal gradient reaching 35 °C to promote natural thermoregulatory behaviour. Crickets (*Acheta domesticus*), enriched with calcium and Reptivite™ powders were offered to lizards three times a week, and water was provided ad libitum.

Behavioural measurements

General procedures

Experimental procedures were performed in 2016, which allowed lizards to acclimate to captive conditions for three years prior to the onset of the study. Three behavioural traits were measured on each individual, including activity, exploration, and boldness, using standard methodologies (Chapple et al. 2011; Michelangeli et al. 2016a, b, 2017; Moule et al. 2016). Assays were repeatedly performed on all individuals at five time-intervals (time 0 and after 2, 4, 12, and 20 weeks). All assays were performed by the same researcher (K.M.B.). Assays at weeks 0, 2, and 4 were used to assess short-term behavioural repeatability and syndromes, whereas those performed in weeks 0, 12, and 20 served to evaluate long-term repeatability and behavioural syndromes.

Lizards were fasted for 48 h prior to an assay to ensure they were in a post-absorptive state during testing (Van Berkum et al. 1989). Behavioural assays were conducted within a constant temperature room (20 °C) in a predetermined order where assays expected to have the greatest impact on behaviour were performed last to minimize carryover effects (Bell 2013). All experimental setups involved an opaque walled test arena (55 cm × 32 cm × 24 cm) with modifications specific to measuring each behavioural trait. Lizards were acclimatized to the experimental arena under a transparent cover for 10 min prior to beginning each trial. All trials were run for 30 min and recorded with a Panasonic HC-V160 video camera suspended above the arena. Video footage was analyzed using the behavioural software J Watcher (Blumstein et al. 2006). Snout-vent-length of each lizard was measured prior to experiments to account for body size effects.

Activity

Activity levels were assessed in a test arena marked with 20 grid squares. The number of transitions lizards made between squares in the 30 min trial period was recorded. Greater number of transitions between grid squares represented higher activity levels.

Exploration

An opaque Perspex partition was placed in the centre of the arena dividing it into two equally sized compartments (start and goal). The partition was trapezium in shape creating a 15 mm gap between the sides of the partition and arena. This required the lizards to climb and squeeze into the gaps to reach the goal compartment. The time it took the lizard to manoeuvre the obstacle was recorded, where lower times were indicative of higher exploratory behaviour. Individuals that did not reach the goal by the end of the trial were assigned 1800s as their score.

Boldness

An individual's readiness to resume risky behaviours after encountering a threat is often used as a measure of boldness (Moiron et al 2020a, b). For reptiles, basking is a necessary, yet risky, behaviour as it generally takes place in open areas where individuals are most vulnerable to predation (Downes and Hoefer 2004). A 40 W heat lamp placed over a ceramic tile at one end of the test arena providing 35 °C basking site, significantly higher than the ambient temperature (22 °C). The other end of the arena was equipped with a shelter site. To simulate a predatory attack, lizards were tapped close to the tail with a paintbrush until they retreated to the shelter site (Michelangeli et al. 2018). The length of time that a lizard took to emerge from the shelter site was used as a measure of its boldness. We note that most lizards did not resume their risky behaviors at every trial, and two lizards never did it.

Statistical analyses

All analyses were conducted using *R* version 3.3.2 (R Core Team 2016), using linear mixed effects models with a Gaussian error distribution.

We were interested to test whether individual differences in behavior were consistent over short and long periods of time (i.e. weeks and months), and explained a significant portion of the behavioural variance observed. To do so, we took a comprehensive approach and partitioned the behavioural variance into its components (among and within individuals), as suggested by Dingemanse et al. (2022), for each behavioural trait separately, accounting for temporal changes in behavior occurring at the individual level ('*lmerTest*' package; Kuznetsova et al. 2013). We ran three separate models for each behavioural trait: one model included the complete dataset (all time intervals), while the short-term model included weeks 0, 2, and 4, and the long-term included weeks 0, 12, and 20. For each model, week, time of day, and SVL were included as fixed effects, housing container ID and lizard ID were the random intercepts, and time (week) for lizard ID was fitted as the random slope. The proportion of among-individual variance over the total behavioural variance was calculated for each model (conditional repeatability), after accounting for the variance explained by the predictors included in the model. However, since our models accounted for variation among individuals in their behaviour over time (i.e. random slopes), the proportion of behavioural variation attributed to among-individual differences changed as a function of week. We followed validated methods from Briffa et al. (2013) to calculate conditional repeatability at the intercept (i.e. scaling the random slope week). Likelihood ratio tests were performed to calculate the significance of both fixed and random effects included in the models.

We also wanted to test whether behavioural syndromes, if any, varied over time in the delicate skink. To do so, the presence of behavioural syndromes was tested by estimating patterns of covariance between pairs of behavioural traits using mixed-effects multivariate models ('*MCMCglmm*' package; Hadfield 2010) with non-informative priors (expected variance V = diag (2); degree of belief nu = 1.002). Models were run for 1,500,000 iterations and, after a burn in of 500,000 iterations, were thinned by 100 iterations, and we visually checked their posterior density plots to ensure proper model mixing and convergence. We partitioned the phenotypic (co)variance into its components: among- and within-individuals, with the former indicating a behavioural syndrome and the latter plasticity integration. The among-individual correlation represents consistent association between individual mean values for a series of behavioural traits over the time period in which measurements were taken, while within-individual correlations indicate how individuals adjust their own behaviour across subsequent measurements (Dingemanse and Dochtermann 2013). Phenotypic correlations result from the joint contribution of correlations at the among- and within-individual level. Inference for correlation estimates was based on the overlap of their 95% credible intervals with zero.

Results

Short- versus long-term variation in individual behaviour

Among-individual variation in behaviour explained a significant portion of the variance observed across all behaviours and time periods, except for exploration in the short-term and boldness in the long-term (Table 1). In other words, behavioural differences among individuals were typically consistent and repeatable over time. As expected, estimates of among-individual variation (skink identity) tended to be higher in the short- than in the long-term models for both activity and boldness, with variation in activity declining to less than half from the short- to the long-term dataset (Table 1). On the contrary, variation among individuals in exploration appeared to be higher in the long-term dataset than in the short-term one (Table 1).

Among-individual variation in behavioural adjustments (behavioural plasticity; the slope for Week) did not explain a significant portion of the behavioural variance observed, except for activity in the short-term (Table 1): individuals appeared to differ from each other in how they adjusted their activity levels over four weeks (short-term analysis), but behavioural plasticity in all behaviours was consistently low when referring to longer time bouts.

The within-individual residual variance (behavioural predictability) also tended to vary between short- and long- term models (Table 1). In particular, the residual variance tended to increase from the short-term to the long-term of over 20% for activity, and over 37% for boldness (Table 1), indicating that individual behaviour was more predictable when animals were assayed over a relatively shorter than longer time window. The opposite trend was observed for exploration, with residual variance that tended to decrease from the short to the long term (Table 1).

Stability of behavioural syndromes

A behavioural syndrome was detected consistently between activity and exploration when considering the full dataset, and the short- and long-term (reduced) datasets (Table 2): a strong negative among-individual correlation between these traits drove the overall negative phenotypic correlation observed throughout the models. Specifically, lizards which made a greater number of transitions in the arena (more active) also took less time to cross the barrier (more exploratory) than others. Boldness, by contrast, was found not to be correlated with any trait at either the among-individual, within-individual, or phenotypic level across datasets.

Table 1 Results of the fixed and random portion of the linear mixed effects models for each behavioural trait. The number of observations (Obs.), individuals (Skink), and social containers (Container) included in each model are provided. Significant fixed and random effects are in bold. The proportion of the variance explained by among-individual differences over the residual variation (conditional repeatability at the intercept) was calculated

Time	Parameter	Activity							Exploration						
		Obs	N	X^2	P	Estimate	SD	Conditional repeatability	Obs	N	X^2	P	Estimate	SD	Conditional repeatability
Full dataset															
	Skink (ID)	283	57	83.58	**< 0.001**	1078.50	32.84	**0.52**	281	57	5.33	**0.02**	0.07	0.26	**0.13**
	Container (ID)		11	2.15	0.14	215.96	14.70	–		11	0.66	0.42	0.01	0.09	–
	Week (slope)			1.28	0.53	12.05	3.47	–			0.26	0.88	< 0.01	0.03	–
	Residual			–	–	1014.63	31.85	–			–	–	0.45	0.67	–
	SVL			3.56	0.06	–	–	–			5.36	**0.02**	–	–	–
	Week			27.03	**< 0.001**	–	–	–			7.89	0.10	–	–	–
	Time of day			13.44	**0.001**	–	–	–			0.77	0.68	–	–	–
Short-term															
	Skink (ID)	171	57	40.66	**< 0.001**	1882.10	43.38	**0.69**	171	57	0.50	0.48	0.02	0.16	0.05
	Container (ID)		11	3.49	0.06	140.50	11.85	–		11	0.83	0.36	0.01	0.11	–
	Week (slope)			6.62	**0.036**	148.30	12.18	–			0.10	0.95	< 0.01	0.05	–
	Residual			–	–	825.70	28.74	–			–	–	0.51	0.72	–
	SVL			3.58	0.05	–	–	–			4.93	**0.03**	–	–	–
	Week			13.34	**0.001**	–	–	–			3.47	0.18	–	–	–
	Time of Day			12.54	**0.002**	–	–	–			1.45	0.23	–	–	–
Long-term															
	Skink (ID)	169	57	26.82	**< 0.001**	898.50	29.97	**0.47**	167	57	7.84	**0.005**	0.13	0.36	**0.27**
	Container (ID)		11	0.06	0.80	< 0.01	< 0.01	–		11	0.16	0.69	< 0.01	0.05	–
	Week (slope)			3.50	0.17	49.63	7.04	–			0.39	0.82	< 0.01	0.03	–
	Residual			–	–	1009.00	31.77	–			–	–	0.34	0.59	–

Table 1 (continued)

Time	Parameter	Activity							Exploration						
		Obs	N	X^2	P	Estimate	SD	Conditional repeatability	Obs	N	X^2	P	Estimate	SD	Conditional repeatability
	SVL			3.39	0.07	–	–	–			5.03	**0.02**	–	–	–
	Week			12.89	**0.002**	–	–	–			3.04	0.22	–	–	–
	Time of Day			13.65	**0.001**	–	–	–			0.08	0.96	–	–	–

Time	Parameter	Boldness						
		Obs	N	X^2	P	Estimate	SD	Conditional repeatability
Full dataset								
	Skink (ID)	190	55	10.45	**0.001**	14,030.00	118.50	**0.31**
	Container (ID)		11	0.06	0.80	< 0.01	< 0.01	–
	Week (slope)			0.27	0.88	699.30	26.44	–
	Residual			–	–	31,450.00	177.40	–
	SVL			1.68	0.20	–	–	–
	Week			6.07	0.19	–	–	–
	Time of Day			0.37	0.83	–	–	–
Short-term								
	Skink (ID)	113	51	8.96	**0.003**	15,284.40	123.63	**0.37**
	Container (ID)		11	0.03	0.86	< 0.01	< 0.01	–
	Week (slope)			0.16	0.92	175.50	13.25	–
	Residual			–	–	25,712.10	160.35	–

Table 1 (continued)

Time	Parameter	Boldness						
		Obs	N	X^2	P	Estimate	SD	Conditional repeatability
	SVL			7.23	**0.007**	–	–	–
	Week			20.21	**< 0.001**	–	–	–
	Time of day			19.96	**< 0.001**	–	–	–
Long-term								
	Skink (ID)	118	51	2.17	0.14	11,421.80	106.87	0.24
	Container (ID)		11	1.06	0.30	3,775.20	61.44	–
	Week (slope)			0.29	0.86	113.40	10.65	–
	Residual			–	–	35,240.10	187.72	–
	SVL			7.42	**0.006**	–	–	–
	Week			22.73	**< 0.001**	–	–	–
	Time of day			20.00	**< 0.001**	–	–	–

Table 2 Results of MCMC general linear mixed effects models testing for bivariate correlations between pairs of behavioural traits on the full dataset (all time intervals) as well as on subsets (short-term: Weeks 0, 2, and 4; long-term: Weeks 0, 12, and 20). The best estimates of correlation coefficients (values above the diagonal) and their 95% credible intervals (values below the diagonal) are presented for among-individual, within-individual, and phenotypic correlations. Significant results corresponding to correlation coefficients whose credible intervals do not overlap zero are in bold

		Full dataset			Short-term			Long-term		
		Activity	Exploration	Boldness	Activity	Exploration	Boldness	Activity	Exploration	Boldness
Activity	Among-individual	**–**	**–0.57**	0.16	**–**	**–0.46**	0.29	**–**	**–0.50**	0.11
	Within-individual	**–**	–0.04	0.11	**–**	–0.07	0.05	**–**	–0.03	0.11
	Phenotypic	**–**	**–0.22**	0.12	**–**	**–0.21**	0.15	**–**	**–0.21**	0.11
Exploration	Among-individual	**–0.80, –0.30**	–	–0.12	**–0.76, –0.11**	–	–0.14	**–0.77, –0.16**	–	–0.13
	Within-individual	–0.17, 0.08	–	–0.09	–0.25, 0.10	–	–0.04	–0.20, 0.15	–	–0.13
	Phenotypic	**–0.36, –0.09**	–	–0.10	**–0.37, –0.05**	–	–0.06	**–0.37, –0.04**	–	–0.13
Boldness	Among-individual	–0.21, 0.52	–0.54, 0.27	–	–0.15, 0.66	–0.59, 0.32	–	–0.37, 0.58	–0.55, 0.33	–
	Within-individual	–0.05, 0.26	–0.25, 0.06	–	–0.17, 0.26	–0.24, 0.17	–	–0.12, 0.33	–0.34, 0.09	–
	Phenotypic	–0.05, 0.29	–0.24, 0.05	–	–0.06, 0.34	–0.23, 0.11	–	–0.10, 0.29	–0.31, 0.07	–

Discussion

The expression and correlation of behavioural differences among our adult skinks were found to be relatively stable across both short- and long-term time intervals, especially for activity-related behaviours. Our results suggest that activity assays conducted over short periods are predictive of longer-term behavioural variation, and that individual variation in activity and exploration are linked to each other in a behavioural syndrome that is stable over time.

Temporal stability in behavioural variation

According to the general assumption that consistent among-individual differences in behaviour have a temporal component, we expected differences in behaviour among individuals (i.e., personality and plasticity) to be consistently higher — and residual within-individual variation (i.e., predictability) to be lower — in the short-time than over longer intervals (Bell et al. 2009; David et al. 2012; Wuez and Kruger 2015). Nevertheless, the expected pattern of decreasing among-individual variation over longer timescales time was only partially supported. For instance, boldness was repeatable in the short timeframe, but such structured variation among individuals in the amount of time that they took to emerge from a shelter disappeared in the long-term. The opposite trend was observed for exploration, for which among- and (residual) within-individual variation varied over temporal scales in the opposite direction. Counter to our initial predictions, individual variation in activity was largely repeatable across all time points. This suggests that estimates of individual variation in activity rates are less likely to suffer from temporal effects compared to estimates on boldness and exploration. Our finding aligns with evidence from Horvath et al. (2017), in which individual variation in the activity levels of adult lizards was found to be less vulnerable to environmental confounds than variation in personality axes related to an individual willingness to take risks. However, boldness and exploration have been found to be highly repeatable across multiple years in other reptiles (e.g., Carlson and Tetzlaff 2020; Payne et al. 2021; De Meester et al. 2022), and evidence from Payne et al. (2021) indicate that boldness levels in lizards typically differ between sexes, with males being bolder than females. So it is possible that by only testing male lizards, our data had lower diversity in boldness levels among the individuals that we would have expected if both males and females were tested — blurring the behavioural repeatability estimates, especially in the reduced datasets.

Findings from other studies have also countered the notion that behavioural differences among individuals are necessarily consistent over long timescales (Kanda et al. 2012; Polverino et al. 2016a; Sakai 2018; Rohrer and Ferkin 2020). For example, meadow voles (*Microtus pennsylvanicus*) were exposed to a novel object test, with the number of approaches towards the novel object (activity), latency to approach (exploration), and latency to move within the test arena (boldness) being measured six times every 60 days (Rohrer and Ferkin 2020). Activity was found to be stable over the long-term, whereas exploratory and bold behaviours were less consistent over time, with repeatability in exploratory behaviour that increased with a vole's age while boldness decreased (Rohrer and Ferkin 2020). Developmental modifications, or fluctuations, in environmental conditions have been suggested to partially explain such inconsistency in the behaviour of animals over ontogeny (Debeffe et al. 2015; Wuez and Kruger 2015; Polverino et al. 2016a;

Polverino et al. 2016b). However, differences in developmental stage or environmental variation are unlikely to explain the results in the present study as lizards were all adults and housed under standard laboratory conditions, which provided a neutral and predictable environment devoid of predators (e.g. David et al. 2012). Specifically, lizards were housed under the same standard conditions for several years, potentially leading to homogenization of their behaviour (e.g. Archard and Braithwaite 2010). However, the different magnitude of behavioural repeatability observed in our study across the three traits (0.05 to 0.69), as also found elsewhere (e.g. Debeffe et al. 2015; McEvoy et al. 2015; Wuez and Kruger 2015; Rohrer and Ferkin 2020), may be due to different ecological importance of these traits for the target species (Bell et al. 2009; Skinner et al. 2022). Alternatively, it is also possible that some of these traits are more sensitive to hormonal or energetic fluctuations than others. A recent meta-analysis revealed that a higher expression of risky behaviours, such as boldness and exploration, decreased survival among individuals in the wild (Moiron et al. 2020a, b); however, this may not apply for captive populations. By contrast, activity may be more directly correlated with an individual's energy budget and feeding rates, rather than survival, whereby maintaining a similar level of activity over longer temporal scales may be a successful strategy for individuals to achieve high level fitness (Biro and Stamps 2010; Rohrer and Ferkin 2020). This view is in line with our own findings, with individual variation in exploration and boldness of the lizards that shifted over time while variation in their activity levels was consistently maintained.

Temporal stability and predictability in behavioural syndromes

Our study found that behavioural syndromes in the delicate skink were stable over time, and therefore short-term assays are predictive of longer-term behaviour. The presence of an activity-exploration syndrome, characterized by a positive relationship between movement frequency and speed to cross the barrier, was present throughout the duration of the study. In addition, the lack of coupling of boldness with other traits is in close alignment with previous work on this species (Michelangeli et al. 2016a, b; Moule et al. 2016; Michelangeli 2018). Our findings are consistent with Michelangeli et al. (2016a, b, 2018) and Moule et al. (2016), who each found the activity-exploration syndrome to be present over short time-periods (days to two weeks). However, it is important to note that the previous works limited their assessment of correlations to only the phenotypic level as opposed to partitioning correlations into the within- and among-individual components, as we have done in this work, which is necessary to reveal "true" syndromes (Dingemanse and Wright 2020; Michelangeli et al. 2020).

The current study differs to our previous studies in one important aspect: the length of time that the lizards were held in captivity prior to the behavioural assays. In the studies of Michelangeli et al. (2016a, b, 2018) and Moule et al. (2016), behavioural assays were performed within weeks of capture. By contrast, our animals had spent several years under captive conditions. Thus, at the onset of the present study, lizards were fully acclimated to lab conditions. Not only did study animals undergo a transition from natural levels of resource availability and predation pressure to predictable availability of food and a reduction in predation, but as a gregarious species, lizards were housed in groups of six individuals. Here we find that a behavioural syndrome is nevertheless present in these lizards, despite the potential drawbacks of acclimation and habituation to captivity and group housing conditions. Thus, our results suggest that future studies of the delicate skink, particularly for activity and activity-exploration syndromes, will not be substantially impacted by the length of time that they keep animals in captivity prior to behavioural assays.

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Data availability All data and code is available on the Bridges data repository: https://doi.org/10.26180/21221012.v1.

Declarations

Conflict of interest We have no conflicts of interest or competing interests to declare.

Ethical approval All animal care and experimental procedures were approved by the Monash University Animal Ethics Committee (BSCI/2017/02 [14659]). All animals were collected in accordance with the appropriate collection and research permits (New South Wales: SL101135, SL101202, SL101203; Victoria: 10006866, 10006867, 10006897).

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