

Sex differences in play behavior, personality, and philopatry in golden-mantled ground
squirrels (*Callopermophilus lateralis*)

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Abstract

Natal dispersal is a primary force in shaping ecological processes and population dynamics. There are several costs to the disperser that may be outweighed by potential benefits, including increased resources or access to mates in a new population site. Personality types or behavioral syndromes appear to outfit some individuals with traits that are advantageous in inducing or surviving dispersal. Social interactions may also be indicators of whether an individual is likely to leave the natal site. This study examined the behavioral traits of boldness and aggression by evaluating trappability and interactions in juvenile golden-mantled ground squirrels, an asocial small mammal. This species contradicts the mammal male-biased dispersal trend. Many female juveniles also disperse, suggesting that dispersal may be mediated by personality in addition to sex differentiated life history strategies.

In order to explain individual variation in dispersal for these squirrels, we used trappability, the frequency an individual entered a baited trap, as a measure of boldness. Interactions between and among litters were scored on a range of aggressive to socially cohesive. Non-behavioral biological traits were measured, as well, including weight at emergence, emergence delay, and growth rate. There was a correlation between trappability and aggressive interactions (both between and among litters) in both males and females, suggesting a behavioral syndrome of aggression-boldness in this species. Females who initiated more interactions were also more likely to be trapped. Socially aggressive and recognitive interactions between littermates drove this correlation, indicating that these females appear to engage more with their siblings, may be more active within the environment, and more willing to take risks. Growth rate also correlated with trappability and may be indicative of trappability being motivated by hunger, although emergence weight and order were not significant variables. This trend presents preliminary evidence for a pace-of-life syndrome in this species with correlations between boldness and an individual's willingness to face risk for food. Finally, we suggest future directions for evaluating the effects of aggression in mating and territorial behavioral contexts.

Introduction

Natal dispersal, the permanent movement of an immature individual away from its birthplace, has far reaching effects on population structure, demography, gene flow, and species distribution (Greenwood 1980, Waser and Jones 1983, Bowler and Benton 2005, Ronce 2007, Armitage et. al. 2011, Blumstein et. al. 2009). Similarly, philopatric individuals who remain or return to their birthplace contribute an equally significant role in shaping these processes. Patterns of dispersal and philopatry vary among taxa and tend to be biased by sex within taxa (Greenwood 1980). In birds, females tend to disperse while males tend to remain philopatric; in mammals, it is the opposite.

Previous research emphasizes inbreeding avoidance, competition for mates, and competition for environmental resources as explanations for male-biased dispersal and female-biased philopatry in mammals (Greenwood 1980, Dobson 1982, Pusey 1987). Males typically compete for females and invest very little in offspring, while females typically invest more time and energy in producing and nursing young. The cost of

dispersal for males is subsequently less than the cost of intrasexual competition and is outweighed by the benefits they receive from gaining greater access to a greater number of females (Dobson 1979). Weaker, younger, or socially subordinate individuals often disperse during times of high population density and environmental stress (Chitty 1967, Krebs 1976, Archer 1970, Watson and Moss 1970, Lidicker 1975). However, these individuals are often equally likely to be male or female. Fluctuations in density also do not appear to change the sex ratio (Armitage 1973, Dunford 1977). While competition as a result of high density may contribute to the number of dispersers overall, it does not appear to be responsible for determining which sex is most likely to leave the natal site (Greenwood 1980). The costs of dispersal also appear to outweigh the potential negative genetic effects of inbreeding. Greater access to females would seemingly promote male dispersal as a means of avoiding inbreeding (Packer 1979, Pusey 1980). Females benefit more by remaining in their natal territory because as the limiting sex, they can choose among potential males. Females can thereby avoid the risks associated with dispersal, such as increased exposure to predators or moving to an unknown environment with fewer resources than the natal area. However, there is little evidence for inbreeding avoidance functioning as the main cause of sex-biased dispersal (Greenwood 1980). The sex subject to the greater cost of inbreeding would be more likely to disperse if this were the case. However, this is not supported in either mammals, which are mostly polygynous, or birds, where more females disperse even though both males and females likely experience similar disadvantages of inbreeding (Greenwood 1980).

A more recent, fairly unexplored concept is personality-dependent dispersal, meaning that the tendency to disperse is associated with boldness, sociability, and/or aggressiveness (Cote et. al. 2010). These behavioral traits, if consistent across multiple contexts, are defined as animal personality. Sih et. al (2004) suggested that behavioral syndromes may be affecting dispersal processes in ways that have not been accounted for by ecological explanations. Linked behaviors (i.e. aggression or shyness in multiple contexts) can limit adaptation in habitats with disparate environmental situations. For instance, aggressive individuals may retain dominance in a ranked society, but their fearless behavior may make them more prone to predation (Sih et. al. 2004). These inherent tradeoffs can inhibit a species' optimal behavior and influence population structure by biasing certain behavioral types for dispersal.

In addition, the ways in which individuals interact in social situations may affect their decision to disperse and reflect their investment in their natal habitat. The Chitty-Krebs hypothesis (Chitty 1967; Krebs 1976) predicts that aggressive individuals would force docile individuals to disperse at times of high population density. Bekoff's social cohesion hypothesis – the idea that more socially interactive individuals remain in their natal group – provides another explanation for socially mediated dispersal (Bekoff 1977). Bekoff's hypothesis was substantiated in work with social yellow-bellied marmots: social network analysis revealed that females who were more integrated in the social system and had more affiliative ties with others were less likely to disperse (Armitage 1986, 2011; Blumstein 2009). However, these factors were not conducive for explaining yearling male dispersal variation. Bekoff's hypothesis has also not previously been applied to understanding asocial, dispersive species which may often engage in intraspecies interactions or have non-sex biased dispersal patterns.

Biological factors, including personality traits, may work cumulatively to shape an individual's inclination to disperse. For example, dispersal rates in birds were found to correlate with body mass (Swingland, 1983), wing shape (Lidicker & Stenseth, 1992), date of birth (Dhont and Huble, 1968), and heritable exploratory behavior (Dingemanse et al. 2003). Disperser mole rats demonstrated higher activity and feeding activity levels than non-dispersers (O'Riain et al. 1996). Similarly, exploratory activity before actual dispersal was correlated with decreased dispersal latency in male house mice (Krackow 2003). The exploratory behavioral trait was also found to be consistent in North American red squirrels and predicted the directionality and distance of dispersal (Haughland and Larsen 2004). However, few studies have compared or ranked the roles that these variables play within the same species.

This study examined biological traits and behavior in juvenile golden-mantled ground squirrels (*Callospermophilus lateralis*), a relatively asocial species of small mammal. The population used for observation has been studied as part of long-term research conducted at the Rocky Mountain Biological Laboratory (Gothic, Colorado) and has demonstrated individual variation in dispersal throughout two decades of monitoring. Nearly all male juveniles born in the population disperse soon after independence, as expected according to Greenwood's (1980) description of male-biased dispersal in mammals. Surprisingly, many of the female juveniles also disperse and only a few remain in the population after their first hibernation. Females from other populations have also been observed traveling through or permanently immigrating to the town site. Since sex-biased patterns in dispersal have previously been documented (Greenwood, 1980) and dispersing individuals may vary in personality traits – such as activity, exploration, and boldness – compared to philopatric individuals (Cote et al. 2010), we evaluated whether there was a sex bias in the personality traits that may be underlying dispersal. Furthermore, personality may account for additional variation within female behavior and golden mantled ground squirrels' deviation from the typical mammal dispersal pattern. Most pups within a litter are of similar weight and share the same habitat at emergence (Wells and Van Vuren, unpublished data). Personality and different rates of development, however, have not previously been considered as measurements of individuality within this species.

Males and females differ in their approaches to risk taking behavior as a result of differing life history strategies (Wolf et al. 2007). In golden-mantled ground squirrels, we would expect that females would be more risk averse because they have a higher expected future reproduction. Male squirrels may be more willing to risk danger for the greater potential of reproducing in the near future in comparison to surviving long enough for the opportunity to reproduce later in life. We hypothesized that innate differences between the sexes may be observable in juveniles and reflected in their interactions and play behavior. Boldness and aggression levels, which are traits that have been associated with high dispersal rates (Fraser et al. 2001; Dingemanse et al. 2003; Sluyter et al. 1995), have been found to differ in juvenile play in rats (Pellis & McKenna, 1992) and a range of social contexts in guppies (Piyapong et al. 2009). Moreover, aggressiveness and boldness have previously been correlated together as a behavioral syndrome (Sih et al. 2004). Interactions between litters and among members of the same litter were therefore used as one measurement of personality - aggression. Aggressiveness is typically defined as the tendency to attack other individuals (Sih et al. 2004). Pups that

initiated and reciprocated more aggressive play behaviors would therefore be considered to score high for this trait. We observed aggressive and socially cohesive play behaviors in golden-mantled ground squirrel pups and analyzed for patterns biased by sex and individual. We used trappability of pups up to three weeks after emergence as another measure of personality - boldness. Entering a trap represents a risk that an individual is willing to take in order to obtain food. Pups that emerged first from the natal burrow, and were captured more frequently during biweekly trapping sessions, were considered to be score high for boldness. Since willingness to re-enter traps could also reflect hunger instead of boldness, we used weights at emergence and growth rate as alternative, hunger-driven explanations for variation in trappability. Overall, we expected to observe one or both of the following outcomes: 1) correlations between aggressive interactions and boldness in males more than females and 2) variation in aggressive traits exhibited by specific females.

Methods

This study was conducted within the town site of the Rocky Mountain Biological Laboratory in Gothic, Colorado. Data consisting of observations and trapping were collected for the purpose of measuring golden-mantled ground squirrel boldness and personality. The time and place of all pup trappings and observations were recorded for analysis. The location of each individual corresponded to a previously designed grid map of the study area. Each grid square represented 7 x7 square meters and was identifiable by a letter-number code. 17 pups from 4 litters born within the town site were used in this study.

Reproductive females were monitored and their main burrows were identified. Subsequently, traps were stationed around the burrow entrance to capture pups on the first day that the first pup emerged from the ground. This allowed for accurate identification of the pups' mother and littermates.

Trappability (the total number of times an individual willingly entered the live trap after initial capture) was used as an indicator of boldness. Individuals were caught using Tomahawk live traps (Model 201, 40.6 x 12.7 x 12.7 cm, Tomahawk Live Trap, Tomahawk, Wisconsin, USA) and bait consisting of peanut butter mixed with 3-4 sunflower seeds. The amount of bait was standardized in order to lure individuals into traps without interfering with their regular caloric intake and growth pattern. The data set used in this study includes trapping sessions conducted twice a week in the morning on nonconsecutive days up until 3 weeks after emergence. During each session, five traps were evenly spaced where the pups were visually observed foraging and playing. Out of a total of 64 captures, individuals were trapped from 0-9 times, including during the specific trapping sessions and incidentally when other individuals were being targeted as part of population census and maintenance. These incidental trappings were included because they indicate a fuller representation of an individual's level of boldness.

Several variables were identified as predictors of trappability: sex, individual, litter, relative emergence delay, emergence weight, growth rate, and interaction types. Relative emergence delay was defined as the lapse of time between each capture of a pup from the same litter. Trapping of a litter began on the day that the first pup was observed aboveground. The time that the first pup of the litter was trapped was set as the standard

for comparison of other pups' emergence. The first pup emergence time was set to 0 and all other pup emergence times were measured in minutes after the first pup was trapped. These times were then converted into percentages for each littermate so that all litters would be comparable during analysis. We expected that higher values for emergence delay would indicate lower boldness overall in terms of trappability.

During the initial trapping of each pup, handling consisted of weighing the animal and obtaining emergence weight, measuring anogenital (AG) distance to determine sex, and providing each pup with numbered ear tags and unique marks on their pelage with black dye. Individuals could then be identified from a distance. Consecutive trapping consisted only of weighing the individual and measuring AG distance. Growth rate was determined for each pup by graphing the weight vs. day of capture, using at least two measurements. We then determined the equation for the line of best fit through the points, with intercept set to zero, and used the line's slope as the pup's post-emergence growth rate.

Interactions between littermates and with other litters were observed daily in the morning and evening. Observations used for analysis took place during June 8, 2012 – July 27, 2012. Interactions were coded as aggressive (behaviors: arched back posture, tail piloerection, tail flicking, forepaws directed forward, chasing, boxing, wrestling), aggressive social (behaviors: rough and tumble, boxing, chasing), recognitive (behaviors: nose to nose, nose to anogenital region, nose to mouth, nose to body) and affiliative social (behaviors: pseudocopulation, social grooming, touching) following Ferron 1985's description of social interactions in this species. For each pup, we scored the number of interactions of each type that were initiated or returned. Mutual interactions were recorded as initiated by all involved because the receptive pup continued the action along with the initiator.

Analysis consisted of using a generalized linear model (JMP® version 10, SAS Institute Inc., 2012) to evaluate sex differences (male vs. female) in each variable predicting trappability. Correlation coefficients using R (version 2.15.1, the R Foundation for Statistical Computing, 2012), R^2 values using Excel (Microsoft® Excel 2002), and a test of fit least squares using JMP were calculated to compare several variables. A two-tailed t-test was used to investigate sex differences in interaction rates and sex differences in trappability. A chi squared test using JMP measured differences in interactions by individual pup and sex.

Results

Sex differences in trappability were tested using a two tailed t-test. This was done in order to check if innate differences between the sexes were responsible for any observed patterns in trap order and frequency. Results demonstrated that there was not a significant difference between males and females in trappability (male mean: 3.6, female mean: 3.7, t value = -0.105). A test of Fit Least Squares supported this result (p = 0.387). This suggested that other variables served as a greater source of variation than sex.

Secondly, weight at emergence was tested as a main predictor variable of trappability. There was no correlation (correlation coefficient = 0.05) between body weight at emergence and the number of times each individual was trapped within 21 days of emergence, not including initial trapping. Similarly, body weight as a result of sex

differences was also not a significant source of variation in the number of times a pup was trapped ($p = 0.8043$) (see Figure 1).

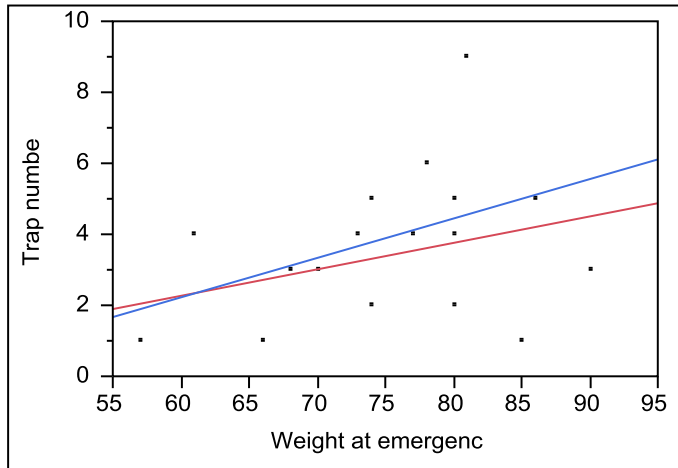


Figure 1: Body Weight vs. Trap Number: Generalized Linear Model

There was no significant correlation between body weight at emergence and the number of times an individual was trapped ($p = 0.2267$), nor was there a difference between male or females in this comparison ($p = 0.8043$) (blue = male, red = female).

Growth rate was also tested because weight at emergence did not take into account some individuals' rapid weight gain during the first three weeks aboveground. For example, a larger pup with a slower developmental trajectory may exhibit a different pattern of trappability than predicted by first weight alone. A higher growth rate appeared to have a positive impact on trap number (GLM, $p = 0.0124$), where faster-growing pups trapped themselves more frequently. However, sex combined with growth rate did not appear to have a significant effect (GLM, $p = 0.2353$). Overall higher growth rates in males and females therefore both contributed to this index of trappability (see Figure 2).

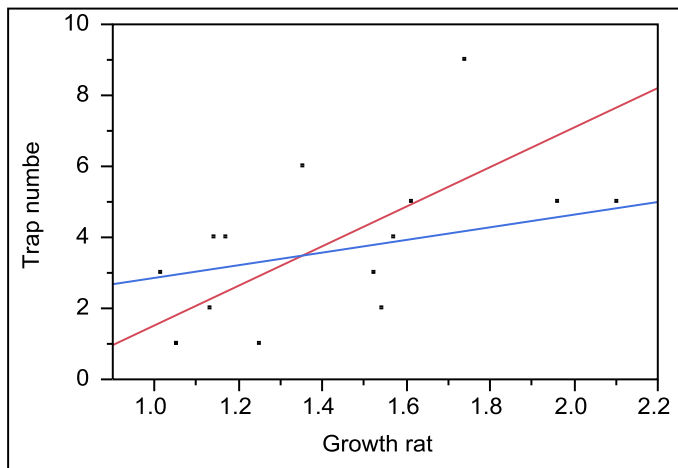


Figure 2: Growth Rate vs Trap Number: Generalized Linear Model

There was a significant correlation between growth rate and the number of times an individual was trapped ($p = 0.0124$), but no differences between the sexes when crossed with growth rate ($p = 0.2353$) (Blue = male, red = female).

Relative emergence delay also did not significantly predict trap number, whether measured alone ($p = 0.7394$) or with sex ($p=0.5755$) (see Figure 3).

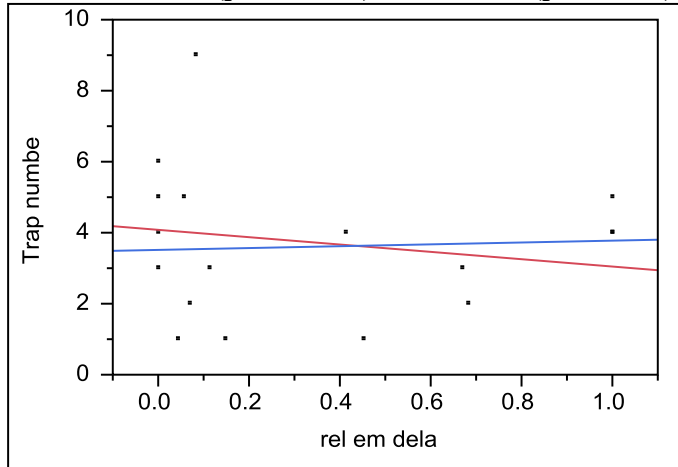
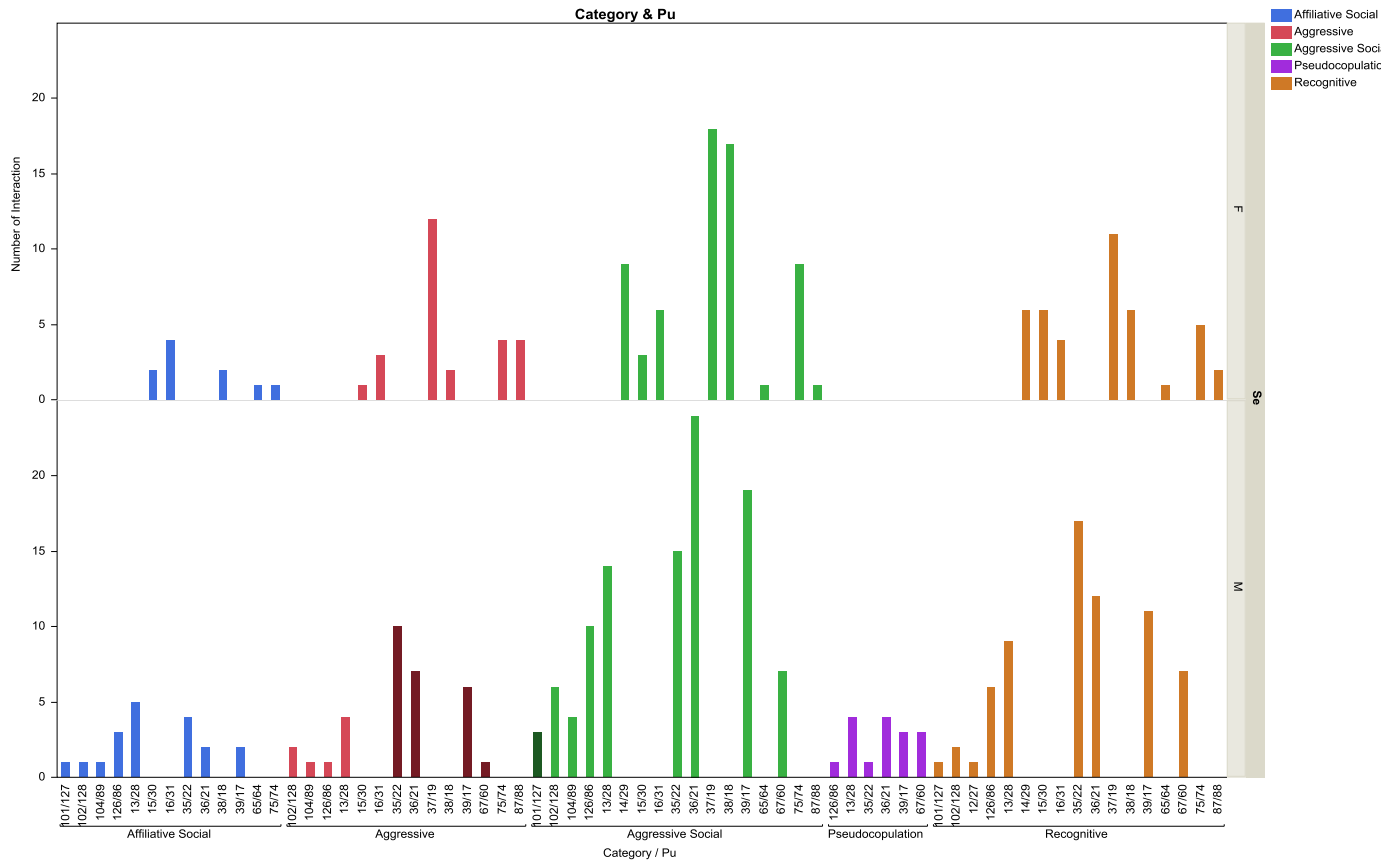


Figure 3: Relative Emergence Delay vs. Trap Number: Generalized Linear Model
There was no significant correlation between the order of emergence and the number of times an individual was trapped both evaluated overall ($p = 0.7394$) or by specific sex ($p = 0.5755$) (blue = male, red = female).

The types of interactions were distributed normally among the individuals (Female mean: 6.6738, Male mean: 6.9872) (see Figure 4). No single individual was visibly more aggressive or cohesive than another. All pups engaged in most types of interactions. The one exception was pseudocopulation- only male pups initiated or returned this behavior.



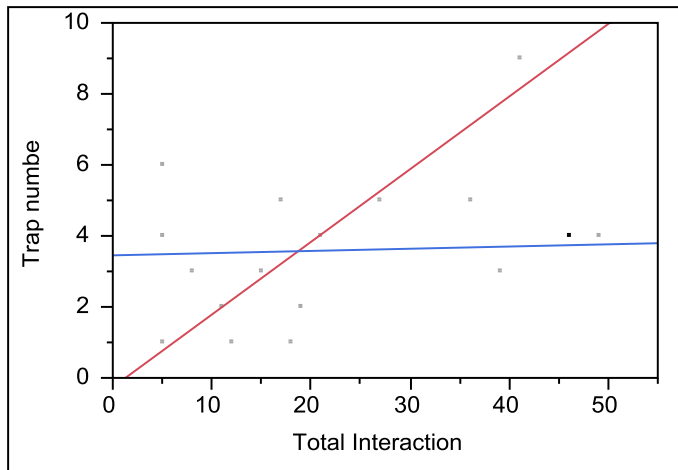


Figure 5: Sex by Interactions: Generalized Linear Model

There was a significant correlation between the number of interactions engaged in by females and trap number ($p = 0.0069$). The slope of the line representing females indicates a range of female behavior; some females did not engage in many interactions and were not frequently trapped while others were highly interactive and trapped much more often (blue = male, red = female).

Sex differences within specific types of behaviors were analyzed. Female trappability was significantly predicted by both aggressive social interactions ($p = 0.0210$) and recognitive interactions ($p = 0.0195$) (see Figure 6). Aggressive ($p = 0.138$) and affiliative social ($p = 0.921$) interactions did not predict trappability for either sex. The individual males who engaged in aggressive social behavior also appeared to engage more in affiliative social behavior ($R^2 = 0.5682$). However, females who were involved in aggressive social behavior were not necessarily involved in affiliative social behaviors ($R^2 = 0.0006$). Moreover, aggressive males ($R^2 = 0.6411$) and aggressive females ($R^2 = 0.3558$) were also likely to engage in aggressive social behaviors. Essentially, the same individuals in both sexes who were aggressive within the litter exhibited aggressive behavior with non-littermates ($R^2 = 0.4166$ for both sexes), but level of aggression was more similar across contexts for males than for females. Aggressive interactions alone, not crossed by sex in our model, were marginally significant in predicting trappability ($p = 0.0552$).

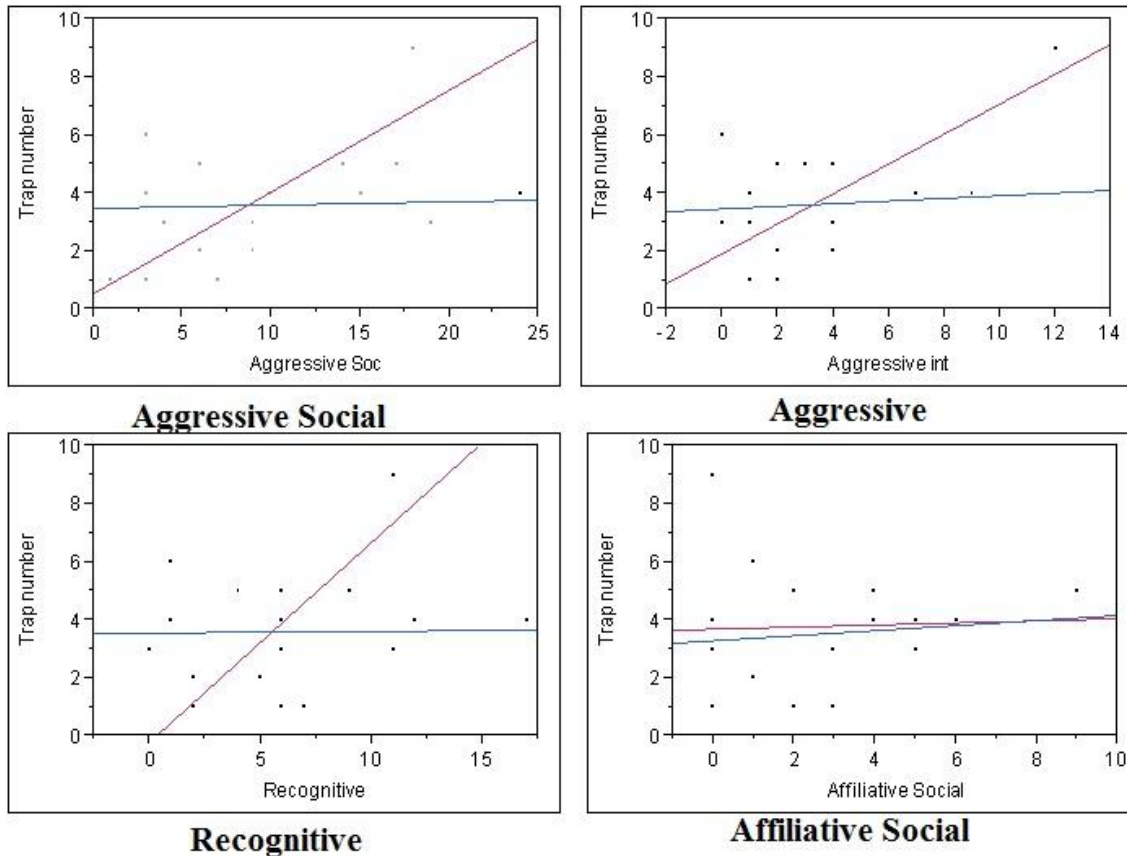


Figure 6: Interaction types vs. Trap Number: Generalized Linear Model

There were significant correlations between trap number and female aggressive social interactions ($p = 0.0210$) and trap number and female recognitive interactions ($p = 0.0195$). Aggressive ($p = 0.138$) and affiliative social ($p = 0.921$) interactions did not predict trap number for either sex. However, aggressive interactions for both sexes (not crossed with trap number in the model), were marginally significant in predicting trap number ($p = 0.0552$) (blue = male, red = female).

Discussion

Differences in behavior, including personality and traits associated with growth rate, were determined to be significant predictors of boldness and characterized by sex. Our model supported trappability as a valid indicator of boldness. There were no innate sex differences within trappability, even though there were slightly more male than female subjects. This suggested that trappability was not driven by whether a pup was male or female. Instead, it appears to be driven by the other predictor variables used within the study.

Included within those variables, weight at emergence and order of initial trapping were not significant predictors of trappability. We expected that weight at emergence could be positively or negatively related to boldness. Smaller pups may be more driven to “catch up” in terms of weight-gain, and take more risks to obtain food, thereby increasing trappability. Conversely, bigger pups may have a faster pace of life syndrome (Reale et al.

2010) and be more driven to obtain food to fuel higher growth (Biro and Stamps 2008). Similar to our reasoning for a possible positive correlation between weight and boldness, we expected that the first pups that emerged would be bigger and therefore possibly bolder than later emerging pups. Order of emergence may serve as an indicator of size and a pace of life syndrome. However, trappability did not appear to be driven by initial size. Since most recently emerged pups of a litter were of similar weight, whether male or female, sex differences did not appear to play a role in whether weight affected boldness. Bigger individuals at emergence were therefore not necessarily bolder.

Growth rate, however, may be an indicator of a pace of life syndrome. Growth rate was a significant predictor of trappability, where faster growing pups were trapped more frequently. Faster growing pups may be more driven to find food and therefore less deterred by risk. While weight at emergence may not be a predictor of trappability, a higher growth rate could result in trappability being motivated by hunger. While differences in sex did not significantly affect growth rate and trappability, females exhibited a slightly tighter relationship between these two variables in this correlation. There may be a greater range of growth rates in females than in males. This may carry over into a greater range of exploratory behavior and contribute to females' displaying a variety of behaviors corresponding to the alternative decisions to disperse or stay in the natal habitat.

For measures of social personality traits, the number of total interactions positively predicted boldness for females, but not for males. Females who initiated or returned more interactions were more likely to be trapped; females who did not initiate or return many interactions were less likely to be trapped. This measurement included all interactions, both aggressive with related and unrelated pups and affiliative within the litter. Sex differences within interactions among a litter and in the number of total interactions were checked against this result to determine its validity. It did not appear that more females engaged in interactions than males overall. When analyzed by litter, some litters appeared to be more interactive than others. However, this is likely due to observation bias. As a result of different litter locations, some were more visible to observers than others. For example, one litter spent much of their day foraging and playing on a steep hillside with high grass while another was more frequently visible in open, rocky habitat. It is unlikely that this bias affected sex differences in our results because sex ratios were fairly balanced within litters. We therefore hold that our results correlating sex and interactions alone were more valid than measuring sex, litter, and interactions. We did not have excess observations of males than females and conclude that highly interactive females are subsequently more likely to take risks within their environment.

Sex differences within specific types of behavior also predicted significant results regarding trappability. Bolder females were both more socially aggressive and engaged in more recognitive interactions. These females appear to engage more with their siblings and may be more active within the environment or more willing to take risks.

Aggressive interactions among unrelated individuals and affiliative social interactions among related individuals did not correlate with trappability. However, aggressively social males also tended to engage in affiliative social interactions. These males may be more interactive with other members of the same litter, especially if they are using play as practice for developing their motor skills (Groos, 1898). This may be in

preparation for dispersal, as previously described in dispersive male belding ground squirrels which had higher motor skill levels than residents (Nunes et al. 2002). Having strong motor skills and practicing aggression in order to compete in a new population may be an especially important technique for males because of male-biased dispersal.

Alternatively, the higher rate of affiliative social interactions in males versus females may be due to differential rates of pseudocopulation behavior. Pseudocopulation behavior, mounting another individual but not truly copulating, was classified as an affiliative (cohesive) behavior in the previous study of social interactions in this species (Ferron 1985). In this study, only males were observed pseudocopulating, which may inflate the overall number of affiliative behaviors compared to females, and may bias the association of this behavior with social aggression in males.

Females did not demonstrate this correlation between affiliative and aggressive behavior toward littermates, even though they are more likely to stay and subsequently may need to form stronger relationships with other females staying in the same habitat. Affiliative interactions with older females who have already established themselves within the area may play a bigger role than cohort interactions in determining which females would be accepted within the population. However, tolerance of juveniles by adult females was not included in this category analysis. Aggressively social males may embody certain traits which promote interactions of all kinds with their littermates. Future research would be required to determine if there is a correlation between pace-of-life syndrome, exploratory activities, and interactiveness within litters. Socially aggressive females may not engage in affiliative social interactions as often as males because of competition, both as pups and as future competitive neighbors if they are philopatric. As previously described, socially aggressive females did engage more in recognitive interactions. Recognition may be necessary for females to differentiate between relatives and non-relatives and affect their future tolerance levels of other individuals sharing the same foraging habitat. The species' overall asocial behavior, however, may inhibit higher levels of affiliative sociality in females.

There appears to be a behavioral syndrome of aggression, social aggression, and boldness in golden-mantled ground squirrel pups of both sexes. Aggressive interactions show a strong trend in predicting trappability: individuals who were more likely to take social risks and play fight with their siblings and more vigorously fight with non-siblings, were also likely to take environmental risks by entering a trap. Moreover, aggressive males were highly socially aggressive, with females showing a slightly less strong pattern. Our results indicate that aggressive individuals exhibit this behavior across multiple contexts and present evidence for an aggression-boldness behavioral syndrome in golden-mantled ground squirrels. Future work will identify whether these syndromes are in fact related to dispersal decisions of individual males and females.

Conclusions

A behavioral syndrome of boldness-aggression in golden-mantled ground squirrels highlights important implications of this behavior that may have different benefits for each sex. Female interactions predicted boldness. Within those interaction categories, social aggression and recognition were driving this correlation. Philopatric females may need to establish their place in the dominance hierarchy of their natal

territory. Fighting, both play and aggressive fights, would allow them to distinguish themselves within the litter and ultimately within the population. Females may also use interactions as juveniles to develop motor skills that would benefit them during courtship. Females who excel at wrestling, chasing, and escaping pseudocopulation initiated by their siblings may be able to exert more choice during mating attempts by males.

Since most males disperse to new populations, juvenile interactions may be most beneficial in enabling them to establish themselves within new populations. Play behavior may allow them to develop the necessary motor skills to compete with other males and to dominate females during courtship. Aggressive and affiliative social behaviors, especially pseudocopulation, wrestling, and chasing, with siblings of both sexes would allow them to practice and refine their skill set. Establishing dominance within a litter and the local population may not be a priority if they are likely to leave the site. Instead, more time spent practicing aggression and engaging in more interactions would most benefit male pups.

Sexual selection may lead to sex differences in personality traits (Schuett et al. 2010). Future research would be helpful in determining whether aggression carries over to mating contexts and/or adult territorial behavior. Additional research can examine the recipients of female aggression to determine if they are predominantly male or female. Alternatively, females may more frequently attack any individual within their territory, no matter the sex. Aggression may play a greater role in competition in multiple mating systems, but additional studies are required to determine the preferred mating strategy in golden-mantled ground squirrels.

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