

## DEMOGRAPHY OF A POPULATION COLLAPSE: THE NORTHERN IDAHO GROUND SQUIRREL (*SPERMOPHILUS BRUNNEUS BRUNNEUS*)

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**Abstract.** We studied the demography of a population of Northern Idaho ground squirrels (*Spermophilus brunneus brunneus*) in Adams County, Idaho. The population was completely censused yearly from 1987 to 1999, during which time it declined from 272 to 10 animals. The finite population growth rate, based on a Leslie matrix model of average life-history parameters, was only 0.72 (i.e., significantly <1.0). Growth rate was more sensitive to proportional changes in juvenile female survival than to any other single life-history parameter. Comparisons with self-sustaining populations of closely related ground squirrel species revealed that juvenile survival and breeding rates of yearling females were anomalously low. We believe that the ultimate cause of the population's collapse was inadequacy of food resources, particularly seeds, due to drying of the habitat and changes in plant species composition, likely the result of fire suppression and grazing. No "rescue" by immigration occurred, probably because *S. b. brunneus* seldom disperse long distances and fire suppression has allowed conifers to encroach on inhabited meadows, shrinking them and closing dispersal routes. The proximate cause of the population's collapse was mortality of older breeding females, which reduced the mean age of breeders. Younger females had lower average pregnancy rates and litter sizes. To place our results in context we developed a new, general classification of anthropogenic population declines, based on whether they are caused by changes in the means of the life-history parameters (blatant disturbances), their variances (inappropriate variations), or the correlations among them (evolutionary traps). Many *S. b. brunneus* populations have disappeared in recent years, apparently due to blatant disturbances, especially loss of habitat and changes in food-plant composition, resulting in inadequate prehibernation nutrition and starvation overwinter. In addition, our study population may have been caught in an evolutionary trap, because the vegetational cues that could potentially enable the animals to adjust reproduction to the anticipated food supply no longer correlate with availability of fat-laden seeds.

**Key words:** anthropogenic causes of population decline; demography; elasticity; evolutionary trap; fire suppression; grazing; life-history evolution; matrix model; Northern Idaho ground squirrel; phenotypic plasticity; population collapse; *Spermophilus brunneus brunneus*.

### INTRODUCTION

The Idaho ground squirrel (*Spermophilus brunneus*) is an endemic species that inhabits five counties in west-central Idaho (Yensen and Sherman 1997). Two morphologically, geographically, and phenologically distinct subspecies have been described (Yensen 1991). The northern subspecies, *S. b. brunneus*, inhabits xeric meadows at 1150–1550 m elevation in Adams and Valley Counties, and the southern subspecies, *S. b. endemicus*, inhabits xeric meadows at 670–975 m in Gem, Payette, and Washington Counties. Currently, the southernmost population of *S. b. brunneus* is located 48 km north of the northernmost *S. b. endemicus* population. Both subspecies are active above ground only 4–5 mo/yr (*S. b. endemicus*: January through May; *S. b. brunneus*: March through July); the rest of the year they hibernate (Yensen and Sherman 1997).

The Northern Idaho ground squirrel is known historically from 36 sites (Yensen 1991), but only 24 of these were still occupied in 1998 (Gavin et al. 1999). The rate of population disappearance has accelerated over the past two decades (i.e., seven populations have disappeared since 1990). Population extinction is probably related to anthropogenic habitat changes. As a result of fire suppression and logging, ancient, age-structured coniferous forests containing open understories and interconnecting meadows have been replaced by dense stands of even-aged, relatively young conifers. These trees have increasingly encroached on meadows, shrinking and isolating them (Arno 1980, Butler 1986, Truska and Yensen 1990). Within extant meadows lack of fire has allowed succession to proceed (from edible grasses and forbs to inedible shrubs). The precarious status of *S. b. brunneus* was officially recognized in 1998 when it was proposed for listing (as "threatened") under the United States Endangered Species Act (Clark 1998). The final rule for listing was published in the spring of 2000 (Clark 2000).

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In 1986, prior to realizing that *S. b. brunneus* was declining, we initiated a behavioral study in a short-grass meadow near Bear, Idaho (e.g., Sherman 1989). We chose the "Squirrel Valley" site because it was the largest and densest of the known populations and it was located on "protected" land (a private cattle ranch with cooperative owners). The Squirrel Valley population, which numbered 272 adults and juveniles in 1987, declined precipitously and by 1999 it contained only 10 individuals. Throughout this 14-yr period we gathered thorough demographic data, based on marking and recapturing the entire population each season. Here we use those data to investigate the demographic dynamics of the population's collapse. Specifically we ask (1) what short-term changes in life-history traits precipitated the collapse, (2) what longer term changes in life-history traits predisposed the population to collapse, and (3) what caused the short- and long-term changes?

Inherent in these questions is a tension between two different temporal scales: the centuries-long scale that brought about landscape changes and predisposed this population to decline, and the decade-long scale during which the final demise occurred. We observed the latter, but are most interested in the former. Resolution of this tension requires integrating Caughley's (1994) "declining-population" and "small-population" paradigms (see also May 1994 and Hedrick et al. 1996). To make the connection we investigated what landscape-scale changes have occurred in this area of Idaho, and the comparative demography of other populations of *S. b. brunneus* and other *Spermophilus* species. We also propose a new, general classification of anthropogenic population declines, and use it as a framework to investigate the demise of the Squirrel Valley population.

## METHODS

### Study area

Squirrel Valley is located in a xeric meadow surrounded by coniferous forests at an elevation of 1315 m (45°00' N, 116°39' W) near the Bear townsite in Adams County, Idaho. For many decades, Bear Meadow (Fig. 1) was grazed by cattle year-round, but beginning in the early 1990s grazing was sharply decreased (John Dyer, *personal communication*). During 1986–1999 there were four concentrations (i.e., population foci) of Northern Idaho ground squirrels in Bear Meadow (Fig. 1): Squirrel Valley, Squirrel Manor (SM), Bear Cemetery (BC), and Lick Creek (LC). Among these, the nearest to Squirrel Valley was Squirrel Manor (~900 m away) and the farthest was Lick Creek (~1800 m away). At every site the ground squirrels' distribution was patchy, apparently due to variations in food abundance and microgeographic habitat features (e.g., soils >0.8 m deep are required for nest and hibernation burrows [Yensen et al. 1991]). Within

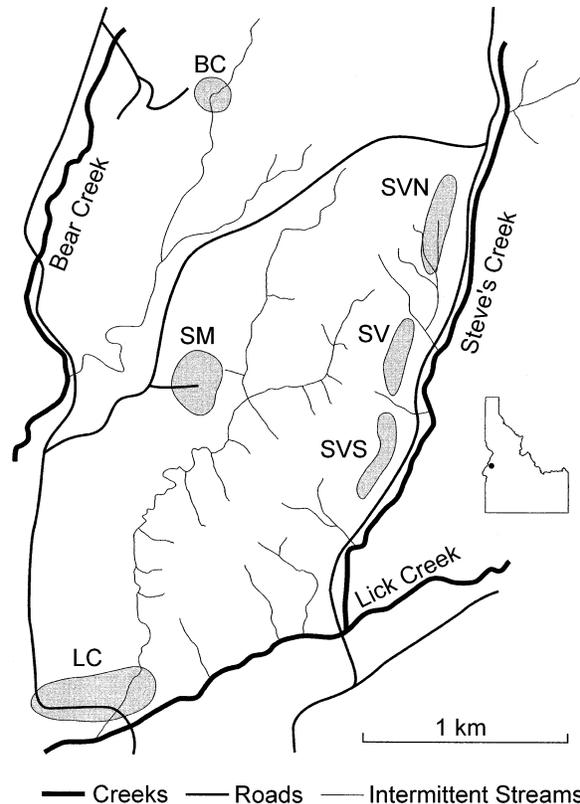


FIG. 1. Map of Bear Meadow, Adams County, Idaho. The shaded areas indicate the concentrations of *S. b. brunneus* within the meadow: Squirrel Valley proper (SV [the main study area]), Squirrel Valley North (SVN), Squirrel Valley South (SVS), Bear Cemetery (BC), Squirrel Manor (SM), and Lick Creek (LC). Bear Meadow is bounded on the west by Bear Creek, on the east by Steve's Creek, and on the south by Lick Creek. Intermittent streams and roads are also shown.

Squirrel Valley there were three areas of high density: the core area (SV proper), plus Squirrel Valley North (SVN) and South (SVS) (Fig. 1). SVN was separated from SV proper by 100 m and two deeply cut intermittent stream beds, and SVS was separated from SV proper by 80 m and one shallow intermittent stream bed. Burrows were scattered at very low densities between SV, SVN, and SVS.

### Trapping and marking

Ground squirrels living in Squirrel Valley proper were captured every year from 1986 through 1999. Trapping commenced at spring emergence from hibernation (usually late March or early April) and usually continued until juveniles dispersed from their natal burrows (late May). The exception was the initial year (1986), when trapping occurred only in late May.

Ground squirrels were captured in single-door, Tomahawk live-traps (13 × 13 × 41 cm; Tomahawk Live Trap, Tomahawk, Wisconsin, USA) and handled without anesthesia, using gloves. The sex and reproductive condition of each animal were recorded (testes scrotal or

nonscrotal for males; pregnant, lactating, and perforate or closed vaginas for females). The animal's mass was determined by restraining it in a soft cloth bag and using a Pesola scale ( $\pm 2$  g; Pesola Company, Baar, Switzerland). At initial capture each animal's age class (juvenile, 1-yr-old, or  $\geq 2$ -yr-old [i.e., "adult"]) was assessed, based primarily on body mass. Age cohorts usually were clear-cut, with the exception of a few immigrant males whose small mass ( $< 130$  g) suggested that they were yearlings, but whose testes were descended, which is uncharacteristic of males  $< 2$  yr old. We categorized these males as 1-yr-olds if their penis was unpigmented (characteristic of known yearlings), and  $\geq 2$ -yr-olds if it was pigmented.

The first time each ground squirrel was handled, we marked it permanently by attaching a small, numbered, noncorrosive (Monel) metal tag (National Band and Tag Company, Newport, Kentucky) to each ear. Within SV every animal also was marked for individual recognition using human hair dye. Ground squirrels were dyed twice per season: at spring emergence and again after molting, which usually occurred coincident with juveniles' appearance above ground (weaning). After marking, each individual was released at its capture location.

The consistency and intensity of our visual marking program enabled us to capture every yearling and adult ground squirrel that appeared on the study area using a "focal animal" regime (Sherman and Morton 1984, Sherman 1989, Hoogland 1995). That is, every time we saw an unmarked animal we followed it until it entered a burrow. Then we surrounded the burrow mouth with four live-traps (two open and two closed), blocked other known or suspected connecting entrances with rocks or sticks, and remained nearby until the animal was caught (usually  $< 10$  min). By the middle of each field season, all residents were marked. This enabled us to efficiently focus on trapping any unmarked individuals that appeared. We are confident that we completely enumerated the SV population every year except in 1986.

#### Dispersal

To assess relatively short-range movements, every year we captured individuals in SVN and SVS as time permitted. In most years trapping was not as thorough as in SV proper, but in 1988 and 1994 we attempted to mark every individual in SVN and SVS. To gauge longer distance movements, beginning in 1992 we captured and eartagged as many animals as possible at the other three population foci in Bear Meadow (Fig. 1) every year, as well as at the four nearest *S. b. brunneus* population sites (located 2–15 km from Bear Meadow; see Gavin et al. 1999). We looked for tagged individuals that had moved from SV, SVN, or SVS to these other populations and vice versa.

#### Lost eartags

Occasionally animals were recaptured that had lost one or both eartags. Loss of a single eartag did not present a problem for estimating survival because of the redundancy of information in the second tag. However, because eartag loss created a permanent slit in the ear, there was no room to attach another one. Instead, we clipped a unique combination of toes and released the animal. During 1987–1999 we recaptured 471 ground squirrels, 27 of which had slits with healed edges in both ears (characteristic of lost eartags), but no missing toes. Among these, 8 were 1-yr-olds. Although they could not be identified individually, they could be assigned confidently to an age cohort. The remaining 19 animals could not be assigned to a cohort. Failure to correct for them would negatively bias survival rates, because lost marks would be counted as having disappeared (died). Therefore, for each year, we compared the number of animals recaptured with lost eartags to the number recaptured with intact eartags using logistic regression. We found no evidence that eartag-loss rate was correlated with age ( $\chi^2 = 0.086$ ,  $df = 1$ ,  $P = 0.77$ ), sex ( $\chi^2 = 0.002$ ,  $df = 1$ ,  $P = 0.96$ ), year ( $\chi^2 = 19.9$ ,  $df = 12$ ,  $P = 0.070$ ), or any of the interactions (collective  $\chi^2 = 25.4$ ,  $df = 27$ ,  $P = 0.55$ ). So, to estimate the rate of double eartag loss, we pooled all observations across age, sex, and years, which yielded a rate of 0.057 (the exact 95% confidence interval for a binomial proportion was 0.038–0.082). In all analyses, if we could not directly correct the data to account for the missing eartags, we adjusted survival rates by dividing by 0.943, the estimated eartag-retention rate (Arnason and Mills 1981, Pollock 1981). Confidence intervals for the corrected survival rates, which are ratios of estimates, were calculated either by a parametric bootstrap procedure (Manly 1997) or by a normal approximations approach (Fieller 1940:45–63, Nisbet et al. 1999).

#### Survival

Ground squirrels that were first captured as juveniles or 1-yr-olds could be confidently assigned to a cohort, but animals first captured as adults could only be assigned a minimum age ( $\geq 2$  yr); the latter were excluded from our survival analyses. We used standard capture–mark–recapture (CMR) techniques for analyses of open populations to estimate survival rates and detection probabilities (Lebreton et al. 1992).

Traditionally the detection parameter in a CMR analysis is interpreted as the probability of observing an animal in a particular year, given that it was present. However we believe that we caught every animal in SV proper each year because (1) ground squirrels are diurnal and easy to see while the vegetation in Bear Meadow is short (usually until emergence of newly weaned juveniles in late May), (2) the SV population was observed every day and strenuous efforts were

made to capture and dye-mark any previously unmarked animals, and (3) by the middle of each field season, every ground squirrel we saw was marked. Nonetheless, 14 of the 471 individuals we recaptured (0.03) were missing for  $\geq 1$  yr and then reappeared. Apparently they had temporarily emigrated from SV and returned. Since we believe our detection probability was 1.0, the "detection probability" we calculated represents fidelity to SV proper, and the additive inverse of the calculated probability represents the frequency of temporary emigration. Interpreting this parameter as a fidelity rate, rather than a detection probability, is consistent with the analytical methods, since random temporary emigration does not bias survival estimates from CMR models (Kendall et al. 1997).

We considered many potential models for survival rates and detection (fidelity) probabilities, including effects of age, sex, and year. We used standard model selection techniques (see the Appendix) to identify the most parsimonious model in each analysis (i.e., the model that explained the most variation in the response variable with the fewest predictors). We then used Program MARK (White and Burnham 1999) to estimate survival rates and detection probabilities from the selected model. Confidence intervals for age- and sex-specific survival rates were calculated on the logit scale (i.e., the log-odds scale) and reported on the nominal scale (corrected for eartag loss). Confidence intervals for the year effects on survival were calculated on the logit scale and reported as odds ratios. These are the odds of survival in a particular year (probability of survival divided by the probability of death) as compared to the average odds of survival across all years. Future life expectancy was calculated as a function of age (Krebs 1978, Caswell 2001), using the estimated survival rates from the CMR analysis.

### Reproduction

Reproduction of females was quantified in six years (1987–1990, 1992, and 1994) by capturing entire litters when they first emerged from their natal burrow. To accomplish this, each female's mating date was determined by direct observation (Sherman 1989), the spot where she excavated her nursery burrow was mapped, and she was observed every 2–3 d throughout gestation and lactation to keep track of which burrow entrance she was using (females often excavate new entrances to their burrow systems). Juvenile *S. b. brunneus* emerge from their natal burrow 50–52 d after their mother mated (Sherman 1989), and pups begin dispersing soon thereafter. We therefore trapped and eartagged entire litters on the first or second day they appeared above ground.

Females of known and unknown ages were included in our analyses; for the latter, minimum possible ages were assigned. Statistical models were then used to identify which factors affected the various components of reproduction. Specifically, to analyze proportions of

successful females, we used logistic regression (SAS PROC GENMOD, SAS Institute 1993), treating each female as a trial and the emergence of  $\geq 1$  pup as a success. To analyze litter sizes, we used a linear model (SAS PROC GLM and PROC MIXED, SAS Institute 1989), with numbers of emergent pups as the response variable and year treated as a random effect (all other effects were fixed). To analyze sex ratios, we used logistic regression, with the number of females in a litter treated as a binomial random variable and litter size as the number of trials. In each analysis, we used Akaike's Information Criterion (AIC, see Burnham and Anderson 1998) to select a parsimonious model. Significance tests of specific terms were made using standard methodology, i.e., likelihood-ratio tests for fixed effects (McCullagh and Nelder 1989) and likelihood-ratio tests modified to reflect the mixture distribution for random effects (Stram and Lee 1994).

### Matrix analysis

After calculating estimates for the various life-history parameters, we constructed an age-structured, females-only matrix model (Leslie 1945, Caswell 1989) for the Squirrel Valley population using the estimated survival and reproductive rates from the models selected for each vital rate. The population growth rate (dominant eigenvalue,  $\lambda$ ), stable age-distribution (right eigenvector,  $\mathbf{w}$ ), and reproductive-value vector (left eigenvector,  $\mathbf{v}$ ) were calculated using MATLAB (Mathworks 1999). The sensitivities of the population growth rate ( $\lambda$ ) to small proportional changes in the matrix elements and vital rates (i.e., the elasticities) were calculated using the formulas given by Caswell (1989).

## RESULTS

During 1986–1999, 1217 *S. b. brunneus* were individually marked in Squirrel Valley proper. Of these, 27 (2%) had lost both eartags, so we actually caught 1190 different individuals. Of the marked animals, 621 (51%) were males and 596 (49%) were females; 972 (80%) were of known age and 245 (20%) were of unknown age. Among the known-age animals, 812 (84%) were first captured as juveniles and 160 (16%) as 1-yr-olds. Among all marked animals, 970 (80%) were never caught again in subsequent years, 148 (12%) were caught in one subsequent year, 55 (5%) were caught in two subsequent years, and 44 (4%) were caught in three or more subsequent years.

From 1987 to 1999 the Squirrel Valley population declined precipitously, from 272 individuals (including 112  $\geq 1$ -yr-olds and 160 juveniles) to just 10 individuals, only two of which were reproductive-age females (Fig. 2). Thus, in just 12 yr the population decreased to  $< 5\%$  of its initial size.

### Dispersal

*Short-range.*—From 1988 to 1991 and in 1993, 17–34 unmarked  $\geq 1$ -yr-olds appeared in SV each year.

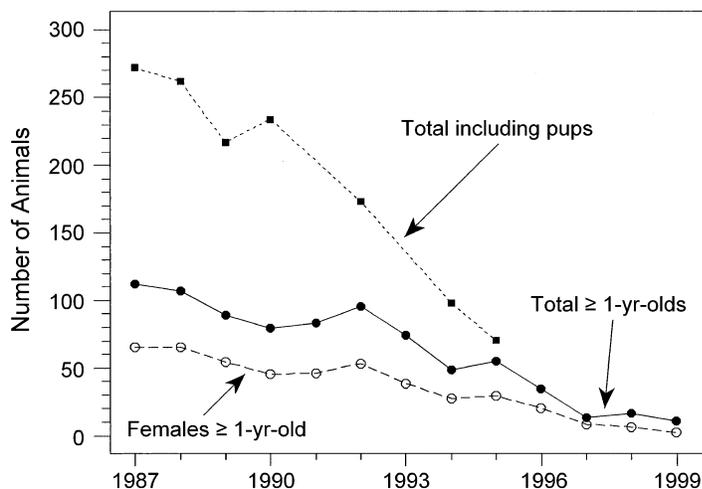


FIG. 2. Number of animals alive in Squirrel Valley, 1987–1999. The solid squares show the total population size, including pups, for those years that pups were trapped. The solid circles show the total population size ( $\geq 1$  yr); the open circles show the female population size ( $\geq 1$  yr). Animals missing for a year or more but captured subsequently are included in the total.

Since the SV population was completely marked each of the prior seasons, the new animals must have been immigrants (1992 was excluded because juveniles were not marked in 1991). In an attempt to determine the origin of these immigrants, we trapped extensively in SVN and SVS (Fig. 1) in two years. In 1988, 72 animals were captured in SVN and 10 in SVS. Of these, seven (8%) had previously been tagged in SV. None of the 82 individuals was ever trapped in SV subsequently. Thus, emigration from SV occurred in 1987–1988, but no individuals marked in SVN or SVS in 1988 immigrated to SV in 1989 or thereafter. In 1994, 83 animals were captured in SVN and 30 in SVS. None of these had previously been tagged in SV. In 1995, eight of these 113 animals (7%) were caught in SV. Thus, in 1994 there was no evidence that individuals that had been marked in SV during 1986–1993 emigrated to SVN or SVS, but immigration to SV from SVS and SVN occurred in 1995.

Of the seven emigrants from SV to SVN and SVS in 1988, three were 1-yr-old males, three were  $\geq 2$ -yr-old males, and one was a  $\geq 2$ -yr-old female; and of the eight immigrants to SV from SVN and SVS in 1994, three were 1-yr-old females, two were 1-yr-old males, two were  $\geq 2$ -yr-old females, and one was a  $\geq 2$ -yr-old male. Thus, 9 of 15 short-range dispersers (60%) were males, and 8 of 15 (53%) were yearlings. Immature males were overrepresented among short-range dispersers; however, this sample size is not adequate to test for age or sex biases.

To further investigate dispersal, we turned to the larger sample of immigrants to SV that were of undocumented origin. We used data from the six years subsequent to seasons in which all litters born in SV had been marked (1988–1991, 1993, and 1995) to be sure that unmarked 1-yr-olds were indeed non-natal individuals. Of 145 immigrants, 60 (41%) were 1-yr-old males, 44 (31%) were  $\geq 2$ -yr-old males, 23 (16%) were 1-yr-old females, and 18 (12%) were  $\geq 2$ -yr-old

females. Immigrants were significantly more likely to be males than females (0.72 vs. 0.28;  $P < 0.001$ , one-sided exact test of a binomial proportion), and slightly more likely to be 1-yr-olds than older (0.57 vs. 0.43;  $P = 0.048$ ). There was no evidence of dependence between the age and sex of the immigrants ( $\chi^2 = 0.031$ ,  $df = 1$ ,  $P = 0.86$ ). An obvious weakness of this analysis is that we do not know the sex and age distributions of the source populations from which the immigrants came. However, they probably were similar to SV (and to other ground squirrel populations [Yensen and Sherman, *in press*]), in comprising (1) more adults ( $\geq 2$ -yr-olds) than yearlings (see *Results: Matrix analysis*), and (2) more females than males among adults (see *Results: Sex ratios*).

*Long-range.*—During 1987–1999 we documented only three long-range ( $>500$  m) dispersal movements. In 1993, an adult female that had been marked in 1987 at SVN was recaptured at SM (1200 m away); in 1995, a 1-yr-old male that had been marked in 1994 (as a pup) at SM was recaptured at SVS (935 m away); and in 1999, an adult male that had been marked in 1994 at the south end of SVS was recaptured at the north end of SV (580 m away).

#### Survival

There were 1283 releases of known-age animals that could be used in our survival analysis (Table 1). The most parsimonious model for survival (see Fig. 3 and the Appendix) revealed significant differences among years and between males and females in four age groups (juveniles, 1-yr-olds, 2–4-yr-olds, and  $\geq 5$ -yr-olds). Survival rates estimated from this model (using the average year effect and correcting for eartag losses) indicated that juveniles of both sexes had extremely low survival rates and that survival rates of males were lower than those of females among all age classes except yearlings (Table 1). For all sex and age classes, the detection probability was 0.91 (95% confidence in-

TABLE 1. Estimated survival rates and sample sizes for Northern Idaho ground squirrels in Squirrel Valley, Idaho, from 1986 to 1998.

Age (yr)	Females				Males			
	$n_x^\dagger$	$L_x^\dagger$	$s_{x^\ddagger}$	95% CI§	$n_x^\dagger$	$L_x^\dagger$	$s_{x^\ddagger}$	95% CI§
0	411	94	0.206	0.16, 0.26	401	31	0.066	0.044, 0.098
1	163	61	0.397	0.30, 0.49	120	46	0.436	0.33, 0.55
2	62	28	0.567	0.45, 0.68	46	16	0.406	0.27, 0.54
3	28	17	0.567	0.45, 0.68	16	7	0.406	0.27, 0.54
4	17	9	0.567	0.45, 0.68	7	1	0.406	0.27, 0.54
5	9	1	0.217	0.05, 0.61	1	0	0.000	0.00, 0.975¶
6	1	1	0.217	0.05, 0.61				
7	1	0	0.217	0.05, 0.61				

Note: The  $x$  subscripts are the respective ages.

$^\dagger$  Survivorship data for animals of known cohort. The statistics shown are the number of animals of the given age known to be alive ( $n_x$ ), and the number of those that survived until the next year ( $L_x$ ).

$^\ddagger$  Survival rate estimates from the selected capture–mark–recapture model, using the average value for the year effect. Survival rates of animals  $\geq 1$  yr are corrected for lost eartags by dividing by the estimated eartag-retention rate.

$^\S$  Confidence intervals for age-0 animals were formed on the logit scale and transformed to the real scale. Confidence intervals for animals  $\geq 1$  yr account for both the variance in the survival estimate and the variance in the eartag-retention rate.

$^||$  Confidence interval determined with a parametric bootstrap procedure.

$^\¶$  Only one male of known age was observed in this age class (he did not survive). The exact 95% confidence interval for a binomial proportion is shown, but this does not take into account the year effect or the eartag-retention rate.

terval = 0.84–0.95), meaning that living SV individuals had a 91% chance of being in SV in a particular year (as opposed to SVN or SVS).

The year effects on survival can be expressed as odds ratios (Fig. 4). For example, the odds of survival in 1993 were 0.46 times the average observed over the course of the study, for all age and sex classes. Estimated odds ratios ranged from 1.72 in 1986 to 0.18 in 1996. Odds ratios of survival apparently declined through time, although the linear trend was not statistically significant (quasi-likelihood test [Lebreton et al. 1992, Link 1999],  $F_{1,10} = 1.87$ ,  $P = 0.20$ ).

Maximum persistence at Squirrel Valley (i.e., apparent longevity) was 5 yr for known-age males and  $\geq 7$  yr for males whose exact age was unknown. Maximum persistence was 7 yr for known-age females and  $\geq 8$  yr for unknown-age females. Interestingly, the oldest female was the long-range disperser from SVN to SM and the oldest male was the long-range disperser from SVS to SV. At birth, a male's future life expectancy (i.e., average life span) was 0.61 yr and a female's was 0.86 yr. As a yearling, a male's future life expectancy was 1.15 more years and a female's was 1.25 more years. Maximum future life expectancies were 1.15 more years for males (as 1-yr-olds) and 1.51 more years for females (as 2-yr-olds).

*Sex ratios*

There was no sex-ratio bias among juveniles at weaning, but among older age classes the sex ratio always was female-biased (Fig. 5). Of the 706 pups captured in 143 litters, 358 (50.7%) were females (95% confidence interval = 47.0–54.5%). Thus the initial ratio of females to males was 1.03:1. Among yearlings and 2-

yr-olds, sex ratios were 1.37:1 ( $n = 282$ ) and 1.36:1 ( $n = 106$ ), respectively. Among 4-yr-olds, the sex ratio rose to 2.43:1 ( $n = 24$ ), and among >4-yr-olds the sex ratio was 11:1 ( $n = 12$ ).

The mother's age was known for 139 of the 143 litters. Among them the sex ratio was not significantly affected by maternal age ( $\chi^2 = 6.86$ ,  $df = 6$ ,  $P = 0.33$ ), total litter size ( $\chi^2 = 12.98$ ,  $df = 10$ ,  $P = 0.22$ ), or year ( $\chi^2 = 2.91$ ,  $df = 5$ ,  $P = 0.71$ ). Thus, the most parsimonious model of sex ratios contained just one parameter: mean fraction of females in a litter.

*Maternity*

*Weaning rates.*—Of the 285 potentially reproductive females ( $\geq 1$ -yr-old) that were monitored from spring emergence until juvenile dispersal, 143 weaned litters (i.e., 50%). The proportion of successful females rose with age (Fig. 6A), an effect that was linear on the logit scale, and significant ( $\chi^2 = 12.96$ ,  $df = 1$ ,  $P = 0.0003$ ). There were no significant differences in age-specific weaning rates among years ( $\chi^2 = 3.48$ ,  $df = 5$ ,  $P = 0.63$ ). The fitted model equation, which we used to generate predicted values for weaning rate, was:  $\text{logit}(\text{weaning rate}) = -0.8361 + 0.3577(\text{age})$ .

*Litter sizes.*—The distribution of litter sizes at weaning was unimodal and symmetric (Fig. 6B). Litter size was  $4.94 \pm 1.88$  pups (mean  $\pm 1$  SD), and the median and modal litter sizes both were 5.0 pups. Mean litter sizes increased significantly ( $P = 0.005$ ) with maternal age from 1 to 4 yr (Fig. 6A). In addition, there were significant fluctuations in mean litter sizes between years ( $\chi^2 = 4.68$ ,  $df = 1$ ,  $P = 0.015$ ), independent of maternal age ( $\chi^2 = 0.059$ ,  $df = 1$ ,  $P = 0.40$ ). That is, litter sizes of females of all ages varied in parallel. We

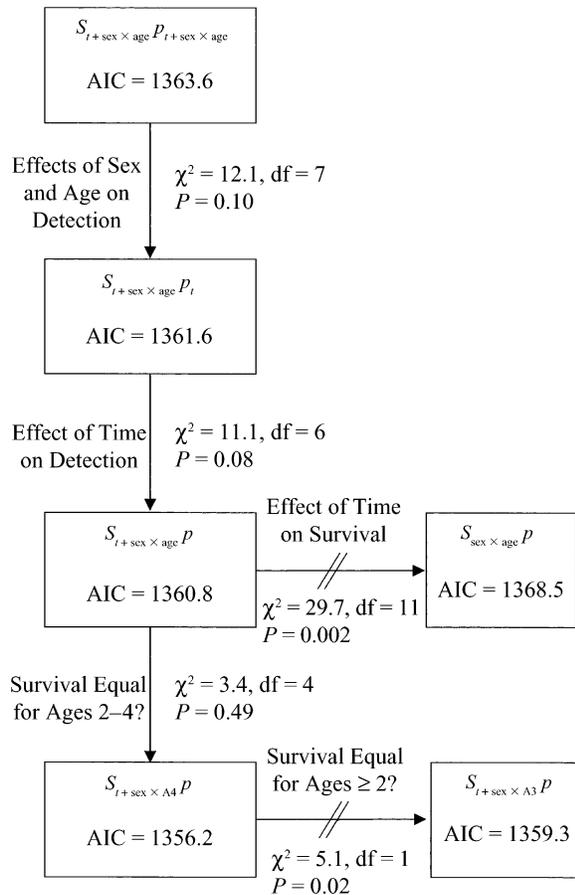


FIG. 3. Model selection schematic for the capture-mark-recapture survival model. The model structure notation indicates whether the survival rates ( $S$ ) and detection probabilities ( $p$ ) varied by sex, age, or time (age indicates that six age classes were used [0, 1, 2, 3, 4, and  $\geq 5$  yr], A4 indicates that four age classes were used [0, 1, 2–4, and  $\geq 5$  yr], and A3 indicates that three age classes were used [0, 1, and  $\geq 2$  yr]). The arrows show the results of likelihood ratio tests for the effects of various factors. Also shown is Akaike's Information Criterion (AIC) for the corresponding models. See also the Appendix.

therefore treated litter size as a linear function of maternal age, with a random year effect. The fitted equation, estimated with SAS PROC MIXED, was: litter size =  $4.0862 + 0.3163(\text{age}) + Y$ , where  $Y$ , the year effect, had a variance of 0.375 (MSE = 3.098). The best linear unbiased predictors of the year effects for litter size were not significantly correlated with the year effects from the survival model ( $r = 0.15$ ,  $P = 0.78$ ;  $n = 6$  yr).

**Temporal variation.**—Between 1987 and 1994 the number of females that successfully weaned at least one pup declined from 31 to 13 (Fig. 7). From 1987 to 1990 the average age of female breeders appeared to increase. However, this was an artifact of the lag between the start of the study and the time when the exact ages of most females in the population were

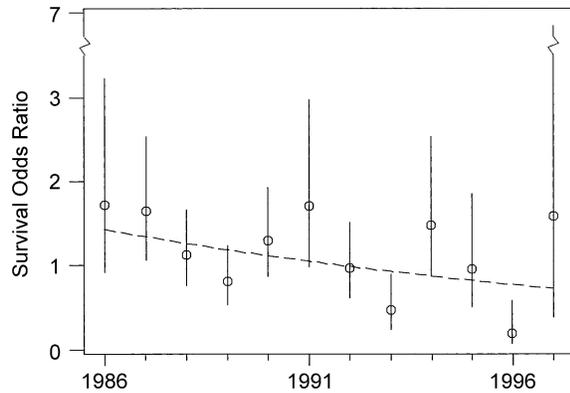


FIG. 4. Year effects from the selected survival model ( $S_{t+\text{sex} \times \text{A4}} p$ ), with 95% confidence intervals. The effects are shown on the odds ratio scale (thus, for example, the odds of survival in 1986 were 1.72 times higher than average). The dashed line is a linear trend fit to the year effects on the logit scale.

known. The average age of female breeders decreased after 1990, by which time ages of most individuals were known. The average litter size followed a trajectory that was similar to those of female numbers and ages; i.e., litter sizes remained relatively constant from 1987 (5.46 pups/litter) to 1990 (5.54 pups/litter) and then declined (to 3.85 pups/litter in 1994).

#### Matrix analysis

The finite rate of increase, calculated from the Leslie matrix (Table 2), was  $\lambda = 0.721$ . This describes a population declining at a rate of nearly 30% per year (see Fig. 2). The stable age distribution ( $w$ ) for the population was dominated by juveniles and yearlings. Indeed, only 0.27 of the stable female population was  $\geq 2$ -yr-old (Table 2). Reproductive value ( $v$ ), defined

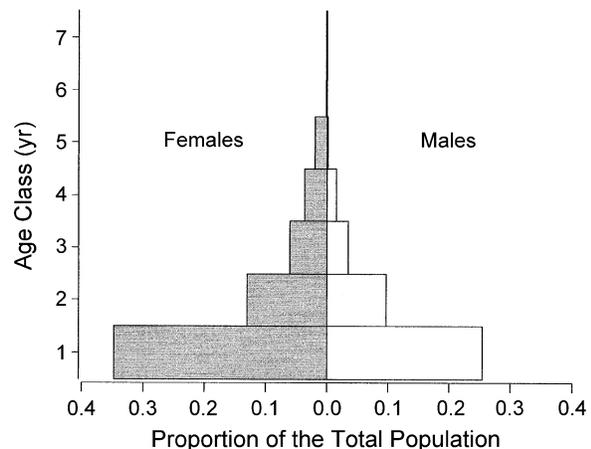


FIG. 5. Population pyramid for *S. b. brunneus* at Squirrel Valley, showing the age and sex composition of the entire yearling and adult population. These are composite data from the years 1986–1998 for animals first caught as either juveniles or yearlings.

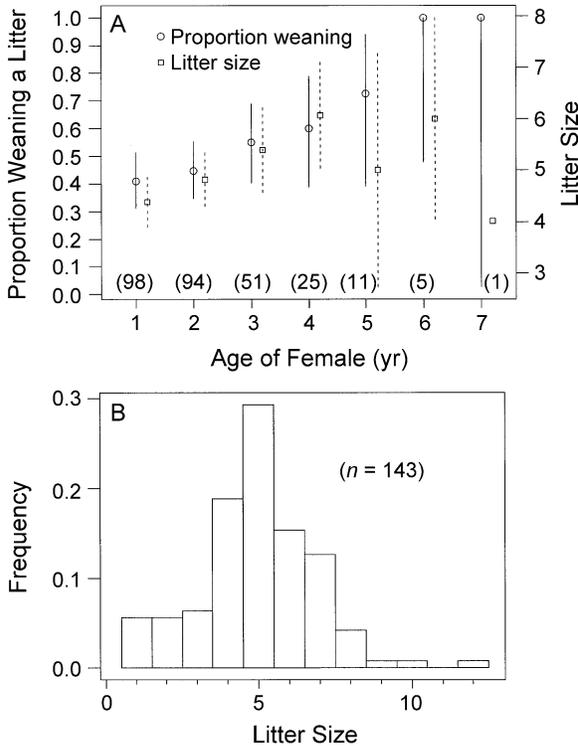


FIG. 6. (A) Observed reproductive rates as a function of dam's age. Open circles are the observed proportion of females weaning a litter (with exact 95% binomial confidence intervals), and open squares are mean litter sizes (with 95% confidence intervals). Numbers of females observed in each age class appear at the bottom in parentheses. (B) Histogram of observed litter sizes ( $n = 143$ ).

as a female's relative contribution to the female population in a given year and all future years, rose until females were 2-yr-old, then declined (Table 2). The elasticities of the vital rates for individual age classes revealed that the growth rate of the population was most strongly influenced by changes in survival of juveniles and 1-yr-olds (Table 2).

Matrix analyses are typically limited by an asymmetry in the treatment of dispersal. "Mortality rates" are actually rates of disappearance and, as such, include individuals that emigrated permanently as well as those that actually died. In contrast, fecundity rates do not reflect immigration. Thus, in general, growth rates calculated using Leslie matrices underestimate true growth rates unless populations are closed. Dealing with this bias motivated development of CMR methods for estimating  $\lambda$  (Pradel 1996, Nichols et al. 2000).

Does this concern undermine our matrix analysis? In most ground-dwelling sciurids, natal dispersal is obligate for males, and breeding dispersal is male-biased (Sherman 1977, Holekamp 1984, Nunes et al. 1997, Olson and Van Horne 1998, Byrom and Krebs 1999). Therefore, rates of disappearance of females more accurately reflect mortality than do disappearance rates of males (e.g., Sherman and Morton 1984). The "sur-

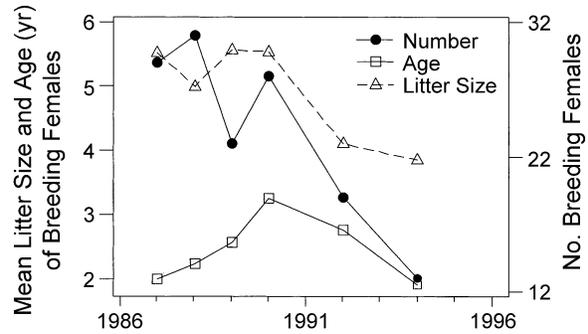


FIG. 7. Temporal demographic changes in Squirrel Valley, 1987-1994. Solid circles show the observed number of successful breeders (females that weaned a litter), open squares show the average age of those breeders, and open triangles show average litter sizes. The initial increase in average age of the breeders is an artifact of the data (see *Results: Maternity, temporal variation*).

vival" rates that might be most biased by emigration are those for males, especially juveniles. Fortunately, our matrix analysis does not include survival rates of males.

Nonetheless, survival rates of juvenile females could potentially be biased. In the early years of our study (1987-1990) the SV population was relatively large (Fig. 2). Although we found that females seldom dispersed, some may have emigrated from SV to areas of lower density where they were not recaptured. If so, their disappearance rate would have overestimated mortality, resulting in an underestimate of the population's growth rate. However, during the latter two-thirds of the study (1991-1999), the population in SV had declined, immigration to SV was minimal, and there was no indication of emigration to any other population site in Bear Meadow or elsewhere (Gavin et al. 1999). Thus, permanent disappearance probably re-

TABLE 2. Matrix analysis of an age-structured Leslie model of female Northern Idaho ground squirrels in Squirrel Valley.

Age (yr)	$m_x$ †	Eigenvectors		Elasticities†	
		$w$ § (right)	$v$    (left)	$s_x$	$m_x$
0	0	0.565	0.578	0.327	0
1	0.854	0.161	1.530	0.247	0.080
2	1.124	0.089	2.128	0.189	0.058
3	1.427	0.070	1.881	0.131	0.058
4	1.749	0.055	1.381	0.076	0.056
5	2.074	0.043	0.558	0.024	0.052
6	2.390	0.013	0.468	0.006	0.018
7	2.688	0.004	0	0	0.006

† Elasticities are for the life-history parameters, not the matrix elements.

‡ Female young weaned in year  $t$  per female  $\geq 1$  yr in year  $t$ , using predicted values of weaning rate, litter size, and sex ratio. The first row of matrix elements was calculated as  $F_x = s_x m_{x+1}$ . (See Table 1 for the survival rates used in the matrix.)

§ Stable age distribution.

|| Reproductive value (scaled so  $\sum w_i v_i = 1$ ).

flected mortality for most of the years that went into the matrix analysis.

#### DISCUSSION

##### *Caughley's challenge*

Between 1986 and 1999 we witnessed the collapse of the largest known population of Northern Idaho ground squirrels (Yensen and Sherman 1997, Gavin et al. 1999). How and why did this occur? These questions capture the dichotomy Caughley (1994) pointed out concerning the nature of investigations of population declines. The proximate question, in the spirit of Caughley's small-population paradigm, asks how the Squirrel Valley population crashed (i.e., the immediate causes of the decline). The ultimate question, in the spirit of Caughley's declining-population paradigm, is why the population was at the brink (i.e., the long-term causes of the decline).

Caughley (1994) challenged us to move away from case-by-case descriptions of declining species in favor of forging general theories about species in decline. Does the SV population offer any general insights into the process of decline? We believe that it does. Here we advance an hypothesis, building on Diamond's (1989) classification of agents of decline and on Sæther et al.'s (1996) categorization of declines in relation to life histories. Then we explore the hypothesis in the context of the Northern Idaho ground squirrel.

##### *A demographic classification of anthropogenic population declines*

Anthropogenic impacts can affect organismal life-history parameters to produce changes in population dynamics. We suggest that anthropogenic population declines can be classified based on whether the means, variances, or correlations among life-history parameters are affected.

*Blatant disturbance.*—Sometimes widespread environmental changes result in major, negative effects on mean values of key life-history parameters. Such environmental changes may (1) affect the demographic parameter with the highest elasticity (or highest sensitivity), (2) produce major changes in some other parameter, or (3) produce small changes in many parameters simultaneously. As an example of (1), the decline of some whale species has been attributed to over-hunting (Brault and Caswell 1993, Fujiwara and Caswell 2001), an impact that most notably reduces adult survival, the key life-history parameter for long-lived, large mammals (Goodman 1981, Caswell et al. 1999). Regarding (2), in peregrine falcons (*Falco peregrinus*) the life-history parameter with the greatest elasticity is adult survival (see Young 1969), but Cade et al. (1988) and Risebrough and Peakall (1988) believe the primary cause of the birds' near extinction was the effects of organochlorine pesticides on reproduction (i.e., a major change in a life-history parameter with a lower elas-

ticity). Regarding (3), large-scale habitat modification (e.g., due to urbanization, clear cutting, or agricultural conversion) obviously impacts multiple life-history parameters simultaneously. All the causes of extinction in Diamond's (1989) "evil quartet" (i.e., overkill, habitat destruction and fragmentation, introduced species, and chains of extinction) fall into this blatant disturbance category.

*Inappropriate variation.*—Changes in the variances of life-history parameters also can bring about population declines. In stochastic environments, the relevant measure of population growth is the expected value of the logarithm of one-time-step growth rates (i.e.,  $E[\log(N_{t+1}/N_t)]$ , Lewontin and Cohen 1969, Tuljapurkar and Orzack 1980, Caswell 2001). Tuljapurkar (1982) showed that this rate decreases with increasing variance in individual life-history parameters. So, even if mean vital rates suggest a population that is growing, the population may decline due to increased variances. A decrease in the temporal (year-to-year) correlation of a vital rate can have a similar effect (Tuljapurkar 1982). Of course, it is difficult to identify changes in variances as opposed to changes in means as causes of population declines, because the altered life-history parameters may appear to be within their natural range of variability, or the natural range of variability may be unknown.

*Evolutionary traps.*—Organisms can respond to environmental stochasticity either facultatively or non-facultatively. The former involves variable behavioral and life-history responses that depend on the state of the environment, whereas the latter involves static responses that accommodate the natural environmental variation. As an example of a facultative response, some ground squirrel species exhibit phenotypic plasticity in reproduction. Individuals may delay sexual maturation if their body masses are too low (Bushberg and Holmes 1985), due for example to food shortages (Dobson and Murie 1987, Dobson and Oli 2001) and droughts (Smith and Johnson 1985). Adverse conditions such as late snowmelt and drought also result in more individuals curtailing reproduction (Phillips 1984, Smith and Johnson 1985). An example of a non-facultative response is that ground squirrels remain in hibernation throughout the winter even when there are several days or weeks of unusually warm weather (e.g., a "January thaw," Michener 1984).

Facultative responses depend on existence of a cue (e.g., day length, temperature, or plant phenology) that reliably indicates the state of some key environmental variable in the future, and thus which behavioral or reproductive choice to pursue presently. However, if anthropogenic changes eliminate the cue, or decouple it from the consequences that have predictably occurred over evolutionary time, individuals' decision rules (Darwinian algorithms) may no longer yield appropriate (adaptive) responses. Disruptions of Darwinian algorithms associated with choices of breeding habitats

were termed “ecological traps” by Gates and Gysel (1978).

More generally, when any aspect of the environment changes suddenly organisms are prone to make inappropriate behavioral and life-history decisions (e.g., when to reproduce, how many young to bear, or when to hibernate). This is because their underlying Darwinian algorithms are only as complex as is necessary to yield adaptive outcomes under normal circumstances, not so complex as to cover all anthropogenically induced contingencies. Schlaepfer et al. (2002) suggested the term “evolutionary trap” to describe the negative results of disassociation of any environmental cue from its expected outcome. Populations that are caught in an evolutionary trap will decline and may even go extinct before individuals with tendencies to ignore the original cue, and pay attention to a more reliable alternative cue, appear and are favored by selection.

Implicit in the evolutionary trap concept is that there are trade-offs in behaviors and life-history strategies, which result in negative correlations among vital rates. For example, ground squirrels that curtail reproduction in drought years presumably benefit through increased adult survival or reproductive success the following year. Indeed, this trade-off has been documented in *S. columbianus* (Neuhaus and Pelletier 2001), which divert energetic resources to survival when reproduction is likely to fail. Anthropogenic impacts that disrupt such correlations among vital rates can impact population growth negatively (Tuljapurkar 1982).

As another example, the yellow-bellied marmots (*Marmota flaviventris*) that reside at high elevations in the Colorado Rockies face an evolutionary trap. Warmer air temperatures that nowadays occur earlier in the season trigger their emergence from hibernation, but the appearance of green forage does not (yet) show a similar advancement in phenology, leaving the early-emergers with little to eat (Inouye et al. 2000). The trade-off here is that if the marmots emerge too early the ground will still be snow-covered and their food supplies will be unavailable, whereas if they emerge too late the young will not have enough time to fatten before inclement weather forces hibernation. Other examples of evolutionary traps are provided by Schlaepfer et al. (2002).

#### *Collapse of the Squirrel Valley population*

*Small-population paradigm: demography of the population collapse.*—Two key demographic factors underlay the collapse of our study population: (1) low survival of juvenile females, and (2) reduced reproductive output by females due to a shift in the age distribution toward younger females. In the initial years of the study the population was large (Fig. 2), and circumstantial evidence suggests that SV was a source of dispersers (i.e., the only documented cases of dispersal were out of SV). However, survival rates of ju-

venile females were low, and year effects in the survival model (Fig. 4) indicated that survival rates apparently decreased across all sex and age classes over the 13 yr of our study.

Major demographic changes occurred at SV after 1990. Between 1990 and 1992 the number of females that successfully weaned litters fell from 28 to 19, their mean age dropped from 3.3 yr to 2.8 yr, and mean litter size fell from 5.5 to 4.1 pups (Fig. 7). The decline in mother's age indicates that mortality rates for older females increased. Alteration in the female age structure coincided with a marked decrease in their average reproduction, apparently because younger females were less successful at weaning litters and had fewer pups (Fig. 6A).

By 1994 the Squirrel Valley population was characterized by a relatively young female age structure, few highly fecund breeders, low juvenile survival, and low immigration. The population was in a steep decline and the only documented cases of dispersal were into SV from neighboring areas. Circumstantial evidence suggests that the nearby subpopulations also were declining. The number of immigrants to SV decreased substantially after 1994 and the density of ground squirrels in SVN and SVS appeared to be much lower in 1994–1999, as indicated by visual surveys of active individuals, numbers of active burrows compared to previous years, and the time and effort it took to capture samples of ground squirrels to identify potential dispersers.

Thus, the proximate cause of the population's collapse was unusually high mortality of older breeding females between 1990 and 1992 against a backdrop of low survival of juvenile females. The change in age structure triggered a population vortex, and the SV population essentially disappeared. Such a collapse is the focus of Caughley's (1994) small-population paradigm. However, as he argued, the important general question is not the immediate reason a small population eventually disappears, but what factors ultimately brought the population to the brink of collapse in the first place.

*Declining-population paradigm: long-term causes of the population collapse.*—The collapse of the Squirrel Valley population caught us off guard, and we did not investigate causal factors throughout the process. However, in retrospect, circumstantial evidence points to two, simultaneous environmental changes as causative factors: (1) fragmentation and shrinking of suitable meadow habitat, due to forest encroachment, throughout the species' range, and (2) changes in the vegetational composition of remaining meadows.

As a result of at least 80 yr of fire suppression, the original age-structured, open-canopy forests and interspersed meadows in Adams and Valley Counties have been largely replaced by dense, even-aged stands of young conifers (Arno 1980, Crane and Fischer 1986, Steele et al. 1986, Barrett 1988, Truska and Yensen 1990). The dry ponderosa pine (*Pinus ponderosa*)/

Douglas-fir (*Pseudotsuga menziesii*) forest types have natural fire intervals of 5–25 yr (Crane and Fischer 1986, Steele et al. 1986). These communities are particularly susceptible to the effects of fire suppression (Bunnell 1995). Forest encroachment has isolated the meadows that are suitable for ground squirrel inhabitation, reduced the sizes of those meadows, and eliminated dispersal corridors along valley bottoms (Yensen and Sherman 1997). Due to demographic isolation, *S. b. brunneus* populations already are genetically differentiated (Gavin et al. 1999). Populations that decline due to stochastic processes (e.g., weather, predation, diseases) are unlikely to be rescued (sensu Brown and Kodric-Brown 1977) by emigrants from neighboring populations, especially given the animals' low vagility even in continuous habitat (Sherman 1989, Gavin et al. 1999; see *Results*).

Even in habitats that remain open, such as Bear Meadow, changes have occurred in the species composition of the ground squirrels' forage due to fire suppression, drying, and grazing, all of which favor drought-adapted, lignified plants (A. H. Winward, *personal communication*). Without fire, meadow succession occurs. As a result, densities of shrubs increase and herbaceous grasses and forbs decline in abundance (Harniss and Murray 1973, Arno and Gruell 1983, 1986, Humphrey 1984). As dense stands of conifers encroach on meadow edges, they draw necessary moisture from the meadows. Cattle grazing creates eroded downcuts on uneven ground that further drain meadows of moisture (Fleischner 1994). Grazing animals also preferentially remove the more palatable and digestible native forbs and perennial bunchgrasses, leaving sod-forming grasses, low-growing weedy forbs, and shrubs. Finally, grazing can destabilize native plant communities, facilitating invasion by exotics (Mueggler 1962, Wing 1969, Collins 1987, Fleischner 1994). Combined effects of these processes on plant species composition have been well documented (Rummell 1951, Mueggler 1962, Wing 1969, Leege et al. 1981, Fleischner 1994), although their individual contributions are difficult to disentangle.

Fire suppression and grazing have been practiced at Bear Meadow for many decades. However, in the early 1990s grazing intensity was dramatically reduced by ranch management. Clearly the observed decline of the Squirrel Valley population did not result from intensification of grazing. Nonetheless, drying, eroded downcuts, and changes in plant species composition are evident in Bear Meadow, as well as at other Idaho ground squirrel population sites. Dyni and Yensen (1996) studied the diet of *S. b. brunneus* in Squirrel Valley just after juveniles were weaned in June 1988. Of the six most important food items (each comprising  $\geq 5\%$  of the diet), three were introduced forage plants (*Poa bulbosa*, *Bromus commutatus*, and *Medicago sativa*) that together constituted 36% of the ground squirrels' diet. The other top three items (*Microseris ni-*

*grecens*, *Lupinus* sp., and seeds of various Asteraceae [genera: *Microseris*, *Agoseris*, *Hieraceum*, and *Crepis*]) are of medium to high palatability to livestock (USDA Forest Service 1993). All the native plants, except *Lupinus*, are reduced in abundance by grazing (A. H. Winward, *personal communication*). The presence of introduced forage plants as a major part of the ground squirrels' diet suggests a long-term shift in plant species composition in Bear Meadow.

At another site studied by Dyni and Yensen (1996), the single most important food of *S. b. brunneus* was *Stipa* sp. seeds (probably *Stipa columbiana*), which comprised 17% of the animals' diet. Seed production of this needlegrass is stimulated by fire, being 30-fold greater on sites burned two years earlier compared to unburned sites (Patton et al. 1988). However, needlegrasses are highly palatable and decrease in abundance when subjected to grazing (Leege et al. 1981). Thus, at least one important *S. b. brunneus* food source is favored by a natural fire cycle and disfavored by grazing.

Taken together, these considerations suggest a synthetic hypothesis for the decline of our study population, as well as other *S. b. brunneus* populations in the vicinity (Yensen and Sherman 1997, Gavin et al. 1999; M. C. Runge, T. A. Gavin, and P. W. Sherman, *unpublished manuscript*). The nonnative and lignified plants and shrubs that now dominate Squirrel Valley and other population sites have different phenologies and nutritional profiles than the food plants the ground squirrels evolved to utilize. In particular, many plants in native meadow communities produce seeds with sufficient endosperm to enable them to persist in the soil until the next fire creates conditions appropriate for germination. These fat-laden seeds are sought by the ground squirrels in late summer, and they provide the animals with the necessary body fat (energy) to survive 7–8 mo in hibernation. By contrast, the plants whose growth is encouraged by the combined effects of fire suppression, drying, and grazing have higher ratios of vegetative to sexual reproduction and flourish and die earlier than the native plants, yielding a food resource that is not suitable for the ground squirrels temporally or nutritionally.

Polyunsaturated fatty acids play an important role in regulating hibernation in rodents (Florant 1998). Reduced availability of seeds containing linoleic acid and alpha-linoleic acid, resulting from changes in plant species composition, may decrease survival of ground squirrels during hibernation (Frank et al. 1998). The effects of changes in nutritional resources should be most severe in juveniles because, among all age classes, juveniles are most susceptible to environmental stress (see Promislow and Harvey 1990), and they have the highest surface-to-volume ratio, hence the greatest heat loss per gram of stored fat during hibernation. Thus, floral changes and loss of fatty seeds may underlie the increased rates of disappearance (mortality) and de-

TABLE 3. Life-history characteristics for ground-dwelling sciurids in the subgenus *Spermophilus*.

<i>Spermophilus</i> species	Survival (juvenile)		Survival (2-yr-old)	Breeding rate of yearlings	Litter size	Sources†
	M	F	F			
<i>b. brunneus</i>	0.07	0.21	0.57	0.41	4.9	1
<i>mollis</i>	0.15	0.30	0.40‡	0.53§	8.0	2, 3
<i>armatus</i>	0.30	0.39	0.42‡	0.60	5.1	4, 5
<i>beldingi</i>	0.31	0.35	0.53	0.65	4.4	6
<i>richardsonii</i>	0.12	0.46	0.65	0.96	7.0	7, 8, 9
<i>elegans</i>	0.19¶	0.40	...	0.00–1.00§	5.9	10, 11, 12, 13
<i>columbianus</i>	0.35	0.40	0.62	0.00–0.86§	2.3–4.6§	14, 15
<i>parryii</i>	0.16	0.42	...	0.47–0.96§	3.5	16, 17, 18

† Sources for these data are (1) this study; (2) Smith and Johnson (1985); (3) Van Horne et al. (1997); (4) Slade and Balph (1974); (5) Rieger (1996); (6) Sherman and Morton (1984); (7) Michener (1985); (8) Michener (1989a); (9) Michener and Locklear (1990); (10) Pfeifer (1982); (11) Zegers (1984); (12) Fagerstone (1988); (13) Stanton et al. (1992); (14) Boag and Murie (1981); (15) Dobson and Murie (1987); (16) Green (1977); (17) Hubbs and Boonstra (1997); and (18) Buck and Barnes (1999).

‡ Survival rate for 2-yr-old females not available, rate shown is for adult females  $\geq 2$  yr (*S. mollis*) or adults  $\geq 2$  yr (*S. armatus*).

§ Rates show considerable temporal or altitudinal variation.

|| Litter size measured in embryos prior to parturition, all other values are measured in pups at weaning.

¶ Survival rate for juveniles did not distinguish between sexes.

creased rates of reproduction in *S. b. brunneus* at Squirrel Valley.

#### A comparative perspective

*Interspecific life-history variation.*—To evaluate the likelihood of our proximate and ultimate explanations for the decline of the population at Squirrel Valley, we considered demographic parameters for other species in the subgenus *Spermophilus*. Detailed demographic studies have been conducted on eight of the 12 Nearctic *Spermophilus* species (Table 3). Because the data are from studies of only one or a few populations, they do not reveal whatever variations may be present across the range of each species. There are four species that are phylogenetically close to *S. brunneus* (Hafner 1984, Hoffmann et al. 1993) for which demographic data are available from studies that lasted longer than six years (i.e., ~two generations). The studied populations of *S. mollis*, *S. armatus*, *S. beldingi*, and *S. richardsonii* were stable or increasing (references in Table 3), so comparisons of their demographic characteristics with those of our population may help us interpret what went “wrong” at Squirrel Valley.

Two factors stand out immediately: *S. b. brunneus* had the lowest rates of juvenile survival and yearling female breeding. In fact, just raising the survival rate of juvenile females and the breeding rate of yearling females to the average values reported for the four related species (i.e., juvenile survival = 0.38, yearling breeding = 0.68) increased the predicted growth rate of the SV population from 0.72 to 1.01. This makes sense because in our population model juvenile survival had the highest elasticity for any single age class (0.33, Table 2). In addition, the breeding rate of yearlings is one measure of the timing of reproductive ma-

turity. Changes in ages at which females mature contributed substantially to changes in population growth rate of *S. columbianus* (Dobson and Oli 2001), as measured by life-table response experiments with a partial life cycle model (Oli and Zinner 2001).

*Intraspecific life-history variation.*—Annual cycles and life-history patterns of ground squirrels are finely tuned to local environments (e.g., Michener 1984, Schwartz et al. 1998; Yensen and Sherman, *in press*). On the one hand, at higher altitudes (and latitudes) vegetational growing seasons and ground squirrels’ active seasons are shorter than at lower elevations. Fewer food resources and less time to obtain them correlate with lower body masses and reproductive rates, especially for yearlings. On the other hand, shorter active seasons reduce the time individuals are susceptible to avian and mammalian predators on the surface, potentially lengthening their life spans. In addition, at higher altitudes the insulative properties of the greater snowpack increase overwinter survival (e.g., Sherman and Morton 1984, Zammuto and Millar 1985). Thus, individual *S. lateralis* and *S. columbianus* in populations at higher elevations emerge from hibernation later, more often do not reproduce as 1-yr-olds, rear smaller litters, and live longer than individuals in lower elevation populations (Bronson 1979, Dobson and Murie 1987). Likewise, in *S. brunneus*, the lower elevation subspecies (*S. b. endemicus*) is physically larger and bears larger litters, but probably has a shorter life span (based on tooth-wear patterns) than *S. b. brunneus* (Yensen 1991, Yensen and Sherman 1997).

Phenotypic plasticity underlies many variations in life-history parameters among sciurid populations at different altitudes (e.g., in ground squirrels, Bronson 1979, Murie 1985, Dobson and Murie 1987; in mar-

mots, Armitage 2000). Temporal variations in life-history parameters within populations also undoubtedly represent plasticity. The evolutionary advantage of phenotypic plasticity is the ability to respond appropriately to environmental variations (Cohen 1966, 1967, 1968, Nichols et al. 1976, Bronson 1979, Charlesworth 1980, Van Horne et al. 1997). Temporal variations in *Spermophilus* demographic patterns apparently represent adaptive responses to environmental stochasticity of two types: length of the active season (i.e., timing of snowmelt) and success of primary productivity (i.e., drought cycle) (Van Horne et al. 1997, Schwartz et al. 1998). For example, adverse environmental conditions (late snowmelt, drought) cause *S. lateralis* and *S. mollis* to reduce or cease reproduction, thus diverting energetic resources to survival when reproduction is likely to fail (Phillips 1984, Smith and Johnson 1985). Body mass of females at emergence strongly affects litter size in adult *S. armatus* (Rieger 1996) and yearling *S. richardsonii* (Michener 1989b). Breeding rates of 1-yr-old females vary between years in *S. columbianus* (Dobson and Murie 1987) and *S. mollis* (Smith and Johnson 1985); in *S. columbianus* at least, yearling females are more likely to reproduce when their food supply is supplemented (Dobson and Kjelgaard 1985, Dobson and Oli 2001). *S. beldingi* (Bachman 1994) and *S. mollis* (Van Horne et al. 1997) allocate food resources to fat as opposed to lean mass in years when food is scarce, which increases the probability of overwinter survival but decreases the likelihood of reproducing in the following year (because of low body mass at emergence).

#### *What happened at Squirrel Valley?*

The most likely proximate hypothesis for the demise of the SV population is starvation. That is, the blatant disturbance to a key portion of the animals' food resource base (seeds of native plants) made it impossible for many individuals (especially young and old females) to reproduce effectively and then store enough fat to survive 7–8 mo in hibernation. Over the longer term, it is possible that the population was caught in an evolutionary trap. In congeneric ground squirrels, condition of the native vegetation at spring emergence is a reliable cue of whether there will be sufficient forage to support reproduction and prehibernatory fattening. The *S. b. brunneus* at Squirrel Valley did not receive an early-season cue that their food base would be nutritionally inadequate (lacking in seeds) and, in many years, unavailable (dried up or eaten by livestock) later in the active season. Thus, they did not respond adaptively to impending food-plant failure by reducing litter sizes or curtailing reproduction in order to fatten early. The consequence may have been increased overwinter mortality, especially for the youngest and oldest females, i.e., those that bore the greatest physiological burdens of gestation and lactation.

We hypothesize that combined effects of fire sup-

pression, introduction of exotic pasture grasses, drying, and grazing have created conditions that are unlike variations to which Northern Idaho ground squirrels have been exposed evolutionarily. This situation occurred so recently (i.e., 80–100 yr) that there has not been sufficient time to select for appropriate physiological or behavioral responses. Across the tiny range of this species, these changes have produced a blatant disturbance by reducing habitat, isolating populations, and minimizing interpopulation exchange. We do not know if the animals at Squirrel Valley and in other populations also were caught in an evolutionary trap, but we suspect so. Unfortunately, we may never find out because there are only 24 remaining populations of *S. b. brunneus* and none contains >100 adults.

Nonetheless, insights gained from understanding the dynamics of the collapse of the Squirrel Valley population may be useful in conserving the remaining populations, e.g., using fire as a tool to remove meadow-encroaching conifers and retard succession of meadows, maintaining the natural fire cycle once it is re-established, reintroducing native grasses and forbs to meadows, and avoiding grazing meadows when seedheads are ripe and ground squirrels are fattening for hibernation (June and July). These suggestions also may be useful in managing remnant populations of other vertebrates and invertebrates that are endemic to shrub-steppe communities (Wisdom et al. 2000).

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## APPENDIX

Details of the analysis of our mark–recapture survival data, including the methods and results for model selection, are available in ESA's Electronic Data Archive: *Ecological Archives* E083-055-A1.