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Personality in a widespread lizard species*

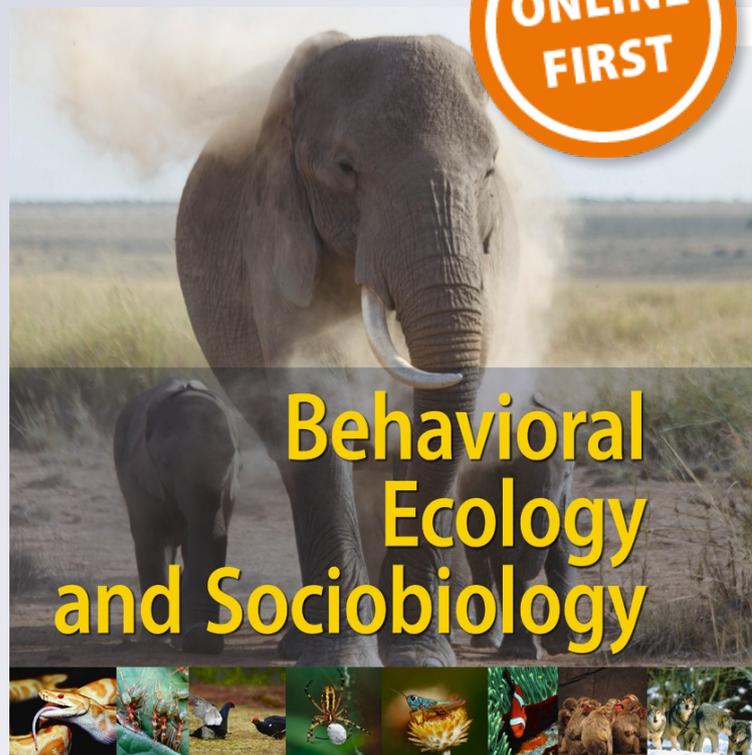
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Are behavioural syndromes sex specific? Personality in a widespread lizard species

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Abstract

Understanding how and why consistent behavioural traits (i.e. animal personality) vary between individuals, and identifying the mechanisms that underlie such variation, is a key focus in behavioural and evolutionary ecology. In many animals, male and female behaviour often diverges in response to different selection pressures and life history trajectories post-maturation. Despite this, animal personality studies spanning several personality traits rarely consider both sexes, ignoring the very strong possibility that key components of personality, behavioural consistency and behavioural correlations, may vary between males and females. Furthermore, such variation can play an important role in ecological processes such as mediating the invasion propensity of a species. Here, we took an animal personality approach to studying the behaviour of a repeatedly successful invasive species, the delicate skink (*Lampropholis delicata*). We investigated whether male and female delicate skinks differed in their personality across five behavioural traits, as sex differences in behaviour could provide a mechanism that explains the delicate skink's successful invasion history via accidental introductions. We found that females were more social than males and showed a trend towards being faster explorers. Both sexes shared the same behavioural syndrome suggesting that it is evolutionarily stable and not easily decoupled by selection. Specifically, skinks that were consistently more active explored environments faster and were more likely to bask with other skinks. In

sum, we found limited evidence of sex-specific personality in the delicate skink suggesting that both sexes might have an equal invasion potential. More broadly, our study highlights the need to consider whether, in fact, differences in personality are important in mediating a species propensity to invade.

Significance statement

Males and females likely differ in their personality because they often face different selection pressures when they are adults. An individual's personality may also determine how likely they are to invade novel environments. Thus, we compared personality traits of males and females in an invasive species, the delicate skink, for what it may reveal about the potential mechanisms that drive the species successful invasion history. We found that females were more social and showed a trend towards being faster explorers than males. Both sexes had positive correlations between activity, exploratory and social behaviour suggesting the presence of a non-sex-specific behavioural syndrome. Our results suggest limited behavioural variation between the sexes and that both sexes may have an equal invasion potential.

Keywords Life history · Behavioural type · Invasion syndrome · Dispersal · Repeatability

Introduction

Within populations, individuals often exhibit consistent individual differences in a range of behaviours across time and/or different contexts. For example, some comb-footed spiders (*Anelosimus studiosus*) are consistently more aggressive during a foraging and mating context than other individuals (Pruitt et al. 2008). These consistent behaviours can also

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become correlated at the population level (Sih et al. 2004). For instance, aggressive comb-footed spiders are also consistently more asocial, whereas passive individuals are consistently more social (i.e. there is an aggressive social syndrome within the population; Pruitt and Riechert 2009). This phenomenon is most regularly referred to as animal personality, but can also be labelled behavioural syndromes, coping styles or temperament (see David and Dall 2016 for discussion on terminology). Animal personality implies limited behavioural plasticity, as an individual is often constrained by their personality type (Sih et al. 2004). Behavioural consistency provides an explanation for why we see maladaptive behaviours in the wild when another behavioural response would be considered more adaptive (Sih and Bell 2008; Wolf and Weissing 2010). Thus, understanding how and why personality varies between individuals, and identifying the mechanisms that underlie such variation, is a key focus in behavioural and evolutionary ecology for what it may reveal about its ecological consequences for population dynamics, species interactions and responses to human-induced environmental change (Wolf and Weissing 2012; Dochtermann and Dingemanse 2013).

One aspect of animal personality research that has surprisingly received little attention is how the sexes may differ in personality (Pruitt and Riechert 2009; Schuett and Dall 2009; Chapman et al. 2013; Fresneau et al. 2014). In many animals, male and female behaviour often diverges in response to different selection pressures and life history trajectories post-maturation. Furthermore, behavioural differences between the sexes, particularly in behaviours associated with reproduction, is a central theme of sexual selection theory (Schuett et al. 2010). Indeed, various studies have reported differences in single behavioural traits between the sexes (e.g. dispersal: Pusey 1987; Pardini et al. 2001, risk-taking: Piyapong et al. 2010). For example, male house sparrows (*Passer domesticus*) are more predictable between and within years in their nestling provisioning rate and parental care than female house sparrows (Nakagawa et al. 2007). However, studies on animal personality spanning several behavioural traits have tended to only focus on one sex, ignoring the very strong possibility that key components of personality, behavioural consistency and behavioural correlations, may vary between the sexes.

Recently, it has been suggested that species that have repeatedly been successful at invading novel environments may be predisposed with a combination of behavioural traits that increase success across the invasion process (Chapple et al. 2012; Sih et al. 2012; Carere and Gherardi 2013). These animals are more prone to enter transportation, survive transit, occupy novel resources, establish a viable population and spread to become invasive (Chapple and Wong 2016). For instance, highly exploratory individuals might be expected to find

their way onto freight or cargo more regularly than less explorative individuals (Chapple et al. 2011). However, if an individual's personality is a key determinant of whether or not they will successfully pass through the invasion process, then invasion front populations will only be made up of a subset of personalities from the source population with implications for the persistence of that species in the invaded range (Wolf and Weissing 2012; Forsman 2014). It is therefore important to ascertain whether there are differences in behavioural variation between the sexes of an invasive organism. If, for example, we find limited behavioural variation between the sexes of an invasive species, then we might predict that the invasion process does not select against the behaviour of one sex and that populations that are introduced to a novel environment will have an equal sex ratio. Alternatively, if personality differs greatly between the sexes then we may predict that the invasion process will favour the behaviour of a particular sex leading to a skewed sex ratio at the invasion front. This has enormous consequences for both population growth and for the native communities in the invaded range (Miller and Inouye 2013; Fryxell et al. 2015).

Accordingly, in the present study, we compared the personality traits of males and females within a native-range population of the delicate skink, *Lampropholis delicata*, a species that has been repeatedly successful at becoming invasive through accidental introductions. Accidentally introduced species rely more heavily on human-mediated dispersal than deliberately introduced species, and thus likely depend on a unique suite of behaviours for invading novel environments (Chapple et al. 2012). The delicate skink is a group-living, small diurnal lizard (adult snout-vent length [SVL] 34–51 mm) that is native and abundant throughout southeastern Australia. It is the only Australian lizard species to have successfully invaded overseas (Kraus 2015). The species was accidentally introduced to the Hawaiian Islands, New Zealand and Lord Howe Island, where it has now become invasive and abundant (Chapple et al. 2013a, b, 2014; Tingley et al. 2016). The delicate skink is also commonly intercepted within freight and cargo being transported overseas (Chapple et al. 2013b, 2016). In this study, we compared males and females from a native population across a range of behavioural traits believed to be important for the early stages of the invasion process: activity, exploratory behaviour, sociability, foraging activity and boldness (Chapple et al. 2012). We hypothesized that males and females would not differ significantly from one another in many of these behaviours, but instead behaviours that are more closely associated with reproductive strategies would be more likely to vary (e.g. social behaviours: Schuett and

Dall 2009; Gyuris et al. 2011; Hedrick and Kortet 2012).

Methods

Animal collection and husbandry

Skinks were captured using mealworm fishing from Lane Cove National Park, Sydney, Australia (33° 47' 17.754" S, 151° 08' 43.968" E) in April 2014 in accordance with the appropriate collection and research permits (New South Wales: SL101203, Victoria: 10006866). We used mealworm fishing as our capture method as it has previously been shown not to retain trapping bias towards particular behavioural types (Michelangeli et al. 2016).

Once captured, skinks were measured for tail length (TL, length from vent to tip of tail), snout-vent length (SVL, length from tip of snout to vent), and their sex determined (via eversion of hemipenes in males). Tail loss (Downes and Shine 2001; Cromie and Chapple 2012) and gravidity (Shine 2003) can influence behaviour in *Lampropholis* skinks; therefore, only adult males and non-gravid adult females (SVL > 34 mm) with long tails (TL > SVL) were retained. Males and females did not differ significantly in size (mean SVL \pm SE; male: 34.95 \pm 0.43 mm, female: 35.61 \pm 1.78, $F_{1, 45} = 1.45$, $P = 0.24$).

Skinks were transported back to Monash University for laboratory behavioural experiments. Upon arrival, all skinks were given a noninvasive unique permanent identification code using different colour combinations of visual implant elastomer (Northwest Marine Technology, WA, USA). Focal skinks (both males and females) were housed individually in plastic containers (25 cm \times 20 cm \times 18 cm). This was done to prevent possible competition between individuals which could alter an individual's behaviour. On one end of each housing container, a basking area was created using heat tape and a flat basking platform (a terracotta tile). This provided a thermal gradient in the housing container (22–35 °C) allowing thermoregulation from 08:00 to 17:00 h. Small plastic pots were added for shelter. UV lighting was placed above the containers and was activated from 08:00 to 18:00 h. All housing containers were in a temperature-controlled room with an ambient temperature of approximately 22 °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™), three times a week and water was made available ad libitum.

Behavioural experiments

We conducted a series of behavioural assays to examine variation and correlation amongst five behavioural traits: activity,

exploratory behaviour, sociability, foraging activity and boldness. Behavioural assays were carried out in a fixed order (in the order presented below), where trials that could have the greatest influence upon behaviour were carried out last to reduce potential carry-over effects (Bell 2012). To test repeatability, or behavioural consistency, individuals were placed through each behavioural assay twice, at least 1 week apart (Bell et al. 2009).

All behavioural assays were conducted in opaque-walled experimental arenas (550 mm \times 320 mm \times 240 mm). The setup of the arena was modified to accommodate the trial being conducted; however, we never conducted two different behavioural assays on the same day but, instead, each behavioural assay was conducted at least 2 weeks apart. Skinks were allowed to acclimate under transparent containers for 10 min prior to the start of each trial. To minimize observer bias by using blinded methods, all trials were recorded using JVC Everio GZ-E100 video cameras. After each trial, the footage was downloaded to a computer for later playback (using JWatcher™; Blumstein et al. 2006) and data analysis. All equipment was thoroughly washed between trials with hot water and scentless dishwashing detergent to prevent scent contamination amongst trials. Since *Lampropholis* skinks are known to modify their behaviours following large meals (Shine 2003), we ensured that lizards were not fed in the 24 h prior to each behavioural trial.

Activity To measure activity levels, skinks were allowed to roam freely in a test arena marked with 20 equal grid squares (8 \times 11 cm). We recorded the number of transitions between grid squares the skink made over 45 min. The greater number of transitions the skink made the higher the activity level (sensu Chapple et al. 2011; Cromie and Chapple 2012; Michelangeli et al. 2016; Moule et al. 2016).

Exploratory behaviour To measure an individual's propensity to explore a novel environment, skinks were placed into a test arena containing an obstacle. The obstacle was in the form of a trapezium-shaped barrier, which divided the test arena into two compartments. Lizards started in compartment 1. The only way lizards could reach compartment 2 was by finding and squeezing themselves through small gaps at either end of the barrier. We recorded the time it took lizards to reach compartment 2 (sensu Chapple et al. 2011; Michelangeli et al. 2016; Moule et al. 2016).

Sociability We conducted a dichotomous choice experiment to measure the social behaviour of skinks. Delicate skinks are often observed either basking in small groups (~2–10 individuals) or alone in the wild (unpublished data). Thus, we offered individual lizards a choice between basking with a group of three conspecifics and basking alone (as per Chapple et al. 2011; Michelangeli et al. 2016). This was achieved by splitting the test arena into three zones: social zone, asocial zone

and a 'no choice' zone. A black marker pen was used to draw five 11 cm segments along the length of the test arena to create the three zones. A basking site, positioned under a 40-W heating lamp, was placed at each end of the arena, on the inner edge of the exterior segments. Each basking site was divided in half by a clear Perspex™ partition (10 cm high), which ran the width of the arena. Three stimulus lizards (same sex as the focal individual) were placed within one of the peripheral sections, enabling focal lizards to see, but not physically interact with them. This left three inner segments, with the two adjoining the basking sites designated as either the 'social zone' (containing same-sex stimulus lizards) or the 'asocial zone' (containing no lizards) and the central one considered to be a 'no choice' or neutral zone. Stimulus lizards (male: $n = 13$, female: $n = 15$) were caught during the collecting trip in April and did not differ in size compared to focal lizards (male: mean SVL \pm SE, focal: 34.95 ± 0.43 mm, stimuli: 34.62 ± 0.45 mm, $F_{1, 33} = 1.74$, $P = 0.54$; female: mean SVL \pm SE, focal: 35.61 ± 1.78 mm, stimuli $F_{1, 39} = 1.22$, $P = 0.38$). No focal lizards were used as stimuli.

The temperature underneath the heat lamps (~ 35 °C) was substantially higher than the ambient temperature (~ 20 °C), prompting the lizards to use the basking sites. Each trial ran for 45 min and we recorded the amount of time focal skinks spent within each zone (sensu Chapple et al. 2011; Michelangeli et al. 2016).

Foraging activity To measure an individual's foraging behaviour, skinks were placed in a test arena with a shelter site at one end. Skinks had not been fed for 3 days prior to experimentation. After an acclimation period, five crickets, of equal size, were dropped into the arena by the observer (MM). This was done from behind a curtain to avoid any disturbance. We then recorded how many crickets were eaten by the skink and the number of failed capture attempts the skink made—failed capture attempts included prey drops (when a cricket was caught but then dropped), and any lunge attacks that failed to capture a cricket—over 15 min (sensu Michelangeli et al. 2016). Using these variables we calculated a foraging score for each skink as follows:

$$\text{Foraging score} = \frac{(\text{Number of crickets eaten} \div \text{total number of crickets offered})}{(\text{Total number of capture attempts} \div \text{number of successful attempts})}$$

Boldness To measure an individual's boldness, we exposed skinks to a simulated predator attack and then measured their basking behaviour after the attack. In reptiles, basking is considered to be a risky behaviour as it exposes individuals to potential predators (Downes and Hoefer 2004). Thus, bolder skinks are expected to bask more than shy skinks after a predatory attack (Downes 2001). Skinks were placed at the centre 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 (~ 20 °C). After the acclimation period, a model of a bird's head was released, striking at a central point 5 cm above the bottom of the arena, before being immediately retracted. Trials ran for 25 min and we recorded the amount of time skinks spent in the open basking site (i.e. underneath the basking lamp) after the attack as our measure of boldness. Not all skinks fled to the shelter site immediately after the 'bird attack'; some instead responded with an initial short boost of activity followed by remaining stationary for a period of time (a common anti-predator behaviour in this species; Downes and Hoefer 2004). Thus, we did not record an individual's re-emergence from shelter time as a measure of boldness.

Statistical analysis

All data were analysed using the statistical program R (R Development Core Team 2012). Statistical significance was assigned at $\alpha = 0.05$. Time spent basking (i.e. boldness) was square root transformed prior to analysis to approximate a Gaussian distribution.

We used Markov chain Monte Carlo general mixed models ('MCMCglmm': Hadfield 2010) to determine if there were any personality differences between male and female skinks. All models followed a Gaussian distribution, except for the model testing foraging behaviour, which required a binomial distribution. Sex and SVL were assigned as fixed factors with skink ID as a random factor. We used non-informative priors (mean = 0, variance = 1000), after we determined that models with more informative priors had no effect on the model outcome. Posterior distributions were examined to confirm homogeneous variances (Gelman and Hill 2007). Models were run for 65,000 iterations and, after a burn in of 10,000 iterations, were thinned by 50 iterations. We found no evidence of autocorrelation between posterior samples. P values were derived from MCMC. We calculated overall between-trial repeatability of behavioural traits and the associated confidence intervals using variance components obtained from the mixed-effects models (the ratio of between-individual variation to total variation; Dingemanse and Dochtermann 2012). We also ran separate models for both males and females to calculate sex-specific repeatability.

We ran principal component analysis (PCA) with data from both sexes followed by nonparametric Spearman rank correlations to investigate the presence of behavioural syndromes (Bell et al. 2009). Three individuals that did not complete the full set of behavioural experiments were excluded from analysis. We also excluded boldness because it had a very low repeatability. Three PCA components were retained based on the Kaiser-Guttman criterion (eigenvalues ~ 1 ; Jackson 1993). In order to test if syndrome structure differed between the sexes, we ran a linear model containing the factor loading

scores as the response variable and sex as the predictor variable. We also used Fisher's Z transformation (Zar 1999) to compare differences in correlation coefficients.

Results

When considering males and females together, we found that all behavioural traits were repeatable, except boldness, which had a very low repeatability estimate (see Table 1). Males and females also did not significantly differ in their behavioural consistency across all five behavioural traits (confidence intervals of repeatability estimates overlap; see Table 1).

Male and female skinks did not differ in activity, in their voraciousness to feed (i.e. foraging scores) or the time they spent basking after a predatory attack (i.e. boldness; see Table 1). Females passed the obstacle faster and more regularly than males, although this

effect was marginally non-significant (i.e. exploratory behaviour; see Fig. 1 and Table 1). However, females were more likely to bask with other skinks (sociability; see Fig. 1 and Table 1), whereas males preferred to bask alone (i.e. were less social). SVL had no effect on any of the behavioural traits.

Kaiser-Guttman analysis of the PCA revealed two factors that explained 66.2 % of the variance (Table 2). Behaviours with a loading of at least 0.4 were considered to contribute to a principal component. PC1 showed strong loadings toward activity and exploratory behaviour whilst also a moderate loading towards sociability. These loadings are reflected by the pairwise correlations between these behavioural traits, as there was a significant positive correlation between activity and exploratory behaviour (see Table 3), but only a non-significant positive association between activity and sociability (see Table 3), and exploratory behaviour and sociability (see Table 3). Thus, PC1 suggests that more active

Table 1 Output from mixed-effects models, showing the effects of sex and SVL (snout-vent length) and the repeatability of behavioural traits in *Lampropholis delicata*

	Coefficient	<i>p</i>	V_p	V_E	Adj repeat
Activity	–	–	1334.65	857.60	0.60 (0.3, 0.76)
Sex (female)	–7.87 (–32.0, 15.1)	0.53	–	–	–
Male	–	–	1029.56	781.01	0.57 (0.24, 0.79)
Female	–	–	1370.42	955.28	0.59 (0.27, 0.78)
SVL	–2.81 (–9.3, 3.5)	0.38	–	–	–
Exploration	–	–	2730.1	3546.1	0.43 (0.20, 0.69)
Sex (female)	393.02 (–50.6, 871.9)	0.09	–	–	–
Male	–	–	5294.22	3178.6	0.63 (0.30, 0.81)
Female	–	–	3006.12	4117.41	0.42 (0.10, 0.55)
SVL	–49.83 (–151.9, 54.1)	0.34	–	–	–
Sociability	–	–	9.83	19.08	0.34 (0.25, 0.42)
Sex (female)	–3.12 (–5.2, –0.5)	0.01*	–	–	–
Male	–	–	6.25	25.9	0.19 (0.05, 0.58)
Female	–	–	10.24	12.50	0.45 (0.10, 0.71)
SVL	–0.55 (–1.2, 0.2)	0.11	–	–	–
Foraging	–	–	34.37	50.33	0.41 (0.14, 0.62)
Sex (female)	–0.15 (–0.4, 0.2)	0.80	–	–	–
Male	–	–	31.41	67.52	0.32 (0.11, 0.65)
Female	–	–	39.36	35.35	0.53 (0.18, 0.76)
SVL	0.05 (–0.3, 0.4)	0.81	–	–	–
Boldness	–	–	9.54	27.75	0.26 (0.03, 0.49)
Sex (female)	–1.73 (–4.5, 0.6)	0.19	–	–	–
Male	–	–	4.51	36.52	0.11 (0.04, 0.28)
Female	–	–	16.48	20.38	0.35 (0.10, 0.65)
SVL	–0.71 (–1.4, 0.7)	0.09	–	–	–

V_A between-individual variation, V_E residual variation (within-individual variance), *Adj repeat* adjusted repeatability ($V_A / V_A + V_E$)

*Significant results

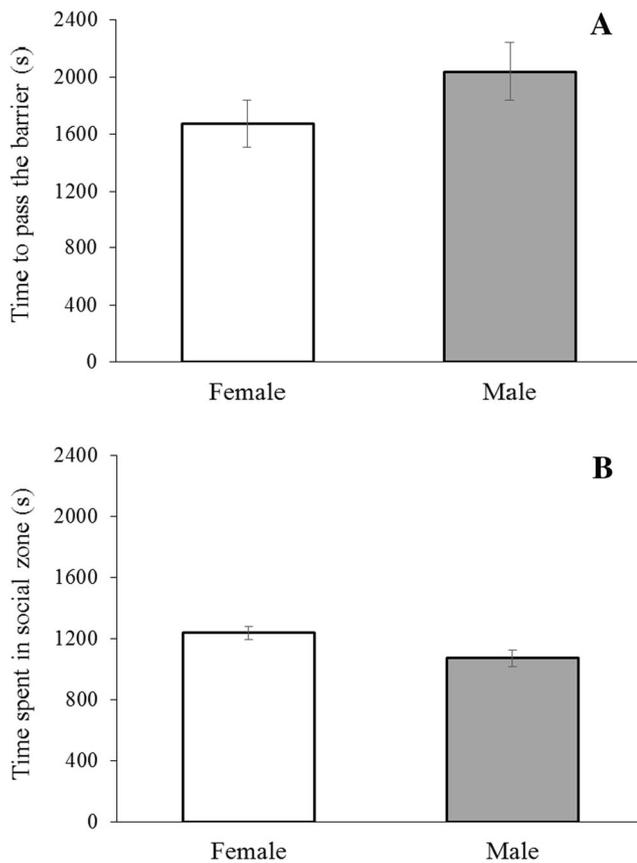


Fig. 1 Sex differences in mean (\pm SE). **a** Exploratory behaviour (i.e. time taken to pass obstacle). **b** Sociability (i.e. time spent in social zone) in the delicate skink, *Lampropholis delicata*

skinks were also faster explorers and tended to spend more time basking with other skinks (i.e. were more social). PC2 was only strongly loaded towards foraging activity, suggesting that this behaviour was not part of any behavioural syndrome. Finally, we found no difference in factor loading scores between the sexes (PC1: $t_{1,84} = -1.50$, $P = 0.137$, PC2: $t_{1,84} = 0.25$, $P = 0.805$) and no difference in the correlation coefficients (see Table 3) suggesting that syndrome structure does not differ between males and females.

Table 2 Component loadings of behaviours observed on two orthogonally rotated principal components. Only behaviours with a loading of at least 0.4 were considered to contribute to a component

	PC1 Activity-exploration-sociability	PC2 Foraging activity
Activity	0.627	
Exploration	0.624	
Sociability	0.525	
Foraging		-0.942
Variance explained %	41.2	25.0
Total explained%	66.2	

Discussion

We found limited sex-specific personality in the delicate skink. Females were more social than males, and our results indicate that females might be faster explorers. However, both males and females share a similar behavioural syndrome, where lizards that are more active tend to be faster explorers and are also more social. This result is supported by our previous studies, where we found correlations between activity, exploratory behaviour and sociability in males (Michelangeli et al. 2016; Moule et al. 2016). Importantly, this is one of only a handful of studies that have found personality differences between the sexes, and one of the first to show these differences in a frequent invader (Cote et al. 2010). We suggest that these personality differences not only reflect different reproductive strategies but, more broadly, may provide a mechanism that could explain the delicate skink's successful invasion history through accidental introductions.

Differences in reproductive or life history strategies might explain the sociability discrepancy between the sexes. Indeed, in reptiles, females tend to be the more social sex (Baird et al. 1996; Strickland et al. 2014). For example, female eastern water dragons (*Intellagama lesueurii*) form stronger social bonds with other individuals of the same sex compared to males (Strickland et al. 2014). Females may be more likely to socialise with other females due to potential anti-predator group benefits (e.g. Downes and Hoefer 2004), enhanced foraging efficiency (e.g. Martin and Lopez 1999) or increased reproductive success/offspring survival (e.g. Cote et al. 2008). Moreover, female delicate skinks often use conspecific cueing to assess suitable nesting environments (i.e. females choose to lay their eggs in the same nesting sites as other females; Paull and Doody unpublished data). On the other hand, males may generally be more asocial to reduce competition and aggressive interactions with other males for resources or copulations with females (e.g. York et al. 2014). However, we did find high levels of variation in sociability in both sexes, suggesting that not all individuals utilise the same life history or reproductive strategies.

Table 3 Spearman rank correlation tests between behavioural traits for the overall population and each sex and differences in correlation coefficients between the sexes

	Correlation	Behaviour 1	Behaviour 2	<i>n</i>	<i>rho</i>	<i>p</i>	Comparison	<i>Z</i>	<i>p</i>
Overall	1	Activity	Exploration	47	0.33	<i><0.01</i>			
	2	Activity	Sociability	47	0.28	0.09			
	3	Exploration	Sociability	47	0.25	0.13			
Male	4	Activity	Exploration	21	0.31	<i>0.04</i>			
	5	Activity	Sociability	21	0.19	0.25			
	6	Exploration	Sociability	21	0.11	0.43			
Female	7	Activity	Exploration	26	0.29	<i>0.03</i>	4 vs. 7	0.07	0.94
	8	Activity	Sociability	26	0.26	0.08	5 vs. 8	-0.23	0.82
	9	Exploration	Sociability	26	0.17	0.35	6 vs. 9	-0.19	0.84

Estimates in italics denote significance

We found that female delicate skinks showed a trend towards being faster explorers than males. In this respect, the coupling of higher exploration and higher sociability in females is an intriguing possibility that may contribute to the species' repeated success as an invader through accidental introductions. For instance, very explorative individuals are predicted to be more regularly transported to new environments than less explorative individuals due to their ability to find their way onto freight and cargo (Chapple et al. 2011, 2012). Similarly, in other lizards, a tendency to explore new environments has been found to promote information gathering (e.g. eastern water skink, *Eulamprus quoyii*, Carazo et al. 2014) and has been linked to an ability to habituate faster to new environments and novel predators (e.g. Iberian wall lizards, *Podarcis hispanica*, Rodríguez-Prieto et al. 2011). Increased exploratory behaviour is also often fundamental to dispersal (Dingemanse et al. 2003; Rehage and Sih 2004), so if females are the more explorative sex, they may also be more likely to disperse and find new areas to colonize than males (e.g. southern snow skinks, *Niveoscincus microlepidotus*, Olsson and Shine 2003). Thus, the combination of sociability, exploration and dispersal could facilitate the invasion of new areas, particularly if females, the regenerative sex, lead the invasion front (i.e. female-biased invasions: Miller and Inouye 2013). However, again, this is only speculation considering we did not find a significant difference in exploratory behaviour between males and females, but we still believe that this is an interesting possibility that could be an exciting avenue for future research.

We also found positive correlations between activity, exploratory behaviour and sociability in the delicate skink, suggesting the presence of a behavioural syndrome. These results support our previous work finding a relationship between these behavioural traits in males only (Michelangeli et al. 2016; Moule et al. 2016). Although sociability was not significantly correlated with activity and exploratory behaviour in this study,

we suggest that this may be because sociability is partly independent of these behaviours (e.g. Cote et al. 2011) or could simply be a result of a smaller sample size compared to our previous study (Michelangeli et al. 2016). The activity-exploratory-sociability syndrome has been found in other organisms, including other invasive species (Cote et al. 2010), but this is the first study to show that the syndrome does not diverge between the sexes. This suggests that the syndrome either develops in males and females due to similar selective environmental conditions or the syndrome is constrained across sexes due to a shared underlying mechanism. As both male and female lizards need to thermoregulate, one such mechanism could be thermal physiology in which an individual's personality is inhibited by their thermal and metabolic requirements (Biro and Stamps 2010).

The activity-exploratory-sociability syndrome has also been associated with dispersal tendency (Cote and Clobert 2007; Cote et al. 2011). For example, in common lizards (*Lacerta vivipara*), social individuals disperse when population densities are low, presumably to find other individuals, whereas asocial individuals tend to disperse when population densities are high (Cote and Clobert 2007). Such a dispersal-related syndrome may be pivotal during the invasion process, as active, explorative and social individuals may have a better opportunity of finding mates in low population densities. Links between these traits in the delicate skink could thus reveal a mechanism that helps drive the success of this species across the invasion process and thus warrants further research.

Conclusions

We found that females were more social than males, and there was some indication that they may also be faster explorers. Our study is also one of the few to find the same behavioural syndrome in males and females (i.e. activity-exploratory-

sociability syndrome; but see Pruitt and Riechert 2009) suggesting that this syndrome is evolutionarily stable and not easily decoupled by selection. In sum, we found limited evidence of sex-specific personality in the delicate skink suggesting that both sexes might have an equal invasion potential. More broadly, our study highlights the need to consider whether, in fact, differences in personality are important in mediating a species propensity to invade.

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Compliance with ethical standards

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Informed consent Informed consent was obtained from all individual participants included in the study.

References

- Baird TA, Acree MA, Sloan CL (1996) Age and gender-related differences in the social behavior and mating success of free-living colored lizards, *Crotaphytus collaris*. *Copeia* 1996:336–347
- Bell AM (2012) Randomized or fixed order for studies of behavioral syndromes? *Behav Ecol* 24:16–20
- Bell AM, Hankison SJ, Laskowski KL (2009) The repeatability of behaviour: a meta-analysis. *Anim Behav* 77:771–783
- Biro PA, Stamps JA (2010) Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends Ecol Evol* 25:653–659
- Blumstein D, Evans C, Daniels J (2006) JWatcher 1.0, <http://www.jwatcher.ucla.edu>
- Carazo P, Noble DWA, Chandrasoma D, Whiting MJ (2014) Sex and boldness explain individual differences in spatial learning in a lizard. *Proc R Soc B* 281:20133275
- Carere C, Gherardi F (2013) Animal personalities matter for biological invasions. *Trends Ecol Evol* 28:5–6
- Chapman BB, Hegg A, Ljungberg P (2013) Sex and the syndrome: individual and population consistency in behaviour in rock pool prawn *Palaemon elegans*. *PLoS One* 8:e59437
- Chapple DG, Wong BBM (2016) The role of behavioural variation across different stages of the introduction process. In: Weis JS, Sol D (eds) *Biological invasions and animal behaviour*. Cambridge University Press, Cambridge
- Chapple DG, Simmonds SM, Wong BBM (2011) Know when to run, know when to hide: can behavioral differences explain the divergent invasion success of two sympatric lizards? *Ecol Evol* 1:278–289
- Chapple DG, Simmonds SM, Wong BBM (2012) Can behavioral and personality traits influence the success of unintentional species introductions? *Trends Ecol Evol* 27:57–64
- Chapple DG, Miller KA, Kraus F, Thompson MB (2013a) 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, Whitaker AH, Chapple SN, Miller KA, Thompson MB (2013b) Biosecurity interceptions of an invasive lizard: origin of stowaways and human-assisted spread within New Zealand. *Evol Appl* 6:324–339
- Chapple DG, Miller KA, Chaplin K, Barnett L, Thompson MB, Bray RD (2014) Biology of the invasive delicate skink (*Lampropholis delicata*) on Lord Howe Island. *Aust J Zool* 62:498–506
- Chapple DG, Knechtmans J, Kikillus H, van Winkel D (2016) Biosecurity of exotic reptiles and amphibians in New Zealand: building upon Tony Whitaker's legacy. *J Roy Soc New Zeal* 46:66–84
- Cote J, Clobert J (2007) Social personalities influence natal dispersal in a lizard. *Proc R Soc Lond B* 274:383–390
- Cote J, Dreiss A, Clobert J (2008) Social personality trait and fitness. *Proc R Soc Lond B* 275:2851–2858
- Cote J, Fogarty S, Weinersmith K, Brodin T, Sih A (2010) Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). *Proc R Soc B* 277:1571–1579
- Cote J, Fogarty S, Brodin T, Weinersmith K, Sih A (2011) Personality-dependent dispersal in the invasive mosquitofish: group composition matters. *Proc R Soc Lond B* 278:1670–1678
- 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
- David M, Dall SR (2016) Unravelling the philosophies underlying 'animal personality' studies: a brief re-appraisal of the field. *Ethology* 122:1–9
- Dingemans NJ, Dochtermann N (2012) Quantifying individual variation in behaviour: mixed effect modelling approaches. *J Anim Ecol* 82:39–54
- Dingemans NJ, Both C, van Noordwijk AJ, Rutten AL, Drent PJ (2003) Natal dispersal and personalities in great tits (*Parus major*). *Proc R Soc Lond B* 270:741–747
- Dochtermann NA, Dingemans NJ (2013) Behavioral syndromes as evolutionary constraints. *Behav Ecol* 24:806–811
- Downes S (2001) Trading heat and food for safety: costs of predator avoidance in a lizard. *Ecology* 82:2870–2881
- Downes S, Hofer AM (2004) Antipredatory behaviour in lizards: interactions between group size and predation risk. *Anim Behav* 67:485–492
- Downes S, Shine R (2001) Why does tail loss increase a lizard's later vulnerability to snake predators? *Ecology* 82:1293–1303
- Forsman A (2014) Effects of genotypic and phenotypic variation on establishment are important for conservation, invasion, and infection biology. *Proc Natl Acad Sci U S A* 111:302–307
- Fresneau N, Kluehn E, Brommer JE (2014) A sex-specific behavioral syndrome in a wild passerine. *Behav Ecol* 25:359–367
- Fryxell DC, Arnett HA, Apgar TM, Kinnison MT, Palkovacs EP (2015) Sex ratio variation shapes the ecological effects of a globally introduced freshwater fish. *Proc R Soc B* 282:20151970
- Gelman A, Hill J (2007) *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, Cambridge
- Gyuris E, Feró O, Tartally A, Barta Z (2011) Individual behaviour in firebugs (*Pyrhocoris apterus*). *Proc R Soc Lond B* 278:628–633
- Hadfield JD (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J Stat Softw* 33:1–22
- Hedrick AV, Kortet R (2012) Sex differences in the repeatability of boldness over metamorphosis. *Behav Ecol Sociobiol* 66:407–412
- Jackson DA (1993) Stopping rules in principal components analysis: a comparison of heuristic and statistical approaches. *Ecology* 74:2204–2214
- Kraus J (2015) Impacts from invasive reptiles and amphibians. *Annu Rev Ecol Evol S* 46:75–97
- Martin J, Lopez P (1999) When to come out from a refuge: risk-sensitive and state-dependent decisions in an alpine lizard. *Behav Ecol* 10:487–492
- 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 TE, Inouye BD (2013) Sex and stochasticity affect range expansion of experimental invasions. *Ecol Lett* 16:354–361
- 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
- Nakagawa S, Gillespie DOS, Hatchwell BJ, Burke T (2007) Predictable males and unpredictable females: sex difference in repeatability of parental care in a wild bird population. *J Evol Biol* 20:1674–1681
- Olsson M, Shine R (2003) Female-biased natal and breeding dispersal in an alpine lizard, *Niveoscincus microlepidotus*. *Biol J Linn Soc* 79:277–283
- Pardini AT, Jones CS, Noble LR, et al. (2001) Sex-biased dispersal of great white sharks. *Nature* 412:139–140
- Piyapong C, Krause J, Chapman BB, Ramnarine IW, Louca V, Croft DP (2010) Sex matters: a social context to boldness in guppies (*Poecilia reticulata*). *Behav Ecol* 21:3–8
- Pruitt JN, Riechert SE (2009) Sex matters: sexually dimorphic fitness consequences of a behavioural syndrome. *Anim Behav* 78:175–181
- Pruitt JN, Riechert SE, Jones TC (2008) Behavioural syndromes and their fitness consequences in a socially polymorphic spider, *Anelosimus studiosus*. *Anim Behav* 76:871–879
- Pusey AE (1987) Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends Ecol Evol* 2:295–299
- R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna (Austria) <http://www.R-project.org>
- Rehage JS, Sih A (2004) Dispersal behaviour, boldness, and the link to invasiveness: a comparison of four *Gambusia* species. *Biol Invasions* 6:379–391
- Rodríguez-Prieto I, Martín J, Fernández-Juricic E (2011) Individual variation in behavioural plasticity: direct and indirect effects of boldness, exploration and sociability on habituation to predators in lizards. *Proc R Soc Lond B* 278:266–273
- Schuett W, Dall SRX (2009) Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*. *Anim Behav* 77:1041–1050
- Schuett W, Tregenza T, Dall SRX (2010) Sexual selection and animal personality. *Biol Rev* 85:217–246
- Shine R (2003) Effects of pregnancy on locomotor performance: an experimental study on lizards. *Oecologia* 136:450–456
- Sih A, Bell AM (2008) Insights for behavioral ecology from behavioral syndromes. *Adv Stud Behav* 38:227–281
- Sih A, Bell AM, 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
- Strickland K, Gardiner R, Schultz AJ, Frère CH (2014) The social life of eastern water dragons: sex differences, spatial overlap and genetic relatedness. *Anim Behav* 97:53–61
- Tingley R, Thompson MB, Hartley S, Chapple DG (2016) Patterns of niche filling and expansion across the invaded ranges of an Australian lizard. *Ecography* 39:270–280
- Wolf M, Weissing FJ (2010) An explanatory framework for adaptive personality differences. *Philos T Roy Soc B* 365:3959–3968
- Wolf M, Weissing FJ (2012) Animal personalities: consequences for ecology and evolution. *Trends Ecol Evol* 27:452–461
- York JR, Baird TA, Haynie ML (2014) Unexpected high fitness payoff of subordinate social tactics in male collared lizards. *Anim Behav* 91:17–25
- Zar JH (1999) Biostatistical analysis. Prentice-Hall, Upper Saddle River, New Jersey