

Food vs. fear:

Behavioral strategies of golden-mantled ground squirrels,

Callospermophilus lateralis

Student: Flannery James

Mentor: Jaclyn Aliperti

Independent Research and Course

Summer 2016

ABSTRACT

Observational studies of behavior provide insight into the fitness consequences of varying behavioral strategies in mammals. The behavior of golden-mantled ground squirrels (*Callospermophilus lateralis*, GMGS), an asocial hibernating species, is constrained by the energetic demands of reproduction, predator avoidance, and a short active season. This study used activity budgets, compiled through daily observations of the GMGS population in Gothic, Colorado throughout the active seasons of 2015 and 2016, to quantify responses to variations in demands for survival across ages and sexes. The percentages of time spent alert and foraging were examined in four groups: adult males, adult females, all adults, and juveniles. The activity budgets of reproductive females were also compared to those of non-reproductive females. Juveniles were found to spend a significantly greater portion of their time foraging than adults ($P < 0.01$). This effect may be due to the time-constrained pressure to store fat for hibernation. Adult females spent more time alert than males ($P = 0.02$), and reproductive females spent more time alert than non-reproductive females ($P = 0.03$). While other behavioral comparisons (foraging ~ sex, foraging ~ reproductive status, alertness ~ age) were not significant, there appears to be a correlation between average body mass and alertness in juvenile males. Future studies might focus on comparisons of temporal variability in activity between different age and sex classes of GMGS in order to account for reproduction-driven fluctuations in behavior and body mass during the active season.

INTRODUCTION

The field of behavioral ecology is important for understanding the consequences of differences in behavior between individuals, which may contribute to their fitness (Lind and Cresswell, 2005). Observing and quantifying the behaviors of free-ranging mammals in their natural habitats is especially difficult due to the large scales of time and space that such research often requires. In addition, behavioral studies focusing on small, asocial mammal species typically receive little interest from researchers, possibly because they are assumed to be relatively uninformative to studies on sociality (Ferron 1985, Jesmer 2011).

Few behavioral studies focus on asocial sciurids. The golden-mantled ground squirrel (*Callospermophilus lateralis*; GMGS) is classified as the least social of five levels of sociality in ground-dwelling squirrels because of the predominance of agonistic interactions between adults (Michener 1983, Ferron 1985). However, despite their seeming lack of a complex social structure, golden-mantled ground squirrels exhibit a wide range of behaviors and interactions, in which males and females play different roles and have different energetic demands in terms of reproduction.

Both sexes are subjected to the constraints of hibernation and reproductive cycles (Blake 1972). Males do not provide parental care to pups, while females have a combined gestation and lactation period of approximately two months (Ferron 1985, Bartels and Thompson 1993). In addition, all individuals must balance the energetic costs of antipredator behavior with the risks of foraging (Grubb and Greenwald 1982, MacWhirter 1991, Verdolin 2006). Because vigilance reduces energy intake (Lima and Dill 1989), examining variations in alert and foraging behaviors is the most efficient way to measure differences in behavioral strategies.

The primary objective of this study was to collect behavioral observations of GMGS to compare variation in activity budgets between a) males and females and b) adults and juveniles throughout the active season. Activity budgets are used to estimate the amount of time spent on certain activities as percentages of the total time that an animal is observed (Bertolino 2004). Variations in activity budgets could reflect differences in behavioral strategies that allow individuals to maximize fitness by balancing the energy expenditures and demands for survival associated with age and sex (Koprowski and Corse 2005). I asked the following:

1. How do behavioral strategies of golden-mantled ground squirrels differ between adult males and adult females with regards to percentage of time spent feeding vs. alert?
2. How do these same behavioral strategies differ between adults and juveniles?

I expected to find that individual reproductive females would respond to the demands of caring for their litters by exhibiting more alert behaviors in the early season. In late summer, after the lactation period, my expectation was that females would exhibit more foraging/feeding behaviors in order to gain the fat necessary for hibernation. I hypothesized that males would spend the majority of their time foraging/feeding because of the weight loss they experience during the breeding season (Bronson 1979) and because they are known to store more fat than females (Blake 1972). I also suspected that juveniles have the highest percentage of time out of any group spent foraging/feeding, because they must triple their body weight in the short period between emergence and hibernation in order to survive the overwintering period (Meister 1996). Overall, this study provides insight into the behavioral dynamics of golden-mantled ground squirrels, a classified asocial species with conflicting demands for survival during the summer.

METHODS

Study site and species.- This study was conducted at a 13 ha site that overlaps the Gothic town site at the Rocky Mountain Biological Laboratory (RMBL) in Gunnison County, Colorado (Fig. 1). The site consisted of several habitat types, dominated by subalpine meadow (Hostetler et al. 2012) and was bordered by aspen groves to the north and east, and by bodies of water (East River and Copper Creek) to the west and south, respectively. The map of the site was gridded into 7x7 m squares (2,653 total). This project was part of the long-term study (over 25 years) on the behavior and population dynamics of GMGS at Gothic.

GMGS represent an asocial, diurnal, and true hibernating species (Bartels and Thompson, 1993). Individuals at this site typically emerge from hibernation in May and reenter hibernation in late August or early September (Kneip 2011). Adult females typically mate soon after emergence and give birth underground to litters of 3-8 pups during July. Juveniles emerge from their natal burrows at approximately 65g and one month of age, and typically disperse within three to four weeks (Jesmer et al 2011). Male GMGS do not provide parental care and focus primarily on avoiding predators and gaining fat to last them through hibernation (Bartels and Thompson, 1993).

While GMGS are generally agonistic, it is likely that individuals differ in behavior due to conflicting survival demands, such as storing fat while remaining agile enough to escape predators. Predators of GMGS at this site included the red fox (*Vulpes vulpes*), the short-tailed weasel (*Mustela erminea*), and the long-tailed weasel (*Mustela frenata*).

Trapping and marking.- GMGS were captured using Tomahawk live traps baited with peanut butter and sunflower seeds. At the beginning of the active season, new individuals were given

uniquely numbered tags, one in each ear, and both new and returning individuals received distinct dye marks for visual recognition through binoculars in the field. Nyanzol-D crystals were mixed with ethanol to make a stock solution, which could be used as a dye for 24 hours after mixing with hydrogen peroxide. Traps were set again in early July to capture emerging juveniles, and later in July and early August to capture immigrants. Individuals were also trapped throughout the season to renew ear tags or a fading dye mark. Ear tag numbers, dye marks, body mass, anal-genital (AG) distance, and reproductive status were recorded at the time of each capture. The AG distance was used to determine the sex of the individual; males have statistically longer AG distances than females.

Behavioral observations.- Observations were recorded daily throughout June and July when the squirrels were most active, approximately 7:30-11:30 and 14:00-18:00 each day following a categorized system for noting individual behavior (Table 1). Focal-animal sampling was used to observe one individual over a period of time (Altmann 1974). An observation was only recorded if the animal could be positively identified by its dye marks. Once an individual was identified, the date, time, ear tag numbers, and activity were recorded at one-minute intervals for up to ten minutes at a time.

Data analyses.- The percentage of time spent foraging was calculated as the number of times that foraging behavior was observed, divided by the sum of the number of times any behavior was observed:

$$\%F = \frac{\#F}{total \# behavioral observations}$$

The percentage of time spent alert (%A) was calculated using the same method. No distinction was made between A4 (alert on all four legs) and A2 (alert on hind legs). When averaging

percentages according to age and sex, individuals with fewer than 10 recorded observations were excluded. The modified Thompson tau test was used to identify and discard outliers in each group (adult females, adult males, all adults, and juveniles). Comparisons between groups were examined using paired *t*-tests.

RESULTS

Population. - Data collected on 63 GMGS were analyzed (Table 2, 3). Thirty-seven individuals (59% of the sample population) were present in 2015, and 26 (41%) in 2016. Five animals appeared in the population both years and were treated as separate individuals each year for the purpose of these analyses. Overall, 19 adult females, 23 adult males, and 21 juveniles (15 females and six males) were observed for this study.

Activity budget. - The percentages of time that an individual was observed foraging and alert (%F and %A) were calculated for each GMGS (Table 3, 4). These percentages were then averaged by group (Table 5). Average %F was found to be significantly different between adults and juveniles ($P = 0.000077$). Adults spent an average of $17.7 \pm 10.3\%$ of observed time foraging and $41.5 \pm 7.8\%$ alert. Juveniles foraged $30.5 \pm 9.6\%$ of the time and were alert $41.6 \pm 17.1\%$. A significant difference ($P = 0.02$) was also found in foraging frequency between adult females (%F $\bar{X} \pm SD = 21.0 \pm 11.8$, %A $\bar{X} \pm SD = 46.5 \pm 12.8$) and adult males (%F $\bar{X} \pm SD = 15.9 \pm 9.6$, %A $\bar{X} \pm SD = 38.7 \pm 6.3$). Reproductive females (%F $\bar{X} \pm SD = 21.3 \pm 12.7$, %A $\bar{X} \pm SD = 49.7 \pm 10.4$) also spent significantly more time on alert behaviors than did non-reproductive females (%F $\bar{X} \pm SD = 20.5 \pm 10.8$, %A $\bar{X} \pm SD = 34.5 \pm 17.0$). Outliers (Table 5, 6) were excluded from calculations of means and standard deviations, and were not included in the paired *t*-tests.

Body mass.- Body mass information at the time of each capture were obtained from trap logs and averaged for each individual. Average body mass was then plotted against %A for four groups: adult males, adult females, juvenile males and juvenile females (Fig. 3). A negative correlation was found between average body mass and %A in juvenile males ($R^2 = 0.89$). Adult males also showed a negative trend, while adult females displayed a slightly positive trend; however, these trend lines explained little of the variation present ($R^2 < 0.10$).

DISCUSSION

Juvenile GMGS were found to spend a significantly larger percentage of time foraging than did adults. Since juveniles have no reproductive demands, their increased foraging implies greater energetic demands for hibernation in juveniles than in adults. Although the typical hibernation period for an adult GMGS is 8-9 months, juveniles may be active and foraging 1-2 months after adults have entered hibernation (Kenagy 1988). Kenagy (1989) found that at midsummer, juveniles had the greatest energetic demands of any age or sex group, supporting the findings that juveniles devote more time to foraging than do adults. Greater female survivorship past one year (Bronson 1979) suggests that behavioral strategies of juveniles differ between males and females in ways not explored in this study, possibly with regard to dispersion. Males disperse farther than females (Meister 1996) which exposes them to greater risks.

The negative correlation found between average body mass and alertness in juvenile males could be due to increased foraging time in larger males, which could detract from time spent alert. Failure to find strong correlations between average body mass and alertness in groups

other than juvenile males could be due to fluctuations in body mass in females and yearling males during the active season (Kenagy et al 1989). Comparing the body masses of all individuals temporally rather than averaging measurements taken at different times may yield more significant results. Because this study did not distinguish between yearlings and older males, it is not possible to examine only the average body masses of older males, which are known to experience fewer changes in mass.

A significant difference was found between adult males and adult females in time spent alert; females spent a higher percentage of their time alert than did males. Females may be more cautious and risk-averse during gestation and lactation, since not only their survival but the survival of their pups depends on their ability to avoid predators. Time spent foraging did not differ significantly between sexes, suggesting that the females' increased alertness came at the cost of another behavior such as grooming or dust bathing.

Although a previous study of GMGS (Kenagy et al 1989) also failed to find significant differences in time allocation for foraging between sexes, females and males do differ in their energetic needs throughout the active season. Reproduction, especially lactation and gestation, are metabolically demanding and are associated with increased nutritional needs (MacWhirter 1991). Lactating females expend more energy than any other group at any time (Kenagy et al 1989). Therefore it is surprising that instead of trading off alertness in exchange for increased foraging bouts and nutrient acquisition, female GMGS are more alert than males.

In addition, reproductive females were found to be significantly more alert than non-reproductive females, yet their foraging habits were not significantly different. In a previous study, female Columbian ground squirrels were found to be less vigilant during lactation (MacWhirter 1991). Reproductive female GMGS have a greater fat content at the beginning of

gestation than at the end (Kenagy 1988), and require 10% more energy throughout the active season than do adult males (Kenagy et al 1989). Adult males lose weight during reproduction (Bronson 1979, Kenagy 1988) but store more fat than do adult females overall (Blake 1972).

Fluctuations in energy demands during the active season suggest that while the amount of time spent foraging does not differ significantly between males and females or reproductive and non-reproductive females over the summer as a whole, behaviors may vary significantly at certain points during the season. The most compelling evidence for this theory comes from Kenagy (1988), who found that reproductive females had notably larger gut contents during lactation than males or nonreproductive females. In addition, a significant difference in foraging between reproductive and nonreproductive females was observed in Columbian ground squirrels (MacWhirter 1991). However, investment in reproduction and parental care can also increase an individual's vulnerability to predation (Lima and Dill 1989).

Further studies might focus on temporal variations in behavior between age, sex and reproductive classes, as well as the behavior of reproductive females during gestation/lactation and after their litters emerge.

LITERATURE CITED

- Altmann, Jeanne. "Observational study of behavior: sampling methods." *Behavior* 49, no. 3 (1974): 227-267.
- Bartels, Molly A. and Doug P. Thompson. "Spermophilus lateralis." *Mammalian Species* no. 440 (1993): 1-8.
- Bertolino, Sandro et al. "Activity budget and foraging behavior of introduced *Callosciurus finlaysonii* (Rodentia, Sciuridae) in Italy." *Journal of Mammalogy* 85, no. 2 (2004): 254-259.
- Blake, B. H. "The annual cycle and fat storage in two populations of golden-mantled ground squirrels." *Journal of Mammalogy* 53 (1972): 157-167.
- Bronson, Michael T. "Altitudinal variation in the life history of the golden-mantled ground squirrel (*Spermophilus lateralis*)." *Ecology* 60, no. 2 (1979): 272-279.
- Ferron, Jean. "Social behavior of the golden-mantled ground squirrel (*Spermophilus lateralis*)." *Canadian Journal of Zoology* 63 (1985): 2529-2533.
- Grubb, Thomas C. and Lewis Greenwald. "Sparrows and a brushpile: foraging responses to different combinations of predation risk and energy cost." *Animal Behavior* 30 (1982): 637-640.
- Hostetler, Jeffrey A. et al. "Stochastic population dynamics of a montane ground-dwelling squirrel." *PLoS ONE* 7, no. 3 (2012).
- Jesmer, Brett R. et al. "Spatial organization in female golden-mantled ground squirrels." *The American Midland Naturalist* 165, no. 1 (2011): 162-168.
- Kenagy, G. J. and B. M. Barnes. "Seasonal reproductive patterns in four coexisting rodent species from the Cascade Mountains, Washington." *Journal of Mammalogy* 69, no. 2 (1988): 274-292.
- Kenagy, G. J. et al. "Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population." *Oecologia* 78 (1989): 269-282.
- Kneip, Eva et al. "Influence of population density and climate on the demography of subalpine golden-mantled ground squirrels." *Journal of Mammalogy* 92, no. 2 (2011): 367-377.
- Koprowski, John L. and Michelle C. Corse. "Time budgets, activity periods, and behavior of Mexican fox squirrels." *Journal of Mammalogy* 86, no. 5 (2005): 947-952.
- Lima, Steven L. and Lawrence M. Dill. "Behavioral decisions made under the risk of predation: a review and prospectus." *Canadian Journal of Zoology* 68 (1989): 619-640.

- Lind, Johan and Will Cresswell. "Determining the fitness consequences of antipredation behavior." *Behavioral Ecology* 16, no. 5 (2005): 945-956.
- MacWhirter, R. Bruce. "Effects of reproduction on activity and foraging behavior of adult female Columbian ground squirrels." *Canadian Journal of Zoology* 69 (1991): 2209-2216.
- Meister, Cecile Josephine. "Behavioral and physiological aspects of natal dispersal in the golden-mantled ground squirrel *Spermophilus saturates*." *ProQuest Dissertations Publishing* (1996).
- Michener, G. R. "Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids." *Advances in the Study of Mammalian Behavior* no. 7 (1983): 528-572.
- Verdolin, Jennifer L. "Meta-analysis of foraging and predation risk trade-offs in terrestrial systems." *Behavioral Ecology and Sociobiology* 60 (2006): 457-464.

TABLES AND FIGURES

Table 1.- Codes for common behaviors.

Activity	Description
F	Feeding or foraging
R	Running
G	Grooming
DB	Dust bathing
SM	Scent marking
A4	Alert on four legs
A2	Alert on hind legs

Table 2.- GMGS population at Gothic.

	Adult females		Adult males	Juveniles		<i>Total</i>
	Reproductive	Non reproductive		Females	Males	
2015	7	5	16	5	4	37
2016	6	1	7	10	2	26
<i>Total</i>	19		23	21		63

Table 3.- Information on adult individuals including sex, percentage of time spent foraging and alert, average body mass (g), and the year they appeared in the study population. Empty cells indicate outliers that have been removed from the data set.

SEX	%F	%A	AVG BODY MASS (g)	YEAR
M	11.8	35.3	191.1	2015
M	19.1	46.8	230.5	2015
M	15.7	34.3	201.5	2015
M	32.5	37.5	139.0	2015
M	32.5	37.5	139.0	2015

M	21.9	32.9	192.0	2015
M	27.8	44.4	157.7	2015
M	5.3	31.6	144.5	2015
M	12.2	44.9	144.0	2015
M	0.0		148.5	2015
M	20.7	32.8	187.3	2015
M	19.9	40.8	200.9	2015
M	7.3		144.8	2015
M	8.3	45.8	205.0	2015
M	5.7	48.6	153.0	2015
M	11.1	39.7	178.7	2015
M		28.8	177.8	2016
M	18.6	45.8	189.5	2016
M		32.0	188.5	2016
M	18.2	29.7	219.3	2016
M	5.3	42.1	174.0	2016
M	31.5	43.3	196.0	2016
M	9.1		177.0	2016
F	16.1	56.4	199.5	2015
F	15.4		134.7	2015
F	6.25	25.0	130.0	2015
F	16.7	58.3	241.5	2015
F	13.0	65.2	196.2	2015
F	36.5	44.1	184.7	2015
F	3.6	64.3	224.0	2015
F	5.9	41.2	222.5	2015
F	33.3	33.3	203.0	2015
F	17.9	51.8	241.5	2015
F	6.2	55.8	194.5	2015
F	36.1	36.1	225.5	2015
F	25.6	46.5	199.5	2016

F	33.3	23.3	197.3	2016
F	24.7	47.2	223.0	2016
F	30.0	32.5	209.0	2016
F	16.0	60.5	217.0	2016
F	43.1	43.1	241.0	2016
F	20.4	53.1	236.4	2016

Table 4.- Information on all individuals GMGS in the study including age (adult or juvenile), percentage of time spent foraging and alert, average body mass (g), and the year they appeared in the study site. Empty cells indicate outliers that have been removed from the data set.

AGE	%F	%A	AVG BODY MASS (g)	YEAR
A	16.1	56.4	199.5	2015
A	15.4		134.7	2015
A	6.25		130.0	2015
A	16.7		241.5	2015
A	13.0		196.2	2015
A	36.5	44.1	184.7	2015
A	3.6		224.0	2015
A	5.9	41.2	222.5	2015
A	33.3	33.3	203.0	2015
A	17.9	51.8	241.5	2015
A	6.2	55.8	194.5	2015
A	36.1	36.1	225.5	2015
A	25.6	46.5	199.5	2016
A	33.3		197.3	2016
A	24.7	47.2	223.0	2016
A	30.0	32.5	209.0	2016

A	16.0		217.0	2016
A		43.1	241.0	2016
A	20.4	53.1	236.4	2016
A	11.8	35.3	191.1	2015
A	19.1	46.8	230.5	2015
A	15.7	34.3	201.5	2015
A	32.5	37.5	139.0	2015
A	32.5	37.5	139.0	2015
A	21.9	32.9	192.0	2015
A	27.8	44.4	157.7	2015
A	5.3	31.6	144.5	2015
A	12.2	44.9	144.0	2015
A	0.0		148.5	2015
A	20.7	32.8	187.3	2015
A	19.9	40.8	200.9	2015
A	7.3	53.7	144.8	2015
A	8.3	45.8	205.0	2015
A	5.7	48.6	153.0	2015
A	11.1	39.7	178.7	2015
A		28.8	177.8	2016
A	18.6	45.8	189.5	2016
A		32.0	188.5	2016
A	18.2	29.7	219.3	2016
A	5.3	42.1	174.0	2016
A	31.5	43.3	196.0	2016
A	9.1		177.0	2016
J	14.9	51.1	71.0	2015
J	21.7	47.8	137.8	2015
J	23.3	63.3	70.5	2015
J	30.8	38.5	60.0	2015
J		58.3	60.0	2015

J	33.3	61.1	56.0	2016
J	40.0		71.0	2016
J	39.3	39.3	45.0	2016
J	43.3	36.7	51.7	2016
J		68.0	46.0	2016
J	24.2	36.4	59.0	2016
J		20.0	52.0	2016
J	40.0	10.0	59.0	2016
J		66.7	59.0	2016
J	45.5	36.4	64.5	2016
J	16.0	44.0	68.0	2015
J	34.4	21.5	85.3	2015
J	33.3	30.3	82.0	2015
J	23.2	19.5	83.0	2015
J		27.3	73.7	2016
J	25.5	55.3	51.0	2016

Table 5.- Average percentages of time spent foraging and alert for adult males, adult females, all adults, and juveniles.

	Adult females			Adult males			Adults			Juveniles		
	$\bar{X}$	<i>SD</i>	<i>OL</i>	$\bar{X}$	<i>SD</i>	<i>OL</i>	$\bar{X}$	<i>SD</i>	<i>OL</i>	$\bar{X}$	<i>SD</i>	<i>OL</i>
%F	21.0	11.8	0	15.9	9.6	2	17.7	10.3	3	30.5	9.6	5
%A	46.5	12.8	1	38.7	6.3	3	41.5	7.8	8	41.6	17.1	1

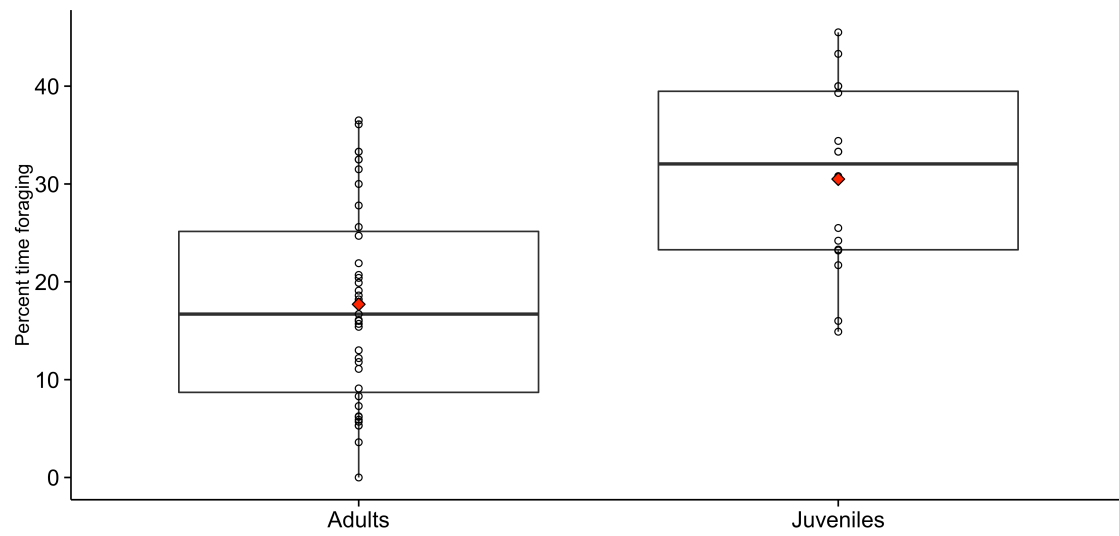
Table 6.- Average percentages of time spent foraging and alert for reproductive and non-reproductive females.

	Reproductive females			Non-reproductive females		
	$\bar{X}$	<i>SD</i>	<i>OL</i>	$\bar{X}$	<i>SD</i>	<i>OL</i>
%F	21.3	12.7	0	20.5	10.8	0
%A	49.7	10.4	0	34.5	17.0	0

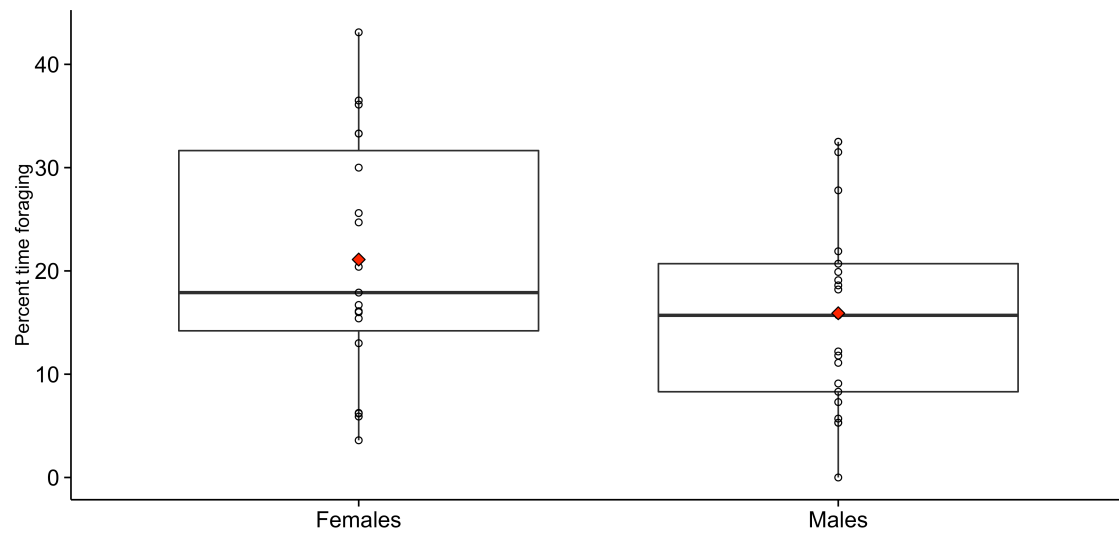


Fig. 1.- Map of the study site in the East River Valley, Gothic, Colorado.

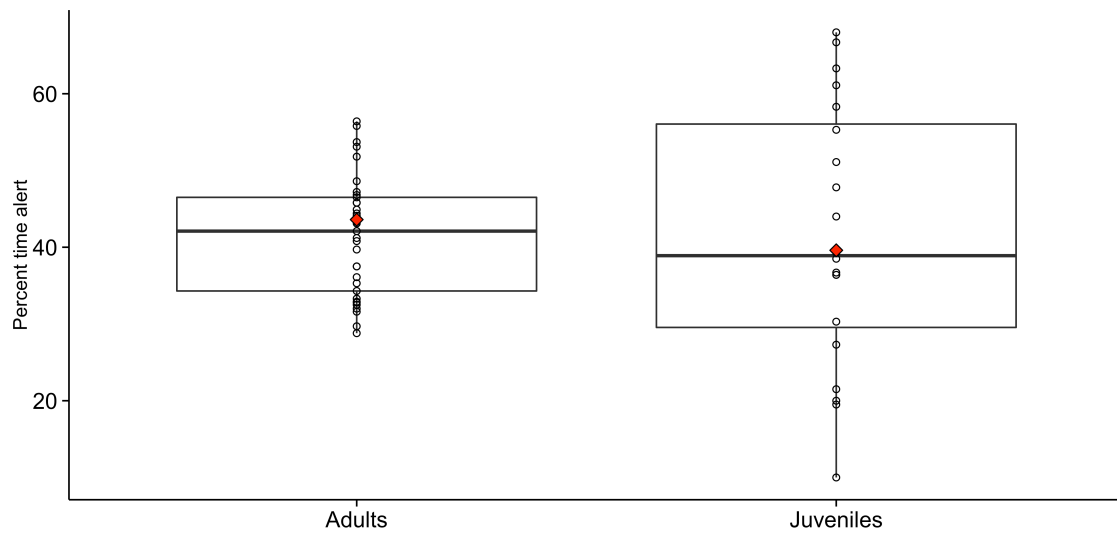
a)



b)



c)



d)

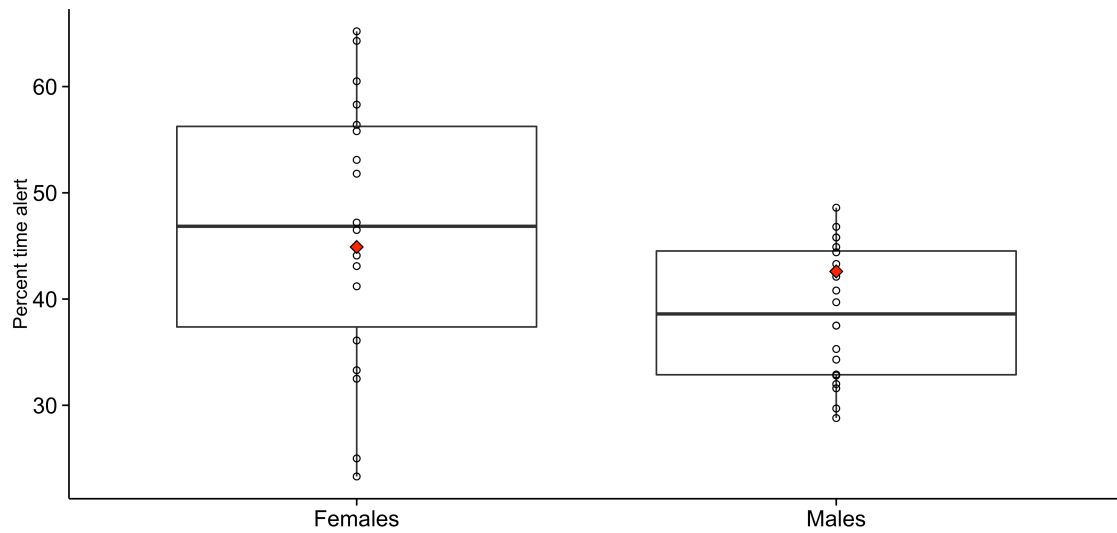


Fig. 2.- Ranges of percentages of time spent foraging between a) adults and juveniles and b) adult females and adult males, and alert between c) adults and juveniles and d) adult females and adult males.

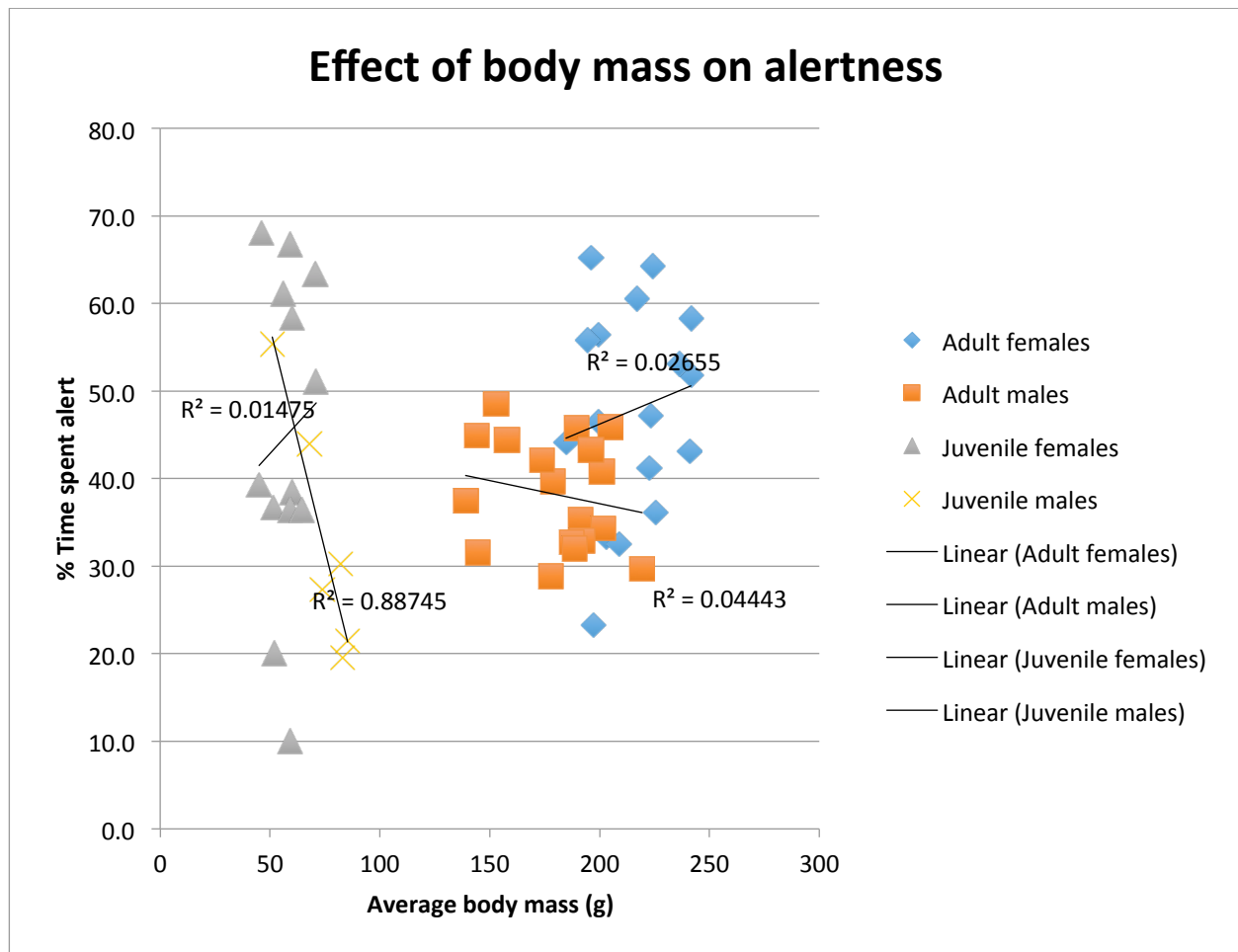


Fig. 3.- Percentage of time spent alert vs. average body mass (g) for adult males, adult females, juvenile males and juvenile females.