

Intense sociability in a “non-social” snake (*Python regius*)

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## **Abstract**

It has been suggested that social behavior in squamates evolved partly due to increased interaction opportunities at communal dens and/or due to vivipary. Ball pythons are not viviparous, are not known to communally den, and are often assumed to be non-social. However, as ball pythons are highly cryptic, little is actually known about their social behavior. Here, we examine social interactions and their relationship to personality in juvenile ball pythons (*Python regius*; n=30) and find evidence, contrary to expectations, that they are highly gregarious. We tested snakes in both an aggregation assay and in individual personality tests. For the aggregation assay, 5 separate mixed-sex groups of 6 snakes were tracked in a large arena for 10 days. For the personality tests, we tested snakes alone for boldness and sociability. We assessed the snakes' social interaction patterns within and between the group and individual assays. We found that ball pythons spent much of their time in one large aggregate and used a home base to facilitate social interaction. The snakes were less consistent in their behavior during individual testing, resulting in flexible, rather than consistent, behavior across contexts. Social complexity is thought to determine the number and nature of social interactions between conspecifics, which often results in only testing species that exhibit highly visible social behaviors. Our findings demonstrate that such biased sampling, which often ignores cryptic behavior, provides an incomplete picture of the biological and ecological factors that influence social behavior.

## **Significance statement**

Juvenile ball pythons are surprisingly social. Animal social behavior is usually assessed in species with easily detectable social interactions, which risks missing social behaviors in less visible species. The ecologies of these social species are often then used to inform theories about the origins of social behaviors. For example, in snakes, social behavior is most commonly tested in species that are known to aggregate in dens. We tested social interaction in ball pythons, who have very different ecologies than the denning snakes typically tested for social behavior. We found that ball pythons had large, stable social groups which were facilitated by the use of a home base. These results challenge many assumptions about the causes of sociability in reptiles.

## Introduction

Snake social interactions can be difficult to observe and quantify, as they are secretive, and their communication is often (but not always) mediated by invisible pheromones (Halpern and Kubie 1984; Doody et al. 2021). Our lack of understanding of snake social behavior is further exacerbated by taxonomic biases, in which reptile behavior is comparatively under-researched compared to mammals and birds (Bonnet et al. 2002; Pawar 2003).

Despite this, researchers are increasingly demonstrating the complex nature of social interactions in snakes and other reptiles (Skinner and Miller 2020; Doody et al. 2021). For example, parental care of neonates has been found in vipers (Greene et al. 2002) and Southern African pythons (*Python natalensis*; Alexander 2018); male red-sided gartersnakes (*Thamnophis sirtalis parietalis*) deceive other males to improve their mating success (Mason and Crews 1985); and female Taiwanese kukri snakes (*Oligodon formosanus*) demonstrate territorial resource defense (Huang et al. 2011). Along with these varied social behaviors, snakes also commonly display a tendency to aggregate, in both laboratory and natural environments (Dundee and Miller 1968; Heller and Halpern 1982; Burghardt 1983; Graves and Duvall 1995; Skinner and Miller 2020). Although aggregations of animals can occur for non-social reasons, such as a mutual attraction to a resource (Gregory 2004; Spiegel et al. 2016), research on snake aggregations has shown patterns that suggest they are driven by social considerations. For example, Butler's gartersnakes (*Thamnophis butleri*) prefer to aggregate with unfamiliar littermates, that were reared on different diets (Lyman-Henley and Burghardt 1994), and plains gartersnakes (*Thamnophis radix*) prefer to aggregate with individuals they have not recently competed with for food (Yeager and Burghardt 1991). Research has suggested that social considerations are particularly important in species of snakes that aggregate at denning sites for mating and brumation. For example, preferred association during den-site aggregation has been demonstrated in timber rattlesnakes (*Crotalus horridus*; Clark et al. 2012) and Arizona black rattlesnakes (*Crotalus cerberus*; Schuett et al. 2017). In addition, laboratory research on eastern gartersnakes (*Thamnophis sirtalis sirtalis*), who also aggregate at den sites for mating and hibernation, has demonstrated coordinated exploration, non-random association patterns, and consistent social personalities (Skinner and Miller 2020, 2022). Overall, snake social interactions can vary depending on kinship, weight, sex, personality (boldness), and previous experience (Skinner and Miller 2020; Doody et al. 2021; Skinner et al. 2024). In addition to strongly implying that social decisions involve sophisticated cognition in snakes, this pattern of results suggests that snakes may be differentially exploiting the benefits of aggregation.

Aggregation has numerous benefits for snakes, including protection from predation, reduced water loss, and improved thermoregulation (Nobel and Clausen 1936; Graves and Duvall 1995; Aubret and Shine 2009). Considering the propensity for large aggregations of snakes to form at den sites in northern climates, it has also been suggested that, along with physiological benefits, access to mates may also drive aggregations (Gregory 1974). Aggregation also entails costs such as resource competition, which may be an important driver of variation in sociability among individuals (Yeager and Burghardt 1991; Riley et al. 2017) and between species (Gardner et al. 2015).

Despite these advances in understanding sociability in aggregative snake species, little is known about how less gregarious snake species interact with conspecifics, though existing work has suggested surprising social behaviors. For example, Erabu sea kraits (*Laticauda semifaciata*)

appear to coordinate hunting with conspecifics and predatory fish (Somaweera et al. 2023); Indian pythons (*Python molurus*) form dominance hierarchies (Barker et al. 1979); and social contact can reduce stress in Southern Pacific rattlesnakes (*Crotalus helleri*), in populations that do and do not den communally (Martin et al. 2023). Patterns of social behavior also occur in other reptile orders often considered less gregarious. For example, research has shown social learning in red-footed tortoises (*Geochelone carbonaria*; Wilkinson et al. 2010) and lizards (bearded dragons; *Pogona vitticeps*; Kis et al. 2015; Italian wall lizards; *Podarcis bocagei*; Damas-Moreira et al. 2018), as well as gaze following in geckos (*Eublepharis macularius*; Simpson and O'Hara 2019). Establishing such patterns of social behavior across reptiles is important not just for improving our understanding of the evolution of sociality, but also for conservation efforts (Choquette et al. 2022), and captive welfare (Burghardt 2013; Martin et al. 2023).

Here, we tested aggregation and social behavior in a snake that is thought to be solitary and is not known to aggregate in large groups, ball pythons (also royal pythons; *Python regius*). We used a similar procedure to that recently used to investigate social behavior in eastern gartersnakes, combining a group aggregation assay with individual tests of sociability and boldness. In gartersnakes, these assays demonstrated preferential associations, coordinated exploration, group effects on boldness, and stable social personalities (Skinner and Miller 2020, 2022). By utilizing a similar process in ball pythons, we can explore to what extent different social behaviors in snakes may be a function of their ecology. As a warm climate, oviparous (i.e., egg laying) species, ball pythons lack many of the characteristics that are thought to influence aggregation and social behavior in squamate reptiles, such as live birth (Halliwell et al. 2017) and seasonal aggregation for mating, gestation, and hibernation (Gregory 1974; Graves and Duvall 1995). As they are primarily ambush predators, spending most of their time stationary, they may also encounter conspecifics less frequently than gartersnakes. We conceptualize social behavior broadly as any interaction between two or more conspecifics (Allaby 2009; Doody et al. 2013; Ward and Webster 2016), avoiding a social/non-social dichotomy (Doody et al. 2013, 2023; Ward and Webster 2016). This approach facilitates cross-species comparisons in the types of social behaviors displayed, and a better understanding of the evolution of sociality (Doody et al. 2013). Under the umbrella of social behavior, we use the term 'sociability' to refer to social attraction (Gartland et al. 2022), and 'sociality' for patterns of social behavior that emerge during repeat interactions (Ward and Webster 2016).

Ball pythons are a relatively small python species endemic to west-central Africa. They are common in the pet trade, probably due to their docile nature (Brashears et al. 2020). Like most species of snake, ball pythons are highly secretive, and little is known about their behavior (Brattstrom, 1974; Aubret et al. 2005; Doody et al. 2021). There has been only one experiment in which the social behavior of a species of python has been observed in a controlled environment (Barker et al. 1979). In this study, one female and four male adult Indian pythons were observed in an enclosed space. The authors observed ritual combat between the males, resulting in the formation of a linear dominance hierarchy. The snakes' social behavior was predictable based on dominance rank, which also determined mating priority. Here we tested social behavior in mixed-sex groups of juvenile ball pythons. Although we did not expect to observe combat in juveniles, we hypothesized that traits found to be important for social behavior in other squamate species, such as sex, size, and personality (Cote and Clobert 2007; Hoss et al 2015; Skinner and Miller 2020, 2022), might influence the structure of intraspecific interactions in these snakes as

well. As ball pythons are not known to be social, we predicted that their networks would be diffuse (i.e., separated individuals with few interactions) and that they would not show preferential associations with some conspecifics over others.

## **Material & Methods**

### *Subjects and Housing*

Subjects were 30 juvenile ball pythons (13 M; 17 F) acquired from 3 local breeders. The snakes were subdivided into 5 cohorts of 6 individuals each. Cohorts 1 and 5 had four females and two males. All other cohorts had three females and three males. Cohorts 1 and 2 consisted of snakes of unknown parentage combined from two separate breeders. Cohorts 3, 4, and 5 consisted of unrelated individuals. When forming cohorts, we prioritized combining unrelated individuals, then having even sex ratios. Ultimately, the composition of our groups was determined by the available animals. A temperature-controlled room with a 12-hour reverse light cycle (lights off at 7 am) and an ambient temperature of 28° C (humidity 50 -70%) was used to house and test the ball pythons. The snakes were housed individually in translucent tubs measuring 84 cm x 44.5 cm x 14.5 cm (ARS-7030 snake rack, ARS Caging, Indianapolis, IN). The snakes had access to shelters (23 cm x 16 cm x 6.5 cm; Cornel's World, Calgary, AB) on both the warm and cool sides of the tub, as well as subsurface heating (32° C) provided by heat tape (THGTape, Cornel's World, Calgary, AB). The snakes had two water dishes, one forward in the enclosure (11.5 cm x 7.5 cm) and one placed over the heat tape (15 cm x 15 cm x 6 cm; Ziplock). Water was changed daily. Snakes were identified by their unique patterning and, during testing, by shapes drawn with nontoxic green nail polish on their heads (Adrienne K).

### *Apparatus*

The aggregation experiment was conducted in a large arena which was an upscaled version of the apparatus described for gartersnakes by Skinner and Miller (2020). The arena walls were made of PVC (120.5 cm x 112 cm x 24 cm), with clear acrylic walls extending the height another 32 cm, to prevent escapes (Fig. S1A). Four square plastic water dishes (15 cm x 15 cm x 6 cm; Ziplock) and six PVC shelters (41 cm x 24 cm x 9; Cornel's World) were evenly spaced within the arena. Pilot testing established that six snakes could easily fit within a shelter. Sixteen square sandstone coasters were placed in the centre of the arena. Each shelter had white paper towels underneath it for cleaning purposes (Fig. S1A). A high-resolution camera (Canon EOS Rebel T5i DSLR) was mounted above the arena and took a picture every 5 seconds during the experiment. During the night cycle, light was provided by red LED light strips attached to the wall 1 meter above the arena (650 nm). Individual snakes could be identified in the pictures.

Individual boldness and sociability tests were carried out in 88 cm x 46.5 cm x 37.5 cm high PVC arenas. The substrate for the boldness test was butcher paper, while the substrate for the sociability test was white paper towel. One black plastic reptile shelter (14 cm x 10.2 cm x 5 cm high; Cornel's World), identical to the shelter in the home tubs, was placed against the middle of one long wall for the boldness test. Two black plastic reptile shelters, identical to those used in the boldness assay, were positioned at the opposing short ends of the arena for the sociability assay (see Fig. S1B). One shelter was designated the Stimulus Shelter and the other one the Control Shelter. For the stimulus shelter, a piece of filter paper with 0.25 ml of a ball python skin lipid solution was placed at the entrance. An equivalent amount of dichloromethane, which was

the solvent used for the stimulus, was placed on filter paper at the entrance to the control shelter. The skin lipid solution was created by extracting skin lipids from ball python sheds, using a procedure adapted from Graves and Halpern (1988) and fully described in Skinner and Miller (2020). A variety of sheds were combined to make the solution including sheds from both adult and juvenile males and females. The sheds were donated by the Toronto Zoo. Before testing, the filter paper was allowed to dry for 15 minutes so that the dichloromethane was evaporated. The location of the stimulus shelter (left or right) was pseudorandomized across trials. Sociability was measured as time near the social stimulus (Cote and Clobert 2007; Waters et al. 2017; Skinner and Miller 2020; Skinner et al. 2022). We placed two arenas beside each other, so that two snakes could be tested simultaneously. 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.

### *Aggregation experiment*

The procedure for the aggregation experiment was based on Skinner and Miller (2020). One day before testing, each snake's head was marked with a green shape using non-toxic nail polish. Shape combinations were unique within each cohort. Testing occurred when snakes were between the ages of 4 and 8 months. Body mass at the time of testing ranged from 119 to 387 g ( $M = 243.17$ ,  $SD = 72.46$ ; Table S1). These weights were within the juvenile range estimated by Aubret et al. (2005). Throughout this document, body mass is used to represent size.

Snakes were released into the enclosure on the evening before the first full day of the experiment. Snakes remained in the experimental apparatus for 10 full days and were removed on the morning of day 11. Each day, at approximately 10:00 and 14:00 (during the relatively dark part of their light cycle), 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 a designated shelter (placed shuffle). Each snake's designated shelter did not change across testing. For the first 8 days of the experiment, the center shuffle pattern was used for both the 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). For days 9 and 10, the center shuffle was used. The placed shuffle ensured that each snake started the test segment alone, so that social choices could be monitored. The center shuffle ensured that the physical movements required to reform groups differed. The water dishes, paper towels, and shelters were changed once daily during the morning shuffle, and the surrounding areas were cleaned with 70% isopropyl alcohol before being thoroughly washed and dried. The entire arena was cleaned with water and isopropyl alcohol on Days 3 and 7. To reduce food-motivated behavior, snakes were kept on their regular feeding schedule during the experiment. They were fed a small frozen-thawed rat on the day they entered the experiment, and again during cleaning on day 7. As ball pythons are nocturnal/crepuscular, shuffles occurred during the snakes' night period (7:00 to 19:00). Red light illuminated the arena 24 hrs a day, but at 19:00 a room light turned on which differentiated 'night' from 'day'. The shuffles, combined with the light cycle, subdivided each day into 4 periods: before the first shuffle (7:00 - 10:00), between the shuffles (10:00 - 14:00), after the shuffles (14:00 - 19:00 pm), and the daytime period when the room light was on (19:00 - 7:00). These periods are hereafter referred to as before shuffle, 1st shuffle, 2nd shuffle, and lights on, respectively. Snakes were undisturbed during the lights on and before shuffle periods.

During testing it became apparent that snakes were aggregating in a homebase shelter. To test if there was something unique about the homebase shelter, on the 1st shuffle of day 9, the homebase shelter was removed and, for cohorts 3, 4, and 5, an additional control shelter was removed (the furthest shelter not directly opposite the preferred shelter). On rare occasions, the snakes would transition their aggregate to a new homebase. In this situation, the most recent homebase was removed. On the morning of day 10, the shelter(s) were placed back into the arena in their original locations. Due to this disturbance, the data for these two days are analyzed separately and only included in the relevant models.

### *Individual behavioral assays*

Snakes completed the individual boldness and sociability assays following the aggregation assay. Cohorts 3, 4, and 5 were tested within 1-2 weeks of completing the aggregation assay. Due to a facility-wide closure at the beginning of the COVID-19 pandemic, cohorts 1 and 2 could not be tested individually until 4 months after their aggregation assay. Snakes were not tested on the day they were fed. Snakes were tested during their night cycle and completed no more than one test per day. The individual boldness and sociability assays are based on Skinner and Miller (2020). Snakes were placed with their heads near the shelter's entrance for the boldness test and, once inside, they were left alone to complete the test. The proportion of the session they spent away from the safety of the shelter was used as a measure of boldness (Jolles et al. 2016; Koenig and Ousterhout 2018; Tang and Fu 2020). For the sociability assay, snakes were placed in an inverted transparent plastic container (27. x 6.5 x 13 cm). The container was placed in the middle of the arena central to both shelters and the snakes were allowed 90 seconds to habituate. The plastic container was then raised, and the snake was free to explore the arena. The time spent in or on the stimulus shelter was used as a measure of sociability. Both boldness and social assays lasted for 20 min and each snake completed each assay twice, with at least one week between trials of the same type. All assays were video-recorded from above using a Panasonic HC-V700 camcorder.

### *Analysis*

Images from the aggregation assay and videos from the individual tests were coded using a custom ethologger program (Fig. S1; see Skinner and Miller 2020; Skinner et al. 2022). For each assay type, the ethologger divided the arena image into multiple zones. There was one zone for each shelter and one zone for the space outside the shelters. As there were six shelters in the aggregation assay, two in the sociability assay, and one in the boldness assay, there were seven, three, and two zones, respectively. We recorded the location of each snake whenever they crossed zone boundaries. We used time sharing the same shelter/zone to codify sociability and to construct social networks. To minimize observer bias, blinded methods were used when behavioral data were recorded and coded.

All statistical analyses were conducted in R version 4.2.1 (R Core Team 2022) using the *DescTools*, *lme4*, *igraph*, *asnipe*, *LambertW*, and *ANTs* packages. We measured the time spent sharing the same shelters/zones and also quantified individual choices such as time spent in a shelter and order of arrival at an aggregation site/shelter. We used mixed-effect linear models to analyze repeated measures data. To account for repeated measures, all of our models contained a random intercept for subject. For the majority of models, we nested subject in cohort. However,

to facilitate model convergence it was sometimes necessary to remove cohort as a random effect. For models that used frame counts as the dependent variable, we used generalized mixed effect models with a negative binomial distribution. To account for any variance resulting from the delay between group and individual testing for cohorts 1 and 2, we added a binomial covariate ‘delay’ to any model that examined the relationship between individual personality measures and behavior in the group.

We used the times that snakes spent together in a shelter/zone to construct weighted association networks, in which the weight of each edge is proportional to the total time each dyad spent together. To quantify sociability, we used the social network measure weighted degree, which is the sum of the weights of all the edges connected to a node (an individual snake). For network-derived models, we confirmed significant findings with 1000 node-label permutations. We did not use network permutations, as many networks were completely connected. As such, we explicitly tested for type 1 error rates by randomizing the independent variables 1000 times while holding the dependent variable constant. This is reported as the random alpha ( $\alpha_R$ ). For individual testing, we used the *rptR* package to test for the repeatability of boldness or sociability across trials (Nakagawa and Schielzeth 2010). In the aggregation experiment, we tested for repeatability in sociability (i.e., consistency in network position) over days using the network rank-order randomization method from Wilson et al. (2013). We looked for association preferences using the edge weight concentration coefficient (McDonald and Hobson 2018) which describes the difference between observed and expected edge weight variance. The larger the difference between the two values, the larger the edge weight concentration coefficient, and the more biased a snake’s relationships are towards certain other individuals.

To test for coordinated exploration, we performed a data permutation. To control for individual differences in sheltering and exploration times, as well as exploration triggered by light level changes, we separately sampled the time spent exploring and sheltering for each individual snake within each portion of the day. Additionally, we constrained sampling to after a snake made its first choice after a shuffle. In other words, the data consisted of time spent in multiple exploration and sheltering events for each individual. Within each time of day, for each individual, the time spent in exploration and sheltering events was shuffled to construct randomized data. The number of individuals co-exploring in these random data streams was then compared to actual co-occurrences. This had the effect of constructing null models that maintained the general data structure while removing any coordination in movements between snakes. We compared the actual mean number of snakes exploring (ignoring times when no snakes were exploring) to a null model consisting of 1000 randomized datastreams.

For all linear models, when the residuals were not normally distributed, we applied data transformations. For proportional data, we used arcsine transformation. For all other variables, we used log transformations or the Gaussianize function from the *LambertW* package. For some models, it was desirable to control for differences in exploration tendencies between snakes. For these models, we included the amount of time each snake spent exploring as a covariate.

## **Results**

### *Individual context: Personality assays*



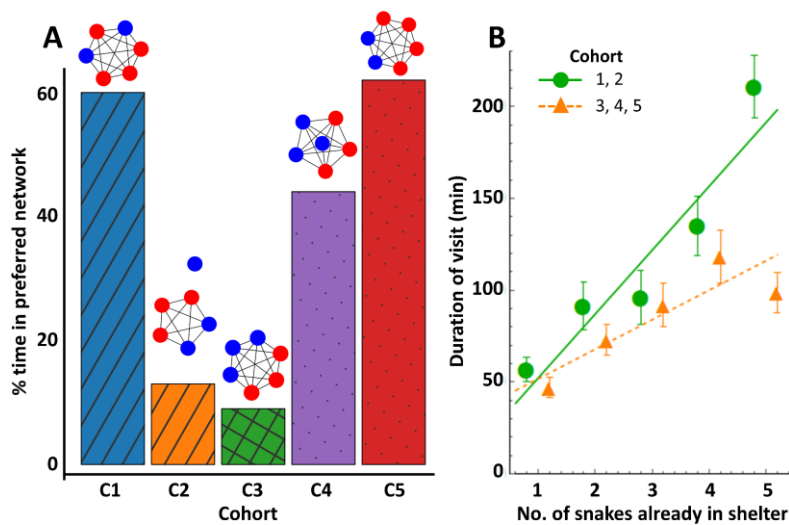
Boldness was highly repeatable across the two solo trials ( $R_{adj} = 0.51$ , CI [0.22, 0.75],  $p < 0.001$ ), and there was no significant effect of body mass ( $F(1, 4.4) = 2.87$ ,  $p = 0.16$ ) or trial ( $F(1, 29) = 0.38$ ,  $p = 0.54$ ) on boldness. Male snakes were bolder than females (mean proportion of time outside the shelter: males, 0.59,  $SD \pm 0.23$ ; females, 0.4,  $SD \pm 0.28$ ;  $F(1, 24.4) = 5.21$ ,  $p = 0.03$ ). We averaged the two boldness trials when looking at the effect of individual boldness scores on group behavior. For sociability, there was no repeatability across trials ( $R_{adj} = 0.07$ , CI [0, 0.44],  $p = 0.36$ ). Analysis of the sociability scores found no effect of body mass ( $F(1, 27) = 2.48$ ,  $p = 0.13$ ) but a significant effect of sex with males tending to prefer the social shelter ( $F(1, 27) = 4.62$ ,  $p = 0.04$ ; mean proportion of session in social shelter = 0.62,  $SD \pm 0.35$ ) and females tending to avoid the social shelter (mean = 0.42,  $SD \pm 0.39$ ). As we found no repeatability across trials, we compared group sociability to the first individual social score (Skinner and Miller 2020). This was done assuming that initial reactions are more representative of sociability, due to the lack of social contact available in the social shelter. We found no correlation between boldness and sociability in the individual tests ( $F(1, 31) = 2.14$ ,  $p = 0.15$ ).

#### *Group context: Aggregation assay*

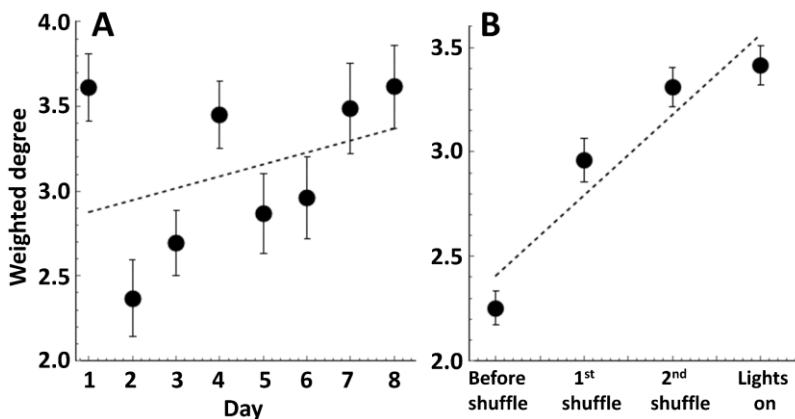
In the aggregation assay, snakes spent most of their time in shelters (mean proportion of session = 0.92,  $SD \pm 0.06$ ), usually in large groups. Although we often placed the snakes alone in shelters during shuffles, in all cohorts except cohort 2, the most common configuration of snakes was all of them together in a shelter (group size: mode = 6, mean = 4.25). The most common configuration for cohort 2 was five snakes together and one snake alone. Across the first eight days of the experiment, some cohorts spent more than half their time all together, with cohorts 1 and 5 spending 60% and 62% of their time, respectively, in one large aggregate. In other words, despite their reputation for being solitary, ball pythons in our apparatus were strongly attracted to others, often preferring to aggregate in the same shelter. Cohorts with more females tended to spend more time in their preferred networks (Fig. 1A;  $M4_{\text{♀}} = 61\%$ ,  $SD = 1.14$ ,  $M3_{\text{♀}} = 22\%$ ,  $SD = 19.15$ ; Kruskal–Wallis  $H(1) = 3$ ,  $p = 0.08$ ). Cohorts also differed in sociability (i.e., mean weighted degree) across days ( $F(4, 23.35) = 62.99$ ,  $p < 0.001$ ), with cohorts 1 and 5 being the most sociable (Fig. S2).

After being shuffled, as snakes traversed the arena and selected shelters, they tended to remain for longer in shelters that already contained more snakes (Fig. 1B;  $F(1, 3351.8) = 45.67$ ,  $p < 0.001$ ). The relationship between the number of snakes in a shelter and the duration of an arriving snake's stay there differed by cohort ( $F(1, 3357.2) = 8.31$ ,  $p < 0.001$ ), being stronger for cohorts 1 and 2 than cohorts 3, 4, and 5 (all  $t$ 's  $> 3.09$ , all  $p < 0.02$ ; post-hoc analyses showed that time spent in a shelter with 1 snake was significantly lower than if there were 2, 3, or 4 snakes already present in the shelter [all  $z < -4.7$ , all  $p < 0.001$ ], and marginally less than if there were 5 snakes [ $z = -2.69$ ,  $p = 0.06$ ]; snakes also remained for less time in shelters with 2 snakes than in shelters with 4 snakes [ $z = -2.78$ ,  $p = 0.04$ ]).

Sociability increased significantly both across days ( $\beta(202.83) = 0.07$ ,  $t = 2.91$ ,  $p = 0.004$ ; Fig. 2A) and time periods within a day ( $\beta(879.7) = 0.39$ ,  $t = 11.00$ ,  $p < 0.001$ ; Fig. 2B). This may have been caused by an increase in the speed or efficiency with which snakes made their final aggregation choices after each shuffle across days ( $F(1, 436.11) = 16.6$ ,  $p < 0.001$ ; Fig. S3). The placement of the snakes during shuffles (centrally or in shelters) had no effect on their aggregation formation time ( $F(1, 436.4) = 1.74$ ,  $p = 0.19$ ).



**Figure 1.** Ball pythons aggregate. **A:** most common social network and the percentage of time that the snakes spent in that configuration (first 8 days), for each of the five experimental cohorts (C1 - C5). The most common configuration for the cohort is represented above each bar; red nodes are female snakes, blue nodes are males. Values were calculated by determining all the social configurations formed across all days, then determining the percentage of the total frames spent in each. **B:** mean duration of visits to a shelter as a function of the number of snakes already in that shelter. Cohorts are grouped by statistical similarity (see main text). Error bars are  $\pm$  standard error of the mean



**Figure 2.** Average sociability collapsed across cohorts for the first 8 days of the group experiment, by day (**A**) or day segment (**B**). Sociability is measured by weighted degree. Error bars are  $\pm$  standard error of the mean

Due to the extremely high sociability the snakes displayed, and the tendency for their networks to be highly connected (often all-to-all) for extended periods, snakes did not spend more time with specific other individuals. Analysis of edge-weight variance showed that the snakes had highly dispersed sociability patterns, with very little preference in their associations. Compared to permuted networks, the mean concentration coefficient (CC) for cohorts 1 and 2 suggested that their association networks were significantly more dispersed than expected by chance (C1,  $CC_{\text{obs}} = 0.001$ , mean  $CC_{\text{rand}} = 0.002$ ,  $SD < 0.001$ ,  $z = -2.36$ ,  $p = 0.02$ ; C2,  $CC_{\text{obs}} = 0.045$ , mean  $CC_{\text{rand}} = 0.053$ ,  $SD = 0.004$ ,  $z = -1.88$ ,  $p = 0.024$ ), whereas the coefficients for cohorts 3, 4, and 5 were not significantly different from the null model (C3,  $CC_{\text{obs}} = 0.006$ , mean  $CC_{\text{rand}} = 0.008$ ,  $z = -1.7$ ,  $p = 0.07$ ; C4,  $CC_{\text{obs}} = 0.01$ , mean  $CC_{\text{rand}} = 0.013$ ,  $SD = 0.002$ ,  $z = -1.72$ ,  $p = 0.057$ ; C5,  $CC_{\text{obs}} = 0.0003$ , mean  $CC_{\text{rand}} < 0.001$ ,  $SD < 0.001$ ,  $p = 0.29$ ).

Unlike the individual tests of sociability, and despite overall increasing sociability, individual snakes were repeatable in their social behavior across days in the group context. Across the first 8 days of the group experiment, all cohorts showed consistent individual differences in sociability as measured by mean weighted degree (i.e., snakes demonstrated a social personality; C1  $p < 0.001$ ; C2  $p = 0.003$ ; C3  $p = 0.05$ ; C4  $p = 0.006$ ; C5  $p = 0.001$ ) during the undisturbed

times of the day (lights on & before shuffle). There were also sex differences in sociability, with large females being more social, while large males were less social (sex by body mass interaction;  $F(1, 22) = 8.98$ ,  $p = 0.007$ ,  $\alpha_R = 0.05$ ; Fig. S4A). There were no main effects of sex ( $F(1, 22) = 0.01$ ,  $p = 0.94$ ,  $\alpha_R = 0.06$ ), batch ( $F(3, 22) < 0.01$ ,  $p = 1.00$ ), body mass ( $F(1, 22) = 0.07$ ,  $p = 0.80$ ), or delay ( $F(1, 22) < 0.01$ ,  $p = 1.00$ ) on sociability. For this model, inspection of the data and Cook's distances (Cook and Weisberg 1982) suggested an influential outlier. Removal of this case did not change the significance of the interaction.

### *Dynamics of aggregation*

Aggregation formation was facilitated by snakes choosing a 'home' shelter, in which they spent the majority of their time. Different cohorts chose different home shelters (shelter use by Cohort interaction;  $\chi^2(20) = 476.44$ ,  $p < 0.001$ ), and some cohorts had 1 home shelter whereas others had 2 (across the first 8 days of the experiment; Fig. S5). When a group had more than one home shelter (e.g., cohorts 4 and 5), it was not because they shared time between the shelters on a daily basis. Instead, transitions sometimes occurred, with the aggregate making a long-term move to a new shelter (Fig. S6). These transitions were rare, and appeared to occur when a snake did not leave the shelter before defecating.

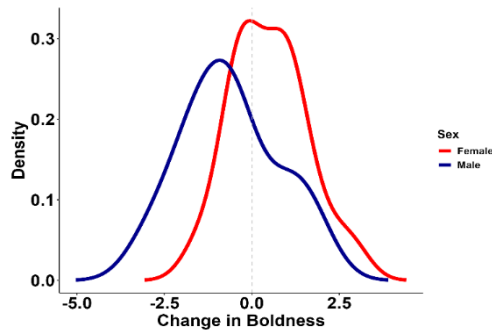
On day 9, we removed each cohort's home shelter for day 8 and, for cohorts 3, 4, and 5, an additional control shelter. Controlling for different overall exploration rates, snakes in these cohorts investigated the location of the missing home shelter more than they did the missing control shelter ( $\chi^2(1) = 37.9$ ,  $p < 0.001$ ). A comparison of models with and without the random effect of identity found a significant effect of individual ( $\chi^2(1) = 5.47$ ,  $p = 0.02$ ,  $\Delta AIC = -3.46$ ), suggesting that increased exploration of the site of the missing home shelter only happened in some of the snakes, which may indicate that some individuals rely on social cues to identify a sheltering site. When the shelters were replaced, on day 10, cohort 4 returned to their previous home shelter, whereas cohorts 3 and 5 remained in their new home shelter (Fig. S7).

Although most aggregation occurred under shelters, randomization models suggested that snakes also tended to explore together; the average number of individuals exploring at any given time period was significantly larger than the number expected by chance (all but one  $p < 0.02$ ). The only exception was in cohort 1 during the 'lights on' period, in which individuals rarely explored and the mean number of individuals exploring was equal to the expected value under a random model (actual mean = 1.00, random model mean = 1.00). Across time periods, there were no significant differences in exploration between males and females ( $F(1, 24.95) = 0.49$ ,  $p = 0.49$ ).

### *Sociability across contexts*

There was no repeatability between the individual social assay and sociability in the group context ( $R_{adj} = 0.14$ ,  $CI[0, 0.5]$ ,  $p = 0.22$ ). Changes in sociability across contexts differed between the sexes, based on body mass, such that the larger a male snake, the more it tended to decrease in sociability across contexts (from individual social assay to the group experiment), while the reverse occurred in females ( $F(1, 22) = 4.45$ ,  $p = 0.046$ ; Fig. S4B). This is the same pattern seen in group social scores in the aggregation context (Fig. S4A). There were no main effects of delay, cohort, body mass, or sex (Table S2).

Boldness (i.e., proportion of time spent out of shelters) was also not repeatable across contexts ( $R_{adj} = 0.12$ ,  $CI[0, 0.45]$ ,  $p = 0.43$ ). Like sociability, males and females differed in their patterns of plasticity. An examination of change in boldness scores ( $\Delta$ boldness) from the individual to group contexts found that males decreased more in boldness than females ( $F(1, 23) = 5.11$ ,  $p = 0.04$ ; Fig. 3). There were no main effects of delay, cohort, or body mass (Table S3).



**Figure 3.** Density distributions of the change in boldness ( $\Delta$ boldness) between the individual assays and the aggregation experiment, by sex. Positive values indicate more time spent outside the shelter in the aggregation assay

## Discussion

We tested 5 groups of 6 juvenile ball pythons each on their social behavior and found that they were surprisingly sociable. In contrast to this species' reputation for being solitary, we found that our snakes spent the majority of their time under shelters together. This occurred despite us placing the snakes alone in identical shelters during shuffle events. In four out of five groups, the most common configuration of the snakes, sometimes accounting for more than 60% of their time, was all the snakes together in a single shelter. In addition, similarly to gartersnakes (Skinner and Miller 2020), juvenile ball pythons spent longer in a shelter if there were more snakes already there when they entered. Unlike the gartersnakes, juvenile ball pythons did not show preferential associations with specific other individuals. These results strongly suggest that our current understanding of ball python social behavior is missing some key factors.

In individual personality assays, juvenile ball pythons - like gartersnakes (Skinner and Miller 2020) - demonstrated consistent individual differences in boldness but inconsistent attraction to the social shelter. Unlike in gartersnakes, we did not find a correlation between boldness and sociability (Skinner and Miller 2020, 2022). We also found no repeatability of personality traits across contexts (from individual assays to the group experiment), but male and female snakes differed in their plasticity across contexts. Compared to the individual tests, the group environment tended to decrease male but not female boldness, while sociability decreased in larger males and increased in larger females.

In the group assay, juvenile ball pythons were highly consistent in their sociability. Surprisingly, this was not due to differences between individuals in social approach tendencies, but instead resulted from the snakes forming large stable social groups under preferred 'home' shelters. Analysis suggested that this was not the result of the quality of any particular shelter, as different cohorts chose different preferred shelters, and snakes switched to a new shelter when their preferred one was removed and did not necessarily return when it was placed back. This suggests that the selection of a preferred shelter may have been a strategy to facilitate aggregation. Coordinated small-group explorations of the arena further maintained group cohesion.

Although stable large groups were the prevailing social pattern, snakes differed in their sociability across the 8 days. Sociability differences were a function of sex and body mass, with large males tending to be less social and large females more social.

### *Aggregation formation*

The snakes had to reform their aggregation after our perturbations (i.e., the twice-daily shuffles). The most obvious way for an individual to join the aggregate would be to find a shelter that already contained some snakes. This was a strategy that at least some of the snakes appeared to follow (as only a subset of snakes preferentially explored the site of a missing home shelter, suggesting some of them had been locating the ‘home’ shelter using social cues). The use of a ‘home base’ - a common preferred shelter - could also facilitate aggregation. The tendency to establish a home base is not unique to juvenile ball pythons. Both rats and mice establish home bases around which their movement is organized when exploring novel environments (Eilam and Golani 1989; see Thompson et al. 2018 for review). Like rats and mice, in the wild, ball pythons are often found living in burrows, where they sometimes cohabitate (Aubret et al. 2005). The choice of a home base could be beneficial for facilitating both navigation around, and aggregation in, preferred burrows. Future research should determine what patterns of home base use and navigation are shared across burrow-living animals.

### *Sociability*

The sociability patterns we find in juvenile ball pythons share some features of the patterns demonstrated in comparable experiments performed on juvenile eastern gartersnakes (Skinner and Miller 2020, 2022). Notably, ball python social networks are denser and more stable than gartersnake networks, even when there are fewer snakes and more shelters (Skinner and Miller 2020, 2022). It is not surprising that these species differ in their social behavior, as eastern gartersnakes inhabit a colder climate, in which they aggregate seasonally for hibernation and mating, whereas ball pythons are from west-central Africa and do not hibernate. However, the difference between the species is in the opposite direction to what we had predicted based on their ecologies, with juvenile ball pythons appearing to be more social than gartersnakes. It is possible that lack of resource competition drives this increased sociability. Resource competition is an important predictor of sociability patterns across taxa (Rubenstein 1978; Dittus 1988; Wittemyer et al. 2005) including squamates (Stamps 1984; While et al. 2009). As ball pythons eat large meals and can go for extended periods without eating, they may be able to more efficiently separate food competition from social interaction than gartersnakes.

A related finding is the lack of preferred associations in these ball pythons. If ball pythons are together a lot of the time, then all (or no) individuals are ‘preferred’ associates, leading to homogenous association patterns in the network. This contrasts with work done on gartersnakes and Arizona black rattlesnakes showing some snakes have preferred associates (Lyman-Henley and Burghardt 1994; Amarello 2012; Skinner and Miller 2020). As differential responding to certain individuals is a hallmark of many definitions of social complexity (Bergman and Beehner 2015; Kappeler 2019), juvenile ball pythons may be less socially complex than seasonally gregarious denning snakes and may have limited social perception abilities. A recent comparative study on self-recognition in ball pythons and gartersnakes found that, unlike gartersnakes, ball pythons do not respond differently to their own marked scent compared to that

of a familiar conspecific (Frieburger et al. 2024). A lack of ability to differentiate between one's own scent and the scent of a conspecific might result in attraction to the scent of any ball python – with little differentiation. However, this would not explain why some snakes avoided the aggregate more than others.

Past social experiences can also influence responses to conspecifics. For example, when first introduced to a social group, socially naive tree skinks (*Egernia striolata*) will show comparatively homogeneous conspecific attraction in relation to individuals with social experience. As individuals gain social experience, their association patterns change (Riley et al. 2018). Similarly, guppies (*Poecilia reticulata*) need up to 12 days to develop familiarity-based schooling preferences (Griffiths and Magurran 1997). It is possible that the lack of social experience among our juvenile ball pythons may have resulted in a reduced repertoire of social responses.

Alternatively, it is possible that ball pythons demonstrate social complexity differently than gartersnakes. Our ball pythons were not consistent in their social behavior across social contexts, adapting their sociability and boldness to the context. The social stimulus in the individual assays consisted of skin lipids derived from both males and females from a wide range of ages. In contrast, in the group context, the social stimulus consisted of similar-aged juveniles. Juvenile ball pythons may detect these compositional differences, and choose when, and for how long, to aggregate based on the social context - a possible form of social competency (Taborsky and Oliveira 2012). Context-dependent social responses have been identified in many taxa including gartersnakes (*Thamnophis sirtalis sirtalis*; Skinner et al. 2024), family living lizards (*Egernia striolata*; Riley et al. 2017), fish (*Neolamprologus pulcher*; Taborsky et al. 2012), as well as birds and mammals (Webster and Ward 2010; Duboscq et al. 2016).

Despite some obvious differences in social interaction between juvenile ball pythons and gartersnakes, in some ways the social patterns displayed by the two species were similar. For example, although the ball pythons had a strong tendency to all aggregate together, they displayed individual differences in sociability - a pattern also seen in gartersnakes (Skinner and Miller 2020). Furthermore, similar to gartersnakes, larger female ball pythons were more social while larger males were less social; social interaction or social opportunity affected boldness in male ball pythons; and ball pythons explored in small groups (Skinner and Miller 2020; Skinner et al. 2022). These similarities suggest that some aspects of sociability may be widespread across snake phylogeny, but more comparisons are needed.

It is also notable that many of these similarities appear linked to effects based on sex and weight. Sex-biased dispersal has been reported in multiple species of snake (Keogh et al. 2006; Dubey et al. 2008) and might partly underlie sex-linked patterns of juvenile sociability. This idea is supported by research on juvenile common lizards (*Lacerta vivipara*) which found that differences in social personality influenced dispersal patterns (Cote and Clobert 2007). Across squamates, it is possible that sex- and body mass-based changes in social attraction could ensure that dispersal occurs when individuals have the best chance of survival. Alternatively, both pythons and gartersnakes display sexual size-dimorphism, with males tending to be smaller than females (Shine 1994; Aubret et al. 2005). This is thought to influence social patterns in many taxa (González-Solís et al. 2000; Ruckstuhl and Neuhaus 2005), possibly due to resource competition. Such similar competition pressures may result in similar social patterns. In ball

pythons, males occupy a different foraging niche than females, feeding more on birds while females feed more on mammals (Luiselli and Angelici 1998). A different foraging niche for male ball pythons could explain the sex differences in sociability we observed. Larger juvenile males may adopt different movement and foraging strategies that allow them to feed on birds but result in less burrow/shelter use. Although larger juvenile male snakes appeared less social than females, most males still demonstrated attraction to the group and to conspecific skin lipids. These patterns mirror those identified in gartersnakes and suggest that balancing the benefits of aggregation with the drawbacks of competition is a complex process for snakes. Recent research has found that patterns of snake social attraction demonstrated in laboratory testing translate into broader patterns of social structure and sociality in the wild (Roth and Lutterschmidt 2011; Skinner et al. 2023), to what extent this occurs in ball pythons will require further research.

### *Conclusion*

Our finding that juvenile ball pythons formed a large stable aggregate was surprising, as there have been no reports of stable aggregations in this species (Gardner et al. 2015). In snakes, much of the evidence for social behavior comes from denning species, such as gartersnakes and rattlesnakes (Heller and Halpern 1982; Lyman-Henley and Burghardt 1994; Clark 2007; Clark et al. 2012; Schuett et al. 2017; Skinner and Miller 2020). Patterns of social behavior in denning snakes conforms well to theories of the development of sociality in squamates as they share mutual benefits at hibernation sites (Gregory 1974; Graves and Duvall 1995) and give birth to live young (a theorized precursor to group-living in squamates; Halliwell et al. 2017). In contrast, ball pythons are oviparous and have no need for communal hibernation. Nevertheless, aggregation could still benefit juvenile ball pythons. For example, social contact likely reduces water loss (Nobel and Clausen 1936; Aubret and Shine 2009), and, through dilution of risk, could protect vulnerable juveniles from predation (Krause and Ruxton 2002).

Irrespective of the benefits they receive from aggregation, our results suggest that juvenile ball pythons are strongly attracted to conspecifics. As secretive animals, snake sociability may occur hidden from view and/or through invisible chemical signals (Halpern and Kubie 1984; Doody et al. 2021). The difficulty in observing some social behavior may be exacerbated in species like ball pythons that often hide in burrows. Studies continue to find surprising patterns of sociability in snakes (Clark 2007; Doody et al. 2021), including aggregation and conspecific attraction in a wide variety of species (Green et al. 2001; Aubret and Shine 2009; Turner 2023). It is possible that many species of snake are highly social, but taxonomic biases (Bonnet et al. 2002; Stahlschmidt 2011) and challenges in observing their social behavior limit understanding of these systems. Although ball pythons have been reported to frequently share burrows in the wild (Aubret et al. 2005), more research is needed to understand these aggregations. If wild ball python aggregations differ from what we have identified here, one possibility might be that resource distributions limit ball python sociability and group living more generally (i.e., the resource distribution hypothesis; Johnson et al. 2002; Gardner et al. 2015).

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**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 and R21003). All applicable international, national, and institutional guidelines for the use of animals were followed.

**Conflicts of interest:** The authors declare no conflicts of interest.

**Author contributions:** MS and NM conceived the ideas and designed methodology; TK and MS collected the data; MS analysed the data; MS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.



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