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Causes and Consequences of Pre-hibernation Body Mass  
in Golden-mantled Ground Squirrels (*Callospermophilus lateralis*)

By

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THESIS

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## ABSTRACT

Mammals that cope with harsh environmental conditions by hibernating show seasonal variation in body mass, as fat reserves are accumulated during summer and depleted during winter. Hence, pre-hibernation mass is often considered a key phenotypic trait in hibernating species that can be an indicator of future survival and reproductive success. We used 30 years of demographic data from a high-elevation population of golden-mantled ground squirrels (*Callospermophilus lateralis*) to identify life-history and environmental variables that influence pre-hibernation mass in females, and to determine if pre-hibernation mass influences overwinter survival or subsequent reproduction. Growth curves revealed female-biased size dimorphism, with adult mass not attained until age 2 years, so we considered three age classes of females, juveniles, yearlings, and adults ( $\geq 2$  years). We found that earlier snow melt during spring is associated with higher pre-hibernation masses of yearlings and adults, and that juveniles emerging earlier from their natal burrows had higher pre-hibernation masses than later-emerging juveniles. Measures of food quantity or quality did not affect pre-hibernation mass for any age class, nor was there an effect of reproductive status. Juvenile females with greater pre-hibernation mass were more likely to survive overwinter and reproduce as yearlings, but we found no such effect for yearlings or adult females. We did not find an effect of snow depth or winter duration on either survival or reproduction. Our results indicate that time appears to be the key variable for golden-mantled ground squirrels to acquire sufficient body mass to survive and reproduce, but the effects vary by age class.

## INTRODUCTION

High elevation environments are characterized by a short growing season during summer and thus a small window of time in which food resources are available to many resident mammals. Food scarcity and harsh environmental conditions over winter pose challenges for mammals who consequently often show seasonal dynamics in body growth and fattening (Davis 1976; Cederlund et al. 1991; Monteith et al. 2013). Fluctuations in body mass are often most dramatic for species that cope with harsh environmental conditions via hibernation, an adaptive life history strategy that involves fat storage during summer followed by a drop in metabolic rate and body temperature during winter, thereby decreasing the “energetic price” of winter (Nedergaard and Cannon 1990). Hibernation occurs in a variety of mammalian taxa but is particularly prevalent in the ground-dwelling squirrels (marmots, prairie dogs, and true ground squirrels). Hibernators accumulate fat reserves prior to hibernation and then subsist entirely, or to a large extent, on stored fat as an energy source in winter (Geiser 2011). Species that hibernate experience higher overwinter survival compared to similar-sized non-hibernating species (Turbill et al. 2011); however, hibernators have a relatively short period of time in which to gain sufficient fat stores to sustain them through the subsequent winter.

A hibernator’s ability to accumulate fat reserves during the summer growing season can be influenced by life history and environmental factors, but previous studies of ground-dwelling squirrels that have investigated factors influencing pre-hibernation mass have typically focused on the effect of a single variable, such as age class or weather. Adult Belding’s ground squirrels (*Urocitellus beldingi*) weighed more than yearlings prior to hibernation (Morton and Parmer 1975), and a longer growing season led to higher pre-hibernation weights for yellow-bellied marmots (*Marmota flaviventer*; Ozgul et al. 2010). Weather factors in particular vary annually and have the potential to affect an entire population, but these influences may change over time

with a changing climate (Ozgul et al. 2010). Climate change is expected to influence climate variability and may impact a hibernator's ability to store sufficient fat during the growing season or prolong winter conditions (Cordes et al. 2020).

Pre-hibernation fat reserves, as indicated by an individual's body mass, are often considered a key life-history trait and can be a determinant of survival (Lenihan and Van Vuren 1996) and reproductive success (Dobson and Michener 1995). Differential survival corresponding to pre-hibernation mass has been documented in a few species of ground-dwelling squirrels, suggesting that the period of fattening is a crucial time in the annual cycle of hibernating squirrels (Armitage et al. 1976; Murie and Boag 1984; Rieger 1996), but the topic remains poorly studied. Pre-hibernation mass also has the potential to influence future reproductive success, having implications for individual fitness as well as population dynamics (King et al. 1991; Dobson and Michener 1995; Hoogland 1995; Neuhaus 2000), but few studies have investigated the relationship between pre-hibernation body mass and reproductive output the following year in ground-dwelling squirrels.

We used 30 years of demographic data from a high-elevation population of golden-mantled ground squirrels (*Callospermophilus lateralis*) to identify life-history and environmental variables that influence accumulation of fat reserves, and to determine if pre-hibernation fat reserves influence overwinter survival or subsequent reproduction. Understanding demographic responses to environmental conditions of hibernating mammals is important for forecasting population dynamics under a changing climate (Ozgul et al. 2010).

## **MATERIALS AND METHODS**

*Study site and species.*—We studied golden-mantled ground squirrels from 1990 through 2020 at the Rocky Mountain Biological Laboratory (2900 m elevation), in the East River Valley of Gunnison County, Colorado, U.S.A. (38°58'N, 106°59'W). The 13-ha study site was

characterized by subalpine dry meadow habitat interspersed with patches of wet meadow and stands of aspen (*Populus tremuloides*), willow (*Salix* spp.), and spruce (*Picea engelmannii*); ground squirrels occurred primarily in dry meadow habitat (Aliperti 2020). Golden-mantled ground squirrels are a small-bodied (150-300 g), primarily herbivorous, diurnal species that breeds once per year and can live up to nine years (Bronson 1980; Kanaziz et al. 2022).

Reproductive maturity is reached at age 1, but many yearling females do not breed (Bronson 1980; Kneip et al. 2011). At our site, females emerge from hibernation in late April or May and subsequently mate. Females give birth to a litter of two to nine juveniles in underground burrows after a gestation of about 28 days (Cameron 1967). Juveniles are weaned after approximately 30 days (Phillips 1981), at which time they appear aboveground and begin foraging independently (Wells et al. 2017). Litters typically emerge from late-June to mid-July at our site and adults begin entering hibernation during August.

We conducted field work each year from late May or early June to late August; in some years we continued field work until early September. We trapped squirrels multiple times during the summer with Tomahawk live-traps (Model 201, Hazelhurst, Wisconsin) baited with black-oil sunflower seeds and peanut butter. We used numbered metal eartags (Model 1005-1 National Band and Tag Company, Newport, Kentucky) for permanent identification and unique dye marks on the fur (Nyanzol D dye, Greenville Colorants, Greenville, South Carolina) for visual identification of all captured squirrels. We recorded sex (anogenital distance), body mass (to the nearest 1 g) and reproductive status for females (color and swelling of nipples) at each capture. Squirrels were observed regularly throughout the active season. We rotated through all sections of the study area at least twice daily, once during the morning and once during the afternoon, and used binoculars to visually identify squirrels at a distance based on their unique dye marks. All

trapping procedures were approved by the institutional animal care and use committees of the University of California at Davis and the Rocky Mountain Biological Laboratory, and met guidelines set by the American Society of Mammalogists (Sikes et al. 2016).

We conducted an annual census at the beginning of each field season by continuing trapping efforts until visual searches revealed that all squirrels in the study area had been identified and dye marked. Females classified as reproductive were monitored closely by searching their home ranges multiple times daily for newly emerged juveniles. The emergence date for a litter was recorded as the day on which the first juvenile was seen aboveground, and all juveniles were trapped within 1-2 days of emergence from the natal burrow. Immigrants were captured and marked whenever they first appeared in the study area, typically as unknown-age adults in early June or as juveniles in August.

Although the age of sexual maturity for golden-mantled ground squirrels is 1 year, the age at which individuals attain adult body mass is unknown. Yearlings often fail to reproduce (Bronson 1979; Kneip et al. 2011), perhaps because they have not reached adult mass; hence, we constructed age-specific growth curves. Age was known for individuals born into the population, and for August immigrants age was based on body mass (Kneip et al. 2011).

*Pre-hibernation mass.*—Juvenile males born in our study area are seldom re-trapped as yearlings, presumably because of male-biased dispersal; hence, our analysis of causes and consequences of pre-hibernation mass was based only on females. Because adult body mass was not reached until age 2 years (see results), we used three age classes, juveniles, yearlings, and adults ( $\geq 2$  years old). Immigrant females trapped during June were either yearlings or adults. We classified immigrants that weighed  $< 190$  g during 1-15 June as yearlings, because 95% of

known-age females that weighed <190 g during 1-15 June were yearlings ( $n = 70$ ; Schlageter *unpublished data*).

We used mass data obtained after 31 July to estimate pre-hibernation masses, based on the assumption that hibernation began during August. That assumption was supported during the years in which field work continued into September; of those yearling and adult females known to be alive 1 August and that survived overwinter, 85% ( $n = 39$ ) were not detected by trapping or observation after 31 August (Schlageter *unpublished data*). During those years of post-August field work, almost all squirrels detected after August were juveniles, indicating that they entered hibernation somewhat later. Squirrels were trapped on various dates after 31 July; to standardize pre-hibernation masses, we calculated the late-season mass gain per day for those females with  $\geq 2$  post-July masses separated by  $\geq 5$  days, by dividing the difference between first and last masses by elapsed time. Using mean daily mass gain for each age class, we standardized pre-hibernation mass to 15 August for yearlings and adults and to 25 August for juveniles, to account for later hibernation of juveniles.

Environmental factors, especially weather, might influence pre-hibernation mass; data on weather variables were obtained from a long-term (1975 – 2022) weather station at the Rocky Mountain Biological Laboratory (Gothic Weather 2022). We expected that time of spring snow melt and summer rainfall would be important (Table 1). At high-elevation sites, snow melt in the spring signals the onset of vegetation growth, hence food availability; thus, early snow melt should increase the amount of time that individuals have to gain mass, resulting in increased pre-hibernation masses (Van Vuren and Armitage 1991; Ozgul et al. 2010). Snow melt date was represented by the first day of exposed bare ground at the weather station (Kneip et al. 2011). Summer rainfall might have either of two effects on pre-hibernation mass: it might enhance the



growth of vegetation and positively influence pre-hibernation mass, or it might reduce the amount of time spent above ground, thus limiting foraging opportunities and negatively influencing pre-hibernation mass (Kneip et al. 2011). We summed rainfall for June and July each year; August rainfall was excluded because squirrels were entering hibernation at this time (Kneip et al. 2011).

We expected that several life history variables could influence pre-hibernation mass. For yearling and adult females, being reproductive could lead to lower pre-hibernation mass because of the energetic cost of reproduction (Moore et al. 2016). Additionally, if squirrels are competing for food resources, we would expect that in years with higher density, pre-hibernation masses would be lower. The study area was constant throughout the study, so as a proxy for density we used population size which was revealed by the annual census. For juveniles we expected that emergence date from the natal burrow would influence pre-hibernation mass because it delimits the amount of time a juvenile has to gain mass before hibernation (Wells and Van Vuren 2018).

*Overwinter survival.*—A squirrel was classified as having survived overwinter if it was recaptured the following year. We expected that greater accumulated fat stores, as represented by pre-hibernation mass, would have a positive effect on overwinter survival (Lenihan and Van Vuren 1996). We used body mass as a proxy for fat stores because it is an accurate indicator of fat stores in golden-mantled ground squirrels during the pre-hibernation period (Wells et al. 2019). We expected two environmental variables to influence overwinter survival: date of first bare ground the following spring and mean snowpack depth during winter. Early snow melt should reduce the amount of time that hibernating squirrels subsist on fat reserves, with positive effects on overwinter survival (Lane et al. 2012). Snowpack has insulating effects in the winter and prevents frost from reaching deep underground (Hardy et al. 2001). As a result, thin snow

cover can decrease hibernaculum temperature and accelerate fat depletion of hibernating mammals (Tafari et al. 2013), with a negative effect on overwinter survival (Patil et al. 2013). Measures of snowpack depth were averaged for the months of October through April.

*Reproductive output.*—We explored the effects of pre-hibernation mass and several environmental variables on two components of reproduction the following year: whether a female was reproductive, and litter size for those females that did reproduce. Consistent with our overwinter survival analysis, we expected that greater snowpack depths and earlier snow melt dates would have positive effects on reproduction and litter size during the subsequent spring.

*Statistical analysis.*—We constructed growth curves for known-aged males and females. For squirrels  $\geq 1$  year old we used body masses recorded 1-15 June. Juvenile masses were recorded within 2 days of emergence from the natal burrow. In order to identify the age at which growth stabilized at adult body mass, we conducted a change point analysis in the R package *chngpt* and fitted a continuous two-phase model for each sex (Killick and Eckley 2014).

To evaluate the effects of life history traits and environmental factors on pre-hibernation body mass we fit a series of linear mixed effects models (LMMs) using the RStudio package *nlme* (R Core Team 2021; Pinheiro et al. 2022). For the juvenile age class, we fit a LMM with density, summer rainfall, and natal emergence day as fixed effects, and year of birth as a random effect. We also ran the same model but with the addition of mother's identity as a random effect, and the outcome was qualitatively the same. For females  $\geq 1$  year old we modeled density, summer rainfall, date of first bare ground, age class (yearling or adult), and reproductive status as fixed effects, and individual identity as a random effect. Dates were entered into the models as integers corresponding to the number of days past 30 April.

To investigate the impact of life history traits and environmental variables on overwinter survival we fit generalized linear mixed models (GLMM's) using the RStudio package *lme4* with a binomial error structure and a logit link function (Bates et al. 2015). For the juvenile model, pre-hibernation mass, snowpack depth, and date of first bare ground were included as fixed effects, and year of birth was included as a random effect. For females  $\geq 1$  year old we included pre-hibernation mass, snowpack depth, date of first bare ground, reproductive status, and age class as fixed effects, and individual identity as a random effect.

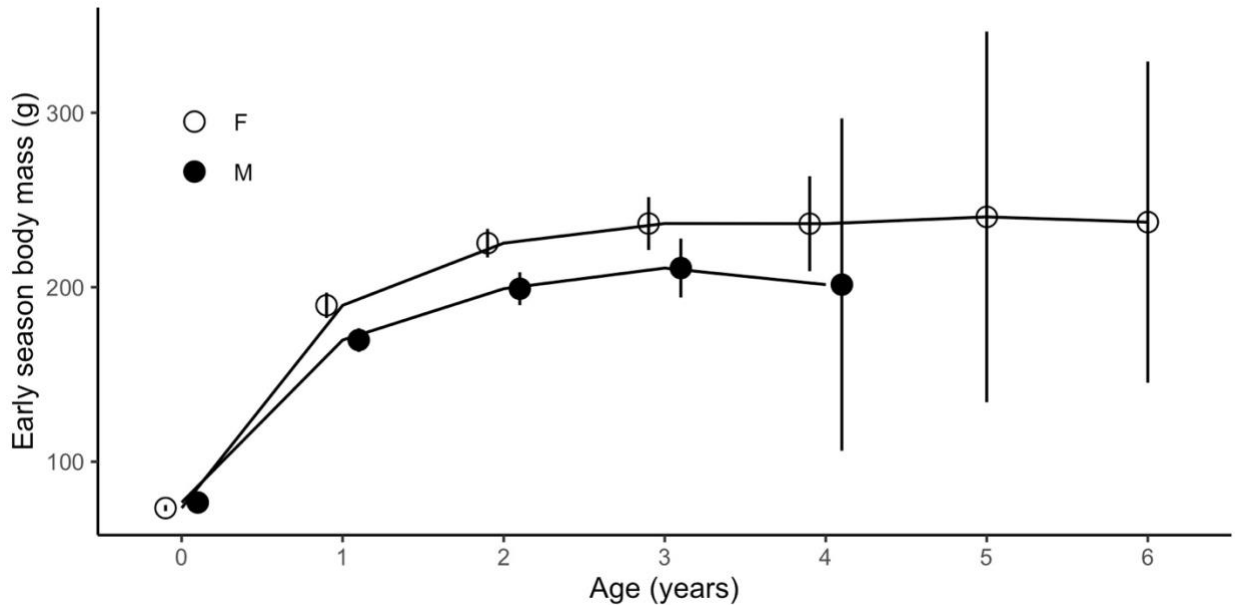
For our reproductive success analyses, we modeled likelihood of reproduction as a function of pre-hibernation mass, mean snowpack depth, and date of first bare ground using a GLMM with a binomial error structure and a logit link function with year as a random effect. At our site most adult females breed (82%; Kneip et al. 2011), resulting in a sample size of non-reproductive adult females insufficient for analysis. As a result, we focused on the probability of reproduction for yearlings, using juvenile pre-hibernation mass as a predictor. We modeled litter size for yearling and adult females in a LMM with pre-hibernation mass, mean snowpack, date of first bare ground, and age class as fixed effects and individual identity as a random effect.

**Table 1.**—Definition of effects used in statistical analyses.

	Definition
<u>Fixed effects</u>	
Population size	Total number of squirrels in the population in a given year
Summer rainfall	June and July rainfall total
Emergence day	Date a juvenile emerged from their natal burrow
Age class	Yearling (1 year old) or adult ( $\geq 2$ years old)
Reproductive status	Whether or not a female initiated reproduction
Mean snowpack	Mean snow depth for October through April
Date of first bare ground	The date when bare ground was first exposed in the spring
Pre-hibernation mass	Estimated body mass on 15 August (yearlings and adults) or 25 August (juveniles)
<u>Random effects</u>	
Year of birth	Year a juvenile was born

## RESULTS

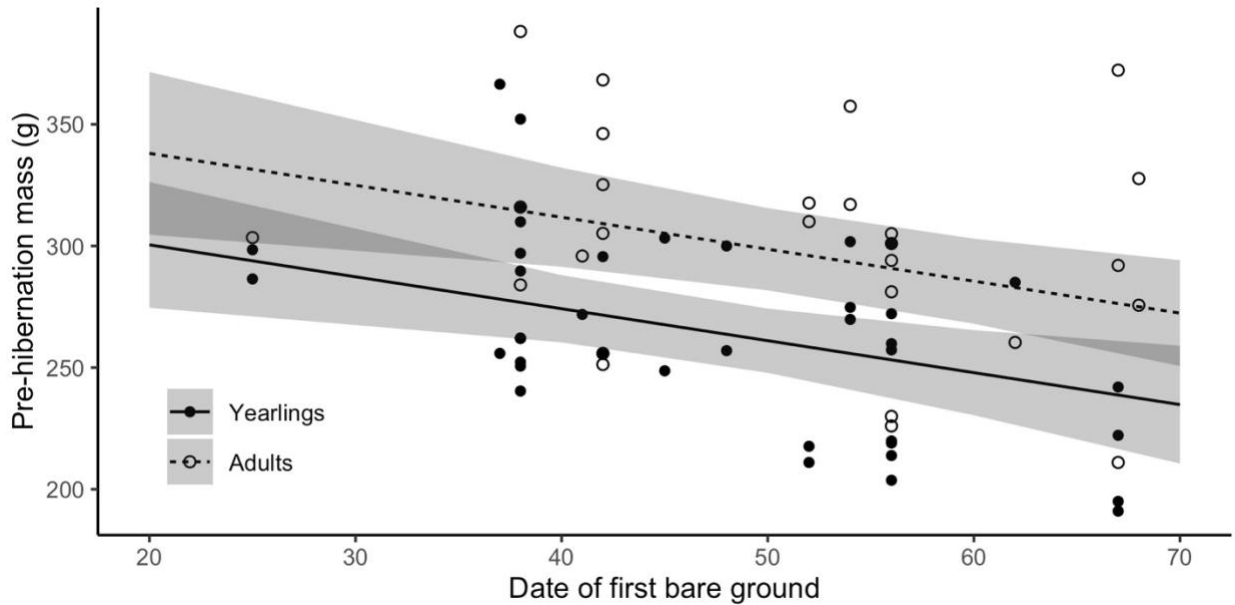
Our change point analysis revealed that mean mass of both male and female golden-mantled ground squirrels stabilized at 2 years of age (Fig. 1). Females weighed consistently more than males beginning at age 1.



**Fig. 1.**—Growth curves for known-age male and female golden-mantled ground squirrels using early season (1-15 June) body mass at the Rocky Mountain Biological Laboratory, Colorado. Vertical bars represent 95% confidence intervals.

*Pre-hibernation mass.*—Female late-season mass gain averaged 2.9 g/day for adults, 2.2 g/day for yearlings, and 2.3 g/day for juveniles. Standardized female pre-hibernation mass values ranged 84 – 303 g for juveniles ( $n = 136$ ), 191 – 367 g for yearlings ( $n = 40$ ), and 211 – 388 g for adults ( $n = 27$ ). In the yearling and adult female analysis, adult age class was positively associated with pre-hibernation mass (LMM  $\beta \pm SE = 37.60 \pm 10.37$ ,  $t = 3.63$ ,  $P = 0.003$ ), and date of first bare ground showed a negative association (LMM  $\beta \pm SE = -1.31 \pm 0.43$ ,  $t = -3.05$ ,  $P = 0.008$ ; Fig. 2). We found no effect of reproductive status (LMM  $\beta \pm SE = -1.17 \pm 12.93$ ,  $t = -0.09$ ,  $P = 0.929$ ) or density (LMM  $\beta \pm SE = 1.74 \pm 1.44$ ,  $t = 1.21$ ,  $P = 0.247$ ) on yearling and

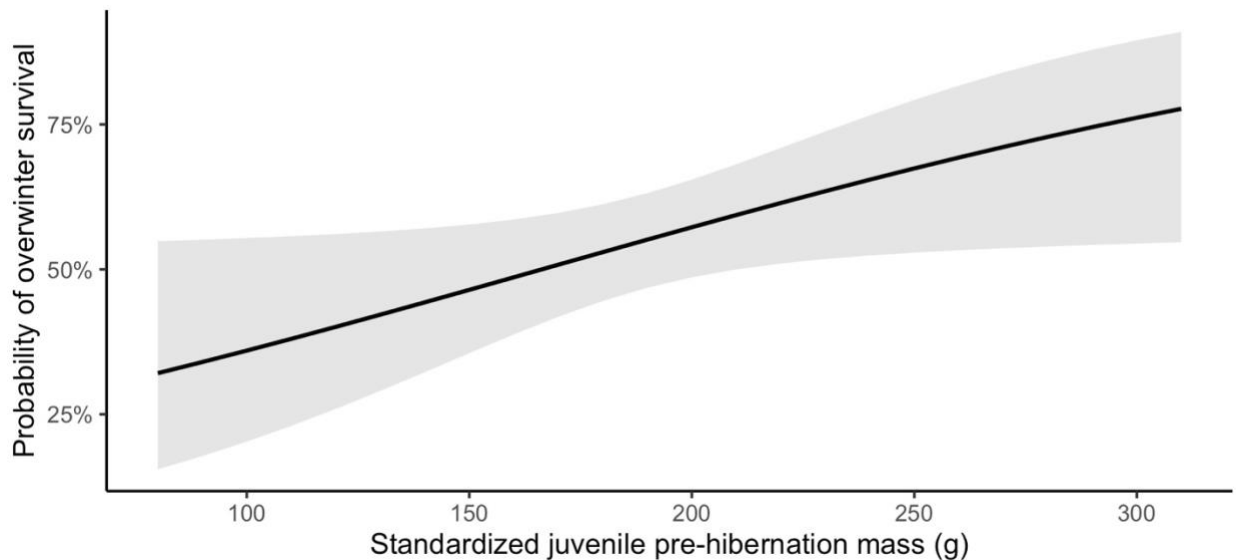
adult pre-hibernation mass. Date of juvenile emergence from the natal burrow ranged 18 June to 14 August and had a positive association with pre-hibernation mass for juvenile females (LMM  $\beta \pm SE = -2.63 \pm 0.22$ ,  $t = -12.15$ ,  $P < 0.001$ ). We found no effect of summer rainfall (LMM  $\beta \pm SE = -1.35 \pm 1.27$ ,  $t = -1.06$ ,  $P = 0.304$ ) or density (LMM  $\beta \pm SE = 0.06 \pm 0.12$ ,  $t = -0.51$ ,  $P = 0.615$ ) on juvenile female pre-hibernation mass.



**Fig. 2.**—Linear regression of date of first bare ground (number of days past 30 April) on pre-hibernation mass of yearling and adult female golden-mantled ground squirrels at the Rocky Mountain Biological Laboratory, Colorado. Points represent raw data; lines represent model output.

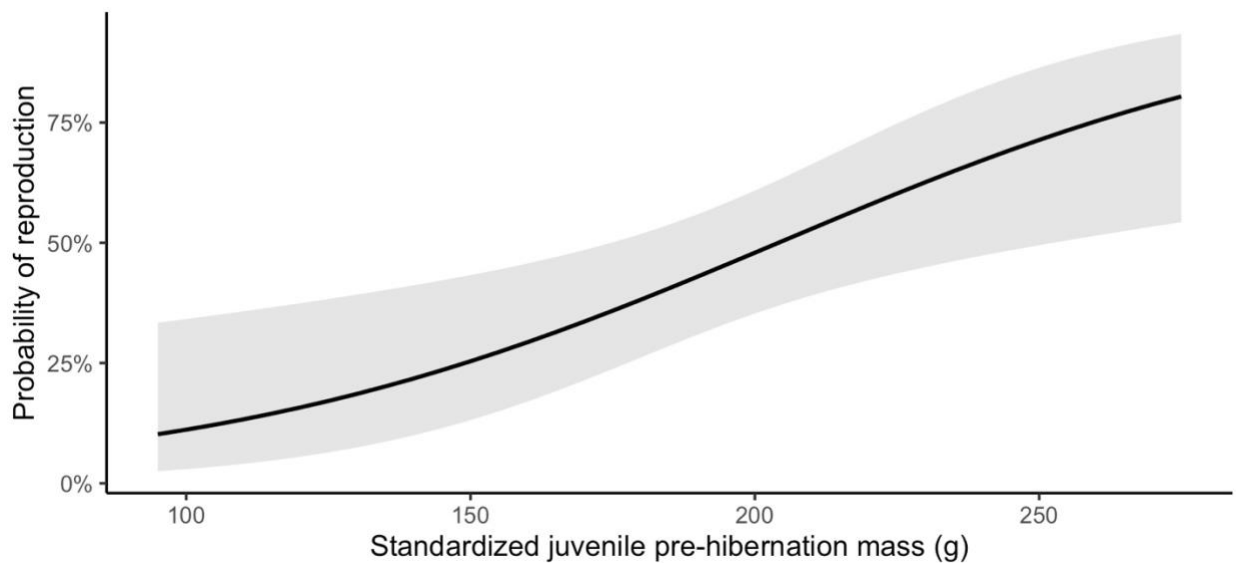
*Overwinter survival.*—Female overwinter survival was 54% for juveniles, 77% for yearlings, and 71% for adults; adult survival was calculated assuming independence among squirrel-year observations. For juveniles, pre-hibernation mass was positively associated with overwinter survival (GLMM  $\beta \pm SE = 0.009 \pm 0.004$ ,  $z = 2.51$ ,  $P = 0.038$ ,  $n = 223$ ; Fig. 3). Hence, a juvenile weighing 250 g on 25 August had a 67% ( $SE \pm 9\%$ ) chance of surviving overwinter, whereas a 100 g juvenile on this date would have only a 36% ( $SE \pm 7\%$ ) chance. We

found no relationship between either mean snowpack (GLMM  $\beta \pm SE = 0.0005 \pm 0.007$ ,  $z = 0.07$ ,  $P = 0.945$ ) or date of first bare ground (GLMM  $\beta \pm SE = 0.006 \pm 0.01$ ,  $z = 0.42$ ,  $P = 0.672$ ) on juvenile overwinter survival. Our analysis of yearling and adult overwinter survival included 100 observations from 64 unique squirrels. We did not find a relationship between overwinter survival and pre-hibernation mass (GLMM  $\beta \pm SE = 0.003 \pm 0.008$ ,  $z = 0.39$ ,  $P = 0.698$ ), mean snowpack (GLMM  $\beta \pm SE = -0.004 \pm 0.01$ ,  $z = -0.33$ ,  $P = 0.745$ ), date of first bare ground (GLMM  $\beta \pm SE = 0.02 \pm 0.03$ ,  $z = 0.70$ ,  $P = 0.486$ ), reproductive status (GLMM  $\beta \pm SE = 0.09 \pm 0.72$ ,  $z = 0.12$ ,  $P = 0.903$ ), or age class (GLMM  $\beta \pm SE = -0.44 \pm 0.84$ ,  $z = -0.53$ ,  $P = 0.598$ ). We evaluated different parameterizations (continuous and categorical) of mean snowpack depth and date of first bare ground to account for the possibility that median values were more favorable than the extremes (Kanaziz et al. 2022). None of the effects of the categorical or continuous parameterizations was significant (results not shown).



**Fig. 3.**—Predicted probabilities of overwinter survival for juvenile female golden-mantled ground squirrels by pre-hibernation mass, adjusted for a mean snowpack of 107 cm and a date of first bare ground of 20 May, at the Rocky Mountain Biological Laboratory, Colorado.

*Reproductive output.*—Pre-hibernation mass was positively associated with the probability of reproduction in yearling females (GLMM  $\beta \pm SE = 0.02 \pm 0.01$ ,  $z = 2.79$ ,  $P = 0.005$ ; Fig. 4). We found no effect of mean snowpack (GLMM  $\beta \pm SE = -0.01 \pm 0.01$ ,  $z = -1.45$ ,  $P = 0.148$ ) or date of first bare ground (GLMM  $\beta \pm SE = -0.03 \pm 0.02$ ,  $z = -1.35$ ,  $P = 0.177$ ) on the likelihood of reproduction for yearling females. Our sample size for the litter size model included 85 observations from 51 unique yearling and adult females. We did not find an association between litter size and pre-hibernation mass (LMM  $\beta \pm SE = 0.006 \pm 0.004$ ,  $t = 1.67$ ,  $P = 0.109$ ), mean snowpack (LMM  $\beta \pm SE = 0.006 \pm 0.006$ ,  $t = 0.99$ ,  $P = 0.335$ ), date of first bare ground (LMM  $\beta \pm SE = -0.013 \pm 0.01$ ,  $t = -1.08$ ,  $P = 0.290$ ), or age class (LMM  $\beta \pm SE = 0.16 \pm 0.38$ ,  $t = 0.41$ ,  $P = 0.688$ ). We evaluated both continuous and categorical parameterizations of mean snowpack and date of first bare ground and neither parameterization had an effect (results not shown).



**Fig. 4.**—Predicted probabilities of positive reproductive status for yearling female golden-mantled ground squirrels by pre-hibernation mass, adjusted for a mean snowpack of 107 cm and a date of first bare ground of 20 May, at the Rocky Mountain Biological Laboratory, Colorado.

## DISCUSSION

Neither male nor female golden-mantled ground squirrels attained adult body mass until 2 years of age, 1 year after the age of sexual maturity, reflecting a pattern of continued growth after sexual maturity that has been reported for several other species of ground-dwelling squirrels (Boag and Murie 1981). We observed female-biased sexual size dimorphism for squirrels  $\geq 1$  year old, based on early-season body masses. The difference between male and female masses likely was affected by changes in female mass during reproduction; most reproductive females were in gestation during early June, and some had given birth. However, the mass disparity between males and females was maintained through August (Schlageter *unpublished data*), after reproduction was concluded. Male-biased sexual size dimorphism is the common pattern in mammals (Isaac 2005), including ground-dwelling squirrels (Boag and Murie 1981; Matějů and Kratochvíl 2013). Female-biased size dimorphism has been reported in some species of ground-dwelling squirrels (Levenson 1990), but the causes are uncertain (Schulte-Hostedde et al. 2004). One explanation is a polygynandrous mating system with relatively low opportunity for sexual selection between males and females, which characterizes the mating system of golden-mantled ground squirrels (Schulte-Hostedde et al. 2004; Wells et al. 2017). Additionally, structural measures (hind foot and condylobasal lengths) of golden-mantled ground squirrels do not differ between males and females (Matějů and Kratochvíl 2013), suggesting that the greater mass of females is due mostly to fat stores. Females initiate reproduction shortly after emergence from hibernation and thus require sufficient fat reserves to both survive hibernation and support the physiological costs of reproduction (Levenson 1990).

In high elevation environments, exposure of bare ground by melting snow signals the onset of the growing season, and hence of food availability for herbivores (Van Vuren and



Armitage 1991). Accordingly, we found that earlier snow melt is associated with higher pre-hibernation masses of both yearling and adult female golden-mantled ground squirrels. Similarly, juveniles that emerged earlier from their natal burrows had higher pre-hibernation masses than late-emerging juveniles. In contrast, measures of food quantity or quality (summer rainfall, density as an indicator of competition) did not affect pre-hibernation mass, perhaps because squirrels in our population are not food limited during the growing season (Kneip et al. 2011). We also did not find an effect of reproductive status on pre-hibernation mass for yearling and adult females. Hence, time appears to be the key variable in determining mass gain in preparation for hibernation; a similar relationship was documented for yellow-bellied marmots (Ozgul et al. 2010). In our study, squirrels remained underground during periods of rain (Kneip et al. 2011), but the resulting loss of time available for feeding was not consequential in influencing pre-hibernation masses. Time might be particularly important for juveniles, which emerge and begin feeding after the plant growing season is well advanced; and may be especially critical for late-emerging juveniles, who are unable to compensate with higher growth rates (Wells and Van Vuren 2018).

We expected that pre-hibernation mass would have a positive effect on overwinter survival for females of all age classes, but we did not find that to be the case for yearling and adult females, in support of a previous study on our population (Aliperti 2020). We did not find a difference in survival rates between yearling and adult females; evidently both age classes gained sufficient levels of fat stores prior to hibernation to survive overwinter, as was reported for Columbian ground squirrels (*U. columbianus*; Murie and Boag 1984) and Richardson's ground squirrels (*U. richardsonii*; Michener and Locklear 1990). Hibernators likely need to reach a certain body fat content to survive hibernation (Rieger 1996), and selection should favor

processes in which animals achieve adequate weight gain in time for hibernation (Armitage et al. 1976). Snowpack depth and date of first bare ground in the spring did not affect overwinter survival for females of any age class. Evidently females had sufficient fat reserves to survive a longer hibernation caused by delayed snow melt, and snowpack was sufficiently deep to provide necessary insulation (Tafari et al. 2013); snowpack absence might have been necessary for an effect on survival (Johnston et al. 2021). In contrast to our findings that reproductive females did not suffer lower overwinter survival, Neuhaus (2000) reported that reproductive female Columbian ground squirrels were lighter at hibernation and suffered lower overwinter survival than non-reproductive females. Perhaps our inability to detect an effect resulted from our relatively small number of non-breeding females ( $n = 22$ ).

In contrast to yearlings and adults, pre-hibernation mass of juvenile females was positively associated with overwinter survival, a finding that has been observed in several other ground-dwelling squirrels, including yellow-bellied marmots (Lenihan and Van Vuren 1996), Columbian ground squirrels (Murie and Boag 1984), Uinta ground squirrels (*U. armatus*; Slade and Balph 1974), black-tailed prairie dogs (*Cynomys ludovicianus*; Foltz et al. 1988), and Richardson's ground squirrels (Michener and Locklear 1990). The difference between the standardized pre-hibernation masses of the lightest and heaviest juveniles was over 200 g, so it is likely that lighter juveniles did not have sufficient fat stores to successfully overwinter (Rieger 1996). Time might be the most important influence, since juveniles emerge from their natal burrow well into the vegetation growing season; accordingly, late-emerging juveniles experienced lower overwinter survival in yellow-bellied marmots (Armitage et al. 1976) and Uinta ground squirrels (Rieger 1996). Additionally, juveniles have higher surface-to-volume

ratios than the other age classes, which may result in more energy expenditure per gram of body weight and thus a greater requirement for pre-hibernation fat stores (Sherman and Runge 2002).

Female pre-hibernation mass was a significant predictor of the probability of reproduction as a yearling, and our results provide a mechanistic explanation for the finding by Wells and Van Vuren (2018) that early-emerging juvenile females were more likely to reproduce as yearlings. Early-emerging juveniles have more time to gain body mass prior to hibernation, increasing their chances of reproducing the following spring. These results imply a fitness advantage for females who mate earlier in the season via increased overwinter survival and subsequent reproduction by their offspring (Armitage et al. 1976). We did not find a relationship between date of first bare ground or mean snowpack and the likelihood of reproduction. Litter size was not influenced by pre-hibernation mass, contrary to results for black-tailed prairie dogs (Hoogland 1995), nor was it influenced by date of first bare ground, mean snowpack, or age class, consistent with a previous study on our population (Kneip et al. 2011).

Females might support reproduction using ingested resources (“income breeder”) or stored resources, either fat deposits or food caches (“capital breeder”; Jönsson 1997). These strategies are seen as two ends of a spectrum, and one species may utilize both to support reproduction (Broussard et al. 2005). Ground squirrels are thought to combine the two strategies, with maternal fat stores at the time of mating influencing reproductive investment and ingested food after mating supporting most energetic needs during gestation and lactation (Broussard et al. 2005; Wells and Van Vuren 2017). Our results support a combined strategy for golden-mantled ground squirrels. Timing of litter emergence in our study area is correlated with time of snow melt ( $r = 0.61$ ,  $P < 0.001$ ,  $n = 27$ ), and most females mate around the time of snow melt or shortly before, as estimated by backdating time for gestation and lactation (58 days) from litter

emergence dates (Schlageter *unpublished data*). Hence, females often mate before substantial growth of spring vegetation, and apparently they are relying on stored fat rather than food caches, as excavation of 48 burrows near our study area during July and August revealed no evidence of substantial caches (Bihr and Smith 1998). Pre-hibernation mass likely influenced the probability of reproduction by yearling females, suggesting the role of residual fat stores in the spring. Most adult females breed each year, and pre-hibernation mass did not affect litter size the next year, possibly because residual fat stores in spring are sufficient to support reproduction. Presumably, gestation and lactation are supported primarily by ingested energy.

Body mass is often considered to be a key-life history trait, and in hibernating species in particular it can be an indicator of future survival and reproductive success (Jebb et al. 2021). Our results indicate that time can be important for golden-mantled ground squirrels to acquire sufficient body mass to survive and reproduce. The effects of climate change on local weather may differ among localities (Inouye et al. 1999). In the Rocky Mountains of Alberta, Canada, the annual time of snow melt has been progressively delayed because of an increasing frequency of late-season storms; the result for Columbian ground squirrels has been later emergence from hibernation and reduced survival, reproduction, or both (Lane et al. 2012). In contrast, at our study site in the Rocky Mountains of Colorado, the annual time of snow melt has progressively advanced (Inouye 2022); for yellow-bellied marmots, the result has been earlier emergence from hibernation and more time to gain mass, which has led to increased survival (Ozgul et al. 2010). Our results indicate that for golden-mantled ground squirrels, earlier snow melt will lead to increased survival and subsequent reproduction, but this effect is limited to the juvenile age class. Hence, our findings are in agreement with those of Falvo et al. (2019), that effects of climate change on a particular species may differ markedly between age classes.

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