

## Beating the odds: effects of weather on a short-season population of deer mice

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**Abstract:** We examined 11 years of data on reproductive success, survival, and population dynamics of two populations (Fortress and Grizzly) of deer mice (*Peromyscus maniculatus*) in the Kananaskis Valley, Alberta, to investigate the extent to which the dynamics of these populations is dictated by weather conditions. Summer population growth was not related to the population growth in the winter preceding the breeding season or to spring population density. Over the summer on the Fortress grid, population growth was positively related to adult survival, whereas on the Grizzly grid, population growth was positively related to nestling survival. Neither summer population growth nor demographic correlates of summer population growth was consistently related to weather patterns. On Fortress, adult survival during the breeding season was negatively correlated with precipitation. On Grizzly, nestling survival during the breeding season was negatively correlated with precipitation. Winter population growth was inversely proportional to the fall population density prior to the winter but neither was related to weather conditions. Climate limits seasonal breeding in these populations, but compensatory responses appear sufficient to accommodate extreme weather conditions during both the breeding and nonbreeding seasons.

**Résumé :** Nous avons examiné des données accumulées durant 11 années sur le succès reproducteur, la survie et la dynamique de population chez deux populations (Fortress et Grizzly) de souris à pattes blanches (*Peromyscus maniculatus*) de la vallée de Kananaskis, Alberta, pour déterminer l'influence des conditions climatiques sur la dynamique de ces populations. La croissance de la population en été n'est pas reliée à la croissance durant l'hiver qui précède la saison de la reproduction. Durant l'été, la croissance de la population de Fortress est en corrélation positive avec la survie des adultes, alors que celle de la population de Grizzly est reliée à la survie des jeunes au nid. Ni la croissance de la population en été, ni les facteurs démographiques reliés à la croissance de la population en été ne sont reliés systématiquement aux variations climatiques. Chez la population de Fortress, la survie des adultes durant la saison de la reproduction est en corrélation négative avec les précipitations. Chez la population de Grizzly, la survie des jeunes au nid durant la saison de la reproduction est en corrélation négative avec les précipitations. La croissance démographique en hiver est inversement proportionnelle à la densité de la population durant l'automne précédent, mais ni l'un ni l'autre de ces variables ne sont influencées par les conditions climatiques. Le climat est un facteur limitant de la reproduction saisonnière chez ces populations, mais celles-ci ont des réactions compensatoires qui semblent suffire pour qu'elles supportent des conditions climatiques extrêmes aussi bien durant la saison de la reproduction qu'en dehors de la saison de la reproduction.

[Traduit par la Rédaction]

### Introduction

Small mammals are endotherms that have the capacity to maintain physiological homeostasis in a changing environment. The metabolic costs of doing so, however, are high. Most small mammals have few somatic energy reserves (Millar 1987; Jönsson 1997), have maintenance costs that are strongly influenced by environmental temperature (Speakman 2000), and support a biomass of offspring greater than themselves during late lactation (Kaczmarski 1966; Migula 1969; Millar 1975). It is not uncommon for their daily energy expenditures to be several times their resting metabolic rates (Speakman

2000). Under these circumstances, it is not surprising that reproduction can fail during inclement weather, a phenomenon that has been recorded many times (e.g., Scott 1993; McDevitt and Speakman 1994; Reid and Krebs 1996; Van Horne et al. 1997; Lewellen and Vessey 1998; Neuhaus et al. 1999; and references therein). However, failure in the nest does not automatically follow from inclement weather, because endotherms also have physiological, metabolic, morphological, and behavioral compensatory mechanisms that enable them to cope with unusual events (e.g., King and Murphy 1985; Corp et al. 1999; Syme et al. 2001). Each event, therefore, should be assessed independently.

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Deer mice (*Peromyscus maniculatus*) in the Kananaskis Valley, southwestern Alberta, Canada, are typical of small mammals in strongly seasonal environments. The initiation of reproduction in the spring varies with environmental temperature (Millar and Gyug 1981) and snow cover (Sharpe and Millar 1991); fat content, as an indicator of body condition, varies with environmental temperature (Millar and Schieck 1986); and precipitation during the breeding season affects the relative mortality of female and male nestlings (Havelka and Millar 1997). Despite these influences, which can vary considerably from year to year, populations of deer mice in the Kananaskis Valley are relatively stable, with small annual differences in fall population densities attributable primarily to differences in reproductive success during the summer (Millar and McAdam 2001). Reproductive success, in turn, depends primarily on the amount of mortality in the nest (Millar and McAdam 2001). Nestling mortality is unrelated to spring population densities (and therefore not likely related to density effects), which leads to the possibility that nest mortality and the dynamics of these populations are dictated by weather conditions. To test the effect of weather, we examined 11 years of data on the survival, reproductive success, and population dynamics of two populations of deer mice in the Kananaskis Valley. The data used here, a subset of the 16 years of data reported in Millar and McAdam (2001), comprise data from the only two grids studied by Millar and McAdam (2001) that were monitored continuously for 11 years, so that analyses of summer and winter demographics could be treated as grid-specific and effects of year-to-year variation in weather could be tested.

## Materials and methods

Mice were monitored using Longworth live traps (a single trap per station, 20-m spacing, baited with oats and cotton bedding) at two sites in the Kananaskis Valley throughout the summers (May through August) of 1987–1997. Details of the trapping regime can be found in Teferi and Millar (1993) but trapping was frequent (twice per week), parturition dates were estimated for all females, females were tracked to their nests using fluorescent-powder tracking (Lemen and Freeman 1985), and intensive trapping at nest sites (5–7 traps per nest site) permitted weaned young to be assigned to particular dams. In this way, both frequency of reproduction and breeding success were determined for all females in all years.

The trapping sites were represented by two trapping grids of 4.4 (Fortress) and 6.0 (Grizzly) ha. The distance between the two trapping grids was approximately 3 km. The home ranges of mice in the Kananaskis Valley are large relative to grid sizes (0.6 ha for females and 1.2 ha for males; Ribble and Millar 1996) but the catchment area was larger than the grids and the same in all years (Millar and McAdam 2001), because grids encompassed optimal ephemeral stream bed habitat (Millar et al. 1985). Thus, given the trapping regime, grid size, and grid placement, our trapping sample is representative of the population. Because weather records for the Kananaskis Valley were available only from the Kananaskis Field Station, which was 35 km north of the study sites, we were only able to examine the demography of these mice in

relation to global weather within the valley. For this reason, we analyze the demographic data in relation to the weather data from each of the two grids separately to avoid pseudo-replication (Hurlbert 1984).

The demographic data available to us were represented by annual summaries of the number of previously tagged and “new” over-wintered males and females resident on the grids in the spring (early May), the number of parturitions (representing an average of 5.25 young each; Millar and Innes 1983) and weaned young, the number of spring residents and weaned young alive in late August, and the number of other mice (immigrants) resident in late August. A detailed description of the population parameters and their calculations can be found in Millar and McAdam (2001).

For all analyses, traditional calendar years were modified into biological years. A biological year began at the beginning of October and ended at the end of September the following year. For example, biological year 1993 began in October 1992 and ended in September 1993. Biological years were further divided into seasons relevant to breeding mice in the Kananaskis Valley. The “nonbreeding” season consisted of October–February, inclusive. The “prebreeding” season was considered to be the spring directly preceding the breeding season and consisted of March. The “breeding” season consisted of April–August, inclusive. The “postbreeding” season followed the breeding season and consisted of September. Thus, a biological year began with the nonbreeding season (October) and ended with the postbreeding season (September). Winter population demographics for a given biological year (year  $x$ ) were calculated over all the biological seasons preceding the breeding season, and included the postbreeding season (year  $x - 1$ ), the nonbreeding season (year  $x - 1$  and year  $x$ ), and the prebreeding season (year  $x$ ). Summer population demographics were calculated over the breeding season (year  $x$ ). For example, winter population demographics for biological year 1993 were calculated over the postbreeding season of biological year 1992, the nonbreeding season of biological year 1993, and the prebreeding season of biological year 1993. Summer population demographics were calculated over the breeding season of biological year 1993.

Weather parameters were collected daily for the 11 years of the study. We used daily minimum temperature (°C), daily maximum temperature (°C), and daily precipitation (mm) to explain variation in population parameters (during summer and winter) over the study period. Winter precipitation values include both rainfall and snowfall, with the assumption that 10 mm of snow is equivalent to 1 mm of rain. For each season, we calculated a mean maximum temperature, a mean minimum temperature, and a mean precipitation from the daily data. To describe variability in weather among years, the coefficient of variation (CV) was used.

All variables were tested for normality using a Shapiro–Wilk normality test (Zar 1984). Although several demographic and weather variables were normally distributed, we examined relationships using nonparametric statistics for consistency and because of our relatively small sample size (11 years). Wilcoxon’s matched pairs tests or Spearman’s rank correlation analyses were used (Zar 1984). Statistical significance was assigned at  $\alpha = 0.05$  or at a Bonferroni corrected  $\alpha = 0.02$  where multiple correlations were performed. The cor-

**Table 1.** Number of over-wintered mice; number of mice born, weaned, and resident in late August; number of young-of-the-year breeding; and number of immigrant deer mice recorded on the Fortress and Grizzly grids in the Kananaskis Valley, Alberta, from 1987 to 1997.

Biological year	Over-wintered adults				Young-of-the-year								Total no. resident in August (I)					
	No. resident in May (A)		No. remaining in August (B)		No. of parturitions (C)		No. born <sup>a</sup> (D)		No. weaned (E)		No. remaining in August (F)		No. of parturitions (G)		Immigrants resident in August (H)			
	Fortress	Grizzly	Fortress	Grizzly	Fortress	Grizzly	Fortress	Grizzly	Fortress	Grizzly	Fortress	Grizzly	Fortress	Grizzly	Fortress	Grizzly		
1987	40	65	9	22	14	35	74	184	23	26	12	15	0	0	7	3	28	40
1988	23	44	7	14	13	22	68	116	30	47	23	27	0	0	7	15	37	56
1989	34	33	12	8	24	15	126	79	38	24	34	16	0	0	12	9	58	33
1990	36	28	11	7	14	15	74	79	26	29	20	22	0	1	4	11	35	40
1991	33	46	8	10	19	14	100	74	45	22	29	16	0	0	1	2	38	28
1992	37	41	1	10	21	32	110	168	22	36	2	20	0	0	3	11	6	41
1993	7	29	0	3	0	10	0	53	0	14	0	4	0	0	1	4	1	11
1994	7	33	2	13	2	21	11	110	7	57	5	34	1	2	0	12	7	59
1995	13	27	2	5	7	21	37	110	21	31	10	12	0	0	4	8	16	25
1996	11	21	5	4	9	10	47	53	20	29	12	19	0	3	3	5	20	28
1997	20	29	5	7	13	28	68	147	22	52	16	24	0	0	2	2	23	33

Note: Values are totals on each grid.

<sup>a</sup>Estimated as the number of parturitions × 5.25 (mean number of offspring for dams in this population; Millar and Innes 1983).

**Table 2.** Summer and winter population growth for deer mice on the Fortress and Grizzly grids in the Kananaskis Valley, Alberta, from 1987 to 1997.

Biological year	Summer population growth		Winter population growth	
	Fortress	Grizzly	Fortress	Grizzly
1987	-0.021	-0.029	na	na
1988	0.028	0.014	-0.006	0.003
1989	0.031	0.000	-0.002	-0.015
1990	-0.002	0.021	-0.015	-0.005
1991	0.008	-0.029	-0.002	0.004
1992	-0.107	0.000	-0.001	0.011
1993	-0.114	-0.057	0.004	-0.010
1994	0.000	0.034	0.056	0.031
1995	0.012	-0.005	0.018	-0.022
1996	0.035	0.017	-0.011	-0.005
1997	0.008	0.008	0.000	0.001

Note: Population growth is an instantaneous rate per week calculated over 17 weeks (early May to late August) for summer and over 35 weeks (early September to late April the following year) for winter: summer,  $r = (\ln \text{ total mice in fall} - \ln \text{ spring density})/17$ ; winter,  $r = [\ln \text{ total mice in spring of year } x - \ln \text{ total mice in fall of year } (x - 1)]/35$ .

rected  $\alpha = 0.02$  was determined as the most conservative  $\alpha$  level at which relatively high Spearman's coefficients of rank correlation ( $>0.70$ ) were significant, given the number of samples in this study. Data are presented as mean  $\pm$  1 SD.

## Results

### Population density and demography

Reflecting the difference in grid size, the number of mice in the spring was significantly higher on Grizzly ( $36.0 \pm 12.3$ ; Wilcoxon's matched pairs  $Z_{[11]} = 2.58, p < 0.01$ ) than on Fortress ( $23.7 \pm 12.8$ ; Table 1). Although not significant, the number of mice in the fall was greater on Grizzly ( $35.8 \pm 13.7$ ; Wilcoxon's matched pairs  $Z_{[11]} = 1.69, p < 0.1$ ) than on Fortress ( $24.5 \pm 17.0$ ; Table 1). The number of mice in the spring ranged from 21 to 65 on Grizzly and from 7 to 40 on Fortress, while the number of mice in the fall ranged from 11 to 59 on Grizzly and from 1 to 58 on Fortress (Table 1).

Summer population growth was negative on at least one grid in 6 of 11 years, although the pattern was not consistent between grids (Table 2). Both grids had negative summer population growth in 1987 and 1993; Fortress had negative summer population growth in 1990 and 1992, whereas Grizzly had negative summer population growth in 1991 and 1995. Positive population growth during the winter occurred on at least one grid in 7 of 10 years (all except 1989, 1990, and 1996; Table 2). There was no significant difference between grids in summer population growth (Wilcoxon's matched pairs  $Z_{[11]} = 0.36, p > 0.05$ ) or winter population growth (Wilcoxon's matched pairs  $Z_{[10]} = 0.66, p > 0.05$ ).

Patterns of reproduction, survival, and immigration are outlined in Tables 1 and 3. Winter immigration rates (Table 3) were higher on Grizzly ( $0.091 \pm 0.009$ ) than on Fortress ( $0.075 \pm 0.009$ ; Wilcoxon's matched pairs  $Z_{[10]} = 2.67, p < 0.05$ ). The number of individuals resident, born, weaned,

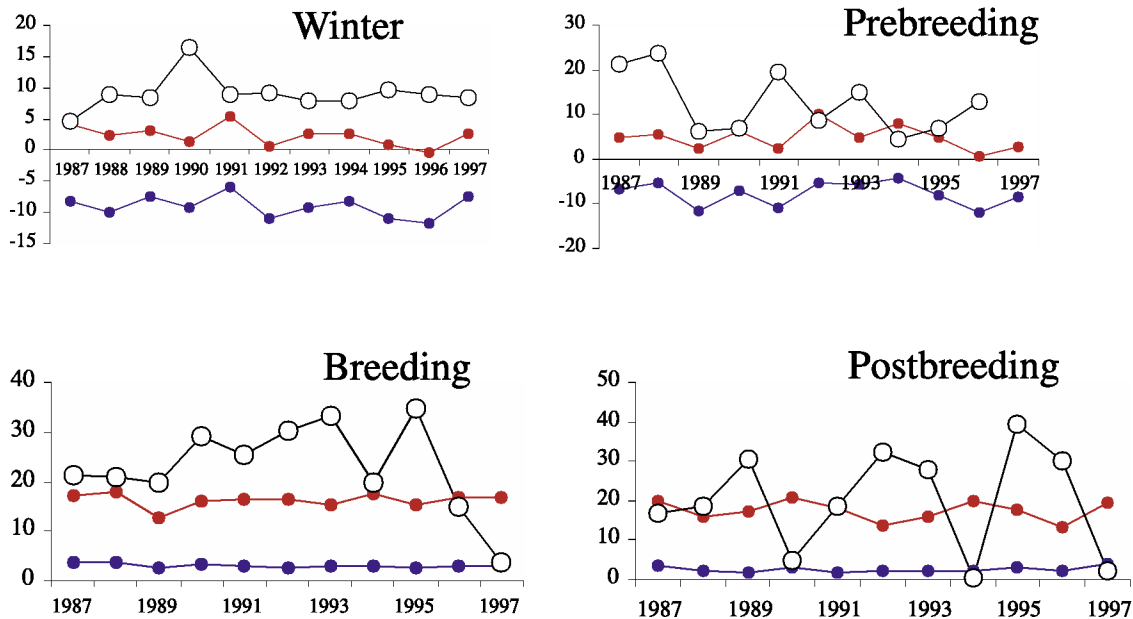
**Table 3.** Proportional demographic responses of deer mice on the Fortress and Grizzly grids in the Kananaskis Valley, Alberta, from 1987 to 1997, derived from values in Table 1.

Biological year	Over-wintered adults												Young-of-the-year						Summer immigrants relative to weaned young (E vs. H)	
	Winter survival (A vs. B*)		Winter immigration (A vs. B*)		Summer survival (A vs. B)		Per capita parturition (C/A)		Nestling survival (D vs. E)		Summer survival (E vs. F)		Per capita parturitions (G/E)		Fortress	Grizzly				
	Fortress	Grizzly	Fortress	Grizzly	Fortress	Grizzly	Fortress	Grizzly	Fortress	Grizzly	Fortress	Grizzly	Fortress	Grizzly						
1987	na	na	na	na	-0.09	-0.06	0.35	0.54	-0.39	-0.65	-0.08	-0.07	0.00	0.00	-0.15	-0.27				
1988	0.06	0.06	0.08	0.10	-0.07	-0.07	0.57	0.50	-0.27	-0.30	-0.03	-0.07	0.00	0.00	-0.18	-0.14				
1989	0.08	0.06	0.08	0.09	-0.06	-0.08	0.71	0.45	-0.40	-0.40	-0.01	-0.05	0.00	0.00	-0.14	-0.12				
1990	0.07	0.05	0.09	0.09	-0.07	-0.08	0.39	0.54	-0.35	-0.33	-0.03	-0.03	0.00	0.03	-0.23	-0.12				
1991	0.08	0.08	0.08	0.10	-0.08	-0.09	0.58	0.30	-0.27	-0.40	-0.05	-0.04	0.00	0.00	-0.48	-0.30				
1992	0.09	0.07	0.08	0.10	-0.21	-0.08	0.57	0.78	-0.54	-0.51	-0.30	-0.07	0.00	0.00	-0.25	-0.15				
1993	0.00	0.03	0.06	0.09	-0.12	-0.13	0.00	0.34	0.00	-0.44	0.00	-0.16	n/a	0.00	n/a	-0.16				
1994	0.00	0.00	0.08	0.10	-0.07	-0.05	0.29	0.64	-0.14	-0.22	-0.04	-0.06	0.14	0.04	n/a	-0.19				
1995	0.03	0.07	0.07	0.08	-0.11	-0.10	0.54	0.78	-0.19	-0.42	-0.09	-0.12	0.00	0.00	-0.21	-0.17				
1996	0.02	0.02	0.06	0.08	-0.05	-0.10	0.82	0.48	-0.29	-0.20	-0.06	-0.05	0.00	0.10	-0.24	-0.22				
1997	0.06	0.07	0.07	0.08	-0.08	-0.08	0.65	0.97	-0.38	-0.35	-0.04	-0.10	0.00	0.00	-0.30	-0.41				

**Note:** Letters are as in Table 1 headings. The instantaneous weekly rate of winter immigration is calculated as  $(\ln \text{winter immigrants})/35$ , where winter immigrants are considered to be [total mice in spring of year  $x$  - total mice in fall of year  $(x - 1)$ ]. Survival is an instantaneous survival rate per week calculated over 35 weeks for winter survival, over 17 weeks (prebreeding to fall) for summer survival of over-wintered adults, over 3 weeks (birth to weaning) for nestlings, and over 8 weeks (weaning to fall) for weaned young of the year. Summer immigration rates were calculated relative to the number of weaned young over 8 weeks. Because no over-wintered adults remained on Fortress in the fall of 1993, a constant (1) was added to the number of over-wintered residents both in May and in August, to calculate over-wintered adult survival; this was also done to calculate survival for nestlings and young of year.

\*Refers to the previous biological year.

**Fig. 1.** Patterns of precipitation (○), maximum temperatures (top ●), and minimum temperatures (bottom ●) in the winter, prebreeding, and breeding seasons on the Fortress and Grizzly grids in the Kananaskis Valley, Alberta, during the 11 years studied (1987–1997). In all cases, values on the y axis indicate millimetres or degrees centigrade for precipitation or temperature, respectively.



and immigrant in summer was generally higher on Grizzly than on Fortress during the study period, although there was a trend during some years (particularly 1989) for the number of mice resident, born, weaned, and immigrant in summer to be higher on Fortress than on Grizzly.

### Weather

Maximum and minimum ambient temperatures ( $T_{\max}$  and  $T_{\min}$ , respectively) were correlated during the winter (Spearman's  $R = 0.89, p < 0.01$ ), prebreeding (Spearman's  $R = 0.86, p < 0.01$ ), and breeding (Spearman's  $R = 0.65, p < 0.05$ ) seasons, but not during the postbreeding season (Spearman's  $R = 0.46, p > 0.05$ ).  $T_{\max}$  and precipitation (Ppt) were not correlated during the prebreeding (Spearman's  $R = -0.27, p < 0.05$ ) or breeding (Spearman's  $R = -0.45, p > 0.05$ ) seasons, but were correlated during the winter (Spearman's  $R = -0.65, p < 0.05$ ) and postbreeding (Spearman's  $R = -0.74, p < 0.01$ ) seasons.  $T_{\min}$  and Ppt were not correlated during the winter (Spearman's  $R = -0.49, p > 0.05$ ), prebreeding (Spearman's  $R = -0.04, p > 0.05$ ), breeding (Spearman's  $R = 0.0, p > 0.05$ ), or postbreeding (Spearman's  $R = -0.34, p > 0.05$ ) seasons.

There was variation ( $CV_{T_{\max}} = 0.72$ ) in temperature during the winter, with 1991 being relatively warm ( $T_{\max} = 5.4^{\circ}\text{C}$ ) and 1996 being the coldest ( $T_{\max} = -0.46$ ) (Fig. 1). Ambient temperatures during the prebreeding season were variable ( $CV_{T_{\max}} = 0.58$ ) among years, with 1992 and 1994 being warm relative to the other years (Fig. 1). With the exception of a slightly cool 1989, breeding season temperatures varied little ( $CV_{T_{\max}} = 0.09$ ;  $CV_{T_{\min}} = 0.12$ ) among years (Fig. 1). Ppt was variable over the years in all seasons (Fig. 1). During the 11 years, there were both wet and dry prebreeding seasons ( $CV = 0.55$ ), with 1989, 1990, and 1994 having relatively little Ppt. The breeding seasons ( $CV = 0.39$ ) of 1990–1993 and 1995 were wet relative to breeding seasons in other years.

### Explanation of summer population growth

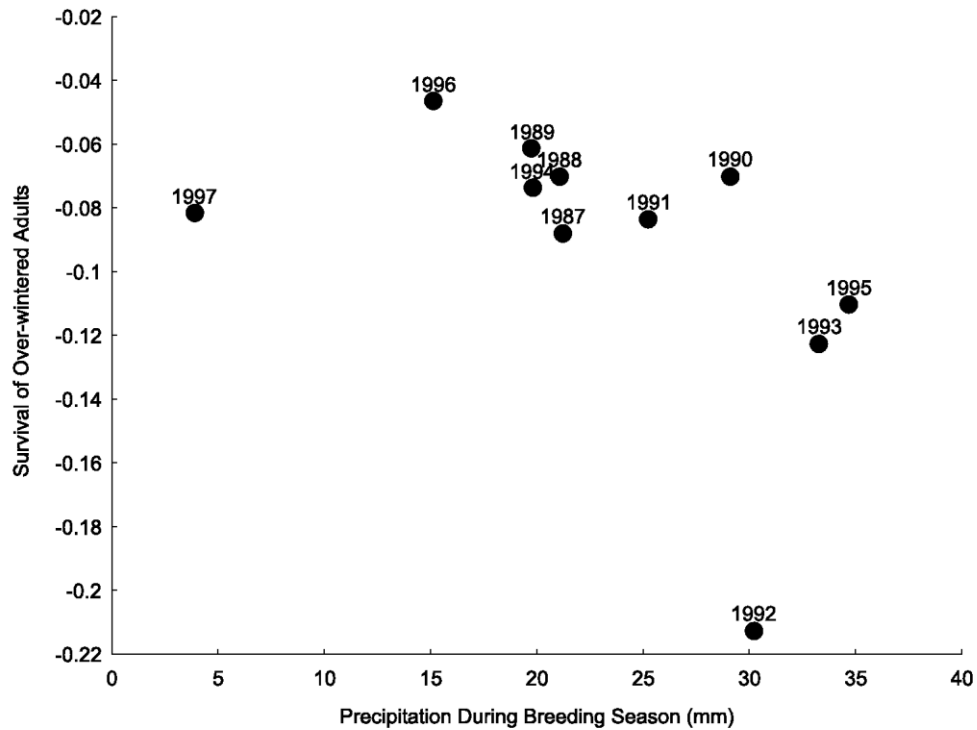
#### Demographics

Summer population growth was not related to the population growth in the winter preceding the breeding season on either Fortress (Spearman's  $R = -0.46, p > 0.05, N = 10$ ) or Grizzly (Spearman's  $R = 0.13, p > 0.05, N = 10$ ). Furthermore, summer population growth was unrelated to spring population density on Fortress (Spearman's  $R = -0.18, p > 0.05, N = 11$ ) and Grizzly (Spearman's  $R = -0.34, p > 0.05, N = 11$ ). To explain variation in summer population growth using demographic parameters, we first assessed summer population growth in relation to each demographic variable and the interrelationship among demographic variables. On Fortress, summer population growth was positively related to the survival of over-wintered adults (Spearman's  $R = 0.71, p < 0.02$ ) and the number of parturitions by over-wintered adults (Spearman's  $R = 0.72, p < 0.02$ ). On Grizzly, summer population growth was positively related to nestling survival (Spearman's  $R = 0.82, p < 0.02$ ). Among the demographic variables used to explain summer population growth, there were no correlations.

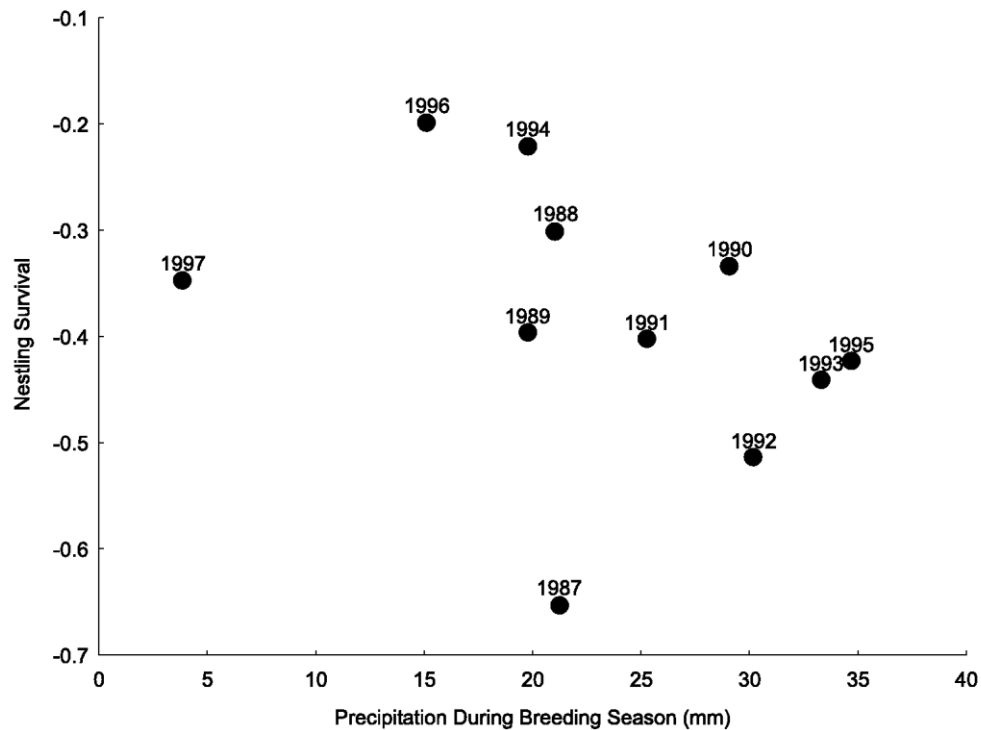
#### Weather

In our analyses, we only included weather parameters in the winter, prebreeding, and breeding seasons, because postbreeding season weather should not affect summer population growth or its correlates (over-wintered adult survival and parturitions). We considered Ppt and  $T_{\max}$  as independent parameters that could influence summer population growth or its correlates, because  $T_{\min}$  and  $T_{\max}$  were correlated in the winter, prebreeding, and breeding seasons. To explain variation in summer population growth using weather parameters, we assessed each weather variable in relation to summer population growth and its demographic correlates. Summer population growth was not related to Ppt or  $T_{\max}$ .

**Fig. 2.** Negative relationship between over-wintered adult survival and precipitation during the breeding season over 11 years (1987–1997) on the Fortress grid in the Kananaskis Valley, Alberta (Spearman’s  $R = -0.70$ ,  $p = 0.016$ ). The year is indicated above each data point.



**Fig. 3.** Negative relationship between nestling survival and precipitation during the breeding season over 11 years (1987–1997) on the Grizzly grid in the Kananaskis Valley, Alberta (Spearman’s  $R = -0.61$ ,  $p < 0.05$ ). The year is indicated above each data point.



on either Fortress or Grizzly. Of the demographic correlates of summer population growth on Fortress (over-wintered adult survival and parturition rate), only over-wintered adult survival was related to Ppt. Over-wintered adult survival on Fortress was negatively influenced by Ppt in the breeding

season (Spearman’s  $R = -0.70$ ,  $p < 0.02$ ; Fig. 2). The demographic correlate of summer population growth on Grizzly (nestling survival) was related to Ppt. Nestling survival was negatively correlated with Ppt in the breeding season (Spearman’s  $R = -0.70$ ,  $p < 0.02$ ; Fig. 3).

## Explanation of winter population growth

### Demographics

On Grizzly, winter population growth was not significantly related to any demographic characteristics, however there was a trend for winter population growth to be negatively correlated with the fall population density of the preceding biological year (Spearman's  $R = -0.70$ ,  $p < 0.05$ ) and positively related to winter immigration (Spearman's  $R = 0.69$ ,  $p < 0.05$ ). On Grizzly, there was also a positive trend between summer growth and the fall population density of the preceding biological year (Spearman's  $R = 0.66$ ,  $p < 0.05$ ). On Fortress, winter population growth was unrelated to demographic variables, although there was a trend for a negative relationship between winter population growth and the fall population density of the preceding biological year (Spearman's  $R = -0.69$ ,  $p < 0.05$ ). On Fortress, there were also strong correlations between the fall population density of the preceding biological year and winter immigration (Spearman's  $R = 0.97$ ,  $p < 0.001$ ) and survival (Spearman's  $R = 0.91$ ,  $p < 0.001$ ), as well as winter survival and immigration (Spearman's  $R = 0.91$ ,  $p < 0.001$ ).

### Weather

In our analyses, we only included the weather parameters of the previous year's postbreeding (autumn) and nonbreeding (winter) seasons, because the weather during the prebreeding and breeding seasons should not affect winter population growth. As with the summer population growth analysis, we considered only Ppt and temperature to be independent parameters that could influence winter population growth. However, because  $T_{\min}$  and  $T_{\max}$  were not correlated in the postbreeding season, we considered  $T_{\min}$  and  $T_{\max}$ , as well as Ppt during the postbreeding season, to be independent parameters that could influence winter population growth. On Fortress and Grizzly, winter population growth was not related to weather conditions during the winter or the autumn preceding the winter. Demographic correlates of winter population growth on Fortress and Grizzly were not related to weather conditions during the winter or the autumn preceding the winter. There was a trend on Grizzly for winter survival to be negatively related to Ppt in the autumn preceding the winter (Spearman's  $R = 0.69$ ,  $p < 0.05$ ).

## Discussion

The summer population dynamics and demography of these two populations, which represent a subset of data used in a broader study (Millar and McAdam 2001), were slightly different from the average for the Kananaskis Valley as a whole. While average summer population growth was influenced primarily by nest mortality over the long term (Millar and McAdam 2001), on Fortress, summer population growth was significantly related to the survival of over-wintered adults and the number of parturitions, whereas on Grizzly, summer population growth was significantly related to nestling survival. In this study, both populations showed sufficient similarities in their seasonal patterns to suggest that some valley-wide phenomenon governs their dynamics in some years. For example, both populations showed no or negative summer population growth in 1987, 1992, and 1993, and both

showed positive population growth in 1988, 1996, and 1997. Similarly, both populations declined over winter, as expected, during a nonbreeding (winter) season in 1989, 1990, and 1996, while both populations increased through immigration during the winter season of 1994. The demographic basis for these seasonal patterns is clear. Summer population growth of both populations was influenced by survival (of either adults or nestlings) during the breeding season. There was a trend on Fortress and Grizzly for winter population growth to be negatively related to fall population density. The general pattern that emerges is one wherein a high level of summer survival (and associated reproductive success) leads to a relatively high fall population density, which then leads to a relatively low level of survival over the winter. This general pattern suggests density-dependent effects on demographics.

Patterns of Ppt and temperature were variable among years, but none of the population or demographic patterns were clearly or consistently related to these variables. Our main significant relationships with the weather were adult survival on Fortress and nestling survival on Grizzly during the breeding season, whereby survival was low in years with high Ppt. The general lack of relationships between the weather and population and demographic patterns was unexpected, because weather is known to constrain seasonal breeding in these populations (Millar and Gyug 1981; Sharpe and Millar 1991), influence sex-specific mortality in successful litters (Havelka and Millar 1997), and influence body condition (Millar and Schieck 1986). These relatively clear effects of weather on reproduction, survival, and physiology do not appear to have strong effects at the population level, perhaps for a variety of reasons. First, small mammals are known to respond behaviorally and physiologically to environmental circumstances by either reducing energy expenditure and (or) increasing cold tolerance (Wunder 1984; Hill 1992). Physiological tolerances and behavioral responses are likely broader than the "normal" variation in weather experienced by these mice. Compensatory mechanisms such as reduced activity and torpor may preclude "extreme" weather having a negative impact on survival or reproduction. Evidence for this in this study can be seen in the demographic responses to extreme conditions. For example, June is a critical month for reproduction, because first litters of the season are nestlings at that time, but extreme weather in June had little impact on demography or population growth. The lowest average daily  $T_{\min}$  ( $3.7^{\circ}\text{C}$ ) was in 1991, but both summer population growth (Table 2) and survival (Table 3) were intermediate in that year. The highest average daily  $T_{\min}$  ( $5.9^{\circ}\text{C}$ ) was in 1987, when summer population growth was negative but not extreme. Similarly, neither high average daily Ppt (57.7 mm in 1992) nor low average daily Ppt (6.1 mm in 1997) was associated with extremes in demography or summer population growth. In winter, the highest population growth was recorded in 1994, but the highest average daily temperature ( $-3.9^{\circ}\text{C}$ ) was in February 1991 and the highest average daily Ppt (23.8 mm) was in 1997. The coldest winter month ( $-20.4^{\circ}\text{C}$ ) was January 1996 and the lowest winter Ppt (0.6 mm) occurred in February 1992, but the greatest winter declines (1990 on Fortress and 1995 on Grizzly) did not occur in these years. Clearly, mice have compensatory mechanisms to deal with extreme weather conditions; perhaps weather impacts populations only when extreme conditions persist long

enough to have an effect on other resources, such as available food, water, or shelter.

Alternatively, the scale at which weather was measured may have been too broad to reveal negative consequences of weather on reproduction and survival. For example, Ppt included both rain and snowfall, but snow cover may be more important to the dynamics of these populations than total Ppt, rain, or snowfall, as has been shown for other northern rodents (Scott 1993; Reid and Krebs 1996). In addition, the effects of weather on demography may be very short term (0–2 months; Lewellen and Vessey 1998) and the seasonal averages used here may have masked short-term effects. Third, local effects may be more important than global effects in the dynamics of these populations, and we have some evidence that this may be true. While the two populations showed similar summer population growth in 6 years and similar winter population growth in 4 years, the remaining years were dissimilar between grids. Local conditions appear to be important to the dynamics of these populations. If so, detailed local studies will be needed to identify the underlying causes.

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