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Source: Journal of Mammalogy, 92(2):367-377. 2011.

Published By: American Society of Mammalogists

DOI: 10.1644/10-MAMM-A-156.1

URL: http://www.bioone.org/doi/full/10.1644/10-MAMM-A-156.1

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Influence of population density and climate on the demography of subalpine golden-mantled ground squirrels

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Temporal fluctuation in abundance is common in many wildlife populations, but the causes and consequences to population dynamics of these fluctuations remain poorly understood. We used long-term (1990–2008) field data to investigate the influence of population size and environmental factors (climatic variables and predation) on the demography of golden-mantled ground squirrels (*Callospermophilus lateralis*). Survival varied by sex and age class, with highest survival for adult females ($\Phi = 0.519$, 95% confidence interval [95% *CI*] = 0.462–0.576) and lowest survival for juvenile males ($\Phi = 0.120$, 95% *CI* = 0.094–0.152). Population size negatively influenced survival with a time lag of 1 year. Among environmental factors, current year's rainfall and intensity of predation substantially influenced survival. Probability of successful reproduction (probability that a female weans $\geq$1 pups) was higher for older females ($\Psi = 0.816$, 95% *CI* = 0.734–0.877) than for yearlings ($\Psi = 0.313$, 95% *CI* = 0.228–0.412). Rainfall negatively influenced probability of successful reproduction of both older and yearling females with a time lag of 1 year. Litter size ranged from 1 to 8 pups, with a mean of 4.8 (95% *CI* = 4.5–5.1). We found no evidence that litter size varied among age classes or over time, or was influenced by population size or environmental factors. Our results suggest that population size and environmental factors do not affect all demographic variables in the same way, and that both density-dependent and environmental factors influence the size of our study population.

Key words: *Callospermophilus lateralis*, climate change, demography, density-dependence, golden-mantled ground squirrels, population dynamics, population regulation, *Spermophilus lateralis*

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Identifying and quantifying the causes and consequences of temporal fluctuations in vertebrate populations is a persistent challenge in ecology (Coulson et al. 2001; Oli and Armitage 2004; Williams et al. 2001). Factors that drive population dynamics can be density-dependent (DD) or density-independent (DID). DD feedback mechanisms play an important role in regulating populations (Hone and Sibly 2002; Royama 1992; Turchin 2003), but several studies suggest that density-dependence and environmental factors (e.g., rainfall and temperature) act synergistically to determine dynamics and thus regulation of populations (Clutton-Brock and Coulson 2002; Coulson et al. 2001, 2008; Leirs et al. 1997). However, the relative roles of DD factors, climatic factors, predation, and intrinsic influences on population dynamics remain poorly understood for most species (Den Boer and Reddingius 1996; Tamarin 1978).

The impact of climatic factors on population dynamics may be intensifying as a result of global climate change. A growing body of evidence demonstrates that the climate of Earth is changing and that these changes will influence both the mean and variance of climatic variables (Bernstein et al. 2007). Consequently, these changes already are affecting the physiology, phenology, and demography of several species, particularly those species occupying high-altitude or high-latitude habitats (Bernstein et al. 2007; Frederiksen et al. 2008; Hughes 2000; Inouye et al. 2000; Jenouvrier et al. 2009; Parmesan 2006; Regehr et al. 2010). Global climate change can affect the length of summer or winter seasons, which in turn can have substantial effects on hibernating species (Inouye et al. 2000; Ozgul et al. 2010). Species distributions and life-history traits also can be altered (McLaughlin et al. 2002). To mitigate the potential ecological consequences of such changes we must understand how fluctuating environmental factors influence the demographic parameters, dynamics, and persistence of populations (Boyce et al. 2006; Jenouvrier et al. 2009). Because

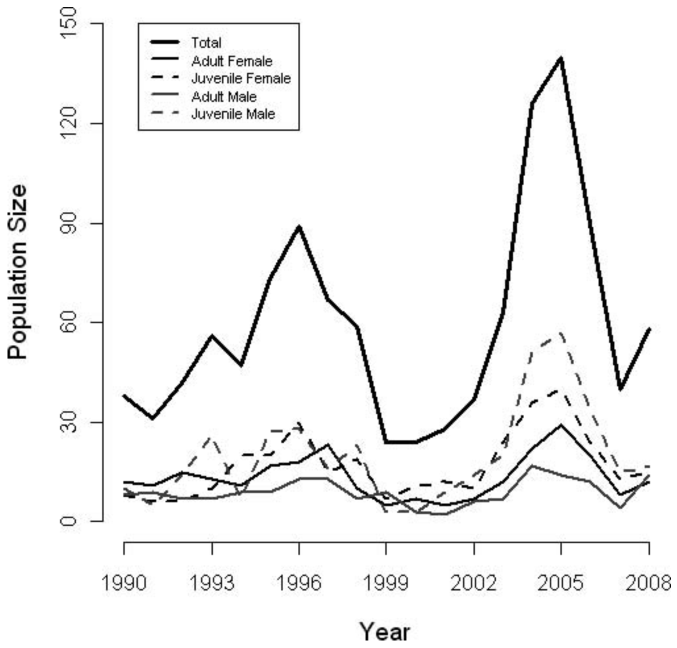

Fig. 1.—Annual variation in population size of the golden-mantled ground squirrel (*Callospermophilus lateralis*) population for the period 1990–2008. Total and age- and sex-specific numbers of squirrels are presented.

population growth rates are determined by demographic parameters (Caswell 2001; Oli and Armitage 2004), population-level impacts of anticipated global climatic change are likely to be mediated through demographic rates such as survival and reproductive rates (Jenouvrier et al. 2009; Krebs 1995, 2002). Therefore, to define the relative roles of population density, predation, and climatic factors in determining population dynamics in stochastic environments, one must 1st understand their relative impacts on vital demographic rates.

The golden-mantled ground squirrel (*Callospermophilus lateralis*; formerly, *Spermophilus lateralis*; hereafter, GMGS—Helgen et al. 2009) is a hibernating species occupying montane habitats in western North America (Bartels and Thompson 1993; Ferron 1985). At a subalpine location in the Rocky Mountains, where climate change has affected phenology and population dynamics of several species (Inouye et al. 2000; Ozgul et al. 2010), a free-ranging GMGS population exhibited substantial fluctuations (Fig. 1). The long-term (19 years) monitoring of this species allowed us to investigate the relative influence of population density and extrinsic factors on GMGS vital rates. Our objectives were to provide estimates of age-specific survival rates, breeding probabilities, and litter size (LS); to evaluate the effects of sex, population size (with and without time lag), and environmental factors (predation, previous and current summer rainfall, and previous and current year's time of snowmelt) on these rates; and to compare the relative influence of DD and DID factors on vital rates.

Materials and Methods

Study area and species.—Our research was conducted at the Rocky Mountain Biological Laboratory near Crested Butte, Colorado (38°58′N, 106°59′W, elevation 2,890 m). The 13-ha study area was situated on a primarily open subalpine meadow that was interspersed with willow (*Salix* sp.) and aspen (*Populus tremuloides*) stands. The meadow was bordered on the west and south by the East River and Copper Creek, and on the north and east by aspen forest.

The GMGS is a diurnal, asocial species whose distribution spans a broad elevational gradient from 1,220 to 3,965 m above sea level, where it occupies open habitats such as rocky slopes adjoining grasslands, areas of scattered chaparral, and margins of mountain meadows (Bartels and Thompson 1993; Ferron 1985). GMGSs hibernate to cope with food shortages during long winters. The entrance to and emergence from hibernation both vary depending on altitude and amount of snowfall (Bartels and Thompson 1993).

At our study site adult squirrels typically emerged from hibernation at about the time of snowmelt or before, in May or early June. The mating season began shortly after emergence, and pups emerged from natal burrows during late June to mid-July. Squirrels entered hibernation by late August or early September. The GMGS is considered omnivorous (Bartels and Thompson 1993), but in our study area its diet consisted mainly of herbaceous vegetation such as grasses and forbs (D. Van Vuren, pers. obs.), whose growth is stimulated by snowmelt. After the onset of vegetative growth, squirrels gain weight rapidly, storing fat for overwinter survival and to sustain gestation the next spring until green vegetation starts growing again (Phillips 1984). Numerous mammalian and avian predators prey on GMGSs (Bartels and Thompson 1993), but in our study area predation only by red foxes (*Vulpes vulpes*), long-tailed weasels (*Mustela frenata*), and short-tailed weasels (*Mustela erminea*) was apparent.

Field methods.—For 19 consecutive years (1990–2008) we conducted livetrapping of GMGSs, augmented by almost daily observations during the active season. Squirrels were trapped during late May to early June for the annual census and marking of the resident population, late June to mid-July for trapping and marking emerging litters, and late July and again late August for weighing squirrels and renewing marks. Observations and opportunistic trapping were conducted almost daily throughout the summer to capture and mark new immigrants and renew marks on residents.

Squirrels were captured with single-door Tomahawk live traps (12.7 × 12.7 × 40.6 cm; Tomhawk Live Trap Company, Tomhawk, Wisconsin) baited with a mixture of sunflower seeds and peanut butter. Newly captured squirrels received a noncorrosive metal tag (National Band and Tag Company, Newport, Kentucky) in each ear. Squirrels were distinctly marked with black fur dye (Nyanzol-D; J. Belmar Incorporated, North Andover, Massachusetts) for visual recognition, and body mass, sex, ear tag numbers, and reproductive condition were recorded. All juveniles were trapped at 1st emergence from their natal burrow; LS was determined, and the mother was recorded as having reproduced successfully. Animal handling followed protocols approved by the Animal Care and Use Committee at the University of California, Davis, and met guidelines of the American Society of Mammalogists (Gannon et al. 2007).

Age was known for 704 squirrels that were captured initially as juveniles at their natal burrow. For an additional 127 squirrels (all adults in 1990 and immigrant adults in subsequent years) exact age was not known; however, immigrant juveniles (<1 year) could be differentiated from adults based on body mass.

Population size and predation.—Squirrels and predators were readily visible during observations. We determined squirrel population size by counting individuals because we continued trapping and marking until all squirrels in the study area were trapped and identified each year; therefore, capture probability was ~ 1 throughout the study period. Predation (*pred*) was measured as an index and was quantified as the sum of observed and inferred predations on squirrels per year. Inferred predation events were recorded if a squirrel abruptly disappeared when red foxes or weasels were active in the study site.

Climatic covariates.—Climatic factors considered in this study included summer (June and July) rainfall during the current ($rain_t$) and previous year ($rain_{t-1}$) and the 1st day that snowmelt exposed bare ground during the current (bg_t) and previous year (bg_{t-1}). These variables were used as temporal covariates in our capture–mark–recapture analysis, and they were selected based on a priori hypotheses that they influence demographic parameters of GMGSs—apparent survival rate (survival), probability of successful reproduction (PSR), and LS. Data on climatic variables were obtained from the United States Environmental Protection Agency Weather Station at the Rocky Mountain Biological Laboratory (http://www.rmbl.org/home/index.php?module=htmlpages&func=display&pid=99) and from B. Barr (Rocky Mountain Biological Laboratory, pers. comm.).

Summer rain can prolong the growth of forbs and grasses that began when snow melted. Therefore, because of its effect on primary production, summer rainfall could be a good predictor of vital rates of squirrels (Sherman and Runge 2002). Summer rainfall was the rainfall total for June and July; August rainfall was excluded because squirrels are approaching hibernation.

The duration of snow cover likely influences the length of the growing season, hence food availability for squirrels (Bronson 1979; Van Vuren and Armitage 1991). During years of food shortage GMGSs may curtail reproduction in favor of survival (Phillips 1984; Sherman and Runge 2002). In addition, time of snowmelt affects the length of time squirrels are exposed to predation (Bronson 1979). Consequently, the 1st day of bare ground (i.e., no snow cover) also could be a good predictor of squirrel demographic parameters.

For the investigation of lag effects data were required from the year preceding the commencement of the study (1989) and were not available for all variables such as summer rainfall and population size. Summer rainfall was obtained by averaging the values from 1990 and 1991. Because the population fluctuated extensively during the study period, lag effects were studied from 1991 to 2008 for all DD analyses.

Survival analysis.—We used multistate capture–mark–recapture models (Williams et al. 2001) implemented in program MARK (White and Burnham 1999) using RMark interface (Laake and Rextad 2009) to estimate survival. We considered 2 states based on 2 age classes (juvenile, <1 year old; adult, ≥ 1 year old) and estimated and modeled the state-specific apparent annual survival (Φ) and recapture (p) rates. Preliminary analyses revealed that capture probability was close to 1.0 (≥ 0.99); therefore, we fixed p to 1.0 for all models. Transition from juvenile to adult state was fixed to 1.0, and that from adult to juvenile state was fixed to 0.0. Survival then was estimated for 4 sex and age classes (juvenile males and females, and adult males and females).

The goodness-of-fit of our fully time-dependent general multistate model was tested with software U-CARE version 2.3 (Choquet et al. 2005), and the overdispersion parameter ($\hat{c}$) was calculated as χ^2 divided by the degrees of freedom (Burnham and Anderson 2002). We found no evidence for lack of fit or overdispersion of data ($\hat{c} = 1.08$; $\chi^2_{35} = 37.785$, $P = 0.343$).

We used Akaike's information criterion corrected for small sample size (AIC_c) for model comparison and statistical inferences and to select the most-parsimonious model from a candidate model set (Burnham and Anderson 2002). Model comparison was based on the differences in AIC_c values (ΔAIC_c). The model associated with the lowest AIC_c value was considered the best, and models with $\Delta AIC_c \leq 2$ were treated as equally representative of the underlying data. The slope parameter (β) and the 95% confidence interval (95% *CI*) for β indicated the direction and magnitude of the relationship between each parameter and covariate (Gaillard et al. 1997; Ozgul et al. 2007).

The stepwise approach was used in the capture–mark–recapture analysis. First, we considered the additive and interactive effects of age class and sex on GMGS survival. Using the most-parsimonious age and sex model as the base model, we tested for the additive and interactive effects of time.

Second, we tested for the additive and interactive effects of current (N_t) and previous year's population size (N_{t-1}) to test for direct and delayed density dependence, respectively. In our terminology N_t with respect to survival refers to a same-year relationship where population size of the current summer affects the survival of the squirrels until the next spring. In this context N_{t-1} denotes the influence of population size the previous summer on survival until the following spring. The size of the study site was constant, so we used population size (not population density) as a time-dependent covariate for these analyses.

Third, we tested for the additive and interactive effects of environmental factors (*pred*, $rain_t$, $rain_{t-1}$, bg_t, and bg_{t-1}). The most-parsimonious model identified in step 1 was used as a base model for these analyses.

Fourth, we tested for the additive and interactive effects of covariates in the best DD (N_{t-1}) and DID ($rain_t$, $rain_{t-1}$, and *pred*) models. We compared AIC_c values for the most-parsimonious model that included the effects of population size only, extrinsic factors only, and both population size and extrinsic factors, to evaluate the influence of DD and extrinsic factors (and combination thereof) on sex- and age-specific survival of GMGSs. To determine the relative importance of our predictor variables, for each variable we summed the Akaike weights for all models in the candidate set that contained the variable (Anderson 2008). The predictor variable with the largest sum of Akaike weights was considered to be the most influential. Finally, to address model selection uncertainty we performed model averaging using all models from step 1 to calculate model-averaged estimate of sex- and age-specific survival (Burnham and Anderson 2002).

Analysis of reproductive parameters.—We considered 2 components of reproductive rates: PSR—that is, the probability that a female weans ≥ 1 pups, conditional on survival (Doherty et al. 2004; Ozgul et al. 2007); and LS—that is, number of weaned juveniles that emerged from natal burrows (Ozgul et al. 2007). We used logistic regression to estimate and model PSR. This approach was adequate because capture probability was 1.0 for every year of the study. Zero-truncated Poisson regression (generalized linear models with Poisson distribution and log link function) was used for LS analysis. We used the same stepwise approach as described previously for the survival analysis to determine the influence of extrinsic and intrinsic factors on LS and PSR. In contrast to survival analysis, however, sex effect was not relevant for reproductive parameters because only the female segment of the population was examined. We considered 2 age classes, yearling (1-year-old) and older ($\geq$2-year-old) females for the analysis of reproductive rates of adult females. Generalized linear model analyses were conducted in program R (R Development Core Team 2009). Population size of the current year included adults only, whereas population size of the previous year included both juvenile and adult females in the analysis of reproductive parameters.

RESULTS

Total population size fluctuated markedly, ranging from 24 GMGSs in 1999 and 2000 to 140 in 2005. The number of individuals of each sex and age class also exhibited similar fluctuations during the study period (Fig. 1).

Survival.—Strong evidence ($\Delta \mathrm{AIC_c} > 50$) was found that both sex and age substantially influenced apparent survival (models 3 and 4 versus model 5; Table 1). The most-parsimonious model showed an additive effect of age and sex (model 1; Table 1a). Annual survival rate was highest for adult females ($\Phi = 0.519$, 95% *CI* = 0.462–0.576) and lowest for juvenile males ($\Phi = 0.120$, 95% *CI* = 0.094–0.152), and survival rates for juvenile females ($\Phi = 0.310$, 95% *CI* = 0.265–0.359) and adult males ($\Phi = 0.247$, 95% *CI* = 0.197–0.306) were intermediate with overlapping *CI*s. We tested for the additive and interactive effect of time on survival (Table 1a) to investigate temporal variation in sex- and age-specific survival. The most-parsimonious model included an additive effect of age, sex, and time (model 1; Table 1b), suggesting that survival varied substantially over time but sex- and age-specific differences remained relatively constant over time (Fig. 2).

TABLE 1.—Analysis of age-specific apparent survival rates (Φ) for the golden-mantled ground squirrel (*Callospermophilus lateralis*) population in Gothic, Colorado, using multistate mark–recapture models. Models testing for the effect of a) *sex* and *age*; and b) *time* using model 1(a) as the base model. Constant survival and time-specific survival models also are included for comparison. In both analyses the most-parsimonious models are in boldface type. Differences in Akaike's information criterion corrected for small sample size ($\Delta \mathrm{AIC_c}$), $\mathrm{AIC_c}$, weights (w_i), and number of parameters (npar) are given for each model. Annual recapture rate and transition rate are fixed for all models; therefore, they are not included in model descriptions. The symbol (.) indicates constant value of the parameter (model with intercept only).

No.	Model	$\Delta \mathrm{AIC_c}$	$\mathrm{AIC_c}$	w_i	npar
(a)					
1	**Φ(*age + sex*)**	**0.00**	**2,071.14**	**0.720**	**3**
2	Φ(*age * sex*)	1.89	2,073.03	0.280	4
3	Φ(*sex*)	34.60	2,105.75	0.000	2
4	Φ(*age*)	63.74	2,134.89	0.000	2
5	Φ(.)	112.29	2,183.43	0.000	1
(b)					
1	**Φ(*age + sex + time*)**	**0.00**	**2,062.28**	**0.790**	**20**
2	Φ(*sex + age * time*)	2.75	2,065.03	0.200	36
3	Φ(*age + sex*)	8.86	2,071.14	0.009	3
4	Φ(*age + sex * time*)	16.55	2,078.84	0.000	37
5	Φ((*age + sex*) * *time*)	18.22	2,080.51	0.000	53
6	Φ(.)	121.14	2,183.43	0.000	1

The analysis of the effect of current (N_t) and previous year's (N_{t-1}) population size on survival indicated that the most-parsimonious DD survival model included an additive effect of age, sex, and N_{t-1} (model 1; Table 2a). N_{t-1} negatively influenced survival ($\beta = -0.011$, 95% *CI* = -0.015 to -0.006) of squirrels of both sexes and age classes (Fig. 3). Other models that had considerable support (Table 2a) also included effects of N_{t-1}, providing strong evidence for delayed DD effects on survival.

The investigation of the impact of climatic factors ($rain_t$, $rain_{t-1}$, bg_t, and bg_{t-1}) on survival revealed that the best extrinsic survival model included an additive delayed effect of summer rainfall ($rain_{t-1}$) and an interactive effect between *age* and summer rainfall of the current year ($rain_t$; model 1; Table 2b). The previous year's summer rainfall, $rain_{t-1}$, positively affected survival, although this relationship fell short of statistical significance because the *CI* for the slope parameter included 0 ($\beta = 0.005$, 95% *CI* = -0.001–0.010). Current year's summer rainfall, $rain_t$, negatively influenced the survival of juveniles ($\beta = -0.008$, 95% *CI* = -0.013 to -0.004) and positively influenced the survival of adults ($\beta = 0.001$, 95% *CI* = -0.004–0.007), although the latter effect was not statistically significant. Because $\Delta \mathrm{AIC_c}$ between models 1 and 2 was <2 (Table 2b), and $rain_t$ had substantial

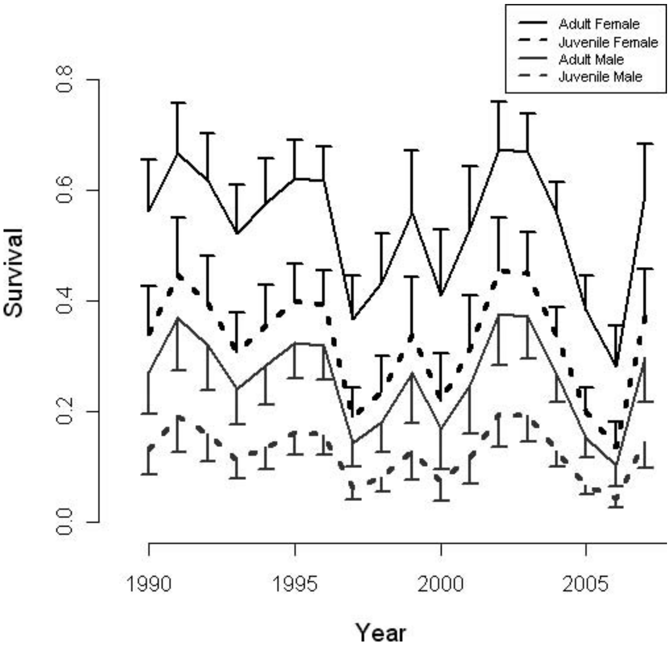

FIG. 2.—Model-averaged annual survival estimates with standard error (*SE*) for adult and juvenile female and adult and juvenile male golden-mantled ground squirrels (*Callospermophilus lateralis*) during 1990–2007. All unique models from Tables 1a and 1b were included for model averaging.

impact on survival of juveniles, we included both models for subsequent analyses.

The analysis of the effect of all environmental factors on survival (Table 2c) showed that the most-parsimonious DID model included an additive effect of *sex*, *age*, and *pred* and an interactive effect of *age* and $rain_t$ (model 1; Table 2c). Predation negatively influenced survival of all age and sex classes ($\beta = -0.033$, 95% *CI* = -0.054 to -0.012).

We compared the best DD (model 1; Table 2a) and DID (model 1; Table 2c) models to evaluate the relative influence of DD and DID factors on squirrel survival. We found strong evidence that both DD (N_{t-1}) and DID ($rain_t$) factors influenced survival (models 1 and 5 versus model 17; Table 2d). The most-parsimonious model (model 1; Table 2d) included an additive effect of N_{t-1} ($\beta = -0.011$, 95% *CI* = -0.015 to -0.006) and an interactive effect between *age* and $rain_t$ (for juveniles: $\beta = -0.007$, 95% *CI* = -0.012 to -0.003; for adults: $\beta = 0.004$, 95% *CI* = -0.001–0.009). These results suggested that N_{t-1} negatively influenced survival of both sexes and age classes. In this final model $rain_t$ had no statistically significant effect on adult survival; however, $rain_t$ had a negative relationship with juvenile survival.

We quantified the relative importance of population density and extrinsic factors by summing the AIC weights for all models from Table 2d that contained each variable. The sum of AIC weights for N_{t-1}, $rain_t$, *pred*, and $rain_{t-1}$ were 0.999, 0.981, 0.360, and 0.305, respectively, indicating that *pred* and $rain_{t-1}$ were considerably less important in explaining survival than the other 2 variables.

Probability of successful reproduction.—Although yearling female squirrels frequently reproduced, older (≥ 2 years) females represented the main reproductive segment of the squirrel population. Although we did not test this statistically, the percentage of adult females reproducing was higher for older than yearling females in all years except 2003 (Fig. 4).

Strong evidence existed for age-specific (yearling versus older females) differences in PSR ($\Delta AIC_c > 30$ for the top 2 models, model 1 versus 2; Table 3a). The estimated PSR for older females was higher ($\Psi = 0.816$, 95% *CI* = 0.734–0.877) than for yearlings ($\Psi = 0.313$, 95% *CI* = 0.228–0.412). We found no evidence for temporal variation in PSR (model 2 versus 3; Table 3a), so we used a model that included the age effect for all subsequent analyses. All models investigating effects of population size on PSR are given in Table 3b. The best DD model showed no evidence for the effect of density on PSR.

The most-parsimonious DID model (model 1; Table 3c) showed evidence for interactive effects of *age* and $rain_{t-1}$ (model 1 versus 8; Table 3c) where $rain_{t-1}$ negatively influenced the PSR of both older ($\beta = -0.004$, 95% *CI* = -0.013–0.006) and yearling ($\beta = -0.033$, 95% *CI* = -0.051 to -0.016) females. When we considered predation as an additional extrinsic factor in our analysis, the best resulting model was still the same as model 1 in Table 3c. Thus, no evidence suggested that predation affected PSR. The most-parsimonious PSR model included only a DID covariate and showed evidence for the interactive effects of *age* and $rain_{t-1}$ (model 1; Table 3d).

Litter size.—Litter size (LS) ranged from 1 to 8 pups (n = 139, mean LS = 4.8, 95% *CI* = 4.5–5.1) with a mode of 5 pups per litter (Fig. 5). Unlike PSR, age of mothers did not influence LS (model 1 versus 2; Table 4a). We found no evidence for temporal variation (model 1 versus 3; Table 4a), DD (Table 4b), or DID (Table 4c) influences on LS. Therefore, the model with constant LS was the most parsimonious, with no evidence for the effect of age of mothers or influence of DD and DID factors on this variable (model 1; Table 4d).

DISCUSSION

The subtle and interactive process by which DD and DID factors impact the vital rates of different segments of structured populations is a phenomenon experienced across taxa (Coulson et al. 2001; Jonzén et al. 2010; Leirs et al. 1997; Ozgul et al. 2006, 2007). DD feedback mechanisms are thought to stabilize populations eventually (Leirs et al. 1997; Royama 1992; Turchin 2003), and stochastic variations in environmental factors tend to have destabilizing effects on population dynamics (Coulson et al. 2000). Consequently, our goal was to disentangle the relative contribution of DD and DID factors on our study population of GMGSs to tease apart their singular and combined effects that likely underlie the extensive temporal fluctuation in GMGS abundance. Understanding these relationships is even more critical when studying a species such as the GMGS that occupies habitats that could be sensitive to climate change.

TABLE 2.—Models testing for the effect of a) current (N_t) and previous (N_{t-1}) year's population size; b) climatic factors such as current ($rain_t$) and previous ($rain_{t-1}$) summer rainfall, current (bg_t) and previous (bg_{t-1}) 1st day of bare ground; c) environmental factors including climatic factors and predation (*pred*); and d) the relative and synergistic effects of the best intrinsic, density-dependent, and environmental factors on the state-specific apparent survival rates for the golden-mantled ground squirrel (*Callospermophilus lateralis*) population in Gothic, Colorado, using multistate mark–recapture models. General model (model a12) is also included for comparison. In all analyses the most-parsimonious models are in boldface type. Not all models are shown for parts a and b. Effects of previous year's rainfall and previous 1st day of bare ground on survival were relevant only to adult animals. Hence, we analyzed the effects of these parameters only for the adult segment of the population. Notation for these parameters therefore are: $rain_{t-1}{:}A$ and $bg_{t-1}{:}A$, respectively. For symbols and table content descriptions refer to the Table 1 legend.

No.	Model	ΔAIC_c	AIC_c	w_i	npar
(a)					
1	**$\Phi(age + sex + N_{t-1})$**	**0.00**	**2,461.82**	**0.177**	**4**
2	$\Phi(sex + age * N_{t-1})$	0.50	2,462.33	0.138	5
3	$\Phi(age + sex * N_{t-1})$	0.69	2,462.51	0.126	5
4	$\Phi((age + sex) * N_{t-1})$	0.85	2,462.67	0.116	6
5	$\Phi(sex + age + N_{t-1} + N_t)$	1.08	2,462.90	0.103	5
6	$\Phi(sex + age * N_{t-1} + N_t)$	1.56	2,463.38	0.081	6
7	$\Phi(age + sex * N_{t-1} + N_t)$	1.76	2,463.58	0.074	6
8	$\Phi((age + sex) * N_{t-1} + N_t)$	1.89	2,463.71	0.069	7
9	$\Phi(age + sex + N_t * N_{t-1})$	2.16	2,463.99	0.060	6
10	$\Phi(sex + age * N_t + N_{t-1})$	2.98	2,464.80	0.040	6
11	$\Phi((age + sex) * N_\mathrm{t} + N_{t-1})$	4.90	2,466.72	0.015	7
12	$\Phi(age + sex + time)$	13.15	2,474.97	0.000	19
(b)					
1	**$\Phi(sex + age * rain_t + rain_{t-1}{:}A)$**	**0.00**	**2,060.13**	**0.236**	**6**
2	**$\Phi(sex + age * rain_t)$**	**0.92**	**2,061.05**	**0.149**	**5**
3	$\Phi(sex + age * rain_t + rain_{t-1}{:}A + bg_{t-1}{:}A)$	1.02	2,061.15	0.142	7
4	$\Phi(sex + age * rain_t + rain_{t-1}{:}A + bg_t)$	1.81	2,061.94	0.095	7
5	$\Phi(sex + age + time)$	2.15	2,062.28	0.080	20
6	$\Phi(sex + age * raint + bg_{t-1}{:}A)$	2.33	2,062.45	0.074	6
7	$\Phi(sex + age * rain_t + bg_t)$	2.62	2,062.75	0.064	6
8	$\Phi(sex + age * rain_t + rain_{t-1}{:}A + bg_t + bg_{t-1}{:}A)$	2.91	2,063.04	0.055	8
9	$\Phi(sex + age * rain_t + bg_t + bg_{t-1}{:}A)$	4.09	2,064.22	0.030	7
10	$\Phi(sex + age + rain_t + rain_{t-1}{:}A + bg_{t-1}{:}A)$	4.31	2,064.44	0.027	6
(c)					
1	**$\Phi(sex + age * rain_t + pred)$**	**0.00**	**2,053.01**	**0.489**	**6**
2	$\Phi(sex + age * rain_t + rain_{t-1}{:}A + pred)$	0.77	2,053.78	0.334	7
3	$\Phi(sex + age * pred + rain_t + rain_{t-1}{:}A)$	5.08	2,058.09	0.039	7
4	$\Phi(sex + age * pred)$	5.40	2,058.41	0.033	5
5	$\Phi(age + sex + pred + rain_{t-1}{:}A)$	5.80	2,058.81	0.027	5
6	$\Phi(age + sex + pred)$	6.84	2,059.85	0.016	4
7	$\Phi(age + sex + pred + rain_t + rain_{t-1}{:}A)$	6.88	2,059.89	0.016	6
8	$\Phi(sex + age * rain_t + rain_{t-1}{:}A)$	7.12	2,060.13	0.014	6
9	$\Phi(sex + age * pred + rain_t)$	7.23	2,060.24	0.013	6
10	$\Phi(sex + age * rain_t)$	8.04	2,061.05	0.009	5
11	$\Phi(age + sex + pred + rain_t)$	8.64	2,061.65	0.007	5
12	$\Phi(sex + age + time)$	9.27	2,062.28	0.005	20
(d)					
1	**$\Phi(sex + age * rain_t + N_{t-1})$**	**0.00**	**2,453.88**	**0.429**	**6**
2	$\Phi(sex + age * rain_t + pred + N_{t-1})$	1.16	2,455.03	0.241	7
3	$\Phi(sex + age * rain_t + rain_{t-1}{:}A + N_{t-1})$	1.63	2,455.51	0.190	7
4	$\Phi(sex + age * rain_t + rain_{t-1}{:}A + N_{t-1} + pred)$	2.89	2,456.77	0.101	8
5	$\Phi(age + sex + N_{t-1})$	7.95	2,461.82	0.008	4
6	$\Phi(age + sex + N_{t-1} + rain_t + rain_{t-1}{:}A)$	8.32	2,462.20	0.007	6
7	$\Phi(age + sex + N_{t-1} + rain_t)$	8.32	2,462.20	0.007	5
8	$\Phi(age + sex + N_{t-1} + pred)$	8.42	2,462.30	0.006	5
9	$\Phi(sex + age + N_{t-1} + rain_{t-1}{:}A + pred)$	9.19	2,463.07	0.004	6
10	$\Phi(sex + age + N_{t-1} + rain_t + pred)$	9.66	2,463.54	0.003	6
11	$\Phi(sex + age + N_{t-1} + rain_t + rain_{t-1}{:}A + pred)$	9.78	2,463.66	0.003	7
12	$\Phi(sex + age * rain_\mathrm{t} + pred)$	14.09	2,467.97	0.000	6
13	$\Phi(sex + age * rain_\mathrm{t} + rain_{t-1}{:}A + pred)$	14.89	2,468.76	0.000	7
14	$\Phi(sex + age + pred)$	20.75	2,474.62	0.000	4
15	$\Phi(sex + age + rain_\mathrm{t} + rain_{t-1}{:}A + pred)$	20.89	2,474.76	0.000	6
16	$\Phi(sex + age + time)$	21.10	2,474.97	0.000	19
17	$\Phi(sex + age)$	21.12	2,475.00	0.000	6

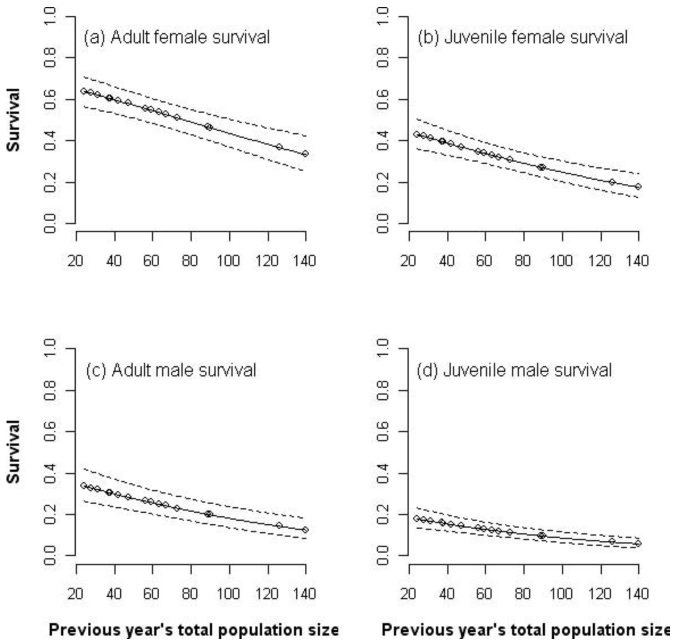

Fig. 3.—Relationship between previous year's population size of golden-mantled ground squirrels (*Callospermophilus lateralis*) and a) adult female survival, b) juvenile female survival, c) adult male survival, and d) juvenile male survival. Dotted lines indicate 95% *CI*s. Circles indicate survival estimates. Parameters were estimated based on model 1 in Table 2a.

Our analysis revealed support for temporal and age- and sex-specific variation on survival. Previous studies on high-elevation sciurid species also have demonstrated the impact of age and sex on survival rates, indicating higher survival for adults versus juveniles and females versus males (Bronson 1979; Schwartz et al. 1998; Sherman and Morton 1984; Sherman and Runge 2002). However, our estimate of juvenile survival rates, especially for males, likely are underestimated because of the confounding effects of dispersal.

Consistent with previous studies that examined reproductive parameters of high-elevation sciurid species (Bronson 1979; Ozgul et al. 2007), we found that older females (≥2 years of age) were the main reproductive segment of the squirrel population. Bronson (1979) reported that many young squirrels failed to reproduce at high-elevation sites. Likewise, yearlings did not reproduce in 9 of 19 years in our study site. Substantial age-specific difference existed in PSR, with older females twice as likely to reproduce as yearlings. Ozgul et al. (2007) reported temporal variation in the PSR of subadult and adult yellow-bellied marmots (*Marmota flaviventris*) in the same area. However, we did not find evidence for temporal variability in PSR. Although Ozgul et al. (2007) and Sherman and Runge (2002) found support for the effect of age and time on LS, respectively, we found no evidence that LS varied among age classes or across years.

We expected that current year's population density would have a negative effect on survival because crowding during the summer reduces per capita food availability and therefore the ability of squirrels to store enough fat for overwinter survival. In addition, high density can promote dispersal of juveniles, thereby reducing their apparent survival. Therefore, we supposed a direct link between the factors affecting fat storage during current summer (e.g., population density) and survival over the coming winter. To our surprise, the results did not show a same-year effect of density on overwinter

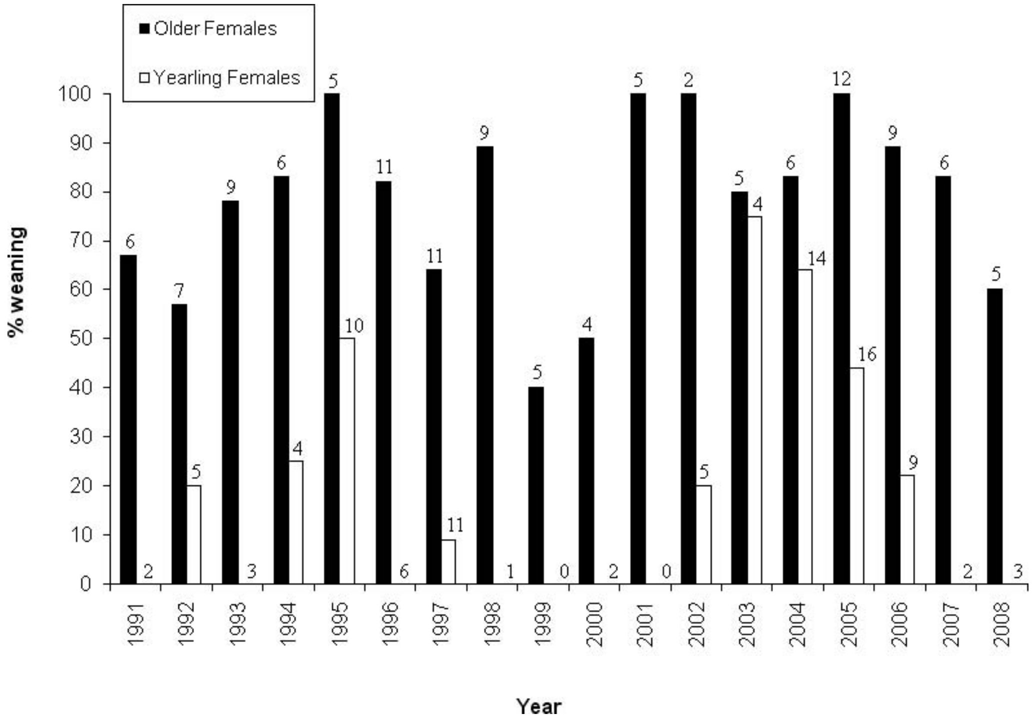

Fig. 4.—Percentage of yearling and older (≥2 years old) golden-mantled ground squirrel (*Callospermophilus lateralis*) females that weaned ≥1 pup during 1991–2008. Numbers above the bars indicate sample sizes.

Table 3.—Models testing for the effect of a) *age* and *time*; b) current (N_t) and previous (N_{t-1}) year's population size; c) environmental factors including climatic factors and predation; and d) the relative and synergistic effects of the best density-dependent and environmental factors on probability of successful reproduction (Ψ) of the golden-mantled ground squirrel (*Callospermophilus lateralis*) population in Gothic, Colorado, using logistic regression. In all analyses the most-parsimonious models are in boldface type. For symbols and table content descriptions refer to the Table 2 legend.

No.	Model	ΔAIC_c	AIC_c	w_i	npar
(a)					
1	**$\Psi(age)$**	**0.00**	**295.96**	**1.000**	**2**
2	$\Psi(.)$	37.11	333.07	0.000	1
3	$\Psi(time)$	52.75	348.71	0.000	19
(b)					
1	**$\Psi(age)$**	**0.00**	**278.57**	**0.194**	**2**
2	$\Psi(age + N_t)$	0.04	278.61	0.190	3
3	$\Psi(age * N_t)$	0.05	278.62	0.189	4
4	$\Psi(age + N_{t-1})$	0.99	279.56	0.118	3
5	$\Psi(age + N_t + N_{t-1})$	2.03	280.60	0.070	4
6	$\Psi(age * N_t + N_{t-1})$	2.05	280.62	0.070	5
7	$\Psi(age * N_{t-1})$	2.22	280.79	0.064	4
8	$\Psi(age * N_{t-1} + N_t)$	3.31	281.88	0.037	5
9	$\Psi(age + N_t * N_{t-1})$	3.48	282.05	0.034	5
10	$\Psi(age + N_{t-1} * N_t)$	3.48	282.05	0.034	5
(c)					
1	**$\Psi(age * rain_{t-1})$**	**0.00**	**279.56**	**0.652**	**4**
2	$\Psi(age * rain_{t-1} + pred)$	1.41	280.98	0.322	5
3	$\Psi(age + rain_{t-1})$	8.01	287.57	0.012	3
4	$\Psi(age + rain_{t-1} + pred)$	8.91	288.47	0.008	4
5	$\Psi(age * pred + rain_{t-1})$	9.79	289.35	0.005	5
6	$\Psi(age * rain_t)$	13.46	293.02	0.001	4
7	$\Psi(age + rain_t)$	14.92	294.49	0.000	3
8	$\Psi(age)$	16.39	295.96	0.000	2
9	$\Psi(age * bg_{t-1})$	17.38	296.94	0.000	4
10	$\Psi(age + pred)$	17.92	297.49	0.000	3
11	$\Psi(age * pred)$	18.00	297.56	0.000	4
12	$\Psi(age + bg_t)$	18.34	297.90	0.000	3
13	$\Psi(age + bg_{t-1})$	18.35	297.91	0.000	3
14	$\Psi(age * bg_t)$	20.33	299.89	0.000	4
(d)					
1	**$\Psi(age * rain_{t-1})$**	**0.00**	**262.20**	**0.662**	**4**
2	$\Psi(age * rain_{t-1} + N_t)$	1.99	264.19	0.245	5
3	$\Psi(age * rain_{t-1} * N_t)$	5.30	267.50	0.047	8
4	$\Psi(age + rain_{t-1} * N_t)$	5.89	268.09	0.035	5

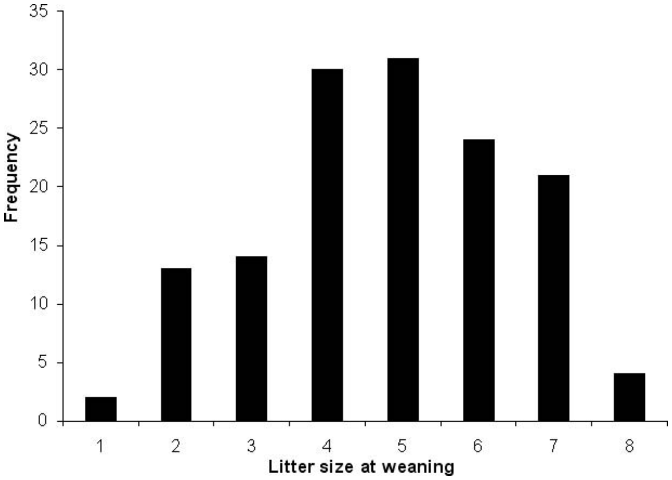

Fig. 5.—Distribution of litter size (n = 139) of golden-mantled ground squirrels (*Callospermophilus lateralis*) during the study period (1990–2008).

survival; rather, we found that GMGS survival was related negatively with the previous year's population density. Our 2nd-best DD model had considerable support ($\Delta AIC_c = 0.50$) and indicated an interaction between age and last year's density. According to this model, high density had a stronger negative effect on survival of juveniles than that of adults. This is not surprising, because juveniles are more likely to disperse and settle in poor habitat within the site or leave the study area permanently. Vital rates are suggested to covary closely with population density in small mammals (Klinger 2007; Leirs et al. 1997; Ozgul et al. 2004), but a lag effect of density on survival was unanticipated. We suggest DD habitat selection as a possible explanation of delayed density effects on survival. High population density in our study area results in increased occupancy of lower-quality habitats (K. Ip, University of California, Davis, pers. comm.), primarily by juveniles. Many of these juveniles originated from high-quality areas where they presumably were able to accumulate sufficient fat reserves for surviving their 1st winter, but subsequently experienced diminished resources for surviving the year after.

Negative DD effects on vital rates can manifest through intraspecific competition, resource availability, and predation (Klinger 2007). The strong effect of predation on temperate populations of small mammals is well established (Hanski et al. 2001), and accordingly, predation negatively influenced GMGS survival in all segments of our study population. Although we found support for predation in the top DID model, predation was not included in the top combined DD and DID model. Because we lacked predator abundance data, we attempted to quantify the effect of predation by recording observed or presumed predation events as they were encountered during field observations. Among small mammals evidence exists for negative DD effects through density-mediated reproductive suppression (Boonstra 1994; Klinger 2007), but our results showed no support for the effect of density on the PSR, nor did evidence exist for the effect of population density on LS.

In our study DID influence was expressed in both survival and reproductive rates, through the interactive effect of age and current year's rainfall on survival of juveniles, and of age and previous year's rainfall on PSR. The literature suggests that increased food availability driven by rainfall improves both vital rates (Klinger 2007), but our results showed a negative correlation between rainfall and survival of juveniles and PSR. Meadow vegetation in our study area is highly productive (Kilgore and Armitage 1978), and it is possible that squirrels experience an abundant food supply regardless of additional growth stimulated by summer rainfall. Instead, periods of prolonged rainfall could have had a negative effect

Table 4.—Models testing for the effect of a) age and time; b) current (N_t) and previous (N_{t-1}) year's population size; c) environmental factors including climatic factors and predation; and d) the relative and synergistic effects of the best intrinsic, density dependent, and environmental factors on litter size (*LS*) for the golden-mantled ground squirrel (*Callospermophilus lateralis*) population in Gothic, Colorado, using Poisson regression. In all analyses the most-parsimonious models are in boldface type. For symbols and table content descriptions refer to the Table 2 legend.

No.	Model	ΔAIC	AIC	w_i	npar
(a)					
1	***LS*(.)**	**0.00**	532.79	0.717	**1**
2	*LS*(*age*)	1.87	534.66	0.282	2
3	*LS*(*time*)	13.69	546.49	0.001	19
(b)					
1	***LS*(.)**	**0.00**	**502.73**	**0.451**	**1**
2	$LS(N_t)$	1.49	504.22	0.214	2
3	$LS(N_{t-1})$	1.55	504.27	0.208	2
4	$LS(N_t + N_{t-1})$	3.43	506.15	0.081	3
5	$LS(N_t * N_{t-1})$	4.54	507.27	0.046	4
(c)					
1	***LS*(.)**	**0.00**	**532.79**	**0.222**	**1**
2	$LS(bg_{t-1})$	0.70	533.50	0.156	2
3	*LS*(*pred*)	1.42	534.21	0.109	2
4	*LS*(*age*)	1.87	534.66	0.087	2
5	$LS(bg_t)$	1.92	534.71	0.085	2
6	$LS(rain_{t-1})$	1.98	534.78	0.082	2
7	$LS(rain_t)$	2.00	534.79	0.082	2
8	$LS(bg_{t-1} + pred)$	2.31	535.11	0.070	3
9	$LS(age + bg_{t-1})$	2.64	535.44	0.059	3
10	$LS(bg_{t-1} * pred)$	4.31	537.10	0.026	4
11	$LS(age * bg_{t-1})$	4.58	537.37	0.022	4
(d)					
1	***LS*(.)**	**0.00**	**500.85**	**0.274**	**1**
2	$LS(bg_{t-1})$	1.41	502.26	0.135	2
3	*LS*(*age*)	1.42	502.27	0.135	2
4	$LS(N_t)$	1.47	502.32	0.131	2
5	*LS*(*pred*)	1.88	502.73	0.107	2

on squirrels by denying them access to food (Bakker et al. 2009); squirrels in our study site remained underground during rainy weather. Hence, GMGSs during rainy summers might have entered hibernation with reduced fat reserves for supporting both overwinter survival and reproduction the following spring.

Our results showed that DD and DID factors did not affect all vital rates in the same fashion. With respect to GMGS survival, both DD (previous year's population density) and DID (current summer rainfall) factors were important. Based on the sum of AIC weights, the relative importance of the 4 most critical variables on survival in decreasing order was: density the previous year, current summer rainfall, predation, and previous summer rainfall. The sum of AIC weights for previous year's density and current summer rainfall were equally high, suggesting that these 2 variables were equally influential. Leirs et al. (1997) found a strong negative effect of direct DD for only adult multimammate rats (*Mastomys natalensis*), but the negative impact of delayed DD in our GMGS population was consistent in all age and sex classes. However, Leirs et al. (1997) did not find a strong extrinsic influence of rainfall, which is surprising in an environment where water is a limiting resource.

For PSR the top combined model included only a DID (rainfall the previous summer) factor showing strong support for the effect of rainfall the previous summer. The strong contribution of DID factors to PSR was consistent with literature suggesting that reproduction of small mammal species is driven primarily by DID factors (Coulson et al. 2000; Klinger 2007).

We conclude that both DD and DID factors influenced demographic variables of GMGSs in our study site, but the pattern of influence differed among variables. Environmental factors influenced both survival and reproduction of squirrels, whereas population density strongly influenced survival only. Climatic variables such as the amount and frequency of precipitation are projected to vary increasingly due to a globally changing climate (Bernstein et al. 2007). Stochastic perturbations to vital rates can have a negative effect on the persistence of populations. The GMGS population inhabits a stochastic, high-altitude environment; hence, increasing perturbations to GMGS vital rates due to changing environmental factors can negatively influence the GMGS population. Future research will focus on predicting GMGS population dynamics using models that incorporate these stochastic processes.

Acknowledgments

This study was supported by the California Agricultural Experiment Station, University of California Davis, and the School of Natural Resources and the Environment and the Department of Wildlife Ecology and Conservation, University of Florida. We thank C. Floyd, K. Jenderseck, and C. Mueller for their contributions to data collection. We thank M. E. Sunquist and V. Rolland for their thoughtful comments on an earlier draft of the manuscript.

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Submitted 5 May 2010. Accepted 16 September 2010.

Associate Editor was Paul T. Stapp.