RESEARCH ARTICLE

Stability and change in gartersnake social networks across ontogeny

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Funding information
Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: RGPIN-2016-06138

Abstract

Developmental studies of sociality in non-human animals can offer important insights into the evolution, function, and plasticity of social behavior, especially in understudied species. We examined the development of social behavior in gartersnakes. We hypothesized that social interactions change as snakes age, but are relatively stable in the short term. To assess developmental changes in social patterns, we examined the social tendencies of a group of 6 eastern gartersnakes over the first year and a half of their lives. We placed the snakes in an arena for 8 days and recorded the time that they spent in physical proximity to each other. We repeated this 8-day process 7 times across the snakes' development. We looked at changes in association patterns and individual differences in sociality (i.e., network position), and examined the effect of group size reduction on social behavior. We found that individuals tended to show repeatable network position across time, but there was a behavioral divide between younger snakes and mature snakes. When male snakes reached sexual maturity, they began initiating most social interactions. Additionally, group member attrition caused the networks to tighten, and the population reduction in combination with sexual maturity created stable social networks. This research shows that social context can have important effects on sociability, and that even a species without permanent social groups will be influenced by its social environment.

KEYWORDS
aggregation, gartersnakes, ontogeny, personality, preferential associations, social networks

1 | INTRODUCTION

Social network stability can be brought about through stable social preferences (Smith et al., 2018) and/or through consistent social interaction patterns (i.e., social personalities; Kulahci et al., 2018). For animals, stability in social interactions can offer a variety of benefits such as reduced conflict and stress (Capitanio & Cole, 2015), improved cooperation (Gerber et al., 2019), and reducing uncertainty during interactions (Dall et al., 2005). Although stability is important, social groups are rarely completely stable, especially when the group's members lack features that encourage cohesion such as kinship (Silk et al., 2014). For example, animal communities shrink and grow, and animals actively respond to such changes in group composition (Farine, 2019). Additionally, certain situations may support behavioral plasticity and override previous social interaction patterns such as conformity (Franks et al., 2020), changing environmental conditions (Taborsky & Oliveira, 2012), and ontogenetic changes (Guenther et al., 2014). This balancing act between stability and change is an active area of research in animal behavior (Bell & Stamps, 2004; Riley et al., 2018; Sih et al., 2004).

Social network analysis provides a method for quantifying stability and change in social behaviors and interactions (Krause et al., 2015). The behaviors quantified vary based on the analysis with some examples being time spent together, grooming behavior, aggressive actions, or coordinated foraging (Canteloup et al., 2021; Jones et al., 2020; Stanley et al., 2018). As social networks quantify

social interactions, consistency in social network measures across time and/or context can provide evidence for social personalities. In this context, social personality refers to individual differences in at least one social behavior. For this behavior to be considered a personality trait, individual animals should be consistent in the behavior across time and/or context but different from each other (Bell et al., 2009). For example, one individual may be consistently attracted to social interactions, whereas another may consistently avoid them (Gartland et al., 2021). Previous work on consistency in ring-tailed lemur (*Lemur catta*) social networks found that individuals displayed consistency across time in a suite of social behaviors (Kulahci et al., 2018), and similar findings have demonstrated temporal consistency in social measures for wild vervet monkeys (*Chlorocebus pygerythrus*; Blaszczyk, 2017) even with changing group membership (Canteloup et al., 2021). Along with temporal consistency, context consistency has also been demonstrated in social network measures. For example, below and above ground consistency in social interactions was found in California ground squirrels (*Otospermophilus beecheyi*; Smith et al., 2018), and consistency in social network measures has also been found across environments in Trinidadian guppies (*Poecilia reticulata*; Krause et al., 2017) and cat sharks (*Scyliorhinus canicular*; Jacoby et al., 2014). In addition, consistency in social network statistics between particular individuals can provide evidence for social bonds. In the studies mentioned above on ring-tailed lemurs (Kulahci et al., 2018) and California ground squirrels (Smith et al., 2018), social bond consistency was found in addition to social interaction consistency. In semi-feral ponies (*Equus caballus*), social bond consistency has been found across years but flexible social bonds were found across seasons (Stanley et al., 2018). Although both social interaction consistency and social bond consistency can be considered part of a social personality (Kulahci et al., 2018), these two consistencies are not always found together. For example, in Australasian gannets (*Morus serrator*), individuals demonstrate consistent social behavior but flexible social bonds across time (Jones et al., 2020).

Maturation has been suggested to be a period of behavioral instability (Bells & Stamps, 2004). One explanation for this behavioral instability is that behavioral reorganization allows individuals to contend with different selection pressures at different stages of development (Bells & Stamps, 2004). A meta-analysis of personality development across ontogeny found that in the majority of situations, animals tended to be consistent within a developmental stage but changed across milestones (Cabrera et al., 2021). Although a minority of studies did find stability in some traits such as boldness and aggression, none of the examined studies found consistency in sociability across life stages (Cabrera et al., 2021). As maturity seems to have a transitory effect on personality, research on social network stability that bridges maturity should offer valuable insight into the factors that may influence stability and change in social networks.

Research on social network stability and change is still an emerging field of research. The work that has been done has mostly studied mammals and birds with long-term and/or complex social interactions (Jones et al., 2020; Kulahci et al., 2018). Little is known about social network stability in reptiles and other animals that are typically considered non-social (Doody et al., 2012). Although the social lives of snakes are still poorly understood, they are not typically considered social animals and are not known to inhabit long-term stable social groups. However, snakes do display complex patterns of social behavior that offer a variety of benefits. Several species of snake have been shown to form aggregates both in the wild (Larsen et al., 1993; Reichenbach, 1983) and in the lab (Aubret & Shine, 2009; Burghardt, 1983; Dundee & Miller, 1968; Heller & Halpern, 1982; Skinner & Miller, 2020). It has been hypothesized that grouping offers snakes a variety of benefits such as reduced water loss (Noble & Clausen, 1936), thermoregulation (Aubret & Shine, 2009), protection from predation (Graves & Duvall, 1995), and access to mates (Gregory, 1984), in addition to more general mechanisms that have been proposed for other taxa, such as protection from predation (Krause & Ruxton, 2002). Furthermore, attraction to conspecifics, by following scent trails, can allow snakes to find preferred overwintering locations (Costanza, 1989). Improved foraging success—often considered one driver of aggregation—likely plays no role in snake aggregation, as they cannot share food (suggesting that foraging competition and kleptoparasitism may actually favor solitary living in snakes; Devine, 1977; Yeager & Burghardt, 1991). Snakes, like other taxa, do not aggregate at random: relatedness, familiarity and even diet can influence aggregation patterns in juvenile Butler's gartersnakes (*Thamnophis butleri*; Lyman-Henley & Burghardt, 1994); brown snakes (*Storeria dekayi*) and gartersnakes (*Thamnophis sirtalis*), when placed together, show preferential aggregation with conspecifics (Burghardt, 1983); and both timber rattlesnakes (*Crotalus horridus*; Clark et al., 2012) and cottonmouths (*Agkistrodon piscivorus*; Hoss et al., 2015) have demonstrated kin recognition in their grouping patterns. Arizona black rattlesnakes (*Crotalus cerberus*) at their den sites preferentially associate with specific members of their group (Schuett et al., 2017), as we have also recently demonstrated for juvenile eastern gartersnakes (*Thamnophis sirtalis*; Skinner & Miller, 2020).

In addition to complex patterns of social behavior, some studies have found that reptiles display personalities that change across ontogeny. For example, decreases in boldness and exploration across the transition from juvenile to adult were found in mourning geckos (*Lepidodactylus lugubris*; Sakai, 2018). In snakes, long-term individual consistency in predator defense behavior has been observed in Mexican black-bellied gartersnakes (*Thamnophis melanogaster*; Herzog & Burgardt 1988) and northwestern gartersnakes (*Thamnophis ordinoides*; Brodie, 1993; see Waters 2017 for review). More recently, long-term consistency in both foraging and feeding behaviors, with a period of instability during the sub-adult phase, has been demonstrated in the northern common boa (*Boa imperator*; Simkova et al. 2017). In eastern gartersnakes (*T. sirtalis sirtalis*), we have found consistent individual differences in sociability along with a reduction in aggregation tendency with increasing age (Skinner & Miller, 2020). Taken together, these data suggest that snakes, like other vertebrates, display individual differences in sociability akin to a "social personality" (Cote & Clobert, 2007), which vary across their lifetimes, possibly in a

systematic manner that has not yet been mapped in detail. As in some fish species (Shaw, 1978), some snakes may only aggregate as juveniles and lead solitary adult lives. Alternatively, the social structures that snake populations form may change with the ages of their constituent members.

Eastern gartersnakes (*T. sirtalis sirtalis*) occupy a large range of habitats from northern Canada to the southern United States and Mexico (Rossman et al., 1996). The gartersnakes used in this study were from Ontario, Canada. As such, they experience cold winters and are known to aggregate for hibernation and for mating. Eastern gartersnakes also display trailing behavior (following other snakes' scent trails), which may be used for finding mates (LeMaster & Mason, 2001) or the communal hibernation site (Costanzo, 1989). After mating in the spring, it is thought that gartersnakes disperse for the summer months (Larsen et al., 1993) – although birthing aggregations during the summer months have been recorded (Reichenbach, 1983). Gartersnakes give birth to live young and do not provide parental care. Vulnerable neonate and juvenile snakes, therefore, face unique ecological challenges not shared by larger, less vulnerable adults. Thus, these snakes may display changes in aggregation patterns over the first year or two of their lives, as a result of gradually decreasing vulnerability to predation and increasing mating drive. To explore these changes, we performed a longitudinal analysis of aggregation behavior on a group of 6 eastern gartersnakes from ~2 months of age until ~16 months of age. We quantified the snakes' interactions using social network analysis. We primarily used weighted degree and dyad strength as measures of sociality and partner preferences, respectively. We looked for both consistency and change in these measures to quantify social interactions across development. We hypothesized that: (1) social behavior would remain relatively consistent but would demonstrate a shift across maturity; (2) overall network structures would remain stable across time, despite behavioral shifts; and (3) males and females would differ in social behavior post maturity. Based on these hypotheses we made the following predictions about the relationship between social behavior and network structure: (1) Snakes would display preferential associations (consistency in dyad strength) that would change as they transitioned into maturity. This change would be reflected through increased associations between opposite sex snakes; and (2) snakes would display consistent individual differences in sociability (weighted degree) as juveniles and as adults, but there would be a behavioral shift as they transitioned to maturity.

Due to the death of one snake and the removal of another individual during the final testing period, we also tested the response of the snakes' social network to node removals. As these removals were unplanned, we had no particular *a priori* hypotheses regarding their effects on the network. However, the experimental removal of nodes from a network has often resulted in behavioral changes that were not predicted by simulations, possibly as a result of social networks rewiring to meet the social needs of the remaining individuals (Farine, 2019). Our two consecutive reductions of the group allowed us to examine whether gartersnakes' social networks adjust to node removal through a form of structural rewiring, as predicted by some theoretical work (Farine, 2019).

2 | MATERIAL & METHODS

2.1 | Subjects and housing

Subjects were six neonate eastern gartersnakes (3 males and 3 females; *T. sirtalis sirtalis*). They were collected from field sites in Ontario, Canada, in August 2018. Upon collection, neonate status was assessed visually, and age was approximated based on the reproductive cycle of eastern gartersnakes in northern climates (Rossman et al., 1996). The snakes were housed in pairs until ~8 months of age. Two pairs consisted of same-sex snakes, and one pair consisted of opposite-sex snakes (Table S1). At 8 months of age the snakes were separated into individual terrariums. Snakes were housed in glass terraria (21 cm × 10.5 cm × 31 cm high). They had access to belly heat (30℃) provided by heat tape (THGTape), and clean water was provided daily. The snakes were fed chopped nightcrawlers (Pagonis live bait, Toronto) with vitamin supplements (Zilla) as needed. The housing facility was maintained at 22℃ with a 12 h day-night cycle. All of the snakes were sexed by probing. The snakes were tested seven times over approximately 16 months, starting when they were about 2 months old. Between replications of the experiment, we controlled snakes' diets, social contacts, and physical environment. We refer to each 8-day test as a session (sessions are numbered 1–7). One female died between sessions 5 and 6, and on day 3 of session 7 there was a successful mating between two snakes. As such, on the morning of day 4 of session 7, the mated female was removed from the experiment for health monitoring. The female snake did not give birth. Snakes were weighed before the start of each session (Table S1).

2.2 | Apparatus

The experiments were conducted in two separate arenas. The first five sessions were conducted in a juvenile arena (identical to the one in Skinner & Miller, 2020). Sessions 6 and 7 were conducted in an adult arena. The juvenile arena was 73 cm × 73 cm × 36 cm high, constructed of polyethylene walls, and was placed on a table covered with waterproof white paper (Figure S1A). The arena contained one black plastic shelter (14 cm × 10 cm × 5 cm high; Cornel's World) and one water dish (a 15 cm × 15 cm × 8 cm clear plastic tub) for each snake. The center of the arena was covered with 12 tumbled sandstone squares. The adult arena was a scaled-up replica of the juvenile arena, made of 120.5 cm × 112 cm × 24 cm PVC walls with the height reinforced by 119 cm × 111 cm × 32 cm clear acrylic walls (Figure S1B). The shelter and water dish layout was identical, but the shelters were increased in size to accommodate the increased size of the snakes (23 cm × 16 cm × 6.5 cm; Cornel's world). The water dishes were square plastic containers

(15 cm × 15 cm × 6 cm; Ziplock). The center was covered by 16 sandstone squares. In both arenas, white paper towels were placed under each shelter for ease of cleaning. A high resolution camera (Canon EOS Rebel T5i DSLR) was mounted above the arena and took a picture every 5 s for all 12 h of daylight. Individual snakes could be identified in the pictures.

2.3 | Procedure

Before testing, each snake's head was marked with colored dots of non-toxic nail polish (Adrianne K). Color combinations were unique within each session. Snakes were re-marked whenever they shed. The snakes were tested at the following ages: session 1, ~2 months; session 2, ~4 months; session 3, ~6 months; session 4, ~8 months; session 5, ~10 months; session 6, ~14 months; session 7, ~16 months. As we removed one snake midway through session 7, this session is divided into two parts, sessions 7.1 and 7.2, for some analyses.

To begin each session, the snakes were released into the enclosure on the evening before the first full day of the experiment. Data from this time period were only used to record courtship behavior (see below). Following this, snakes remained in the experimental apparatus for 8 full days. Each day, at approximately 10 am and 2 pm, all the snakes were removed from the arena and replaced into it, either as a group in the center of the arena (Center shuffle), or each snake individually into its designated shelter (Placed shuffle). The Center shuffle pattern was used for both morning and afternoon shuffles on odd-numbered days (days 1,3,5,7) and the Placed shuffle was used on even-numbered days (days 2,4,6,8). As there were 6 shelters for the 6 snakes, the snakes did not need to aggregate at all. Once a day, during the morning shuffle, the water dishes, paper towels, and shelters were replaced, and the areas around the shelters were cleaned with 70% isopropyl alcohol, and washed and dried thoroughly. On the mornings of Days 3 and 7 the entire arena was cleaned with water and isopropyl alcohol. During this time, snakes were placed in individual holding containers and fed nightcrawlers (chopped or whole, depending on their age).

All methods followed the Canadian Council on Animal Care guidelines and were approved by the Wilfrid Laurier Animal Care Committee. Subjects were collected from the Waterloo, Ontario, area under a Wildlife Scientific Collector's Authorization from the Ontario Ministry of Natural Resources (No. 1090896).

2.4 | Coding

To codify snake social interactions, a high-resolution image was taken of the testing arena every 5 s during the testing period. These images were coded using a custom ethologger program (Figure S1; see Skinner & Miller, 2020). The ethologger divided the image of the arena into seven zones: one for each of the six shelters, and one zone to represent all the space outside the shelters. We recorded the location of each snake whenever they crossed zone boundaries. We

used time sharing the same shelter/zone to construct the social networks used in most of our analyses. In addition to these networks, we also coded courtship behavior. To quantify courtship, we looked for the characteristic chin rubbing behavior demonstrated by males who are courting a female snake (Rossman et al., 1996). Courtship behavior was only coded when the snakes' heads could be seen (i.e., when snakes were outside the shelter). We totaled the number of frames in which males demonstrated courtship, stopping when the snakes separated. One experimenter coded the data, and all data was checked for errors before analysis. Although the ethologger kept track of the snakes' locations, the coder was essentially blind to a snake's location after it entered a shelter.

2.5 | Statistical analysis

All statistical analyses were conducted in R (R Core Team 2017) using the *DescTools*, *lme4*, *rcompanion*, *igraph*, *asnipe*, and *ANTs* packages. We used mixed-effect linear and general linear models to analyze repeated measures data. All of our models contained a random intercept for subjects and either session or day as a fixed effect, depending on the analysis timescale. For some models, we also included session as a random intercept or random slope. As the snakes were tested 7 times, long-term analysis was on the scale of session (between-session) and short-term analysis was on the scale of days (within-session). When the residuals of our models were not normally distributed, we applied data transformations. For proportional data, we used arcsine transformation. For all other variables, we used Tukey's ladder of powers to find the appropriate transformation (Tukey, 1977). As rank-order consistency is effective for measuring snake behavior (Šimková et al., 2017; Skinner & Miller, 2020; Waters et al., 2017), we used Kendall's test of concordance to test if individuals had consistent ranks. We examined rank-order consistency across sessions and within each session. In all situations in which we found significant *p*-values, we confirmed these values by comparing our data to 10,000 permutated networks in which individual ranks were randomized (Krause et al., 2017; Wilson et al., 2013). In all situations, we report the more conservative *p*-value. As session 7.2 only had 4 individuals we dropped it from this analysis. Since snakes were shuffled (removed from and then returned to the arena) twice a day, data for most analyses were subdivided into three periods: Morning (from lights-on to the first shuffle), Midday (first shuffle to second shuffle), and Afternoon (second shuffle to lights-out).

To quantify social interactions, we primarily used "weighted degree." We quantified the time snakes spent with others using their average weighted degree (the cumulative proportion of time they spent in the same zone as others). Gartersnakes demonstrate repeatable individual differences in the time they spend with other snakes in a group environment. These individual differences have been shown to correlate with individual tests of sociability, and appear to be a consistent measure of social behavior in these snakes (Skinner & Miller, 2020). We, therefore, used "weighted degree" and "average weighted degree" to look for consistency in aggregation

behavior over time. To examine the snake's social preferences for particular individuals, we looked at variability in the snakes' rank order preferences for each other within each session compared to randomized preferences.

Finally, we developed a method for comparing the amount of time snakes spent in a particular network configuration to the probability of that configuration occurring if snakes only controlled their dyadic interaction strengths. We first calculated all possible unweighted undirected networks of a certain size. We then weighted those networks such that the averaged (weighted) network matched the strengths of all the dyadic interactions observed in our data. In other words, we set the probability of any particular network to be equal to the social preferences of our snakes. We could then compare our actual networks against these predicted networks (see SI Text A for details). We used this to determine whether or not snakes controlled for large-scale features (i.e., more than dyads) of their association networks.

3 | RESULTS

The snakes spent the vast majority of their time in the shelters ($88 \pm 10\%$ of the time; Figure S2). Therefore, the reported networks primarily describe the time each snake spent in the same shelter as another (see Figure S3 for networks). We did not observe any systematic changes in behavior across the 8 days of each session, as we might have expected if some of our effects resulted from social or environmental habituation (Figure S2).

3.1 | Partner preferences

We examined whether snakes preferentially associated with specific partners, as we have previously observed in this species (Skinner & Miller, 2020). In order to test for preferred associations with particular individuals, we ranked each snake's associations with all possible partners and then performed a ranked test looking for consistency in the rank of associates across days for each session (Stanley et al., 2018). To perform these tests, we tested the observed network ranks compared to 10000 random networks, using the network consistency function from Wilson et al. (2013). The rank order test suggested that preferences for particular partners increased as snakes aged with the highest proportion of snakes showing significant preferences in session 6 (p's < 0.01 for 5 of 6 snakes) and session 7.2 (p's < 0.05 for 3 of 4 snakes) and session 4 (p's < 0.01 for 4 of 6 snakes). No snake demonstrated a preference for particular individuals in session 1 or session 5 (all p's > 0.15; Table S2).

The solidification of aggregation preferences resulted in snakes spending an increasing amount of time in particular social network configurations. To quantify these preferred networks, we examined the proportion of time spent in each configuration, and compared it to the predicted probability of that configuration occurring, while controlling for overall sociability and for the strength of the

connection between each pair of snakes (see SI Text A for details). The most common configurations often accounted for a large proportion of session time (e.g., in session 6, snakes spent 63% of their time in their most preferred network). Snakes spent more time than predicted in their preferred networks (Figure S4a) and less time than predicted in their less preferred configurations (Figure S4b), strongly suggesting that they consider more than just dyadic interactions in their affiliative behavior decisions (i.e., if snakes only cared about the time they spent with specific single partners, all the points in Figure S4 should cluster around the diagonal).

Since each snake was frequently released into its designated shelter, it is possible that snakes developed a stereotypical response performed after release, which re-formed the same networks each time, independent of social considerations. We, therefore, tested whether preferred network formation depended on release pattern. We found that release patterns (Central or Placed) had no effect on the formation of preferred networks (F(1, 22.3) = 0.004, $p = 0.95$).

Thus, over the course of their development, young gartersnakes become more selective in their associations, and increasingly spend the majority of their time in networks that reflect both partner and larger-scale preferences. However, a particular configuration may not be preferred by all the members of that network. More social individuals may initiate and maintain contact, and thus play an outsized role in determining the form of the network. Therefore, we next examined individual differences in sociality and interaction initiation.

3.2 | Sociality

To explore the development of consistent aggregation behavior, we used snakes' rank-order consistency in weighted network degree. In other words, were snakes' positions within the network, or overall levels of social contact, consistent across time? All significant values were confirmed using network permutations (see Methods). Between-session rank-order consistency was significant (Kendall's W = 0.54, $p = 0.02$). When broken down by time period, consistency was significant for mornings (W = 0.39, $p = 0.03$) and midday (W = 0.51, $p = 0.008$) but not for afternoons (W = 0.36, $p = 0.07$). Visual inspection of the data suggested that individual differences in average weighted degree began to emerge in session 2 and tended to strengthen and stabilize over time (Figure 1). This was particularly true for the least ("R") and most ("GG") social snakes. We compared each pair of sessions to each other using Spearman's rank order correlations. Although it was difficult to reach significance with our small sample size, the coefficients provide an effect size for the number of individuals that occupied the same rank-order across any two sessions. We found an ontogenetic shift, with earlier sessions being more similar to each other and later sessions being more similar to each other (Table S3). This shift occurred between sessions 3 and 4, when at least one male snake hit sexual maturity (see below).

Within-session rank-order consistency in degree (across the 8 days of each session) began to emerge in session 3 and reached
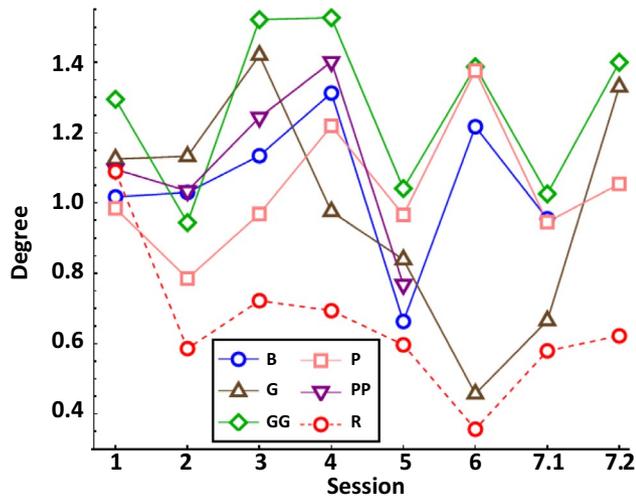
FIGURE 1 Weighted degree for each subject across sessions. Rank order consistency emerged early, especially at the extremes. For example, snake "R" is the least social snake from session 2 onwards; snake "GG" is the most social from session 3 onwards
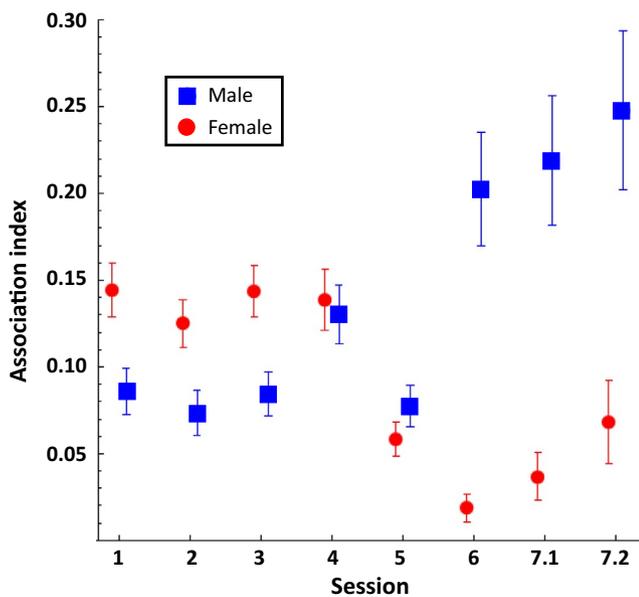

FIGURE 2 Owned weighted degree across sessions by sex. Male snakes primarily drive social interactions from session 6 onwards. Error bars show ± SEM

significance in sessions 4, 6, and 7.2 (Figure S5; Table S4). Sex differences in social interactions emerged in session 4. To quantify this, we apportioned a dyad's shared weighted degree (how much time two snakes spent together) by the proportion of times each snake initiated an interaction. For example, if two snakes spent 100 min together and they equally initiated the interactions, then each snake owned (was responsible for) 50 min (or half the total time). As snakes regularly visited shelters, sometimes for only a few seconds, we counted an "initiated interaction" as initiated time spent with a snake, or group of snakes, which was longer than the initiating individual's average stay length. We found a

significant main effect of session ($F(7, 1480) = 4.74$, $p < 0.001$), no effect of sex ($F(1, 4) = 0.10$, $p = 0.763$), and a significant interaction between session and sex ($F(7, 1480) = 10.74$, $p < 0.001$; Figure 2). The association pattern began to change in session 4 and by session 6 males were primarily initiating long-term interactions. To test this, we compared the results of the mixed-effect model to the results from 10000 generated networks in which the sex identities of the nodes were randomly permutated. The interaction was significant for session 4 ($p = 0.04$), marginal for session 5 ($p = 0.05$) and significant for sessions 6, 7.1, and 7.2 (all $ps < 0.001$). Although courtship behavior also emerged in session 4, it does not alone explain the network patterns that emerged in later sessions (SI text B).

3.3 | Node removals

As one female snake died between sessions 5 and 6, and another female snake was removed during session 7, we compared our social network data to node deletion simulations. As we had detected effects of sex on association patterns, we simulated both random deletions and targeted deletions of females. To reflect our data, we simulated the deletion of one snake for sessions 6 and 7.1, and two snakes for session 7.2. For both random and targeted deletions, the simulation calculated the network diameter and global efficiency. Network diameter is the longest path between two individuals (nodes). Global efficiency is a statistic that captures the spread of information (or a pathogen) through a social network, with high values indicating faster spread (Romano et al., 2018). The simulated node removals predicted a decrease in network diameter and stable global efficiency. In agreement with the simulations, our actual networks showed a decrease in diameter. However, unlike the simulations, the global efficiency values for our data demonstrated a large increase after the removal of each snake (Figure S6).

To test the significance of these differences, we extracted each simulated network, and permuted the links between individuals 10000 times using the function provided in the ANTs R package for network analysis (Sosa et al., 2020). We then calculated the global efficiency and network diameter for each random network (see Methods). The increase in global efficiency in our data was significantly larger than in the randomized simulated networks (all $ps < 0.001$). For network diameter, there was no significant difference between the data and the permuted networks for one deletion (all $ps > 0.43$) but the network diameter was smaller than would be expected by chance for two deletions (all $ps < 0.001$). In other words, when snakes were removed from our networks, the diameter of the network shrank, as expected. However, the efficiency of the network also increased significantly more than would have been predicted, even by targeted removals of females. This result suggests, in line with recent theoretical predictions (Farine, 2019), that the remaining snakes shifted their interaction patterns, including males shifting their focus to a new preferred female, and creating a more connected network.

4 | DISCUSSION

By repeatedly placing the same 6 young eastern gartersnakes (*T. sirtalis sirtalis*) into an enclosure where we could monitor all their social interactions, we show that snakes demonstrate consistency in social behavior, but that its structure changes across development. As they aged, snakes became more selective in their associations (Table S2), leading to the group spending more time in their most preferred configurations (Figure S4) and individual differences in sociability solidified over the first few months of life (Figure 1). As the snakes crossed into maturity, the male snakes began initiating more social interactions than female snakes (Figure 2). Along with this shift in interaction pattern, the consecutive removal of two female snakes caused the remaining snakes to "rewire" their associations, increasing the connectivity of the networks (Figure S6).

4.1 | Preferential associations

The snakes in our experiment demonstrated no association preferences as neonates (at 2 months old), weak association preferences during their early development, and strong preferences after maturity. This change in association pattern could be the result of changes in recognition. It is possible that snakes, like some species of fish (see Griffiths, 2003, for review), may require a particular amount of contact time before they can recognize each other. To complicate the challenges of recognition, previous research on young gartersnakes has shown that familiarity and diet can influence grouping patterns (Lyman-Henley & Burghardt, 1994). As the snakes in this experiment were equally familiar with each other and were all on the same diet, we may have removed the most important perceptual cues for sorting in young snakes. Aggregation can offer a variety of important survival benefits such as thermoregulation (Graves & Duvall, 1987), protection from water loss (Nobel & Clausen 1936), and protection from predation (Graves & Duvall, 1995). As a result, for particularly vulnerable young snakes, finding a group may be more important than finding any particular group. A similar lack of preference for phenotypic sorting while shoaling has been found in small Trinidadian guppies (whereas large guppies choose size matched groups; Rodgers et al., 2011). It has been suggested that reduced sorting preferences when grouping may be the result of learning, with younger individuals improving in their decision making over time. An alternative explanation is that quickly choosing a group, rather than choosing the ideal group, may be more important for reducing the risk of predation in more vulnerable populations (Rodgers et al., 2011). It has been suggested that speed of decision making is an important trait in snakes (Simkova et al., 2017) and in a comparison of three species of gartersnakes, it was found that the common gartersnake (*Thamnophis sirtalis*) was the quickest to make decisions in an open-field task (Herzog & Burghardt, 1986). In summary, young snakes need time to either develop or demonstrate individual recognition of conspecifics. We suggest that young gartersnakes may use

different cues for recognition compared to older snakes, may quickly choose any group over specific individuals due to safety concerns, or may be incapable of individual recognition. Future research should attempt to parse out that factors influence the reduced preferential associations we found in younger compared to older snakes.

In contrast to their younger selves, the snakes in our experiment demonstrated strong preferences for particular individuals as they transitioned to maturity. As snakes age, the primary functions of aggregation change. Access to mates may drive aggregation in some species (Gregory, 1984), something that may be especially important for species with short active seasons like gartersnakes in northern climates (Larsen et al., 1993). With the onset of maturity, larger females become more attractive, increasing their reproductive output (Shine et al., 2006). This may have led to the increase in preferential associations we saw between male and female snakes as they passed maturity, even when courtship behavior was not observed (as in our session 6). An ontogenetic shift in preferential associations has also been found in Arizona black rattlesnakes (*C. cerberus*) with juvenile-juvenile preferred associations being less common at a den site than associations between adults or between adults and juveniles (Schuett et al., 2017). Additionally, in some groups of wild vervet monkeys (*C. pygerythus*), adults have more stable relationships than juveniles (Borgeaud et al., 2016) and in wild olive baboons (*Papio anubis*) juveniles have fewer social bonds than adults (Fedurek & Lehmann, 2017). In gartersnakes, the changing strengths of preferential associations that we observed across development may, therefore, be the result of changing ecological demands and the differential utility of associating with particular conspecifics. In our snakes, male-female preferential bonds appeared to override any pre-existing preferences among the snakes. Future research should test same-sex groups of mature snakes to see if same-sex bonds can be maintained (and are equally strong) among adults. As adult female snakes are known to aggregate for gestation (Graves & Duvall, 1995), preferential associations in adults may be limited to females.

4.2 | Consistency in sociability

Our snakes demonstrated consistent individual differences in the time they spent with others (their weighted degree), suggesting that sociality is a personality trait (Bell et al., 2009). The study of social network statistics as personality traits is a growing field (Krause et al., 2010,2017), but consistency in social network measures has been found in giraffes across seasons (*Giraffa camelopardalis*; Prehn et al., 2019), house sparrows across time (*Passer domesticus*; Plaza et al., 2020), and both cat sharks (*S. canicular*; Jacoby et al., 2014) and guppies across contexts (*P. reticulata*; Krause et al., 2017). Thus, our data add to a growing body of literature that suggests that social network statistics show repeatability similar to other measures of animal personality. In our data, young snakes were more variable in sociality within a session (on short timescales) but consistent across sessions. As they aged, snakes became more consistent at shorter timescales (days). These results suggest that consistency in network

measures may be driven by several distinct processes that operate and vary on different timescales.

Snakes began to demonstrate individual differences in sociality early in their development, showing moderate to high rank-order consistency across the first three sessions of our data (~2–6 months of age). Social patterns changed as the group transitioned to maturity/sub-adulthood (in session 4, ~8 months of age; Table S4). Some individuals increased in behavioral consistency across time, while maintaining their individual differences (e.g., snake "R" was the least social individual across almost all sessions, and became increasingly asocial as he aged). A similar pattern has been found in humans, with personalities tending to strengthen with age (Caspi et al., 2005; Roberts & DelVecchio, 2000) and has also been observed in mice (*Mus musculus*; Brust et al., 2015) and mosquitofish (*Gambusia holbrooki*; Polverino et al., 2016). Past social experiences may result in snakes finding a social niche, which they continue to exploit as long as there are benefits (e.g., non-social snake R continues to avoid competition, whereas social snake GG gets access to a possible mate).

4.3 | Sex-related effects

Before maturity, in this group of snakes, males and females were approximately equal in their tendency to initiate lengthy social interactions. However, as the male snakes matured, they became the primary initiators of social interactions (Figure 2), creating stable social networks between interested males and their preferred female(s). Female snake size – a key factor in determining female quality in gartersnakes (Shine et al., 2001,2006) – probably drove these preferences. Although size differences in our age-matched snakes were small, the preferred females tended to be slightly larger (Table S1). For these female snakes, consistency in post-maturity sociability was contingent on their popularity. As the male snakes began aggressively pursuing female snakes, the females had little control over their socialization. This shift to male-initiated social interactions could be a strategy used by male snakes to improve reproductive success in a highly competitive mating system. In the gartersnake mating system, numerous male gartersnakes will often simultaneously court a single female snake. In this situation, it may benefit male snakes to associate with particular females outside of mating season if it influences female mate choice. Although familiarity appears to have little effect on the mate choices of male gartersnakes (Shine et al., 2012), further research could examine if social contact outside of mating times (e.g., our session 6) influences female mate choice. Additionally, future research should test if these observed patterns generalize to larger aggregates of mixed-sex snakes.

4.4 | Node removals

Despite our removals of snakes from the experiment being accidental and random, their effects were extreme, causing a structural rewiring of the social network, as predicted by some recent theories (Farine, 2019). Sociable male snakes collapsed their social interactions around particular female snakes, resulting in a significant increase in preferred associations (Table S2). Global efficiency, a measure of information flow through the network, increased with the removals (Figure S6), probably as a result of male snakes searching for a preferred female. This, combined with the shrinking number of acceptable females, resulted in an increase in overall network connectivity, as male snakes searched more widely. Overall, the removal of nodes stabilized social networks and increased the amount of time spent in preferred social groups. Future work should try removing individuals that are either central or on the periphery of the network to see how network position affects this rewiring process. Animal networks have been shown to adjust to the removal of individuals by forming new associations (Firth et al., 2017), changing their association patterns (Naug, 2009), or changing their behavior to compensate for the missing individual (Annagiri et al., 2016).

The collapse of social networks in snakes may have important consequences. Along with many other taxa, reptiles are experiencing severe population decline due to environmental change and human-animal conflict (Böhm et al., 2013). For example, Snake Fungal Disease (SFD) – a contagious and often fatal illness – is of growing concern (Lorch et al., 2016). Our data suggest that the removal of key individuals could exacerbate the spread of contagious pathogens, such as SFD, through already vulnerable populations. Identifying social tendencies across snake species, and the structures of their social networks, may help identify populations that are particularly vulnerable to SFD. Our data also suggest that it is important to consider social interactions in conservation efforts. Even outside of mating times, male access to females appears to be important for eastern gartersnakes (*T. sirtalis sirtalis*). If this social access is equally important in other species of snake, it could help explain the concerning lack of site fidelity frequently observed in male snakes after translocation (Nash & Griffiths, 2018).

We note that the conclusions we can draw from these data are limited due to our small sample size. In addition, we carefully controlled the environmental conditions and feeding schedules of our lab-housed snakes. This eliminated extraneous variables but meant that the snakes did not experience brumation or seasonal fluctuations (e.g., in resource availability) that might have otherwise influenced their social behaviors and/or growth rate. This should be considered when interpreting our findings, and future research should attempt to verify these findings under more naturalistic conditions. However, as long-term studies of both personality and social network structure are rare in any species, this study offers important insights into the changes that occur in social behavior over time. Further work on developmental changes in snake sociability will help flesh out our understanding of this neglected taxon.

for the snake image used in the graphical abstract. The research was funded by the National Science and Engineering Research Council of Canada (NSERC) grant RGPIN-2016-06138.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICAL APPROVAL

All experimental procedures conformed to Canada Council on Animal Care guidelines and were approved by the Wilfrid Laurier University Animal Care Committee (AUP R17004). The snakes were collected from the Waterloo, Ontario area under a Scientific Collector's Permit from the Ontario Ministry of Natural Resources.

DATA AVAILABILITY STATEMENT

All the data reported in this paper are archived at https://osf.io/vykqp/?view_only=0febe8aa56124460adb3906cf2771666.

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REFERENCES

Annagiri, S., Kolay, S., Paul, B., & Sona, C. (2016). Network approach to understanding the organization of and the consequence of targeted leader removal on an end-oriented task. *Current Zoology*, *63*, 269–277. https://doi.org/10.1093/cz/zow058

Aubret, F., & Shine, R. (2009). Causes and consequences of aggregation by neonatal tiger snakes (Notechis scutatus, Elapidae). *Austral Ecology*, *34*, 210–217. https://doi.org/10.1111/j.1442-9993.2008.01923.x

Bell, A. M., & Stamps, J. A. (2004). Development of behavioural differences between individuals and populations of sticklebacks, Gasterosteus aculeatus. *Animal Behaviour*, *68*, 1339–1348. https://doi.org/10.1016/j.anbehav.2004.05.007

Bell, H., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: A meta-analysis. *Animal Behaviour*, *77*, 771–783. https://doi.org/10.1016/j.anbehav.2008.12.022

Blaszczyk, M. B. (2017). Consistency in social network position over changing environments in a seasonally breeding primate. *Behavioral Ecology Sociobiology*, *72*, 1–13. https://doi.org/10.1007/s00265-017-2425-y

Böhm, M., Collen, B., Baillie, J. E. M., Bowles, P., Chanson, J., Cox, N., Hammerson, G., Hoffmann, M., Livingstone, S. R., Ram, M., Rhodin, A. G. J., Stuart, S. N., van Dijk, P. P., Young, B. E., Afuang, L. E., Aghasyan, A., García, A., Aguilar, C., Ajtic, R., … Zug, G. (2013). The conservation status of the world's reptiles. *Biological Conservation*, *157*, 372–385. https://doi.org/10.1016/j.biocon.2012.07.015

Borgeaud, C., Sosa, S., Bshary, R., Sueur, C., & van de Waal, E. (2016). Intergroup variation of social relationships in wild vervet monkeys: A dynamic network approach. *Frontiers in Psychology*, 7:915. https://doi.org/10.3389/fpsyg.2016.00915

Brodie, E. D. (1993). Consistency of individual differences in anti-predator behaviour and colour pattern in the garter snake, Thamnophis ordinoides. *Animal Behaviour*, *45*, 851–861. https://doi.org/10.1006/anbe.1993.1106

Brust, V., Schindler, P. M., & Lewejohann, L. (2015). Lifetime development of behavioural phenotype in the house mouse (Mus musculus). *Frontiers in Zoology*, *12*, S17. https://doi.org/10.1186/1742-9994-12-s1-s17

Burghardt, G. M. (1983). Aggregation and species discrimination in newborn snakes. *Zeitschrift Für Tierpsychologie*, *61*, 89–101. https://doi.org/10.1111/j.1439-0310.1983.tb01330.x

Cabrera, D., Nilsson, J. R., & Griffen, B. D. (2021). The development of animal personality across ontogeny: A cross-species review. *Animal Behaviour*, *173*, 137–144. https://doi.org/10.1016/j.anbehav.2021.01.003

Canteloup, C., Puga-Gonzalez, I., Sueur, C., & van de Waal, E. (2021). The consistency of individual centrality across time and networks in wild vervet monkeys. *American Journal of Primatology*, *83*:e23232. https://doi.org/10.1002/ajp.23232

Capitanio, J. P., & Cole, S. W. (2015). Social instability and immunity in rhesus monkeys: The role of the sympathetic nervous system. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*, 20140104. https://doi.org/10.1098/rstb.2014.0104

Caspi, A., Roberts, B. W., & Shiner, R. L. (2005). Personality development: Stability and change. *Annual Review of Psychology*, *56*, 453–484. https://doi.org/10.1146/annurev.psych.55.090902.141913

Clark, R. W., Brown, W. S., Stechert, R., & Greene, H. W. (2012). Cryptic sociality in rattlesnakes (Crotalus horridus) detected by kinship analysis. *Biology Letters*, *8*, 523–525. https://doi.org/10.1098/rsbl.2011.1217

Costanzo, J. P. (1989). Conspecific scent trailing by garter snakes (Thamnophis sirtalis) during autumn Further evidence for use of pheromones in den location. *Journal of Chemical Ecology*, *15*, 2531–2538. https://doi.org/10.1007/bf01014729

Cote, J., & Clobert, J. (2007). Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 383–390. https://doi.org/10.1098/rspb.2006.3734

Dall, S., Giraldeau, L., Olsso, O., McNamara, J., & Stephens, D. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, *20*, 187–193. https://doi.org/10.1016/j.tree.2005.01.010

Devine, M. C. (1977). Copulatory plugs, restricted mating opportunities and reproductive competition among male garter snakes. *Nature*, *267*, 345–346. https://doi.org/10.1038/267345a0

Doody, J. S., Burghardt, G. M., & Dinets, V. (2012). Breaking the social-non-social dichotomy: A role for reptiles in vertebrate social behavior research? *Ethology*, *119*, 95–103. https://doi.org/10.1111/eth.12047

Dundee, H., & Miller, M. (1968). Aggregative behavior in habitat conditioning by the prairie ringneck snake, Diadophis punctatus arnyi. *Tulane Studies in Zoology and Botany*, *15*, 41–45.

Farine, D. R. (2019). Structural trade-offs can predict rewiring in shrinking social networks. *Journal of Animal Ecology*, *90*, 120–130. https://doi.org/10.1111/1365-2656.13140

Fedurek, P., & Lehmann, J. (2017). The effect of excluding juveniles on apparent adult olive baboons (Papio anubis) social networks. *PLoS One*, *12*, e0173146. https://doi.org/10.1371/journal.pone.0173146

Firth, J. A., Voelkl, B., Crates, R. A., Aplin, L. M., Biro, D., Croft, D. P., & Sheldon, B. C. (2017). Wild birds respond to flockmate loss by increasing their social network associations to others. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20170299. https://doi.org/10.1098/rspb.2017.0299

Franks, V. R., Ewen, J. G., McCready, M., & Thorogood, R. (2020). Foraging behaviour alters with social environment in a juvenile songbird. *Proceedings of the Royal Society B: Biological Sciences*, *287*, 20201878. https://doi.org/10.1098/rspb.2020.1878

Gartland, L. A., Firth, J. A., Laskowski, K. L., Jeanson, R., & Ioannou, C. C. (2021). Sociability as a personality trait in animals: methods, causes and consequences. *Biological Reviews*. https://doi.org/10.1111/brv.12823. Epub ahead of print.

Gerber, L., Connor, R. C., King, S. L., Allen, S. J., Wittwer, S., Bizzozzero, M. R., Friedman, W. R., Kalberer, S., Sherwin, W. B., Wild, S., Willems, E. P., & Krützen, M. (2019). Affiliation history and age

similarity predict alliance formation in adult male bottlenose dolphins. *Behavioral Ecology*, 31, 361–370. https://doi.org/10.1093/beheco/arz195

Graves, B. M., & Duvall, D. (1987). An experimental study of aggregation and thermoregulation in prairie rattlesnakes (Crotalus viridis viridis). *Herpetologica*, 43, 259–264.

Graves, B. M., & Duvall, D. (1995). Aggregation of squamate reptiles associated with gestation, oviposition, and parturition. *Herpetological Monographs*, 9, 102. https://doi.org/10.2307/1466999

Gregory, P. T. (1984). Communal denning in snakes. In R. A. Seigel, L. E. Hunt, J. L. Knight, L. Malaret L, N. L. Zuschlag (Eds.). *Vertebrate ecology and systematics: A tribute to Henry S. Fitch*, Vol. 10 (pp. 57–76); University of Kansas Museum of Natural History Special Publications.

Griffiths, S. W. (2003). Learned recognition of conspecifics by fishes. *Fish and Fisheries*, 4, 256–268. https://doi.org/10.1046/j.1467-2979.2003.00129.x

Guenther, A., Finkemeier, M. A., & Trillmich, F. (2014). The ontogeny of personality in the wild guinea pig. *Animal Behaviour*, 90, 131–139. https://doi.org/10.1016/j.anbehav.2014.01.032

Heller, S., & Halpern, M. (1982). Laboratory observations of aggregative behavior of garter snakes, Thamnophis sirtalis. *Journal of Comparative and Physiological Psychology*, 96, 967–983. https://doi.org/10.1037/0735-7036.96.6.967

Herzog, H. A., & Burghardt, G. M. (1986). Development of antipredator responses in snakes: I. Defensive and open-field behaviors in newborns and adults of three species of garter snakes (Thamnophis melanogaster, T. sirtalis, T. butleri). *Journal of Comparative Psychology*, 100, 372–379. https://doi.org/10.1037/0735-7036.100.4.372

Herzog, H. A., & Burghardt, G. M. (1988). Development of antipredator responses in snakes: III. Stability of individual and litter differences over the first year of life. *Ethology*, 77, 250–258. https://doi.org/10.1111/j.1439-0310.1988.tb00208.x

Hoss, S. K., Deutschman, D. H., Booth, W., & Clark, R. W. (2015). Post-birth separation affects the affiliative behaviour of kin in a pitviper with maternal attendance. *Biological Journal of the Linnean Society*, 116(3), 637–648. https://doi.org/10.1111/bij.12604

Jacoby, D. M. P., Lauren, N. F., David, W. S., & Darren, P. C. (2014). Shark personalities? Repeatability of social network traits in a widely distributed predatory fish. *Behavioral Ecology Sociobiology*, 68, 1995–2003. https://doi.org/10.1007/s00265-014-1805-9

Jones, T. B., Green, J. A., Patrick, S. C., Evans, J. C., Wells, M. R., Rodríguez-Malagón, M. A., & Arnould, J. P. Y. (2020). Consistent sociality but flexible social associations across temporal and spatial foraging contexts in a colonial breeder. *Ecology Letters*, 23, 1085–1096. https://doi.org/10.1111/ele.13507

Krause, J., James, R., & Croft, D. P. (2010). Personality in the context of social networks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 4099–4106. https://doi.org/10.1098/rstb.2010.0216

Krause, J., James, R., Franks, D., & Croft, D. (2015). *Animal social networks (UK ed.)*. Oxford University Press.

Krause, J., & Ruxton, G. (2002). *Living in groups (Oxford Series in Ecology and Evolution)*. 1st ed. Oxford University Press.

Krause, S., Wilson, A. D. M., Ramnarine, I. W., Herbert-Read, J. E., Clement, R. J. G., & Krause, J. (2017). Guppies occupy consistent positions in social networks: Mechanisms and consequences. *Behavorial Ecology*, 28, 429–438.

Kulahci, I. G., Ghazanfar, A. A., & Rubenstein, D. I. (2018). Consistent individual variation across interaction networks indicates social personalities in lemurs. *Animal Behaviour*, 136, 217–226. https://doi.org/10.1016/j.anbehav.2017.11.012

Larsen, K. W., Gregory, P. T., & Antoniak, R. (1993). Reproductive ecology of the common garter snake thamnophis sirtalis at the Northern limit of its range. *American Midland Naturalist*, 129, 336. https://doi.org/10.2307/2426514

LeMaster, M. P., & Mason, R. T. (2001). Evidence for a female sex pheromone mediating male trailing behavior in the red-sided garter snake, thamnophis sirtalis parietalis. *Chemoecology*, 11, 149–152. https://doi.org/10.1007/PL00001845

Lorch, J. M., Knowles, S., Lankton, J. S., Michell, K., Edwards, J. L., Kapfer, J. M., Staffen, R. A., Wild, E. R., Schmidt, K. Z., Ballmann, A. E., Blodgett, D., Farrell, T. M., Glorioso, B. M., Last, L. A., Price, S. J., Schuler, K. L., Smith, C. E., Wellehan, J. F. X., & Blehert, D. S. (2016). Snake fungal disease: An emerging threat to wild snakes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371, 20150457. https://doi.org/10.1098/rstb.2015.0457

Lyman-Henley, L. P., & Burghardt, G. M. (1994). Opposites attract: Effects of social and dietary experience on snake aggregation behaviour. *Animal Behaviour*, 47, 980–982. https://doi.org/10.1006/anbe.1994.1131

Nash, D. J., & Griffiths, R. A. (2018). Ranging behaviour of adders (Vipera berus) translocated from a development site. *Herpetological Journal*, 28, 155–159.

Naug, D. (2009). Structure and resilience of the social network in an insect colony as a function of colony size. *Behavioral Ecology Sociobiology*, 63, 1023–1028. https://doi.org/10.1007/s00265-009-0721-x

Noble, G. K., & Clausen, H. J. (1936). The aggregation behavior of Storeria dekayi and other snakes, with especial reference to the sense organs involved. *Ecological Monographs*, 6, 269–316. https://doi.org/10.2307/1943244

Plaza, M., Burke, T., Cox, T., Flynn-Carroll, A., Girndt, A., Halford, G., Martin, D. A., Sanchez-Fortún, M., Sánchez-Tójar, A., Somerville, J., & Schroeder, J. (2020). Repeatable social network node-based metrics across populations and contexts in a passerine. *Journal of Evolutionary Biology*, 33, 1634–1642. https://doi.org/10.1111/jeb.13703

Polverino, G., Ruberto, T., Staaks, G., & Mehner, T. (2016). Tank size alters mean behaviours and individual rank orders in personality traits of fish depending on their life stage. *Animal Behaviour*, 115, 127–135. https://doi.org/10.1016/j.anbehav.2016.03.013

Prehn, S. G., Laesser, B. E., Clausen, C. G., Jønck, K., Dabelsteen, T., & Brask, J. B. (2019). Seasonal variation and stability across years in a social network of wild giraffe. *Animal Behaviour*, 157, 95–104. https://doi.org/10.1016/j.anbehav.2019.08.018

Reichenbach, N. G. (1983). An aggregation of female garter snakes under corrugated metal sheets. *Journal of Herpetology*, 17, 412. https://doi.org/10.2307/1563599

Riley, J. L., Guidou, C., Fryns, C., Mourier, J., Leu, S. T., Noble, D. W. A., Byrne, R. W., & Whiting, M. J. (2018). Isolation rearing does not constrain social plasticity in a family-living lizard. *Behavioral Ecology*, 29, 563–573. https://doi.org/10.1093/beheco/ary007

Roberts, B. W., & DelVecchio, W. F. (2000). The rank-order consistency of personality traits from childhood to old age: A quantitative review of longitudinal studies. *Psychological Bulletin*, 126, 3–25. https://doi.org/10.1037/0033-2909.126.1.3

Rodgers, G. M., Ward, J. R., Askwith, B., & Morrell, L. J. (2011). Balancing the dilution and oddity effects: Decisions depend on body size. *PLoS One*, 6, e14819. https://doi.org/10.1371/journal.pone.0014819

Romano, V., Shen, M., Pansanel, J., MacIntosh, A. J. J., & Sueur, C. (2018). Social transmission in networks: Global efficiency peaks with intermediate levels of modularity. *Behavioral Ecology Sociobiology*, 72, 154. https://doi.org/10.1007/s00265-018-2564-9

Rossman, D. A., Ford, N. B., & Richard, A. S. (1996). *The garter snakes: Evolution and ecology (animal natural history series*, Vol. 2. University of Oklahoma Press, Norman.

Sakai, O. (2018). Comparison of personality between juveniles and adults in clonal gecko species. *Journal of Ethology*, 36, 221–228. https://doi.org/10.1007/s10164-018-0551-2

Schuett, G. W., Clark, R. W., Repp, R. A., Amarello, M., & Greene, H. W. (2017). Social behavior of rattlesnakes: A shifting paradigm. In

G. W. Schuett, M. J. Feldner, C. F. Smith, & R. S. Reiserer (Eds.). *Rattlesnakes of Arizona*, Vol. *2* (pp. 61–244). Eco Publishers, Rodeo.

Shaw, E. (1978). Schooling Fishes. *American Scientist*, *66*, 166–175.

Shine, R., O'Connor, D., LeMaster, M. P., & Mason, R. T. (2001). Pick on someone your own size: Ontogenetic shifts in mate choice by male garter snakes result in size-assortative mating. *Animal Behaviour*, *61*, 1133–1141. https://doi.org/10.1006/anbe.2001.1712

Shine, R., Webb, J. K., Lane, A., & Mason, R. T. (2006). Flexible mate choice: A male snake's preference for larger females is modified by the sizes of females encountered. *Animal Behaviour*, *71*, 203–209. https://doi.org/10.1016/j.anbehav.2005.04.005

Shine, R., Webb, J. K., Lane, A., & Mason, R. T. (2012). Familiarity with a female does not affect a male's courtship intensity in garter snakes thamnophis sirtalis parietalis. *Current Zoology*, *58*(6), 805–811. https://doi.org/10.1093/czoolo/58.6.805

Sih, A., Bell, A., & Johnson, J. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution*, *19*, 372–378. https://doi.org/10.1016/j.tree.2004.04.009

Silk, M. J., Croft, D. P., Tregenza, T., & Bearhop, S. (2014). The importance of fission-fusion social group dynamics in birds. *Ibis*, *156*, 701–715. https://doi.org/10.1111/ibi.12191

Šimková, O., Frýdlová, P., Žampachová, B., Frynta, D., & Landová, E. (2017). Development of behavioural profile in the Northern common boa (Boa imperator): Repeatable independent traits or personality? *PLoS One*, *12*, e0177911. https://doi.org/10.1371/journal.pone.0177911

Skinner, M., & Miller, N. (2020). Aggregation and social interaction in garter snakes (Thamnophis sirtalis sirtalis). *Behavioral Ecology Sociobiology*, *74*, 1–13. https://doi.org/10.1007/s00265-020-2827-0

Smith, J. E., Gamboa, D. A., Spencer, J. M., Travenick, S. J., Ortiz, C. A., Hunter, R. D., & Sih, A. (2018). Split between two worlds: Automated sensing reveals links between above- and belowground social networks in a free-living mammal. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*, 20170249. https://doi.org/10.1098/rstb.2017.0249

Sosa, S., Puga-Gonzalez, I., Hu, F., Pansansel, J., Xie, X., & Sueur, C. (2020). A multilevel statistical toolkit to study animal social networks: The animal network toolkit software (ANTs) R package. *Scientific Reports*, *10*, 12507. https://doi.org/10.1038/s41598-020-69265-8

Stanley, C. R., Mettke-Hofmann, C., Hager, R., & Shultz, S. (2018). Social stability in semiferal ponies: Networks show interannual stability alongside seasonal flexibility. *Animal Behaviour*, *136*, 175–184. https://doi.org/10.1016/j.anbehav.2017.04.013

Taborsky, B., & Oliveira, R. F. (2012). Social competence: An evolutionary approach. *Trends in Ecology & Evolution*, *27*, 679–688. https://doi.org/10.1016/j.tree.2012.09.003

Tukey, J. W. (1977). *Exploratory data analysis*. Addison-Wesley.

Waters, R. M., Bowers, B. B., & Burghardt, G. M. (2017). Personality and individuality in reptile behavior. In J. Vonk, A. Weiss, & S. A. Kuczaj (Eds.). *Personality in nonhuman animals* (pp. 153–184). Springer. https://doi.org/10.1007/978-3-319-59300-5

Wilson, A. D. M., Krause, S., Dingemanse, N. J., & Krause, J. (2013). Network position: A key component in the characterization of social personality types. *Behavioral Ecology Sociobiology*, *67*, 163–173. https://doi.org/10.1007/s00265-012-1428-y

Yeager, C. P., & Burghardt, G. M. (1991). Effect of food competition on aggregation: Evidence for social recognition in the plains garter snake (Thamnophis radix). *Journal of Comparative Psychology*, *105*, 380–386. https://doi.org/10.1037/0735-7036.105.4.380

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