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ARTICLE

Exploratory and defensive behaviours change with sex and body size in eastern garter snakes (*Thamnophis sirtalis*)

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Abstract Phenotypic traits are important to consider when examining behaviour because they can help explain behavioural trait variation. Behaviours such as exploration, boldness, and defense may vary between individuals because different intensities of a behaviour may be advantageous for males versus females, or at different body sizes. We tested the hypothesis that exploration, boldness, and defensive behaviours are related to body size, sex, and reproductive status in eastern garter snakes, *Thamnophis sirtalis*. We also tested whether the measured behavioural traits were consistent through time (i.e., whether eastern garter snakes could have personalities) and whether the measured behavioural traits were related to one another (i.e., whether behavioural syndromes could be present in eastern garter snakes). Males and non-gravid females were more likely to flee than gravid females when faced with an attack. Males and non-gravid females were also more active after the attack than before the attack, whereas gravid females were more active before the attack. Furthermore, longer females explored less than smaller females, with a more precipitous decline of exploration as a function of size in gravid females than in non-gravid females. In contrast, longer males explored more than smaller males. Although we did not detect behavioural syndromes, within individuals the measured behavioural traits were repeatable through time, suggesting that eastern garter snakes could have personalities.

Keywords Behavioural syndrome · Consistency · Boldness · Repeatability · Personality · Reproductive status

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Introduction

Behaviour often varies between individuals within a population, and several proximate mechanisms can underlie this behavioural variation. Factors such as body size (Herzog et al. 1992; Krause et al. 1998; Bell and Stamps 2004; Glaudas et al. 2006) or sex (Scudder and Burghardt 1983; Herzog and Burghardt 1986; Shine et al. 2000; van Oers et al. 2005) can predict an individual's relative placement on a behavioural axis. For example, a study exploring the reaction of cottonmouths to predatory stimulation indicated differences in antipredator response between neonates and adults (Glaudas et al. 2006). In addition, Scudder and Burghardt (1983) found that male banded water snakes responded more aggressively to predator stimulation than females. Likewise, Durso and Mullin (2014) found that in plains hog-nosed snakes, larger snakes death-feigned for a longer period of time than smaller ones, and that this relationship was stronger in females. Thus, it seems plausible that sex and body size play an important role in predicting an individual's behaviour.

Personality represents individual patterns in behavioural traits that are consistent through time and across situations (Jacobs 2009). Many behavioural studies fail to test the assumption of individual consistency (e.g., Scudder and Burghardt 1983; Riechert and Hedrick 1993; van Oers et al. 2005; Bell and Sih 2007) because difficulties arise when testing for a behaviour multiple times on one individual. For instance, results on subsequent behavioural trials may differ due to varying environmental conditions during the tests (Archer 1973; Mettke-Hoffmann et al. 2006). In addition, performing the same standardised test on an individual to determine whether the behaviour is consistent may result in habituation, therefore producing different results through time (Groves and Thompson 1970; Archer 1973; Herzog et al. 1989; van Oers et al. 2005). Habituation is important in the context of personalities because greater ability to habituate may be associated with improved fitness (Rodríguez-Prieto et al. 2010).

Behavioural syndromes, on the other hand, are groups of correlated behavioural traits that occur across various contexts (Sih et al. 2004). A behavioural syndrome differs from a personality in that personality simply refers to an individual displaying consistent behavioural traits, whereas a behavioural syndrome describes a phenomenon whereby one behavioural trait (e.g., foraging) is correlated to one or more other behavioural traits in a population (e.g., exploration) (Jacobs 2009). For instance, Riechert and Hedrick (1993) found that aggressive female desert grass spiders also displayed more boldness following a simulated predatory attack. A similar result was found in sticklebacks, with individuals with high activity scores also being bolder when faced with a predator (Bell and Stamps 2004). Behavioural syndromes are important in the context of personalities because they can help predict an individual's placement on a related behavioural axis by comparing multiple behaviours.

In this study, we test the hypothesis that exploratory, boldness, and defensive behaviours are a function of sex, female reproductive status, and body size in eastern garter snakes, *Thamnophis sirtalis*. While eastern garter snakes apparently exhibit consistent behaviours (e.g., Herzog and Burghardt 1986; Shine et al. 2000), it remains unclear which factors predict these behaviours and whether these consistent behaviours represent personalities. In addition, in red-sided garter snakes, some individuals are more likely to strike than others (Shine et al. 2000), but it remains unknown whether some behavioural traits are correlated to others as part of a behavioural syndrome. Garter snakes are viviparous; therefore gravid females carrying developing young may defend themselves and forage differently than males due to their reproductive state (Graves 1989; Brown and Shine 2004; Sperry and Weatherhead 2012). Also, Shine et al. (2000) found that smaller male garter snakes were more likely to flee from a predatory stimulus than larger females. It is possible that larger individuals are more inclined to defend themselves because they may have a better chance of successfully dissuading a predator compared to a smaller snake (Glaudas et al. 2006). Larger snakes may also exhibit higher activity due to an increased endurance over smaller snakes (Pough 1977). Female snakes exhibit different defensive behaviours than males, and defensive behaviour and boldness are usually interrelated (Sih et al. 2004). Based on these findings, we tested the predictions that larger snakes should be more exploratory, bolder, and more defensive than smaller snakes. Similarly, females should be more exploratory, bolder, and more defensive than males, especially when they are gravid. To examine whether eastern garter snakes could have personalities, we also tested whether an individual's behaviour was consistent through time. Finally, we investigated whether there were behavioural syndromes by looking for correlations between the various behaviours.

Materials and methods

Study animals

We used eastern garter snakes as model organisms in this study. Snakes are ideal candidates for studying behaviour because they exhibit a variety of defensive behaviours and are among the most precocial animals, meaning that behaviour in younger snakes can be compared easily to that in older snakes (Herzog and Burghardt 1986). We chose eastern garter snakes as study species because they are abundant in our study area, and because there is a body of literature on this species for comparison. For the behavioural trials, we collected 42 garter snakes opportunistically following the breeding season, between May and July 2013 at the Queen's University Biological Station (latitude 44.57, longitude −76.32), approximately 100 km southwest of Ottawa, Ontario, Canada. For the consistency trials, we caught 19 garter snakes at hibernacula in October 2013 in areas surrounding Ottawa, Ontario (latitude 45.42, longitude −75.68) and Gatineau, Québec (latitude 45.48, longitude −75.70).

Snakes were kept in captivity for a maximum of 2 weeks while conducting trials, and released back at their capture site. Snakes were housed in plastic containers (30.5 × 48.5 × 31.5 cm), provided ad lib water, and fed earthworms once per week if they were kept in captivity for more than 1 week. Newspaper was used as substrate and replaced as needed. All methods were approved by the University of Ottawa Animal Care Committee (protocol number BL-278), which follows the guidelines of the Canadian Council for Animal Care.

Behavioural trials

We conducted three groups of trials, each with the purpose of eliciting a different type of behavioural response: exploratory, boldness, and defensive. We conducted these trials twice for each individual to test for individual consistency: once after a minimum of 1 day acclimation to captivity, and the second occurring 2 days later. We did not randomize the order of trials, but conducted all trials in the same order (exploratory, boldness, and defensive) for two reasons. (1) The exploratory trial was conducted first so that the test arena was indeed a novel environment for the snake. (2) The defensive trial was conducted last because it was potentially the most stressful for the subjects, and could therefore impact any subsequent trials. Although following the same order of trials did not allow to control for potential carry-over effects (e.g., Hsieh and Liu 2005), we deemed that this cost was outweighed by the benefits of always having the exploratory trial first and the defensive trial last. To minimize potential carry-over effects, we left at least 30 min between subsequent trials for each snake. We covered the sides of a 60 × 30.5 × 31.5 cm terrarium with paper to block all visual stimuli outside of the terrarium, and we recorded all trials with a video camera. In snakes, cloacal sac odours may alarm conspecifics to danger (Graves and Duvall 1988) so we replaced the paper in the terrarium between trials.

We examined exploratory behaviour by placing the snake in the middle of the terrarium and recorded the time spent exploring and the area explored over 5 min. We placed a grid of 5 × 5 cm squares on the bottom of the terrarium to quantify the area explored. Using this grid, we counted the total number of squares that the head of the snake passed over during the trial, and calculated the total percentage of squares that the snake passed over.

Second, we evaluated boldness by placing the snake in a refuge (half of a PVC pipe: L = 25.5 cm, H = 9.5 cm) in the terrarium. We left the snake in the refuge for a 30-second acclimation period, and then uncovered the entrance to determine how long it took for the snake to exit the refuge (latency to leave), for a maximum of 5 min. We determined latency to leave as the time it took for the snake's entire head to be exposed for at least 10 s.

Lastly, we recorded defensive behaviour by placing the snake in the terrarium for a one-minute acclimation period before dropping a model predator claw (shaped like an osprey claw: 19.3 cm long, 5.3 cm wide at the top, 2.1 cm wide at the base with four 6.7 cm talons; Fig. 1) above the snake (after Jonsson et al. 1996). We dropped the model from approximately 50 cm above the bottom of the terrarium and allowed it to stop approximately 10 cm above the middle of the snake's body. We categorized defensive behaviour as one of six responses with their corresponding defensive score in parentheses: flee (−2), aversion (−1), no reaction (0), tense (1), S-pose (2), or strike (3). We defined S-pose as the shape of the snake when it is partially coiled in an "S" shape and is ready to strike [see Shine et al. 2000, and Hailey and Davies's (1986) "viperine display"]. The categories were determined through pilot tests that indicated the presence of these different reactions. The scores are arranged in a scale from least defensive (flee) to most defensive (strike), similar to the scale used by Shine et al. (2000). If a snake exhibited multiple behaviours, we added the scores from each behaviour. We also recorded

Fig. 1 Model claw used to elicit defensive behaviours in eastern garter snakes

movement for a full minute before and after the predatory attack. Movement was recorded as the number of seconds the snake was moving; the timer started whenever the snake was moving, and stopped whenever the snake was still. We calculated the difference between time active after versus before the model predator attack by subtracting the time spent active after the attack from the time spent active before the attack.

We used simple regressions (package: stats; function: lm) to examine the relationship between each of the measured behaviours, sex and reproductive status, and snout-vent length (SVL). We used each behaviour (percent area explored, latency to leave refuge, defense score, and difference in time active before and after predator attack) as dependent variables, and sex and reproductive status, SVL, and their interaction as independent variables.

We used paired *t* tests in R (package: stats; function: *t* test) to assess the consistency between the two sets of behavioural trials (e.g., latency to emerge in trial A versus trial B conducted 2 days later).

We examined the correlations between the five measured variables using Spearman's rank correlations (package: stats; function: cor.test; R Core Team 2013). We used a Spearman's rank correlation because our variables were not measured on the same scale, and Spearman's correlations are widely used in behavioural studies (e.g., Bell and Sih 2007; Höjesjö et al. 2011; Nyqvist et al. 2013).

Consistency trials

To further test for individual consistency, we conducted a separate set of trials using one behavioural test multiple times, over a longer duration. We put another group of snakes through the defensive behaviour trial every other day for 10 days following a 1-day acclimation period, for a total of 5 trials per snake. We calculated the repeatability of the individual defense scores as the percent measurement error (ME; Yezerinac et al. 1992). A ME of 0 % represents perfect repeatability of a measurement, whereas a ME of 100 % represents within individual variance that is equal to the among individual variance.

Results

Behavioural trials were conducted on a sample of 42 snakes, 22 of which were males (SVL range = 222–617 mm), 21 were non-gravid females (SVL range = 236–571 mm), and 9 were gravid females (SVL range = 467–641 mm). The consistency trials were conducted on a sample of 19 snakes, 13 of which were males (SVL range = 318–517 mm) and 6 were non-gravid females (SVL range = 316–582 mm).

Snakes that explored more of the terrarium also spent more time exploring ($\rho = 0.71$, $p < 0.001$), but no other pairs of behaviours were correlated (Fig. 2). We eliminated the time spent exploring variable from the subsequent analyses because percentage explored and time spent exploring are strongly correlated and most likely represent the same behaviour.

The relationship between percentage of area explored and body size differed between males and gravid females ($t = 2.49$, $p = 0.02$; Fig. 3), but did not differ between gravid and non-gravid females ($t = 1.93$, $p = 0.06$) or between non-gravid females and males ($t = 1.09$, $p = 0.28$). Longer females (both gravid and non-gravid, but the relationship was stronger in gravid females) explored less than shorter females, whereas longer males explored more than shorter males (model $R^2 = 0.26$, $p = 0.05$). Latency to emerge was not related to body size ($t = 1.48$, $p = 0.15$) or to sex and reproductive status ($t = 0.92$, $p = 0.36$). On the other hand, males ($t = 3.07$, $p < 0.01$; Fig. 4) and non-gravid females ($t = 2.52$, $p = 0.02$) were more likely to flee (lower defense score) than gravid females when attacked by a mock predator claw; males and non-gravid females did not differ significantly in their defense scores ($t = 0.36$, $p = 0.72$; model $R^2 = 0.26$, $p < 0.01$). Males ($t = 2.46$, $p = 0.02$; Fig. 5) and non-gravid females ($t = 2.39$, $p = 0.02$) were more

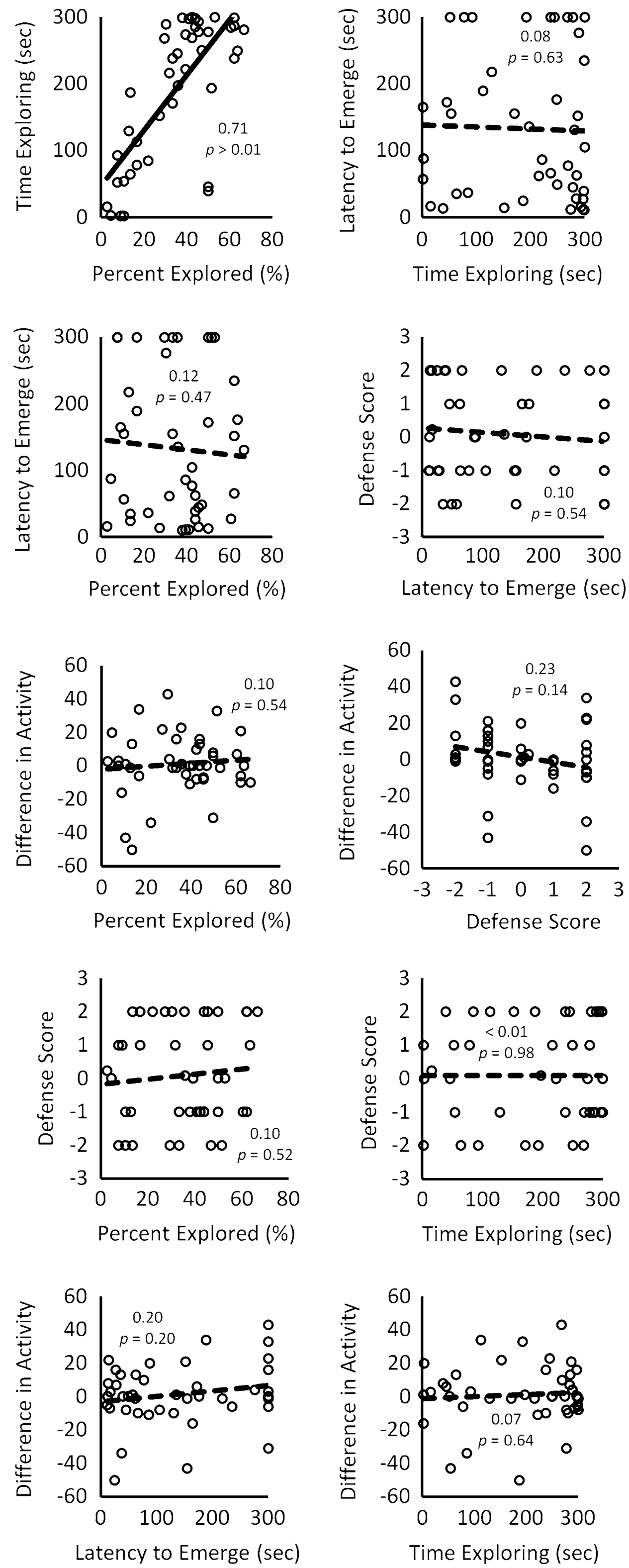

Fig. 2 Correlations between the five measured variables representing exploration, boldness, and defensive behaviour in eastern garter snakes. *Each plot* shows a Pearson's correlation coefficient along with a *p* value for the correlation below it

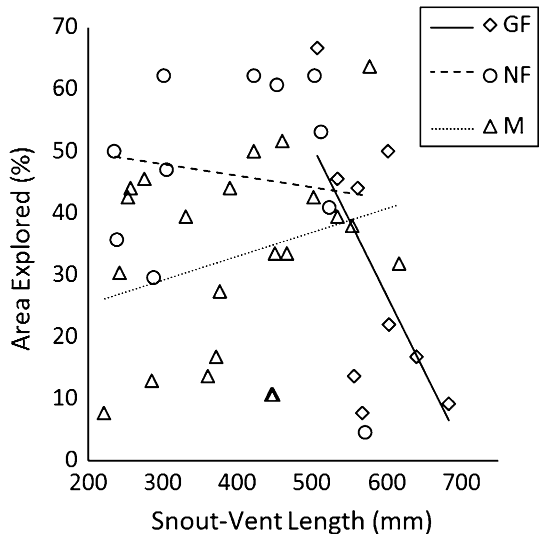

Fig. 3 Percent area explored in a novel arena varies by body size (snout-vent length) and reproductive status [*GF* gravid females ($n = 9$), *NF* non-gravid females ($n = 11$), and *M* males ($n = 22$)] in eastern garter snakes

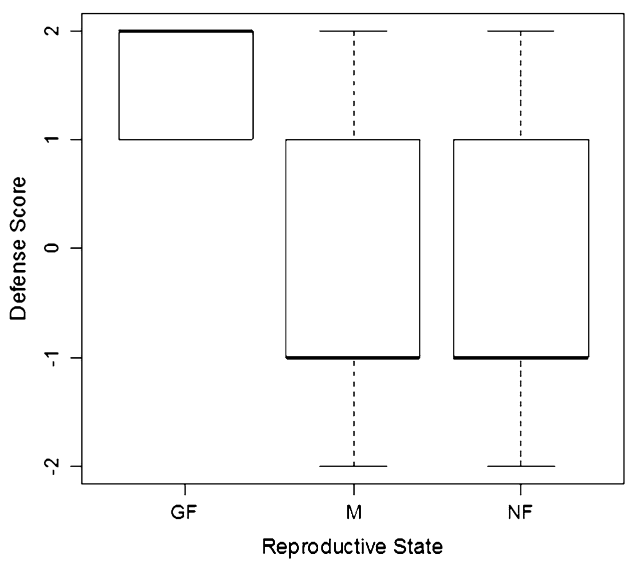

Fig. 4 Defense score varies with reproductive state [*GF* gravid females ($n = 9$), *NF* non-gravid females ($n = 11$), and males ($n = 22$)] in eastern garter snakes. *Boxes* represent the interquartile range and the *bold horizontal lines* within the box represent the median. Whiskers represent the minimum and maximum values

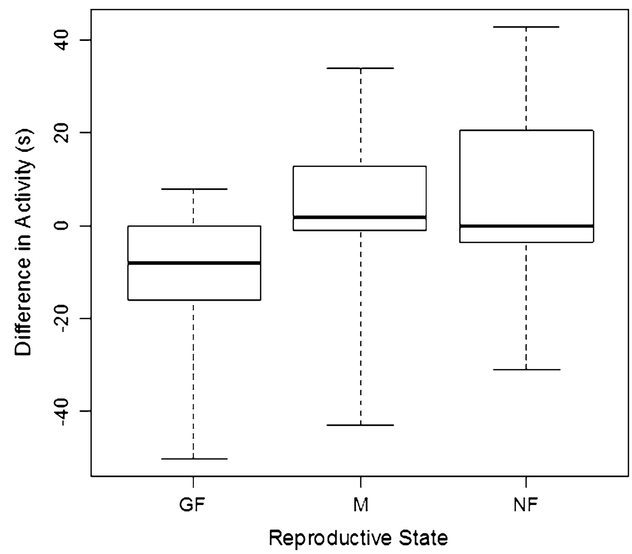

Fig. 5 Difference in activity before and after a model predator attack varies with reproductive state [*GF* gravid females ($n = 9$), *NF* non-gravid females ($n = 11$), and *M* males ($n = 22$)] in eastern garter snakes. *Boxes* represent the interquartile range and the *bold horizontal lines* within the box represent the median. *Whiskers* represent the minimum and maximum values

Table 1 Exploratory, boldness, and defensive behaviour in eastern garter snakes. Paired t-tests between the 5 measured behavioural variables show that they are consistent between trials. $df = 41$. Trial A refers to the mean ± S.E. For that variable in the first trial, and Trial B refers to the same in the second trial

Variable	Trial A	Trial B	t value	p value
Percentage explored	36 ± 3	35 ± 3	0.17	0.87
Time spent exploring	198 ± 16	195 ± 17	0.13	0.90
Latency to emerge	136 ± 17	143 ± 18	0.52	0.61
Defense score	0.1 ± 0.2	0.2 ± 0.2	0.37	0.71
Difference in activity	1 ± 3	7 ± 4	1.42	0.16

active after the predator attack than before the attack, whereas gravid females were more active before the attack; males and non-gravid females did not differ significantly in their difference in activity before and after the attack ($t = 0.27$, $p = 0.79$; model $R^2 = 0.16$, $p = 0.04$).

Amongst the 42 snakes that underwent the 3 behavioural trials twice, behaviour was consistent between the first and second trial (Table 1). Amongst the 19 snakes that underwent the defensive behavioural trial 5 times, the defense scores were not significantly different across all five trials ($F = 0.644$, $p = 0.633$). While taking into account within and among individual variation, defense score was repeatable through time (ME = 65.9 %).

Discussion

Male, non-gravid female, and gravid female garter snakes differed in how size affected exploratory behaviour, as well as in their defensive behaviour. Variation in exploration as a function of body size suggests that different intensities of exploration could be favoured at different sizes, and these differences could be explained by varying levels of hormones (e.g., Bell and Stamps 2004; Dammhahn and

Almeling 2012) associated with maturation and reproduction. The variation in exploration between small males and large males may be related to the fact that smaller snakes are targeted more often by avian predators (Shine et al. 2001). Therefore, smaller males could be more reluctant to expose themselves for exploration and foraging. Moreover, gravid females are more sedentary than non-gravid females (Charland and Gregory 1995), presumably due to reduced locomotory ability (Shine 1980; Kissner et al. 1997). We observed a sharp decrease in the area explored as a function of body size in gravid females.

Male and non-gravid female garter snakes were more likely to flee than gravid females. A similar finding was obtained by Shine et al. (2000): male red-sided garter snakes fled more often than females. Although Shine et al. (2000) did not find an effect of gravidity in females, this may be because their experiment was conducted during spring emergence when females are not yet gravid. This difference between males and females could be a result of differences in testosterone levels. King (2002) found that female garter snakes struck more frequently than males, but when injected with testosterone, struck less frequently. Because we found that non-gravid females were similar to males in their defensive behaviours, however, testosterone may not be the sole factor underlying these patterns. Furthermore, gravid females also may be more reluctant to flee due to locomotory costs associated with carrying developing young (Shine 1980; Kissner et al. 1997). Our results support this hypothesis: gravid females in our experiment were more defensive and less likely to flee than non-gravid females. Brodie (1989) also suggested that altered defensive behaviour may not only be a result of the decrease in locomotory function, but also a result of changes in physiology during pregnancy.

Gravid females were more defensive than non-gravid females and males and, in addition, gravid females decreased activity more following a simulated predator attack than males and non-gravid females. There were notable behavioural differences during the simulated predatory attack. Males and non-gravid females tended to flee during the predator attack (thus augmenting activity), whereas gravid females tended to go into the ready-to-strike S-pose during the predator attack. It is reassuring that, in our experiment, these behavioural differences were reflected in both the activity scores and the defensive scores.

An important assumption behind examining behavioural traits is that they are consistent through time (Jacobs 2009), but few studies actually test for repeatability. The behavioural traits that we measured in eastern garter snakes were consistent through time. This is an important assumption to test because we could not conclude to the presence of a personality in the absence of individual consistency. It has been found that behaviour of ectotherms may be less repeatable than that of endotherms, due to their stronger responsiveness to environmental factors (Bell et al. 2009), but our results clearly demonstrate that snake behavioural traits can be repeatable.

Even though the behavioural traits of garter snakes was repeatable and thus indicates that garter snakes may have personalities, we found no evidence for the presence of a behavioural syndrome. Either the exploratory and defensive behaviour axes are unlinked in garter snakes and the boldness axis is not present in garter snakes, or our methodology was inadequate to measure these behavioural traits accurately. It is also possible that these behavioural traits are linked to other behavioural axes that we did not investigate here.

Trap bias can impact results of behavioural studies if trapping selects for a particular behavioural phenotype (Carter et al. 2012). For instance, bold individuals are most likely to enter a novel object, and therefore trapped individuals may be bolder than the mean for the population. By catching snakes by hand, we avoided this potential issue. It is still possible, however, that the snakes we caught were more exploratory or bolder and thus more likely to be captured. Another potential limitation to consider is whether behavioural assays conducted in captivity reflect phenotypes in the wild (Biro 2012). Snakes were allowed a one-day acclimation period to relieve capture stress, but acclimation may differ between individuals (Biro 2012). The suggestion to overcome this limitation by measuring each behaviour 10 times per individual (Biro 2012) is not ideal because of possible habituation effects (Edwards et al. 2013). Comfortingly, our results on the effect of phenotype on behaviour mirror those of Shine et al. (2000) on red-sided garter snakes, and their results were obtained under natural conditions.

Another limitation that must be considered is that by using wild caught snakes, we cannot control for prior experience that may affect behaviour during our trials. To minimize the impact of this potential confounder, we used a large sample of snakes so that the chances of a systematic confounding between prior experience and our variables of interest (sex, SVL) were small. Furthermore, Weldon and Burghardt (1979) found that prior experience with predators did not affect defensive response in crotaline snakes. Other behavioural studies using amphibians and reptiles also show no effect of experience (Bachmann 1984; Burger et al. 1991; Sih and Kats 1994).

In summary, we found individual consistency in behavioural traits and effects of size and sex and reproductive status on exploratory and defensive behaviours. Our results pave the way for more detailed investigations of how intrinsic factors can be used as predictors of exploratory, boldness, and defensive behaviours, and whether snakes exhibit personalities and behavioural syndromes. By connecting variation in behaviour to phenotypic traits, we can better understand what drives behavioural variation.

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