

Early-life trade-offs in golden-mantled ground squirrel sociality and growth rate

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ABSTRACT

The golden-mantled ground squirrel (*Callospermophilus lateralis*) was first classified as an asocial sciurid in 1983, and little follow-up research has effectively challenged this notion since the early literature. The only recognized social behavior in the species has been documented between young littermates, between a mother and her litter, and occasionally across unrelated or partially related litters of overlapping home ranges. However, little research has been conducted on the potential impacts of pup sociality on early life fitness. In this study, the early-life behaviors of golden-mantled ground squirrels were observed in eight litters in the Gothic Townsite of the Rocky Mountain Biological Laboratory during the first two weeks after pup emergence when sociality is at a peak. A multiple linear regression model was used to compare the relationship between time spent socializing and pup growth rate. This model also accounted for the additive effect of pup age on growth rate and the potential interaction between sociality and litter size (i.e., having more littermates may impact sociality). While the final study model was just shy of significant ($p = 0.0565$), the estimate value of -2.127 showed a consistent, meaningful negative effect ($-2.127 \pm \text{std.} = 1.030 = -1.097$ or -3.157). Unfortunately, due to high predation rates, roadkill events, and natural loss of litters, the low sample size limits conclusions we can draw from these results. Patterns of early-life sociality in an asocial species such as the golden-mantled ground squirrel are important to understand as they may play an important role in juvenile fitness or later life success.

Key words: Golden-mantled ground squirrel (*Callospermophilus lateralis*), social behavior, growth rates, juvenile fitness, early life trade-offs

INTRODUCTION

The evolution of mammalian sociality is a complex topic of behavioral biology, the study of which has been important to understanding the benefits of conspecific kin groups versus territoriality. According to ecological theory, conspecific sociality evolves within a species when the benefits of remaining in a close kin group outweigh the costs (Silk, 2007). While this socioecological theory has been well studied in primates, carnivores, and undulates, there is relatively little known about the sociality of small mammals. High alpine ground squirrels have been largely understudied in this aspect perhaps due to their relatively isolated populations. One of the more studied ground squirrels is the yellow-bellied marmot (*Marmota flaviventer*). Yellow-bellied marmots are considered social and live what has been described as a “harem-polygynous society,” where one male plays a dominant role in a family group of several matrilineal females (Armitage, 1987). For this species of sciurid, it is believed that this socio-reproductive strategy developed as an adaptation to living in alpine environments with short growing seasons. In these environments, there are clear benefits of sociality and delayed dispersal on the ability of this species’ yearlings to devote their energy to fat storage in preparation for long winter hibernation (Armitage 1981; Armitage, 2011).

Another species, whose sociality has been less investigated, is the golden-mantled ground squirrel (*Callospermophilus lateralis*) of the Rocky Mountains of the U.S.. This species has long been classified as a solitary and asocial sciurid (Armitage, 1981; Michener 1983). Unlike related rodents in the sciurid family such as the yellow-bellied marmot (*Marmota flaviventer*), they do not live in cohesive adult family groups and instead disperse soon after natal emergence and develop well-defended individual territories, the inner home ranges of which are usually between 1.14–13.52 ha. (Jesmer *et al.*, 2011). Golden-mantled ground squirrels (sometimes called GMGSs) seldom engage in social behaviors as adults such as grooming, social resting, or other displays of kinship (Michener, 1983; Jesmer *et al.*, 2011). The only consistent social behaviors observed in these ground squirrels have occurred between littermates, between a litter and their mother, and occasionally between pups across different litters when home ranges overlap (Ferron, 1985).

Even these observed “social behaviors” are often antagonistic, particularly between pups of different litters. Pups within a litter, however, have been observed to engage in cohesive mock-fighting behaviors including chasing, rough and tumble wrestling, boxing with front paws, as well as pseudocopulation, and more neutral cognitive behaviors such as greeting nose-to-nose or nose-to-anogenital region (Ferron, 1985). Previous student studies at the Rocky Mountain Biological Laboratory (RMBL) have also shown some sex-specific differences in play behavior and growth rates. For example, one student paper discovered that faster-growing male pups tended to exhibit less risk-taking behaviors (Wells unpublished).

One other exception to GMGS asociality has been observed in what Michener described as neutral or tolerating behavior between “single-family female kin groups” (1983). These tolerating behaviors are most often established when anywhere from 1-5 daughters of a given squirrel only disperse only partially and establishing territories which border the area surrounding their natal burrow (Wells & Van Vuren, 2017). When daughters establish these border territories, there have been increased rates of observed tolerating behaviors between mother and yearling daughters than between non-kin squirrels. However, these higher kin density home ranges have recently been associated with lower survival rates, supporting the hypothesis of a social fitness cost rather than reward (Kanaziz, 2022). So why do pups spend time and

energy on more social behaviors during their first two weeks after emergence? While adult social behavior in GMGSs has shown a negative correlation with survivorship, there is little to no literature examining the potential tradeoffs in social behavior and fitness of juveniles which exhibit much higher rates of social behavior.

The purpose of this study was to determine whether there is a clear fitness trade-off between pup sociality and fitness (measured by growth rate). This study was conducted on this spring's litters of a historically studied population of reproductive female GMGS surrounding the Rocky Mountain Biological Laboratory in Gothic, Colorado. Exploring these questions can provide insight into whether sociality has negative consequences even to pre-dispersal individuals of this asocial species. Early-life socialization may have short-term impacts on pup survivability as well as the establishment of adult home ranges and reproductive success later in life. While the negative consequences of sociality are more evidenced, it is possible that some level of sociality sustained through adulthood may allow for more successful alarm-calling networks which assist predator avoidance, more reproductive success, or tolerating behaviors in overlapping home ranges which provide high quality foraging and increase overall population success. We hypothesized that pups which spend more time socializing with their littermates will grow at a slower rate than less social pups. We predicted that this effect will be seen because by spending more time and energy socializing during their limited above-ground hours will detract from important learned foraging behaviors and will therefore have a negative effect on fitness via growth rate and squirrels' ability to hibernate through the cold subalpine winters (Wells *et al.*, 2022).

METHODS

Study Site:

The study site for this project encompassed approximately 0.15 square kilometers of the Rocky Mountain Biological Laboratory townsite in Gothic, Colorado (Figure 1). Litters included in this study were those of historically and/or newly immigrated reproductive female golden-mantled ground squirrels with established territories in the townsite. Starting in June of 2022, all adult female squirrels which showed signs of being reproductive were trapped and, if they possessed existing ear tags from previous seasons, were remarked using a unique Nyanzol-D fur dye marking; squirrels which were new immigrants or were otherwise missing ear tags were administered uniquely numbered tags on both ears and similarly marked with a unique dye pattern. After all reproductive females were accounted for, a total of nineteen litters were expected for the season. However, due to litter loss during pregnancy or lactation, roadkill incidents, predation by a local red fox family which had inhabited the townsite the previous winter, or simply due to spatial observational challenges, only eight litters persisted as reliable study subjects this season.

Gothic Townsite 2022



Figure 1. Rocky Mountain Biological Laboratory GMGS study site in Gothic, Colorado, June-July 2022.

Growth Rate, Sex, and Census Data

Golden-mantled ground squirrel pups were trapped by repeating previously established safe methods using Tomahawk live traps (Model 201, 40.6 X 12.7 X 12.7 cm, Tomahawk Live Trap, Tomahawk, Wisconsin, USA) (Jesmer *et al.*, 2011). Traps were baited using a mixture of peanut butter and sunflower seeds and set out in early morning and afternoon when pups were observed outside of their burrow. Trapped pups were guided into a conical Emlen canvas handling bag within which they could be marked, measured, and weighed along with the bag (the bag weight was then subtracted from the total mass after ear release.) Pups from each litter were trapped only twice due to time and labor constraints, once at emergence when they were first observed above ground and then as close as possible to 14 days after emergence. The mass measurements taken at these two points were then used to estimate an average growth rate in grams/day for each pup during their first two weeks above ground while behavioral observations were also being taken.

While the average age of pups at emergence is around 30 days, as the study went on it was clear that the age at emergence for each Gothic litter varied considerably. Growth measurements were therefore taken relative to the number of days since each litter emerged (e.g., one litter's

day 1 may be another litter's day 7 and so on.) As stated before, mass was recorded while pups are safely contained in a conical canvas handling bag (Emlen bag) using a 300-gram Pesola scale. Upon the first trapping of each pup, additional data were recorded including pup sex, hair samples, buccal swabs, and fecal samples. Pup sex was determined by measuring the length of the anogenital distance (Wells & Van Vuren, 2017). Small hair samples were taken for DNA and hormonal analysis for long-term census data by pulling small sections of hair from the rump of the pup. Buccal samples were taken using (type?) mouth swabs and brushing them on the inside of each cheek for a total of 30 seconds. Fecal samples were only taken if the squirrel naturally defecated during handling, and both fecal and buccal samples were transferred to 1.5 mL microcentrifuge tubes, labeled, and stored in a freezer unit for preservation prior to analysis. These data were important for long term genetic, hormonal, and population health records within the townsite as well as a comparison of sex-specific trends in average growth rates and sociality. Just as with the reproductive females, each new ground squirrel pup was uniquely marked as a variation of their mother's mark using Nyanzol-D fur dye for easier identification during field observations.

Age Estimations

Age estimations at emergence are commonly approximated to be 30 days because this is how long it typically takes to wean a litter (Phillips, 1981). However, after encountering several litters which far exceeded emergence mass expectations, it was believed that unusually high predation rates this season may have resulted in more cryptic emergence behaviors and some squirrels may have hidden their pups underground for a longer period than usual. To account for this discrepancy in age at emergence which may impact growth rate due to non-linear growth, pup age at emergence was estimated using standardized morphological measurements from previous research on stages of development in GMGS pups. Measurements taken included left hind foot length, ear length, and length of the longest whisker. Two measurements were taken for the foot due to lack of specificity in previous study methods, one being just the foot base from the heel to the beginning of the digits and second being the total length from the heel to end of the third digit excluding the nail. These measurement methods were repeated as closely as possible to earlier studies which tracked the development of these features over known ages of golden-mantled ground squirrels from birth to 77 days in one study and 40 days in another (Clark & Skryja, 1969; McKeever, 1964). Using known ages and measurements of foot, ear, and whisker from McKeever (1964), three separate age models were created using each feature from which Gothic pup ages could be estimated and then averaged across models to get the most accurate age estimate possible. Because discrepancies in age at emergence were only considered after several litters emerged at drastically different weights, pups which were caught at emergence but not initially measured were simply measured when re-trapped at 14 days and to determine their age at emergence, their age estimates from the second trapping measurements were subtracted by 14 days. As stated earlier, these age estimates were later used to correct for differences in growth rates of pups that may have been attributed to age rather than social or foraging behavior.

Behavioral Measurements:

Social behaviors of pups were documented using an observational field method which utilized the unique dye marks given to each individual. Each litter (and pup) was observed for a minimum of 60 minutes and a maximum of 90 minutes between July 1-30 for approximately two

weeks for each litter while they remained close to their natal burrow before dispersal. During this time, observational periods were split up into 10-minute increments in either the morning (8am-12pm) or afternoon (1pm-5pm). To avoid confounding weather variables which may impact activity (e.g., GMGSs are not generally active in the rain), litters were generally only observed a maximum of twice a day (once in the morning and once in the afternoon). During each 10-minute observation periods, litters would be observed from a far enough distance that their behavior was minimally disturbed using binoculars. Observable squirrels which were both above ground and visible were tracked as closely as possible and their dominant behaviors were recorded at each minute interval. Behaviors were mostly split into three main categories: foraging (F), alert on four or two legs (A4/A2), or socializing. Other infrequent behaviors which were not significant enough to include in analysis were grooming, dustbathing, or stretching. Social behaviors were classified using Ferron's 1985 social behavior ethogram, with all observed social behaviors among littermates being classified as recognitive or cohesive (Table 1). The total number of each behavior type observed within different litters was then compared. To account for anticipated inconsistencies between the total time during which each litter was able to be observed, the total time each pup spent engaged in each behavior was translated to a proportion out of the total time they were observed between July 1 and July 30.

Table 1. Ethogram of social behavior from Ferron 1985, *Canadian Journal of Ecology*.

Recognitive (neutral)	Cohesive (Mock-fighting)	Cohesive (body contact)
1. Nose to nose	1. Rough + tumble	1. Pseudocopulation
2. Nose to anogenital region	2. Boxing (slow)	2. Social grooming
3. Nose to mouth	3. Chasing (slow)	3. Paw touching
4. Nose to body/tail	...	...

Accounting for Mortality

Due to unusually high levels of predation from the mother red fox and her kits living in the townsite, some litter sizes changed drastically within the observational study period. Because this had the potential to impact the ability of pups to socialize due to a reduced number of littermates, an average litter size was taken across all observational periods for each litter. This average litter size was later accounted for during data analysis to standardize the impact of increased social opportunity in larger litters. Additionally, the total number of minutes any given pup was observed for was dependent on their survival between observation periods. To avoid underestimating any given behaviors for unknowingly depredated pups, squirrels which were not seen for four consecutive 10-minute observational periods were assumed to be dead and behavioral recordings for that pup were halted at that time; observational data was only later assessed for the time intervals when they were believed to be alive.

Statistical Analysis

Using R Studio, multiple Tukey box-and-whisker plots were created to compare minimums, maximums, averages, and trends in types of behavior as well as growth rates between litters. Normality in the data was evaluated using basic histograms to display distributions and determine which datasets needed transformations to be normalized. The distribution of growth rates (which was not normally distributed) was first transformed using a Box-Cox transformation and the proportion of time social was transformed with a log function. Additionally, simple linear models were plotted for each behavior type (foraging, alert, and social) in relation to growth rate and the resulting p-values (as well as estimates, std. errors, and t-values) were examined for meaningfulness or significance; these models were then re-run isolating just male and female pups to identify any differences. To assess whether litter size had a clear impact on rates of sociality, a simple linear regression of these variables was also tested. Following the simple linear regressions, a multiple linear regression was used to determine the most accurate relationship between sociality and pup growth rate by accounting for the interactive effect of litter size on sociality as well as the impact of age at emergence on growth rate. The outputs of this model (estimates, std. error, p-value, and t-value) were once again examined for meaningfulness or significance. To ensure there were no direct correlations between the independent variables used in the multiple linear regression and therefore confounding effects, correlation values were examined using a Pearson's product moment correlation coefficient, Kendall's *tau* or Spearman's *rho* test. Finally, a linear regression model of the interaction between sociality and growth rate while accounting for differences in litter size was conducted.

RESULTS

Average growth rates of all litters fluctuated between 2.00 grams/day and 3.50 grams/day. It is important to note, however, that the lowest estimate came from the 188/155 litter which only had one surviving pup after two weeks (while observational protocols had not yet ceased for this pup as four observational periods had not yet passed where it wasn't seen) and therefore only had one measurable growth rate at 2.00 grams/day. Contrastingly, the 439/778 litter had the largest surviving cohort of six pups and had a range (2.29-3.21 grams/day). However, despite having a larger litter, this was a narrower range when compared to a smaller litter of 4 pups like 677/596 (2.50-3.50 grams/day) (Figure 2). Average age at emergence varied considerable between litters with the youngest litter (276/872) emerging at only 23 days old and the oldest litter (188/155) emerging at nearly twice that at 40 days old.

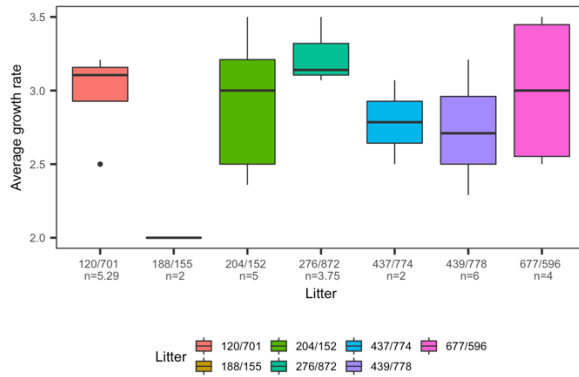


Figure 2. Average growth rate between first emergence and 14 days of litters in the Gothic townsite from July 1-July 30.

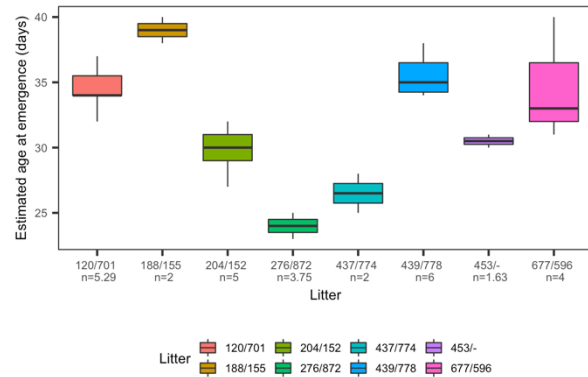


Figure 3. Average estimated age at emergence across litters in the Gothic townsite from July 1-July 30

The proportion of time which litters spent foraging also showed some variation but mostly fell between 0.1 and 0.3 (or 10% to 30%) with a minimum of 0.017 and maximum of 0.414 (Figure 4). The proportion of time which litters exhibited alert behaviors was generally lower than foraging with a minimum of 0.0 and only two pups over 0.2 (Figure 5). The proportion of time which litters engaged in some form of social behavior varied less drastically between litters than either foraging or alert behavior. The most social litter was 188/155 which showed the two highest proportions of time spent socializing for a litter averaging close to 0.2 while all other litters averaged below 0.1 and half were below 0.05 or only 5% of time spent socializing (Figure 6).

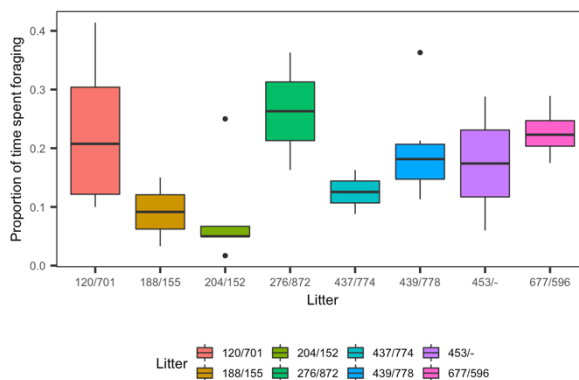


Figure 4. Proportion of observed time spent foraging across GMGS litters in the Gothic townsite from July 1-July 30.

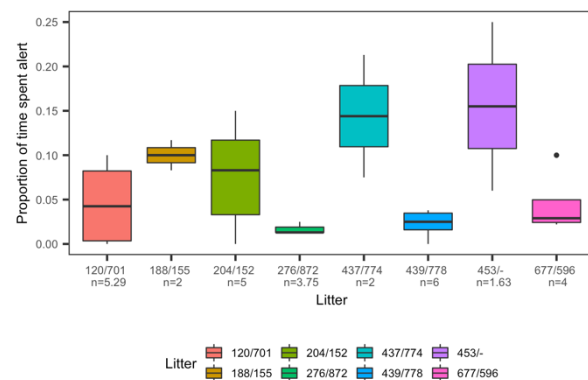


Figure 5. Proportion of observed time spent alert (one four or two legs) across GMGS litters in the Gothic townsite from July 1-July 30.

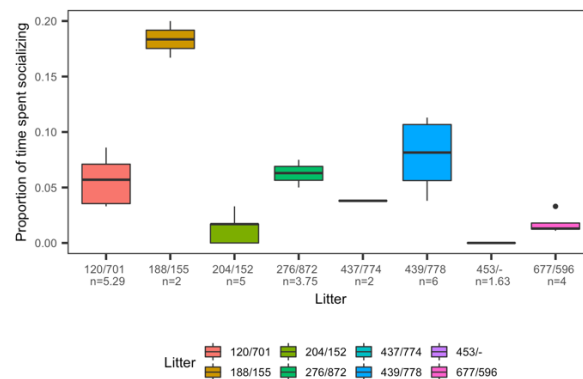


Figure 6. Proportion of observed time spent socializing with littermates across GMGS litters in the Gothic townsite from July 1-July 30.

A simple linear regression of the proportion of time pups spent foraging compared to their growth rate showed a slight positive trend but did not show significance (Estimate= 0.9770, std. error= 0.9359, t-value= 1.044, p-value= 0.309) (Figure 7). Similarly, a linear regression of the proportion of time spent alert compared to growth rates showed no significance (Estimate= -1.0010, std. error= 1.7868, t-value= -0.56, p-value= 0.582) (Figure 8), and neither did the proportion of time spent socializing (Estimate= -1.9573, std. error= 2.5372, t-value= -0.771, p-value= 0.449) compared growth rates (Figure 9). However, both showed slight negative trends, particularly in time spent socializing compared with growth rate. Finally, a linear regression comparing the size of each litter compared to the proportion of time spent socializing was also not significant and showed no obvious trends (estimate= -0.001134, std. error= 0.006200, t-value= -0.183, p-value= 0.856) (Figure 10).

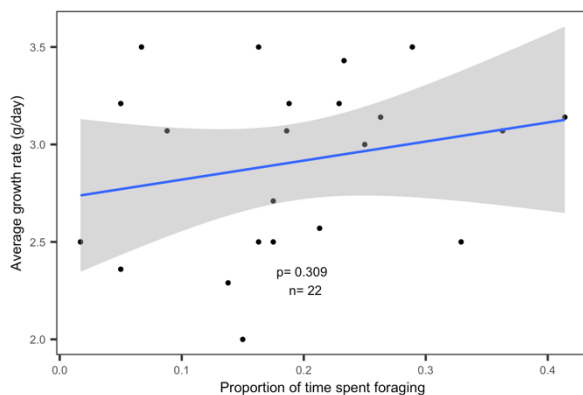


Figure 7. Proportion of time spent foraging for individual GMGS pups compared to average growth rates in the Gothic townsite between day of emergence and 14 days after emergence.

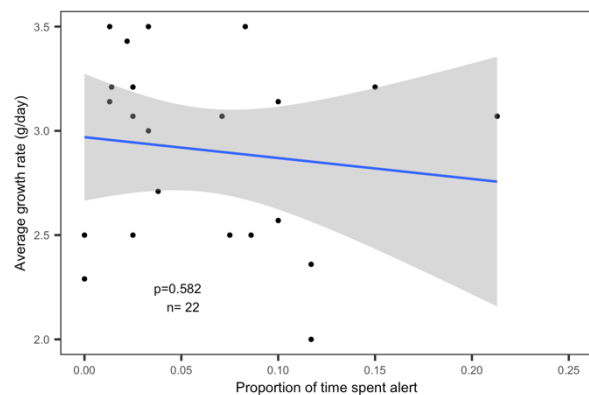


Figure 8. Proportion of time spent alert for individual GMGS pups compared to average growth rates in the Gothic townsite between day of emergence and 14 days after emergence.

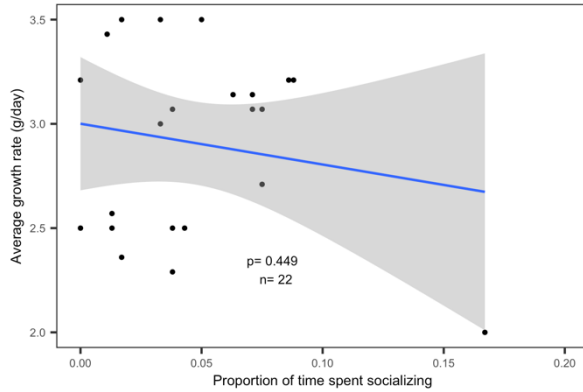


Figure 9. Proportion of time spent socializing for individual GMGS pups compared to average growth rates in the Gothic townsite between day of emergence and 14 days after emergence.

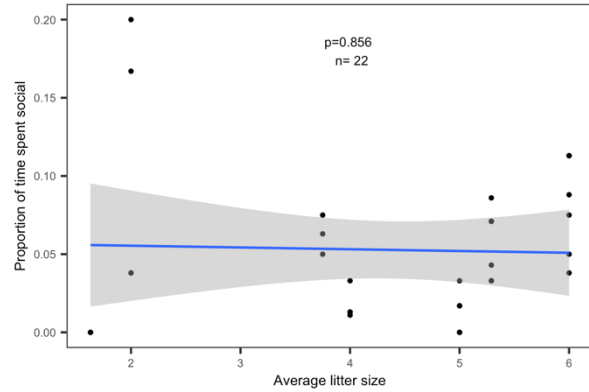


Figure 10. Average size of each GMGS litter compared to the proportion of time the litter spent socializing in the Gothic townsite between July 1-July 30.

The results of the final multiple linear regression model on sociality versus growth rate (correcting for litter size and age at emergence) differed quite a bit from the simple linear regressions, with the final mathematical model shown below*. After transforming the average growth rate data and proportion of time spent social into normal distributions, the impact of proportion of time spent social on growth rate was just shy of significant (Estimate= -2.127, std. error= 1.030, t-value= -2.067, p-value= 0.0565) (Table 2). However, when looking at the estimate plus or minus the standard error, there is a consistent and meaningful negative relationship between time spent social and growth rate ($-2.127 \pm \text{std.} = 1.030 = -1.097$ or -3.157). The p-value of the full model was 0.06809 and therefore also not statistically significant.

$$* \frac{\text{Average growth rate}^{\lambda-1}}{\lambda} = \log((\text{Proportion of time social} + 1)) * (\text{Average litter size}) + (\text{Age at emergence})$$

Table 2. Final multiple linear regression model results showing estimate, standard error, t-value, $\text{Pr}(> |t|)$, and full model p-value.

	Estimate	Std. Error	t value	$\text{Pr}(> t)$
(Intercept)	0.901	0.097	9.307	1.28e-07 ***
$\log(\text{Prop_time_social} + 1)$	-2.127	1.030	-2.067	0.0565 .
Avg_litter_size	-0.020	0.020	0.983	0.3413
Age_at_emergence	-0.005	0.003	-1.618	0.1264
$\log(\text{Prop_time_social} + 1):$ Avg_litter_size	0.552	0.255	2.161	0.0472 *
P-value = 0.06809				

Finally, a linear regression model of the proportion of time pups spent socializing and the average growth rate of pups with correcting for the interaction between litter size and sociality showed an opposite effect of sociality on growth rate for large and small litters. While for larger

litters (6 pups), greater socialization showed a decrease in growth rate, for smaller litters (2 pups), greater socialization showed an increase in growth rate (Figure 11). The results of this model showed a significant interaction between the proportion of time spent socializing and average litter size when impacting growth rate (Estimate= -0.501906, std. error= 0.232212, t-value= -2.161, p-value= 0.0472). The same linear regressions isolated for male and female pups showed no clear differences in trends between sex.

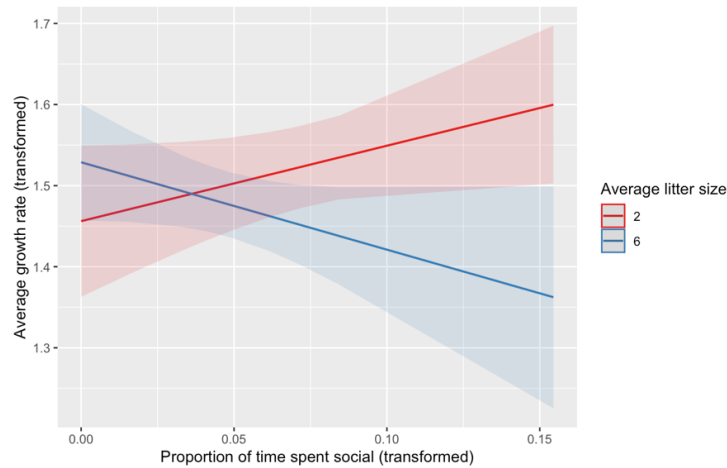


Figure 11. Linear regression model of proportion of time spent social (normalized) and average growth rate of pups (normalized) correcting for the interaction between litter size and sociality divided by small litters (2 pups) and large litters (6 pups).

DISCUSSION

Interpretation of results

On their own, the simple linear regression models yielded no near-significant or meaningful results. The multiple linear regression of the effect of sociality of pups on their growth rates which accounted for litter size and age at emergence showed a negative effect which was also just shy of significant ($p = 0.0565$) (Table 2). However, by looking at the estimated effect of -2.127 and the small standard error of 1.030, it is seen that there is a consistent and meaningful negative effect within the range of error -1.097 and -3.157). The ultimate results of the study, while insignificant, therefore meaningfully supported the hypothesis that with greater rates of social behavior there is a decrease in growth rate due to a tradeoff effect.

Additionally, while there was a significant interaction found between litter size and sociality and their interactive effect on growth rate, this result is likely to be an outlier due to the unusually small sample size for remaining small litters. While several small litters of two pups, including 188/155, 437/774, and 453/-, persisted long enough to be observed for the two-week period without being observationally deemed dead, at the 14th day, only one of these pups (one from 188/155) was able to be re-trapped while the others were never weighed a second time. This means that this “significant” trend for small litters is only hinging on the growth rate of one pup, which is not a reliable result. Re-trapping the other individuals may have proven difficult

for many reasons. Firstly, trapping is not always successful even when pups remain alive and close to a litter and therefore does not have a 100% success rate. Second, it is possible that these un-trapped pups were predated or killed by traffic close to their 14th day after emergence. Finally, due to the late emergence of many litters including 188/155 and possibly others as the age estimates are not exact, these other pups may have already partially dispersed into areas far enough from their natal burrow that they were unable to be relocated. This idea is also supported by field observations of many pups venturing significantly beyond their mothers' home ranges before 14 days lapsed.

There are also several possible explanations for the meaningful negative yet insignificant relationship between sociality and growth rate. Firstly, while sociality may have an impact on growth rate that this study was unable to detect due to the small sample size (a mere 20 surviving squirrel pups), there may also be a greater effect of age on growth rate than initially anticipated. Despite attempting to correct for age at emergence using the McKeever estimates, a follow-up study by Clark & Skryja in 1969 showed different results for the development of measured features at the same ages as McKeever studied. Namely, they found larger sizes of hind foot at the same ages as McKeever measured, which may have resulted in an underestimation of age in this study which used McKeever's measurements as the standard. Because it is unlikely that the growth of pups is linear in their first two weeks after emergence, it is likely an oversimplification of pup development to use linear models of ear, whisker, and foot growth to estimate age. This is supported by an alternative model of growth created in the same study by McKeever which reflected a non-linear and negative growth rate as pups aged. Specifically, this alternative model tracked the weight of GMGS pup eye lenses over known ages, as this is another measure of growth and development observed via the endocrine system (McKeever 1964). The results of this model showed a logarithmic growth curve, suggesting that early growth in golden-mantled ground squirrels may be greater in young under 60 days old and then decrease as they age past this threshold. If this is true, it would make sense that age would account for a more significant factor in growth than sociality which our model was unable to account for even accounting for a likely underestimated measure of age.

Litter size may also play a role in growth rate which was underrepresented in this study as many of the pups from the smaller litters were predated or otherwise disappeared before their growth rates were accounted for. In another study of declining litter sizes in European ground squirrels (*Spermophilus citellus*), a close relative to golden-mantled ground squirrels, mean pup body mass was shown to decrease with increasing litter size (Hubert *et al.*, 2001). This difference in pup size in turn resulted in higher growth rates in the young of larger litters than in smaller litters. However, rather than foraging rates, this was attributed to differences in weaning date because the differences in growth rate evened out once they reached approximately 60 days and were foraging on grasses entirely. This suggests that, particularly for those litters which emerged earlier, there may have still be inconsistencies in growth rates between litters due to the size of the litters.

While this limited seasonal study yielded no strongly significant results, some other interesting patterns were observed. First, the data show some (while insignificant) positive relationship between proportion of time pups allocated to foraging and their growth rates. This would be an expected result given that after weaning, foraging is the primary source of food source for young squirrels (Figure 2). This result may very well have been significant given a more consistent observational method or greater sample size. The lack of evidence of influence of alert behavior on growth may be explained by the fact that alert behavior is far less

energetically costly than social behaviors which are more rigorous and may exhaust calories from juvenile squirrels faster.

Another interesting trend was seen in the lack of a significant relationship between litter size and time spent socializing (Figure 10). The results of this comparison were unusual because it would be expected that larger litters would have more opportunity to socialize and would therefore display higher rates of social behaviors. The results from this study instead suggest that the overall sociality of a litter may be driven by factors other than the size of the litter. For example, if one pup in a litter is much more social than the others, it may be driving the sociality of a litter rather than all pups in a litter being more social due to a larger array of playmates. That the initiator of social interactions within litters was not reliably accounted in this study (as dye-marks were hard to keep track of on especially small pups, particularly at a distance) may have therefore skewed average social rates within litters to reflect the sociality of just one or two hyper-social individuals. This explanation is supported by another recent study on golden-mantled ground squirrel behavior which found both quantifiable and repeatable differences in individual squirrel's behaviors, suggesting that squirrels have individual personalities and exhibit different levels of sociability (Aliperti, 2021).

Finally, while the interaction model between sociality and growth effecting litter size showed significant results predicting an opposite, positive effect of increased socialization on growth rates on smaller litters, this result which be reasonably accepted due to the exceptionally small sample size for small litters. However, it is still possible that this result was true and further analysis into the differences in a sociality and growth trade-offs between large and small litters may expose an unexpected pattern here.

Potential sources of error:

There were several considerable sources of error due to the limitations of a seasonal field study during a high-predation period with five active red foxes (mother and kits) in the townsite. It is important to note that high traffic through the Gothic townsite during the summer may have resulted in altered behaviors in pups. For example, several tour groups and kids' programs walked past burrows during observation periods and pups often prematurely retreated to burrows. Furthermore, due to the brevity of the Education Program here at Rocky Mountain Biological Laboratory, behavioral data collection was only possible for three weeks and all mass measurements had to be completed by July 29. Because data collection did not actually start until July 3, observations of some litters were delayed until almost a week after emergence. It was decided soon afterwards that behavioral observations would only be taken during the first two weeks after emergence due to the unusually fast rates of partial or full dispersal observed from the Gothic litters after just a couple weeks. Perhaps the largest source of error, however, was the small sample size as the number of observable litters quickly dwindled with high predation rates from a resident family of red foxes. What started as an expected sample size of 19 litters was quickly reduced to just eight from depredation, roadkill incidents, naturally lost litters, or otherwise spatially too challenging to reliably observe. Three litters were knowingly orphaned before emergence and, while they did manage to emerge, were entirely depredated by the end of the week. High rates of predation also may have influenced play behavior as pups were observed to be far more cryptic and skittish than in previous seasons.

As stated before, it was also possible that age estimations were inaccurate due to a lack of clarity in the reference paper from McKeever (1964). Specifically, the authors failed to specify whether foot measurements included or excluded the digits. Furthermore, the more recent study

from Clark & Skryja in 1969 which attempted to replicate McKeever's found numerous differences in development of juvenile golden-mantled ground squirrels which may have resulted in an underestimation of ages at emergence. Due to the challenging nature of live trapping in a populated tourist location and earlier dispersal rates, trapping efforts on day 14 was unsuccessful for many squirrels and many trapped a day, or two past 14 days may have had overestimated growth rates.

Finally, due to the crypsis of this season's litters there may have been some level of observation bias present. For example, it was easier to observe some of the more obvious behaviors such as rough-and-tumble play compared to more subtle recognitive social behaviors which may occur for just a second or two. Additionally, there were many minutes of observational time during which individuals were not accounted for and assumed to be inactive while they may have been engaging in additional social or foraging behaviors out of sight.

Future studies

Adult social dynamics have shown to influence survival in Golden-mantled ground squirrels, particularly for maternal individuals which drive population size (Kanaziz *et al.*, 2022). Some research has shown that in another species of ground squirrel, the Belding's ground squirrel, higher rates of juvenile play behavior were associated with greater territoriality and vigilance during gestation. Additionally, rates of social play significantly influenced the success of yearling females in weaning a litter (Nunes, 2014). Therefore, while the influence of play behavior on growth rate has not yet been sufficiently investigated in golden-mantled ground squirrels, early-life sociality may very well play an important role in reproductive success or other important traits related to individual fitness or population success. While small-scale, this study at the Rocky Mountain Biological Laboratory serves as an important step toward understanding the role of pup sociality in the life history of an otherwise asocial species.

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