



Snake personality: Differential effects of development and social experience

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Abstract

Personality traits are consistent across time and context, by definition, but the expression of personality in behavior is affected by both developmental and environmental factors. Little is known about the long-term effects such factors have on stability and change in personality traits, especially in understudied species. Research on species with different ecologies than more commonly studied mammals and birds can provide valuable insight into environmental influences on the stability of personality. We performed two experiments to investigate boldness and sociability in Eastern gartersnakes (*Thamnophis sirtalis*) in the laboratory. We first examined the developmental trajectories of these personality traits across the first 8 months of snakes' lives. Next, we tested whether one month of social isolation could drive changes in either trait. Boldness and sociability displayed two different patterns of consistency and change. Across early development, gartersnakes display a shy–social correlation and are consistent in their boldness but not their sociability. Social isolation in contrast leads to changes in boldness for some snakes, while sociability remains consistent. These patterns of change are moderated by both sex and weight and may serve to drive male-biased dispersal of larger snakes early in life, and their re-settlement later on. In females, trait flexibility may help to balance the benefits of socializing while minimizing competition over food. These results highlight how the dynamics of personality development and stability may vary across taxa, driven by differences in ecology.

Significance statement

How personality traits are expressed in response to developmental changes and environmental pressures is an active area of research. Many studies of personality in non-human animals look for consistency in personality across short periods of time, and in response to moderate environmental change—methods that may miss important developmental changes. Here, we tested for changes in gartersnake personality during the first 8 months of development—an important time period for dispersal and resettlement, and in response to a change in their social environment. We found evidence that the expression of personality is trait-specific. For gartersnakes, boldness is consistent across time but changes in response to the social environment, whereas sociability displays the opposite pattern. These patterns of personality expression are different from more typically studied laboratory animals and emphasize the importance of studying species that experience a variety of selective pressures and social environments.

Keywords Personality · Behavioral Syndromes · Isolation · Dispersal · Sociability · Boldness Development

Introduction

Personality traits are behavioral biases that differ across individuals and can be identified by the repeatability or consistency of the relevant behavior across time and/or context (Stamps and Groothuis 2010). For example, a social individual is one that consistently displays a stronger preference than other members of the population for interacting with conspecifics (Gartland et al. 2022). Although the context in which a behavior is assayed will likely modulate how

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the behavior is displayed (e.g., a stressful situation might increase sociability in all individuals; Owens et al. 2012), the repeatability of personality will be displayed in the consistency of the *relative* behaviors across a population. A behavior is therefore considered reflective of a personality trait when between-individual variance in its expression is high compared to the within-individual variance (Bell et al. 2009). In other words, individuals behave differently from each other but similarly to themselves across time and/or contexts. Personality traits often correlate with each other, clustering into what are sometimes termed behavioral syndromes (Sih et al. 2004). How traits cluster differs across species: For example, bighorn sheep (*Ovis canadensis*) display a docility–boldness syndrome (Réale et al. 2009), guppies (*Poecilia reticulata*) display a boldness–sociability syndrome (Croft et al. 2009), and great tits (*Parus major*) display an exploration–aggression syndrome (Groothuis and Carere 2005).

The expression of personality traits in observable behavior results from an interaction between an internal bias and external (environmental) factors. For example, the intensity of foraging behaviors may be affected by local resource distributions, and this will modulate the expression of innate individual differences. What we measure in studies of personality is the outcome of this interaction. Thus, despite consistency being a key hallmark of personality traits, it is worthwhile to also explore how external factors alter the expression of these traits in individual behaviors. Here, we explore plasticity in behavior across two environmental dimensions: developmental time and the social environment. We study Eastern gartersnakes (*Thamnophis sirtalis*), a species whose ecology enforces several developmental transitions with potentially differing personality requirements, and whose social structures are complex and variable (Skinner and Miller 2020, 2022). Though personalities have been documented in some reptiles (*Lacerta vivipara*, Cote and Clobert 2007; *Terrapene carolina*, Carlson and Tetzlaff 2020; and *Thamnophis sirtalis*, Skinner and Miller 2020), behavioral consistency across development has not been examined in reptile species to the extent that it has been in birds, fishes and mammals (Waters et al. 2017).

Eastern gartersnakes are found across North America (Rossman et al. 1996). The snakes tested in this experiment were from Ontario, Canada. As such, they experienced cold winters and would aggregate to hibernate during the colder months and mate in groups after emerging from hibernation in the spring (Reichenbach 1983; Rossman et al. 1996). Eastern gartersnakes give birth to fully independent babies during the summer months and do not provide parental care (Rossman et al. 1996). After dispersing from their natal sites, these baby snakes must eventually resettle and find a group for hibernation and mating (Rossman et al. 1996). Additionally, though little work has been done on gartersnake

dispersal, research on population gene flow in other species of snake has suggested that sex-biased dispersal—primarily of males—may occur in snakes (*Rhinoplocephalus nigrescens*; Keogh et al. 2006; *Stegonotus cucullatus*; Dubey et al. 2008). Thus, gartersnakes (especially males) might benefit from the ability to restructure their personality across their development to face the varying challenges of differential dispersal, resettlement and survival without parental care.

Personality and development

The requirement for personality traits to demonstrate consistency appears to be at odds with the inevitable changes in behavior that occur over the course of development (Cabrera et al. 2021). Developmental changes in personality often occur across sexual maturity (Cabrera et al. 2021), possibly due to the different selective pressures faced by adults and juveniles (Bell and Stamps 2004). Less work has focused on developmental plasticity across major life history events outside of maturation (Cabrera et al. 2021), such as dispersal and colonization (Cote and Clobert 2007; Howze et al. 2012). As personality differences play an important role in dispersal (Cote et al. 2010a, b), certain species may experience different pressures during and after dispersal and colonization that could select for plasticity over stability.

Numerous conflicting theoretical predictions have been made about how personality traits should change over time, such that they become more consistent (Stamps and Groothuis 2010; Sih et al. 2015), or less consistent (Bell et al. 2009; Stamps et al. 2018). For example, differences between individuals may decrease over time, as they conform to ecological demands and become more like each other (Carlson and Tetzlaff 2020), or they may increase over time as particular behaviors are reinforced by past successes (Sih et al. 2015). Measurements of repeatability that cross important developmental milestones are important for addressing such predictions (Stamps and Groothuis 2010; Cabrera et al. 2021).

One approach to the study of changes in personality across development is to explicitly address the relationship between the two sources of variance (between- and within-individual) across time (Kok et al. 2019; Carlson and Tetzlaff 2020). For example, individual Eastern box turtles (*Terrapene carolina*) act more consistently when older (a decrease in within-individual variance) but also act more like each other (a decrease in among-individual variance; Carlson and Tetzlaff 2020). Other research on long-term personality consistency has given conflicting results. Increased consistency across time has been found in lake frogs (*Rana ridibunda*; Wilson and Krause 2012), zebrafish (*Danio rerio*; Thomson et al. 2020), and in the northern common boa (*Boa imperator*; Šimková et al. 2017), whereas a decrease in consistency has been found in yellow-bellied

marmots (*Marmota flaviventris*; Petelle et al. 2013), sticklebacks (*Gasterosteus aculeatus*; Bell and Stamps 2004) and dumpling squid (*Euprymna tasmanica*; Sinn et al. 2008).

Developmental analyses of behavior can also help elucidate how correlations between behaviors, often referred to as behavioral syndromes (Sih et al. 2004), change. Although research on behavioral syndromes in reptiles is rare (Conrad et al. 2011), a negative correlation between prey acceptance and catch latency has been found in the Northern common boa (Šimková et al. 2017), and a negative correlation between sociability and boldness has been observed in juvenile gartersnakes (Skinner and Miller 2020). Although correlations in personality traits suggest limits to plasticity (Sih et al. 2004), major life-stage transitions could facilitate behavioral plasticity by decoupling traits (Bell and Stamps 2004). This decoupling of traits during major life-stage transitions may happen when divergent pressures on traits occur due to different environmental pressures (Bell and Stamps 2004). A decoupling of traits across life stages has been found in the Navarro River population of three-spined sticklebacks. In these individuals, a boldness–aggression–activity syndrome was found to weaken across the transition to adulthood but strengthened again when the fish were mature (Bell and Stamps 2004).

Here, we assayed two frequently studied personality traits—boldness and sociability—in Eastern gartersnakes every two months for the first 8 months of their lives, to track developmental changes in the expression of their personalities.

Personality and the social environment

Along with ontogenetic shifts in personality, the social environment may also play an important role in determining continuity and change in the expression of personality traits. For example, many species have been shown to alter their behavior—in ways that may depend on their personalities—when alone or in a group (e.g., Guayasamin et al. 2017; Skinner and Miller 2020). In humans, the impact of the social environment on personality is well documented and trait plasticity in response to social environments has been recorded even in late adulthood (Lodi-Smith and Roberts 2012). Stable environments can generate stable personalities (Roberts and Caspi 2003), whereas changes to the environment can encourage personality change (Ardelt 2000). In non-human animals, accumulating evidence suggests that changes to the social environment encourage behavioral plasticity (Riley et al. 2018; Munson et al. 2021; Skinner and Miller 2022), whereas animals in consistent social environments demonstrate fairly consistent social behavior (Jacoby et al. 2014; Skinner and Miller 2022).

In order to test if stability in social grouping could partially explain patterns of personality consistency in Eastern

gartersnakes, we performed a second experiment in which we isolated a subset of the snakes from their long-term social groups for one month, before assaying their personalities one more time. As gartersnakes are relatively independent, but aggregate seasonally for mating and hibernation, the transition between group-living and isolation should be relatively common in this species and may have an effect on the expression of their personalities in behavior.

Experiment 1

In this experiment, we examined repeatability in boldness and sociability during the first 8 months of snakes' lives. We also looked for consistency across development in the boldness–sociability correlation that has been previously identified in this species (Skinner and Miller 2020). As gartersnakes must balance social attraction with the need for dispersal during their early development, we hypothesized that they would demonstrate plasticity over time in their sociability. More specifically, we predicted that differences in sociability would decrease as individuals shifted their behavior to conform to developmental needs. In contrast, we hypothesized that boldness would be consistent across development, similar to what has been found in lizards (Payne et al. 2021) and turtles (Carlson and Tetzlaff 2020). Additionally, because life-stage transitions in snakes depend on size (Shine and Charnov 1992), rather than directly on age, and (as noted above) the ecology of the two sexes varies, we hypothesized that both sex and size would have an effect on the expression of both boldness and sociability. Based on recent literature, we used weight as a proxy for size (Feldman and Meiri 2013). Though there is clear evidence for genetic effects on the expression of personality (Lane and van Oers 2017), we were unable to determine relatedness in our subjects and so could not address the extent to which within and between clutch differences in personality contribute to overall variability in snake personality.

Methods

Subjects and housing

Subjects were 52 Eastern gartersnakes (25 M/27 F) purchased from local breeders and reptile zoos. The snakes were neonates when acquired. Snakes were housed in same-sex groups of 2–6, in 20-gallon glass aquariums (51 × 26 × 30.5 cm) with mesh lids (during tests 1–4) or in plastic boxes with mesh lids (46 × 31 × 17 cm; during test 5). The snakes had access to belly heat (30° C) provided by heat tape (THGHeat) placed under their tanks. Shelters were placed on both the cool and warm sides of the tank. Tanks were lined with paper towels (tests 1–4) or had cypress

mulch bedding (Zoo Med Laboratories Forest Floor Bedding). Clean water was provided daily. The housing room was maintained at 22° C with a 12 h light cycle (lights on at 7 am). The snakes were fed a diet of chopped nightcrawlers (Pagonis Live Bait, Toronto) with vitamin supplements (*Zilla*) as needed.

Apparatus

The boldness assay was conducted in a Styrofoam box measuring 40.6 cm × 45.7 cm × 33 cm high (see Fig. S1). There was one black plastic reptile shelter (14 cm × 10.2 cm × 5 cm high; Cornel's World), identical to the shelter in the home tank, placed against the center of one long wall. Sociability assays were conducted in a 54.6 cm square testing arena made from 24 cm high PVC boards. The bottom of the arena was lined with butcher paper. Two black plastic reptile shelters, identical to those used in the boldness assay, were placed at 45 degree angles in the far corners opposite to the start location (see Fig. S1). One shelter was designated the Stimulus Shelter and the other one the Control Shelter. The stimulus was created by extracting skin lipids from shed juvenile gartersnake skins, using the process described in Skinner and Miller (2020). The skin lipid mixture was produced from sheds taken from both female and male snakes. For each sociability assay, 0.25 ml of the lipid solution was dripped onto a piece of filter paper, which was taped to the floor at the entrance to the Stimulus Shelter. As a control, 0.25 ml of dichloromethane (the solvent used in our lipid extraction procedure) was placed on a second piece of filter paper and placed at the entrance to the Control Shelter. The filter papers were both allowed to dry for at least 15 min before being placed in the arena, to allow the dichloromethane to evaporate. The side on which the Stimulus Shelter was placed was pseudorandomized across trials.

We placed two sociability and two boldness assay arenas beside each other, so that four snakes could be run at a time. Each arena was covered with a clear sheet of acrylic to prevent escapes. All trials were recorded using a camcorder (Panasonic HC-V700) mounted above the arena.

Procedure

The procedures we used closely followed the methods of Skinner and Miller (2020). Snakes were individually marked with 1–3 colored dots on their head with non-toxic nail polish (Adrienne K) prior to each experiment. Snakes were re-marked after shedding and closely monitored to ensure consistency of the dot pattern identity. Snakes were tested individually and were not tested on days when they were fed (Mondays and Thursdays). Each snake completed their assays within two weeks and did not complete more than one assay in a day. The snakes were tested 4 times over the

course of a year (labeled T1–T4), with an approximately 2-month interval between each test; snakes were approximately 2 months old at the time of the first test. All snakes were tested at each time point. Snakes were weighed each time they were tested (see Table S1). We attempted to avoid testing snakes during shedding, but this was not always possible due to the timed nature of the experiment.

To begin each assay, snakes were gently removed from their home tanks and placed in a bucket with a clean paper towel in it. Buckets were covered with clear plastic lids to prevent escapes. The two snakes to be run on the boldness assay were placed in one bucket and the two snakes to be run in the sociability assay in another. Snakes were transported in the buckets to the testing room and spent no more than 5 min in the buckets before being placed into the arenas.

For the boldness assay, snakes were placed with their heads close to the entrance of the shelter and allowed to slither into the shelter to start the trial. The proportion of the session that the snake spent outside of the shelter was recorded as a measure of boldness (Jolles et al. 2016; Koenig and Ousterhout 2018; Tang and Fu 2020). For the sociability assay, snakes were placed under a clear plastic container (11.43 cm diameter × 8.25 cm) in the arena, in the center of the wall opposite both shelters, and allowed to habituate for 90 s. Snakes were then released into the arena by raising the plastic container. The proportion of the session that the snake spent in or on the Stimulus Shelter as a proportion of the total time spent in or on either shelter was recorded as a measure of preference for the social stimulus. Both sociability and boldness assays lasted 20 min.

Analysis

Videos were coded manually, using a custom ethologger program, by clicking on which area of the enclosure the snake was in at each point in the session. The snake's location was determined by the position of its head. We used 2 zones for coding the boldness assay: inside the shelter and over half of the body outside the shelter. We used 3 zones in coding the sociability assays: in or on the Stimulus Shelter, in or on the Control Shelter, and away from both shelters. To minimize bias, blinded methods were used when all behavioral data were recorded and analyzed. Data were analyzed using *Mathematica* (v.12.0, Wolfram Research) and R (R Core Team 2020).

Statistical analyses were performed in R (v4.02, R Core Team 2020). We used data transformations on data with skewed distributions. We used arcsine transformations for the boldness and sociability data. For analyses of the effect of weight on personality, we fitted mixed-effect linear models using the *lme4* package. As our data contained repeated measurements of the same individuals, all the models contained random intercepts for 'individual.' We fitted models

by maximum likelihood ('ML') in order to compare models using the ANOVA function. As models with weight as a fixed effect were a better fit than models with time in all analyses, we progressively added weight followed by a weight-by-sex interaction to our models and chose preferred models based on the lowest AIC. Models within two units of the lowest AIC were considered equal (Cavanaugh and Neath 2019). We then refit preferred models by restricted maximum likelihood (REML). To test the overall effects for each factor, we used the ANOVA function on the best-fit models.

To estimate repeatability, we used the function rptR with 1000 permutations per model. In addition to providing repeatability estimates, the rptR function provides estimates of among-individual and within-individual variance (Nakagawa and Schielzeth 2010). We included individual as a random effect and time as a fixed effect in these models, and we therefore report the R value adjusted for time ($R_{adj|time}$). We note that as we tested each snake once at each time point, within-individual variability occurs across extended time points (2 months apart).

Results

We tested for a boldness–sociability correlation across all time points and within each time point. Across time points, we found a negative relationship between these traits (Fig. S2; $\beta = -0.45$, $t(188.7) = -3.75$, $p < 0.001$). The inclusion of sex did not improve this model's fit. We examined the correlation at each time point for each sex. We found that boldness and sociability were negatively correlated at T1 in males (aged 2 months; $\rho(24) = -0.51$,

$p = 0.01$) but not in females ($\rho(24) = -0.25$, $p = 0.22$). There were no significant correlations at any other time point (Table S2; all $r < 0.31$, all $p > 0.13$).

We found that changes in both boldness and sociability across time are dependent on weight (which serves as a proxy for age) and varied by sex. There was a significant effect of weight on boldness, such that larger snakes tended to be bolder (Fig. 1A; $F(1, 177) = 8.69$, $p = 0.004$). Male and female snakes did not differ in boldness ($F(1, 153.4) = 0.02$, $p = 0.89$), and the interaction between weight and sex was not significant ($F(1, 177.9) = 2.38$, $p = 0.13$). For sociability, there was a significant interaction between sex and weight (Fig. 1B; $F(1, 190.4) = 8.28$, $p = 0.005$), such that larger female snakes tended to be more social, whereas larger male snakes were less social. There was a significant main effect of sex ($F(1, 164.51) = 8.84$, $p = 0.003$), with male snakes tending to be more social than females, and no main effect of weight ($F(1, 190.4) = 0.03$, $p = 0.87$; all main effects in the sociability analysis should be treated with caution due to the interaction effect). In other words, we found that boldness increased across development in both males and females, but sociability decreased in males and increased in females.

We next examined the repeatability of boldness and sociability across development in detail (Table 1). Boldness was consistent across development, with low variance both between and within individuals, which remained consistent across all pairs of time points. Sociability, on the other hand, had low consistency across development. Snakes displayed consistency in their sociability between 2 and 4 months of age, but not between any other ages. This effect was driven by comparatively high variance within individuals and

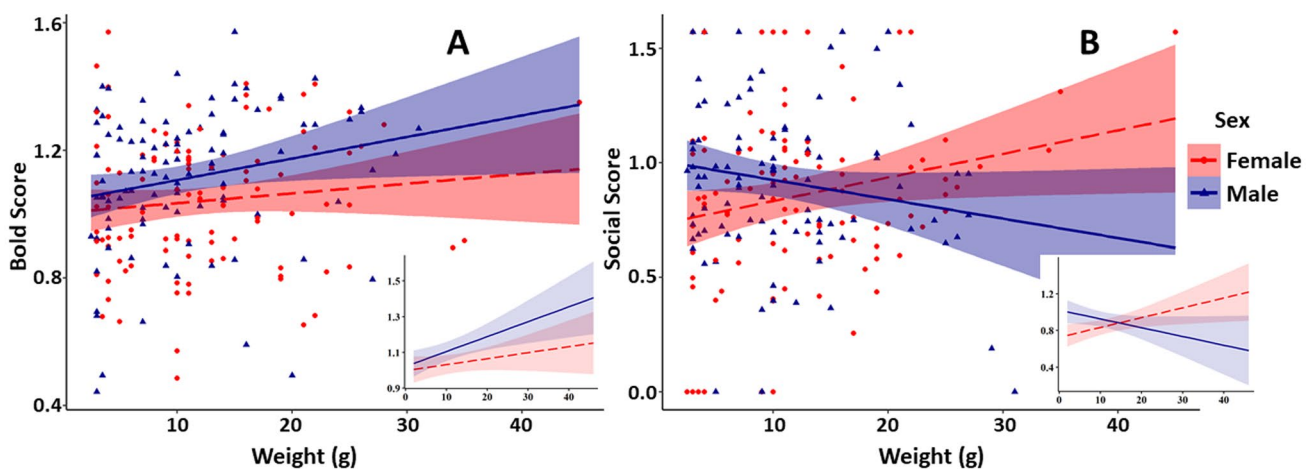


Fig. 1 Boldness (A) and sociability (B) scores as a function of weight. Regression lines with 95% confidence intervals (CI) and raw transformed data are shown separately for male (blue triangles, solid lines) and female (red circles, dashed lines) snakes. The inset to each

panel shows the LMM prediction (lines) with 95% CI (shaded areas) for the model. Inset axes are the same as those for the main panels. Removal of outlying observations based on Cook's distance did not change the statistical relationships

Table 1 Repeatability (first column) and variance decomposition for boldness (top half of the table) and sociability (bottom half) across development. The first row of each half gives the overall values, followed by comparisons of each consecutive pair of tests. The first column gives the adjusted R (R_{adj}) and 95% confidence intervals (in square brackets). Significant values (whose 95% CI does not include 0) are bolded. The other two columns give the mean between- or within-individual variance \pm SD

	Repeatability (R_{adj} [95% CI])	Between-individual variance	Within-individual variance
Boldness	0.21 [0.08, 0.39]	0.009 \pm 0.095	0.041 \pm 0.203
T1 vs T2	0.28 [0.21, 0.52]	0.013 \pm 0.112	0.033 \pm 0.182
T2 vs T3	0.46 [0.22, 0.66]	0.018 \pm 0.133	0.021 \pm 0.145
T3 vs T4	0.28 [0.01, 0.52]	0.014 \pm 0.116	0.035 \pm 0.187
T4 vs Expt. 2	0.08 [0.00, 0.51]	0.005 \pm 0.069	0.057 \pm 0.239
Sociability	0.04 [0.00, 0.17]	0.005 \pm 0.073	0.110 \pm 0.332
T1 vs T2	0.37 [0.09, 0.59]	0.064 \pm 0.253	0.089 \pm 0.298
T2 vs T3	0.08 [0.00, 0.28]	0.000 \pm 0.000	0.122 \pm 0.350
T3 vs T4	0.09 [0.00, 0.29]	0.000 \pm 0.000	0.123 \pm 0.351
T4 vs Expt. 2	0.22 [0.00, 0.64]	0.021 \pm 0.146	0.08 \pm 0.278

decreasing variance between individuals (Fig. S3). In other words, during their early development, snakes demonstrated consistency in boldness but not their sociability.

Discussion

In this experiment, we tested for changes in personality traits and a boldness–sociability behavioral syndrome during the first 8 months of development in Eastern gartersnakes. We found a correlation between boldness and sociability that was much stronger in young male snakes than both females and older snakes. Additionally, we found that boldness and sociability have different developmental trajectories: Boldness scores were significantly repeatable throughout, whereas sociability scores were only repeatable when the snakes were young (up to 4 months of age), and sociability increased with weight in females and decreased in males, whereas boldness increased across development in both sexes.

Boldness–sociability correlation

Across the first 8 months of their lives, gartersnakes that are bolder tend to be less social. This is consistent with previous findings showing a negative correlation between boldness and sociability in this species (Skinner and Miller 2020). Similar correlations have also been found in mammals (*Ovis aries*; Sibbald et al. 2009), fish (*Gasterosteus aculeatus*; Ward et al. 2004) and birds (*Parus major*; Snijders et al. 2016). This negative relationship may represent a trade-off

between the benefits of sociability—such as dilution of predation risk—and the benefits of resource access without competition. As gartersnakes often socialize while hiding (Skinner and Miller 2020) and cannot share food (Yeager and Burghardt 1991), this is a likely explanation for our results. The strongest negative correlation was present in male snakes at \sim 2 months of age, and the relationship weakened as the snakes aged. As gartersnakes are completely independent at birth and disperse shortly after, the presence of a strong shy–social correlation in young male snakes may drive male-biased dispersal. Boldness has been shown to influence dispersal patterns in a range of taxa (mammals: *Marmota flaviventris*, Petelle et al. 2013; fish: *Rivulus hartii*, Fraser et al. 2001; and birds: *Parus major*, Dingemanse et al. 2003). In reptiles, common house lizards (*Lacerta vivipara*) that are non-social are more likely to disperse from areas with more conspecifics (Cote and Clobert 2007). We therefore propose the following dynamic in young male gartersnakes: The negative correlation between boldness and sociability pushes the boldest, least social males away from their natal groups and facilitates dispersal; the weakening of this correlation over time allows for the eventual resettlement of those males in new areas.

Stability and change across development

We found that boldness remained consistent over development, while sociability changed. The stability we observed in boldness was the result of low between-individual and within-individual variability. In other words, the snakes in our study did not change much in their boldness over time but maintained their individual differences. Though we only followed their development for the first 8 months of life, it seems likely that the trade-offs that are selected for individual differences in boldness are important throughout a snakes' lifetime. For gartersnakes, boldness during development is most likely a balance between sheltering for safety and resource acquisition through foraging. Boldness was found to be consistent in the long-lived sleepy lizard across a 6-year field study (*Tiliqua rugosa*; Payne et al. 2021), and a long-term analysis of boldness traits in the northern common boa found that the snakes maintained rank order concordance across development, even though mean levels changed (*B. imperator*; Šimková et al. 2017). Though these results suggest that consistency rather than plasticity in boldness may be the norm in reptiles, future research should determine to what extent boldness expression changes during periods of vulnerability such as pregnancy or ecdysis.

In contrast to boldness, we found that sociability was repeatable across our first two tests (up to 4 months of age) but not thereafter. This effect was the result of a sharp decrease in between-individual but not within-individual variance. In other words, snakes became more similar to

each other in sociability as they aged. Such canalization of behavior is predicted when survival pressures push individuals toward the same particularly adaptive behaviors (Bell et al. 2009; Stamps et al. 2018). This has been found to influence repeatability estimates in some species (*Kryptolebias marmoratus*; Edenbrow and Croft 2012; *Alexandrium fundyense*; Wohlrab et al. 2017). In our case, the canalization of social behavior may be the result of a post-dispersal restructuring of social personality. This type of plasticity may be important for gartersnakes, as they are known to hibernate communally and are thought to follow conspecific scent trails to hibernation sites (Costanza 1989). Periods of uniformly high sociability may facilitate such communal hibernation. It should be noted that canalization did not eliminate variability in social behavior. Instead, differences in social behavior between individuals decreased in relation to high within-individual variability. Alternatively, standard social housing conditions in the laboratory may have reduced differences in social attraction (but see Experiment 2).

Proximal causes of behavioral change

Both boldness and sociability were affected by weight, but in different ways. Weight has important implications for garter-snake reproduction, as size dictates the onset of sexual maturity in snakes (Shine and Charnov 1992). Additionally, larger female snakes tend to have larger clutches (Fitch 1985) and produce higher concentrations of a sex pheromones that makes them more desirable to male gartersnakes (LeMaster and Mason 2002). Although adult female gartersnakes tend to be larger than males, size is also important for males, with larger male snakes successfully mating more often and mating with larger females (Shine et al. 2000). Though data on the exact size that triggers transitions to maturity in Eastern gartersnakes are limited, we estimate that the transition to maturity occurs at approximately 29 g in males and 59 g in females (Parker and Plumber 1985; Feldman and Meiri 2013). These values suggest that some of the juvenile snakes in our experiment were approaching maturity by the end of the study, and two male snakes may have reached maturity (Table S1). This suggests that some of the changes in personality we observed might play a role in meeting the sex-specific challenges of adulthood (discussed below).

The more a snake weighed in our study, the bolder it tended to be, a result that aligns with most of the literature. For example, under controlled feeding conditions, larger neonate keelback snakes (*Tropidonophis mairii*) are bolder (Mayer et al. 2016). Research on fish (*Brachyrhaphis episcopi*) has suggested that higher boldness may in turn lead to increased weight gain by conferring a foraging advantage (Brown et al. 2007). In gartersnakes, some individuals may be born bigger and bolder (similar to keelback snakes; Mayer et al. 2016), which, in turn, facilitates differences

in resource acquisition, which maintain both body size and personality differences (Luttbeg and Sih 2010).

In contrast to boldness, the relationship between weight and sociability was more complex: Larger females tended to be more social than smaller females, but larger males tended to be less social than smaller males. As gartersnakes will fight over food (Yeager and Burghardt 1991), and female gartersnakes tend to be larger than males (Krause et al. 2003), females may have an advantage in food competition (Andrews 1982). As such, larger female snakes may be able to exploit the benefits of sociability while still out-competing smaller snakes for food. Males, on the other hand, may choose to be less social in order to minimize food competition and grow faster. Though limited, data on sociability and weight appear to show a variable relationship in other taxa as well. Male prairie voles (*Microtus ochrogaster*) with a high or low level of sociability had reduced mass compared to males with an intermediate level of sociability (Sabol et al. 2020). Similar to our findings, research on mosquitofish (*Gambusia affinis*) has found that sociability is related to weight, but the relationship is opposite to what we report here—heavier males tend to be more social than lighter males, and heavier females tend to be less social than lighter females (Cote et al. 2010b). Other species, such as greylag geese (*Anser anser*), show no link between sociability and body size (Kralj-Fišer et al. 2010). This variability across species suggests that some behavioral phenotypes may be more advantageous than others for meeting sex-specific challenges, and that this depends on the species' ecology.

Experiment 2

The social environment in which an individual makes choices can also have a large effect on the expression of personality traits in behavior. Consistent social environments may lead to consistent behavioral patterns, which might then be altered by sudden changes in the social environment, such as isolation (Munson et al. 2021). Research on social isolation has found that it can affect numerous behaviors, including social behavior (Hol et al. 1999), boldness (Jolles et al. 2016) and exploration (Liedtke et al. 2015). This research has often emphasized the effects of early social isolation on social behavior (Caine et al. 1983; Hol et al. 1999; Ryabushkina et al. 2020) and the importance of early developmental windows during which behavior can be altered by changes to the social environment (Einon and Morgan 1977; Faulk and Dolinoy 2011). However, social isolation can have noticeable effects on behavior even outside developmental windows (Jolles et al. 2016; Munson et al. 2021), possibly by reducing conformity pressures or by upsetting established social niches (Munson et al. 2021). We socially isolated a subset of our snakes—who had been living in small groups since birth—for one month, while leaving the remaining snakes

in their groups. We hypothesized that social isolation would change either boldness, sociability or both, though we had no a priori predictions of the directions of these changes.

Methods

Subjects, apparatus and procedures

Subjects were a subset of 18 juvenile Eastern gartersnakes (10 female, 8 male) from Experiment 1. All snakes were approximately 10 months of age at the start of the experiment. Nine snakes (5 female, 4 male) were isolated for one month, while the other 9 remained cohabitated in small groups of 3–4. The snakes were sex- and size-matched so that each isolated snake had a similar paired control that remained in social housing. Housing conditions were identical to those described for Experiment 1. Isolated snakes were kept in the same housing, but alone. No food competition was necessary for group-housed snakes as they all received sufficient food. However, despite ample food, gartersnakes will compete for food and food fights inevitably occur (Yeager and Burghardt 1991). We observed group-housed snakes, while they were feeding and carefully separated any snakes that latched onto the same piece of food. Enclosures were placed next to each other on a plastic rack and had mesh lids, so the isolated snakes could still detect the odors of the other snakes in the room and even see them through the walls of the enclosures (when not inside shelters). The testing arenas and procedures were identical to those in Experiment 1.

Analysis

Statistical analyses were performed on the changes in sociability and boldness scores from the pre-manipulation test (T4 in Experiment 1) to the post-manipulation test, denoted ΔSocial and ΔBold , respectively. Scores were calculated such that negative values indicate a decrease in sociability or boldness and were transformed using the *Gaussianize* function from the *LambertW* package in R. As sex and weight were important factors in the Experiment 1 data, a linear model was run on ΔSocial and ΔBold , with isolation status, weight and sex as fixed factors.

Data were coded as described in Experiment 1, but by a different researcher. The coder for Experiment 2 therefore also coded two videos (4 snakes per video) from Experiment 1. Inter-rater reliability was high between coders, with an intra-class correlation of 0.91.

Results

We found no effect of isolation on change in sociability, nor any interaction with sex or weight (ΔSocial model: $R^2=0.23$, $F(7,10)=0.45$, $p=0.85$). We did, however, find that isolating snakes had an effect on their boldness (ΔBold model: $R^2=0.71$, $F(7,10)=3.56$, $p=0.03$; Fig. 2). There was a significant three-way interaction between isolation status, sex and weight on ΔBold (Table 2; $F(1,10)=5.11$, $p=0.047$), such that weight had a larger effect on change in female boldness than it did on male boldness. In other words, isolation had little effect on male boldness, but lighter females decreased more in boldness as a result of isolation

Fig. 2 Change in boldness (ΔBold ; y-axis) in Experiment 2 by sex (panels), isolation status (isolated = pink dot-dash line; paired = solid green line) and weight (x-axis). Values below the black horizontal line indicate that snakes decreased in boldness between tests, whereas values above the line indicate that snakes increased in boldness. Dots show the raw data, and lines give model predictions

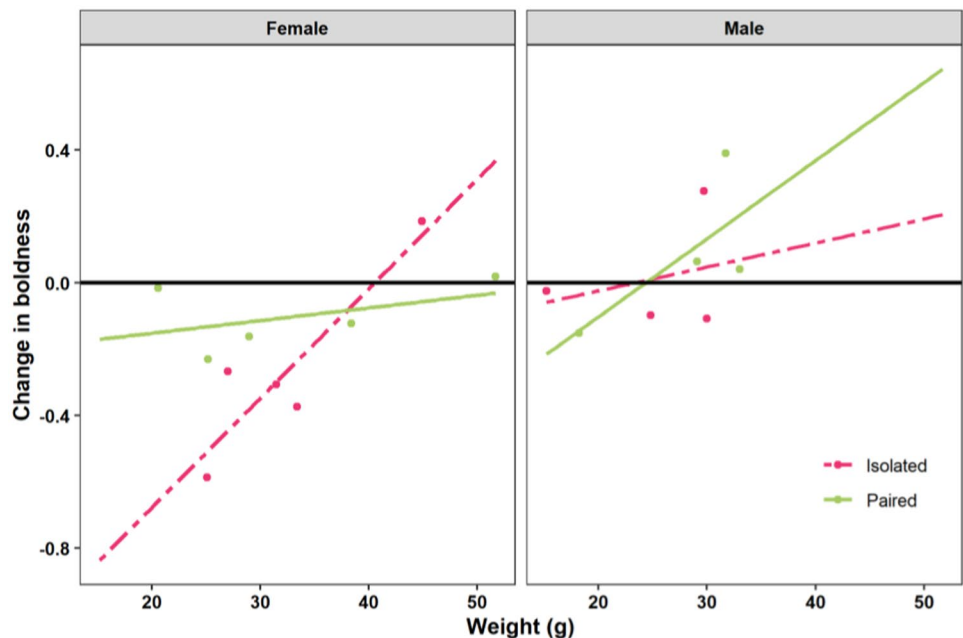


Table 2 Results of an ANOVA on the Δ Bold model. LL and UL represent the lower and upper limit of the partial η^2 confidence interval, respectively

Predictor	Sum of Squares	df	Mean Square	F	<i>p</i>	partial η^2	partial η^2 90% CI [LL, UL]
(Intercept)	0.37	1	0.37	13.79	0.004		
Isol	0.19	1	0.19	7.09	0.024	0.41	[0.04, 0.63]
Sex	0.21	1	0.21	7.91	0.018	0.44	[0.05, 0.65]
Weight	0.25	1	0.25	9.49	0.012	0.48	[0.08, 0.68]
Isol. x Sex	0.17	1	0.17	6.29	0.031	0.39	[0.02, 0.61]
Isol. x Weight	0.15	1	0.15	5.55	0.040	0.36	[0.01, 0.59]
Sex x Weight	0.10	1	0.10	3.90	0.077	0.27	[0.00, 0.54]
Isol. x Sex x Weight	0.14	1	0.14	5.11	0.047	0.34	[0.00, 0.58]
Error	0.27	10	0.03				

than heavier females. Due to the interaction effect, all other effects should be treated with caution (Table 2).

Discussion

In contrast with some previous research in reptiles (Ballen et al. 2014; Hoss et al. 2015; Riley et al. 2017), we found no effect of social isolation on sociability in juvenile Eastern gartersnakes. Research on tree skinks (*Egernia striolata*) has demonstrated that social isolation at an early age increases sociability. However, when pair-housed and isolated individuals were later housed together as adults, formerly isolated lizards adapted their social behavior to reflect their new social environment (Riley et al. 2018). The social plasticity demonstrated by tree skinks may be the result of a non-obligatory social system, in which social isolation is a natural part of development (Riley et al. 2018). In northern climates, gartersnakes must aggregate with conspecifics for hibernation and mating (Rossman et al. 1996). Under such conditions, there may be severe costs to variability in social behavior, and individuals may be reflexively drawn to large groups (Skinner and Miller 2020). Additionally, as social isolation may be part of their seasonal experience—since gartersnakes spend large amounts of time foraging by themselves during the summer months—isolation may have little effect on social behavior in adults.

Additionally, due to the variable nature of gartersnake social contexts, isolation may not be the most effective method for investigating social personality in this species. Instead, systematic manipulation of gartersnake social networks may be a more promising direction for investigating social trait plasticity in this species. For example, the removal of key females from gartersnake social groups can increase the consistency of social behavior in the remaining individuals (Skinner and Miller 2022). Whether or not such changes to the social environment can facilitate long-term changes in sociability is a promising area for future

research. Alternatively, neonatal and/or prolonged isolation may impact social behavior. For example, immediate post-birth social isolation reduces affiliative social behavior in a pit viper (*Agkistrodon piscivorus*) with maternal care (Hoss et al. 2015). Equivalent testing with gartersnakes, that do not provide parental care, would provide valuable insight into the development of social behavior in snakes.

Although social isolation did not affect social behavior, it did decrease boldness scores in female snakes, especially smaller ones. In mangrove killifish (*Kryptolebias marmoratus*), individuals reared in social isolation were bolder than individuals reared with conspecifics (Edenbrow and Croft 2012), and three-spined sticklebacks (*Gasterosteus aculeatus*) that were socially isolated for 48 h before testing displayed higher levels of boldness than individuals that were housed in small groups (Jolles et al. 2016). Within the limited research that has been done on this effect in reptiles, social isolation was found to have no effect on boldness in tree skinks (*Egernia striolata*; Riley et al. 2017). In contrast, social isolation during early development made young veiled chameleons (*Chamaeleo calypratus*) cower from conspecifics and increased their latency to attack prey in a foraging task (Ballen et al. 2014).

It has been suggested that resource competition may be an important cause of behavioral plasticity in squamates (Ballen et al. 2014; Riley et al. 2017). Gartersnakes cannot share food, and food fights can be detrimental (Yeager and Burghardt 1991). As such, the ability to adapt boldness to social conditions may allow female snakes to better compete for valuable resources when near conspecifics. As female snakes tend to be heavier than males, the largest female snakes may not need to be especially bold to compete for resources. In contrast, as size is also related to fecundity in female snakes (Fitch 1985), smaller females must out-compete conspecifics in order to increase their growth. When we isolated these smaller female snakes, they no longer needed to compete for food and may have decreased their boldness in response to their novel situation.

General Discussion

Across our two experiments, boldness and sociability in juvenile Eastern gartersnakes displayed two different patterns of plasticity and consistency. Sociability changed over the course of development, but resisted change due to social isolation, whereas boldness demonstrated long-term consistency but changed in response to social isolation. As snakes grew, individual differences in social behavior disappeared. Size increases led to increased sociability in females and decreases in males. Boldness increased with weight, but snakes maintained their individual differences across development. Removal from social competition (i.e., social isolation) caused a reduction in boldness in smaller female snakes.

Taken together, our results tell a complex story about plasticity in the behavioral expression of personality across development and changes in social context, suggesting that male and female Eastern gartersnakes may have evolved different methods of dealing with the challenges of social competition. As male snakes grow, they become bolder and less social and may generally avoid social competition in order to maximize their resource acquisition. That is, males may trade off some of the benefits of sociability for increased time and energy spent foraging, which may increase their ability to disperse away from their natal group. In contrast, as female snakes grow, they become bolder and *more* social. As body mass is important for reproduction in female gartersnakes (Fitch 1985; Rollings et al. 2017), smaller females may prioritize resource acquisition over sociability.

These sex-based strategies may have evolved in response to differential patterns of social contact in male and female snakes. In northern climates, Eastern gartersnakes aggregate for hibernation and mating (Rossman et al. 1996). Female gartersnakes additionally aggregate during the summer months for gestation (Reichenbach 1983). Our results suggest that female snakes may adjust the expression of their boldness to compensate for these challenges, with smaller females reducing their boldness when isolated more than heavier or group-housed females (Experiment 2). These findings align with prior research that has demonstrated complex social behavior in situations of resource competition in gartersnakes (Yeager and Burghardt 1991; Lyman-Henley and Burghardt 1994).

Previous research has shown that, despite the constraints on behavior imposed by personality types, the expression of personality traits in behavior may display plasticity across ontogeny (Cabrera et al. 2021) or in response to changes in the social environment (Munson et al. 2021). Our findings add to a growing body of the literature that suggest that the interactions between internal

response biases (what we usually term personality) and external factors, which combine to shape individual behaviors, are often system-specific (Riley et al. 2018; Cabrera et al. 2021). We extend this literature by suggesting that, in snakes, plasticity in personality traits can occur during early development, can differ between males and females and can also differ by personality trait (boldness or sociability). Our research also confirms the importance of studying traits in conjunction (Sih et al. 2004) and supports the need for personality research across the taxonomic spectrum.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-022-03227-0>.

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Data availability All the data reported in this paper are archived at https://osf.io/pwxau/?view_only=b57b34321999424fa9d26cf9da2a147d.

Declarations

Ethics Approval All experimental procedures conformed with Canada Council on Animal Care guidelines and were approved by the Wilfrid Laurier University Animal Care Committee (AUP R17004).

Conflicts of interest The authors declare no conflicts of interest.

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