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POPULATION DYNAMICS OF A DIVERSE RODENT ASSEMBLAGE IN MIXED GRASS-SHRUB HABITAT, SOUTHEASTERN COLORADO, 1995–2000

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ABSTRACT: We followed seasonal and year-to-year population dynamics for a diverse rodent assemblage in a short-grass prairie ecosystem in southeastern Colorado (USA) for 6 yr. We captured 2,798 individual rodents (range, one to 812 individuals per species) belonging to 19 species. The two most common species, deer mice (*Peromyscus maniculatus*) and western harvest mice (*Reithrodontomys megalotis*), generally had population peaks in winter and nadirs in summer; several other murid species demonstrated autumn peaks and spring nadirs; heteromyids were infrequently captured in winter, and populations generally peaked in summer or autumn. Interannual trends indicated an interactive effect between temperature and precipitation. Conditions associated with low rodent populations or population declines were high precipitation during cold periods (autumn and winter) and low precipitation during warm periods (spring and summer). Severity of adverse effects varied by species. Heteromyids, for example, were apparently not negatively affected by the hot, dry spring and summer of 2000. Cross-correlations for the temporal series of relative population abundances between species pairs (which are affected by both seasonal and interannual population dynamics) revealed positive associations among most murids and among most heteromyids, but there were negative associations between murids and heteromyids. These results have important implications for those attempting to model population dynamics of rodent populations for purposes of predicting disease risk.

Key words: Abiotic environment, Colorado, grass-shrub habitat, population dynamics, rainfall, rodents, temperature.

INTRODUCTION

In 1993, the first cases of hantavirus pulmonary syndrome were diagnosed in humans in New Mexico, Arizona, and Colorado (USA) (Nichol et al., 1993). The principal vertebrate host of the novel etiologic agent of this disease, Sin Nombre virus (SNV; family *Bunyaviridae,* genus *Hantavirus*), has been identified as the deer mouse (*Peromyscus maniculatus*) (Childs et al., 1994). Subsequent intensive surveys of wild rodent populations in the Americas have shown that there are many hantaviruses, each associated with an essentially specific rodent host in a long-term, perhaps co-evolutionary relationship (Morzunov et al., 1998).

If we are to understand the dynamics of rodent-borne virus infections and their relationships with short- and long-term meteorologic events, it is necessary to conduct long-term, prospective monitoring of multiple rodent populations and the hantaviruses they harbor. We undertook such studies by establishing sites at three ecologically diverse locations, two in western Colorado and one in southeastern Colorado; an interim summary of results at two sites in western Colorado (on the western slope of the Rocky Mountains) has been published (Calisher et al., 1999). The habitat types of the western slope sites are montane shrubland and semidesert shrubland, respectively. The third study area, located in southeastern Colorado, is ecologically distinct from the western slope sites, and the rodent assemblage there is more diverse. A primary goal of our long-term studies is to develop predictive models of risk of human hantavirus disease. Such models will require an understanding of temporal changes in the abundance of hantavirus host species and their competitors and the influence of environmental factors on rodent population dynamics. Abiotic factors, including temperature and precipitation, are hypothesized to form the first tier of a trophic cascade that supports host populations (Yates et al., 2002). This article provides an overview of the dynamics of rodent populations in southeastern Colorado between 1995 and 2000 and their association with abiotic environmental factors. In a companion article (Calisher et al., 2005), we relate these changes in host abundance to changes in prevalence of infection with hantaviruses.

Although our longitudinal studies were designed principally to study the population dynamics of the deer mouse, the reservoir of SNV, several species in the rodent assemblage at the Pinyon Canyon Maneuver Site (PCMS) are hosts for other hantaviruses. The white-footed mouse (*Peromyscus leucopus*) is host for New York-1 (Hjelle et al., 1995) and Blue River (Morzunov et al., 1998) viruses; the brush mouse (*Peromyscus boylii*) hosts Limestone Canyon virus (Sanchez et al., 2001); the western harvest mouse (*Reithrodontomys megalotis*) hosts El Moro Canyon virus (Hjelle et al., 1994); the hispid cotton rat (*Sigmodon hispidus*) hosts Black Creek Canal (Rollin et al., 1995) and Muleshoe (Rawlings et al., 1996) viruses; and the meadow vole (*Microtus pennsylvanicus*) hosts Prospect Hill virus (Lee et al., 1982). The pinyon mouse (*Peromyscus truei*) often has antibody to a hantavirus and may host an undescribed hantavirus, or it simply may be subject to frequent spillover infection from other host species (Calisher et al., 2005). Finally, the white-throated woodrat (*Neotoma albigula*) hosts an arenavirus, Whitewater Arroyo virus (Fulhorst et al., 1996; Calisher et al., 2001a). Thus, the population dynamics of all these species are of interest to disease ecologists. Secondly, the ecology of any one species is best understood in the context of the community of which it forms a part. Therefore, we present data on population dynamics of all the principal members of the rodent assemblage at our study site.

MATERIALS AND METHODS

The PCMS, Las Animas County, southeastern Colorado, comprising more than 1,040 km^2, was acquired by the US Department of the Army in 1983 and is under the management of Directorate of Environmental Compliance and Management, Fort Carson, Colorado (USA). Prior to this acquisition, the area had been grazed by domesticated and wild ungulates and had supported small populations of humans since the late 1870s. The climate is dry continental, and elevations range from 1,300 to 1,700 m (US Department of the Army, 1980; Andersen et al., 1989; Shaw et al., 1989). Topography consists of broad, moderately sloping uplands; vegetation is dominated by short-grass prairie but includes pinyon pine (*Pinus edulis*)–one-seeded juniper (*Juniperus monosperma*) woodland (Costello, 1954).

After initial rodent sampling of numerous sites, we selected three for longitudinal studies: 1) Pinyon Juniper (PJ2; 37°33.014′N, 103°59.549′W, altitude 1,676 m), on three sides a hilly pinyon pine-juniper woodland site with surface limestone and extending on the fourth side into short-grass prairie; 2) Mouth of Red Rock Canyon (MRC; 37°32.759′N, 103°49.352′W, altitude 1,493 m), a meadow with grasses and forbs and with a permanent water source; and 3) Red Rock Canyon (RRC: 37°32.169′N, 103°49.105′W, altitude 1,463 m), a site near MRC, within a shallow canyon. At PJ2 and MRC, webs, each consisting of 145 traps arranged along 12 lines radiating from the center, were established as described (Mills et al., 1999) using 7.6×8.9×22.9 cm Sherman live-traps. Because of lack of sufficient space within the canyon to establish a web at the RRC site, a grid consisting of three parallel trap lines, each 240 m long, was installed. Trap stations were 10 m apart, with 25 traps per line; trap lines were approximately 50 m apart.

The PJ2 site is at Big Arroyo Hills, also known as Bear Spring Hills. This area is typical of shallow limestone breaks. Other than rare flooding from snowmelt, there is no water source at this site. The MRC site is a relatively flat, open plot with a creek flowing from a pond formed by a natural spring at the west side and running approximately southeast, forming a

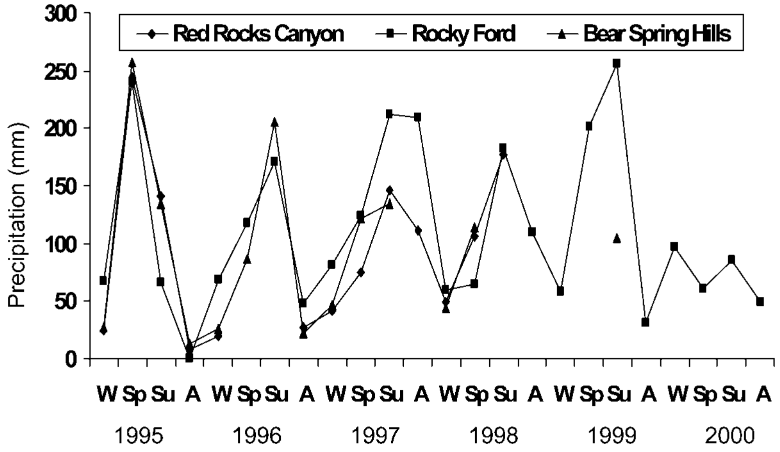

FIGURE 1. Quarterly precipitation as recorded at three weather stations near Pinyon Canyon Maneuver Site, southeastern Colorado, 1995–2000.

marshy area for approximately 100 m from the outlet of the pond. The remains of a homestead are near the center of the web. The east side of the plot, which extends from the mesa above as a rocky hillside, ultimately becomes a field with sparse grasses and forbs. The RRC site, which is about 1.6 km south of MRC, is a rocky slope on the north side, flat in the center, and partly flat and partly rocky slope on the south side. The creek running through it usually is a dry bed.

In this area, skies are cloudless or contain only a few clouds >300 days each year, and the microenvironment can be warm even when the air temperature is low. Data for all daily temperatures and amounts of precipitation were available for the period 1951 to 2000 for the Rocky Ford weather station (Colorado State University, Fort Collins, Colorado, USA), approximately 55 km from MRC. Although some data were available from a station at Bear Spring Hills, which is approximately 20 km from the MRC site, and from another site at RRC, adjacent to the MRC site, these data were incomplete and were used only for comparison to Rocky Ford data.

Rodents were trapped under license from the Division of Wildlife, Colorado Department of Natural Resources. Collection of rodents and safety procedures followed were those recommended by the Centers for Disease Control and Prevention (Mills et al., 1995; Calisher et al., 1999). Except for January 1996 (two nights), trapping was done for three nights approximately every 6 wk between January 1995 and November 2000, depending on weather and site conditions; we terminated regular trapping efforts at the PJ2 site after June 1998 because of logistical considerations. For other logistical reasons and because we did not begin efforts each year on the same date, trapping effort (numbers of trap nights) was not equal among years.

Rodents were lightly anesthetized by gently shaking them from the trap into a plastic Ziplock bag containing two tea strainers holding gauze pads soaked in methoxyflurane or isoflurane. Animals were examined and species, gender, reproductive condition, weight, standard measurements, and the presence of any scars or ectoparasites were recorded. A sequentially numbered stainless-steel tag (National Band and Tag Co., Newport, Kentucky, USA) was inserted into the cartilage of an ear of each animal, and an approximately 0.2-ml blood sample was taken from the retro-orbital plexus. The animal was then released at the exact location at which it had been collected.

As a measure of relative abundance, trap success was calculated as the number of individuals captured per 100 trap nights. Trap nights were the number of traps set multiplied by the number of nights they were left. Data were analyzed using SPSS (Norusis, 1993) and SAS (SAS Institute, Inc., 2000).

RESULTS

Environmental factors

Available data during the study period (Fig. 1) indicate that, although absolute values often differed, the temporal pattern of precipitation at RRC was similar to that at Rocky Ford (Pearson correlation coefficient, $r=0.81$, $P=0.001$) and almost identical to that at Bear Spring Hills ($r=0.9979$, $P<0.0001$). There are no temperature data for RRC, but the patterns of monthly mean minimum and mean maximum temperatures for Rocky Ford and Bear Spring Hills were nearly identical ($r=0.99$, $P<0.0001$ for both comparisons; data not shown). Temperatures at Rocky Ford varied seasonally. Winters (January–March) were cold (mean minimum and mean maximum temperatures were −7.1 C and 11.9 C, respectively); summers (July–September) were hot (12.9 C, 32.2 C); springs (April–June) were warm (7.3 C, 26.5 C); and autumns (October–December) were quite cool (−4.1 C, 15.2 C). Analysis of the deviations of the mean temperature values from the 50-yr (1951–2000) mean (Fig. 2) indicates that overall temperatures during the study period were generally warmer than in previous years. There were 16 quarters during which the mean maximum temperature was warmer than the 50-yr quarterly mean temperatures and eight quarters during which this value was less than the 50-yr mean. There were five quarters during which the deviation was greater than or equal to two standard deviations from the mean (three greater and two lower; Fig. 2A). Seventeen quarters had mean minimum temperatures greater than the 50-yr average, compared to seven quarters during which the mean minimum temperature was lower than the average. Two quarters had mean minimum temperatures greater than or equal to two standard deviations above the mean (Fig. 2B).

For the 50-yr period from 1951 to 2000, total annual precipitation at Rocky Ford ranged from about 156 mm (1964) to 507 mm (1999), with the greatest precipitation occurring from May to August of each year. During the period from 1995 to 2000, annual precipitation totals were 321, 340, 463, 371, 507, and 244 mm, respectively, with a mean of 374 mm. Taken on a quarterly basis for 1951–2000, a mean of 34 mm of precipitation occurred in the January–March periods, 108 mm in April–June, 115 mm in July–September, and 39 mm in October–December.

We compared precipitation each quarter from 1995 to 2000 with mean average quarterly precipitation from 1951–2000. Differences from the 1951–2000 means were more than two standard deviations greater than the 50-yr mean during five quarters (Fig. 2C).

Unusually high precipitation during a cold period (fall or winter) occurred during two quarters, autumn 1997 and winter 2000. Only during autumn 1997, however, were temperatures significantly colder than the average for that quarter. Prolonged drought during warm weather (spring and summer) occurred during a single period, spring and summer 2000, which coincided with maximum temperatures that averaged 2–3 C above normal. Rainfall during this period was 63% of normal. Only four other spring-summer periods during the 50-yr history had less rainfall.

Trapping summary

We accumulated 36,195 trap nights: 9,715 at PJ2, 17,255 at MRC, and 9,225 at RRC. In all, 6,155 captures of rodents were recorded from January 1995 to November 2000 (Table 1). Of these, 3,788 (61.5%) were of the genus *Peromyscus,* 2,174 (35.3% of all captures) of which were deer mice. An additional 884 (14.4% of all captures) were western harvest mice. The remaining 1,483 (24.1% of all captures) belonged to nine genera and 13 species.

Seasonal population dynamics

Except for hispid cotton rats, populations of all frequently captured species fluctuated similarly at MRC and RRC. Therefore, these sites were combined for displaying population dynamics for all species except cotton rats (Figs. 3–5). Because of its early termination and low numbers of captures, PJ2 was omitted from the figures.

Muridae, Sigmodontinae: Relative abundance of deer mice, as indicated by trap success, generally peaked during au-

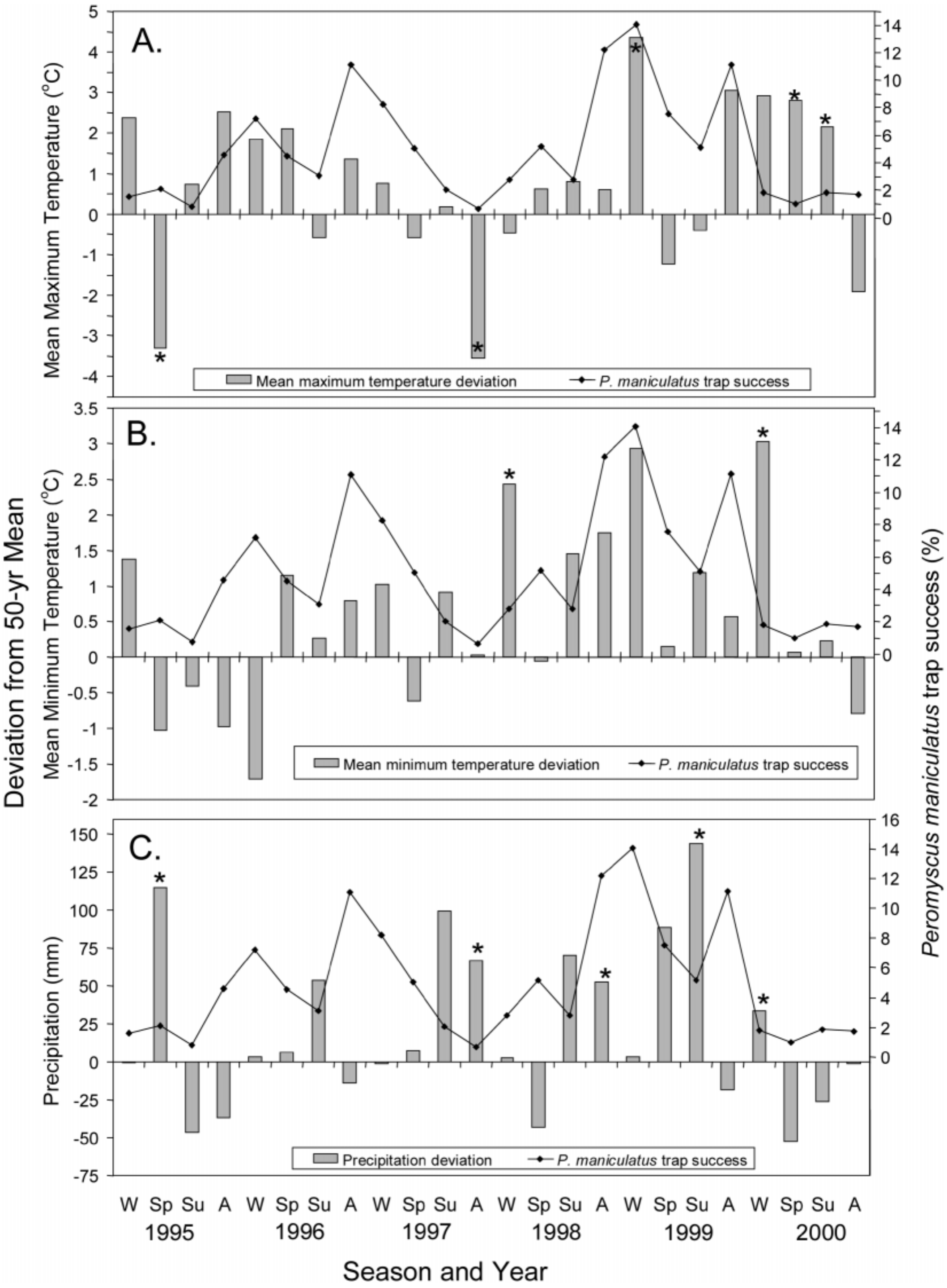

FIGURE 2. Deviations from the 50-yr mean (1951–2000) for quarterly mean maximum (A) and mean minimum (B) temperatures and quarterly precipitation (C) at Rocky Ford weather station (Colorado State University, Fort Collins, Colorado, USA). Asterisks indicate deviations that are at least two standard deviations from the 50-yr mean. The line shows quarterly trap success (number of individuals captured per 100 trap nights) for deer mice (*Peromyscus maniculatus*).

TABLE 1. Total captures of rodents belonging to 11 genera and 19 species at Pinyon Canyon Maneuver Site, southeastern Colorado, January 1995–November 2000, by site and number of individuals.

Species	Total captures	Total individuals captured[a]			
		MRC	RRC	PJ2	Total
Peromyscus maniculatus	2,174	294	478	47	819
Peromyscus truei	1,166	94	186	145	425
Reithrodontomys megalotis	884	343	117	60	520
Sigmodon hispidus	393	121	129	0	250
Neotoma albigula	340	74	70	20	164
Peromyscus leucopus	274	23	67	2	92
Perognathus flavus	249	80	37	93	210
Dipodomys ordii	184	60	22	1	83
Peromyscus nasutus	157	2	57	0	59
Onychomys leucogaster	156	49	14	5	68
Chaetodipus hispidus	64	29	15	0	44
Neotoma mexicana	39	0	25	2	27
Tamias quadrivittatus	20	0	17	0	17
Peromyscus boylii	17	1	2	0	3
Neotoma micropus	15	2	6	3	11
Microtus pennsylvanicus	11	8	0	3	11
Tamias minimus	6	0	6	0	6
Spermophilus variegatus	5	0	5	0	5
Microtus mexicanus	1	1	0	0	1
Total	6,155	1,181	1,253	381	2,815

[a] MRC = Mouth of Red Rock Canyon; RRC = Red Rock Canyon; PJ2 = Pinyon Juniper.

tumn (October–December) or winter (January–March), decreased during spring (April–June) to a trough in summer (July–September), before increasing again in autumn (Fig. 3A). Exceptions were observed during autumn 1997 and winter 2000, when populations crashed (Fig. 3A). Similar effects were seen for most rodent species at our study sites. A third exception to the general pattern was that the usual population increase did not occur in autumn 2000, following the hot, dry spring-summer period.

Population abundance for western harvest mice (Fig. 4A) was similar to that described for deer mice, except that the western harvest mice had high relative abundances in summer 1997 and a period of near-zero population levels followed by slow recovery in summer 1998 to winter 1999.

Seasonal population dynamics for other *Peromyscus* species appeared somewhat distinct. Highest relative abundances of white-footed mice most often occurred in autumn (Fig. 5A), with lows in the spring. Exceptions were again noted with the almost universal population crashes in autumn 1997 and winter 2000. The pattern for pinyon mice was generally similar to that of white-footed mice, except for the relatively high trap success in spring 1995 and spring 1998 and the fact that the peak density in 1998 was delayed from fall to winter.

Northern grasshopper mice (*Onychomys leucogaster*) were captured at all three sites but were never abundant (specific trap success never exceeded 1%; Fig. 5A). Their populations also often demonstrated autumn peaks and spring lows, but decreased to zero captures in the summer 1998–spring 1999 period. Grasshopper mice did not seem to be adversely affected by the cold, wet autumn of 1997.

Because the patterns of occurrence of hispid cotton rats differed at MRC and RRC, trap success rates for the two sites are shown separately (Fig. 5B). Relative abundances at the two sites were generally

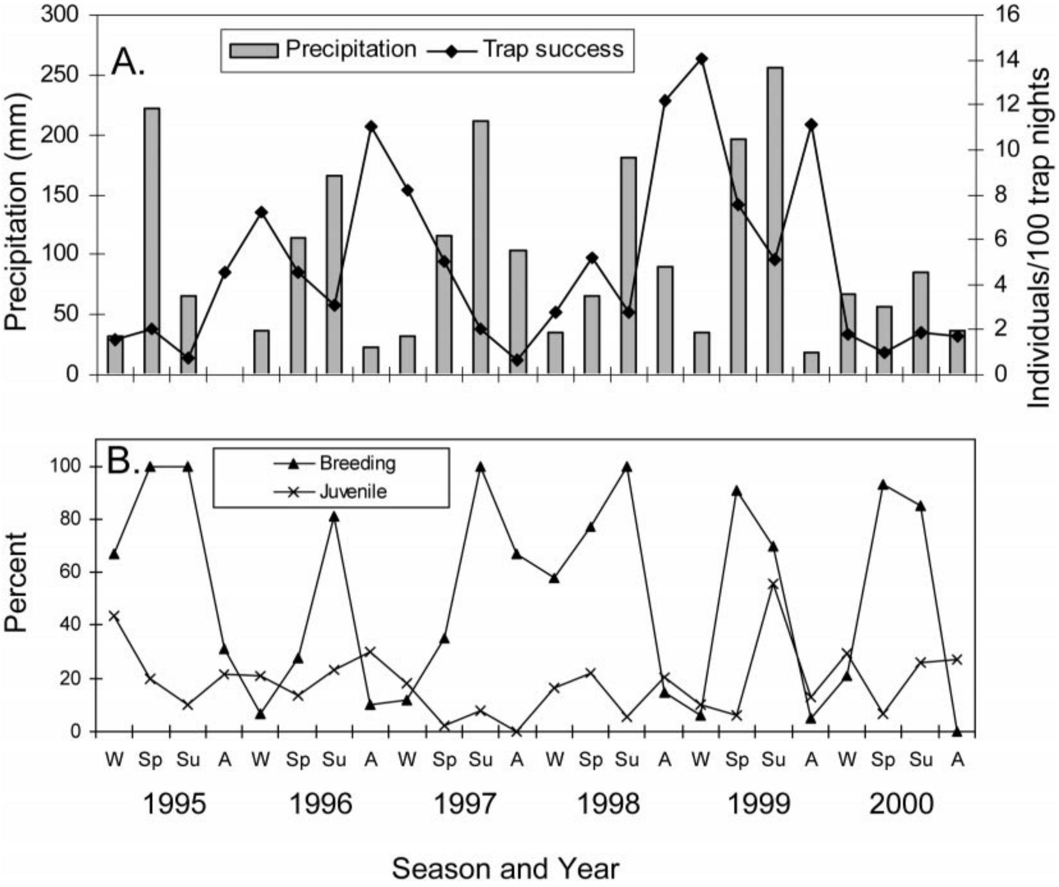

FIGURE 3. Quarterly trap success for deer mice (*Peromyscus maniculatus*) and total quarterly precipitation (A); percent of adults in reproductive condition and percent of captures consisting of juveniles (B), at two mark-recapture sites in southeastern Colorado, 1995–2000.

coincident, peaking in summer–fall, except that the sharp increase in relative abundance at RRC for the summer–fall 1999 period did not occur at MRC.

Of three species of woodrats captured (Table 1), only white-throated woodrats were captured in sufficient numbers to provide meaningful temporal analysis. The seasonal pattern was consistent each year, with relative abundance peaking in summer and lowest in winter (Fig. 5B).

Heteromyidae: Despite the much lower effort at PJ2, silky pocket mice (*Perognathus flavus*) were more common at that site than at MRC or RRC (Table 1). Hispid pocket mice (*Chaetodipus hispidus*) and Ord's kangaroo rats (*Dipodomys ordii*) were captured almost exclusively at MRC and RRC. Because of the consistently low relative abundances for the three heteromyid species (rarely exceeding 1% specific trap success), seasonal trends were not clear. The decreased heteromyid trap success in winter (Fig. 5C) may represent the entrance of these individuals into seasonal torpor rather than any decline in relative abundance.

Muridae, Arvicolinae: The few captured meadow voles and the Mexican vole (*Microtus mexicanus*) at MRC and PJ2 (Table 1) represent the first reports of these species at PCMS.

Sciuridae: We captured five rock squirrels (*Spermophilus variegatus*), all at RRC. Likewise, Colorado chipmunks (*Tamias quadrivittatus*) and least chip-

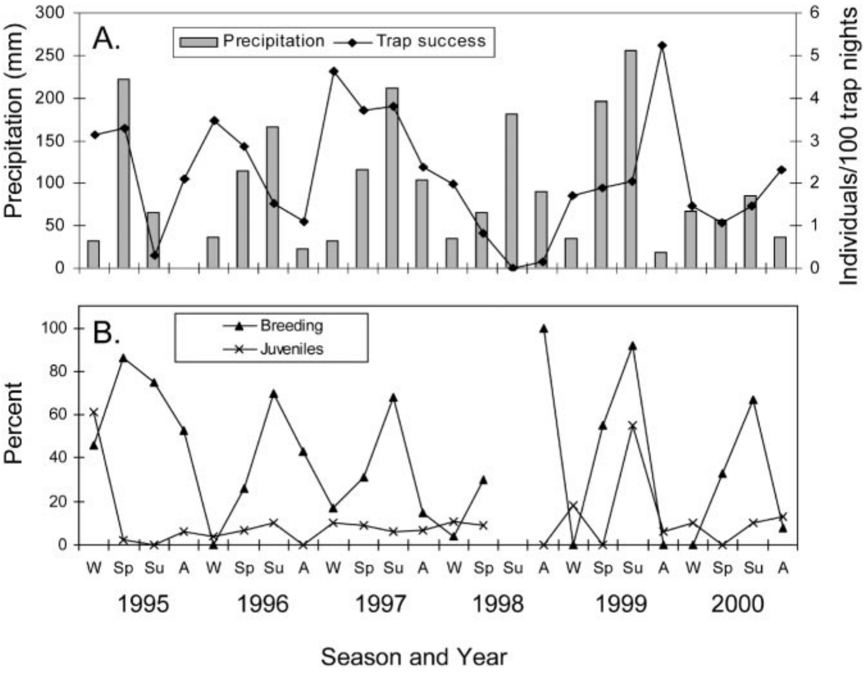

FIGURE 4. Quarterly trap success for western harvest mice (*Reithrodontomys megalotis*) and total quarterly precipitation (A); percent of adults in reproductive condition and percent of captures consisting of juveniles (B), at two mark-recapture sites in southeastern Colorado, 1995–2000.

munks (*Tamias minimus*) were captured only at RRC (Table 1).

Interannual population dynamics

Although population patterns were generally similar from year to year, there were several clear exceptions. The most dramatic exceptions were the population declines in autumn 1997 and winter 2000 (Figs. 4 and 5). The only species that did not exhibit abrupt population declines during these quarters were Ord's kangaroo rat and, perhaps, the northern grasshopper mouse. The autumn 1997 decline coincided with unusually high precipitation accompanied by cold temperatures. A second interannual phenomenon was the irruption of hispid cotton rats that occurred only at RRC during spring–autumn 1999. Finally, the unusually dry and warm spring–summer 2000 period was associated with low relative abundances in spring–autumn 2000 for all species except the three heteromyids and perhaps the grasshopper mice (Figs. 3–5).

Population dynamics of species pairs

We calculated correlation coefficients for trap success indices over time for all pairwise combinations of the 10 commonly captured species at PCMS. Of the 45 pairwise cross-correlations, 27 species pairs had positive correlations and 18 had negative correlations in species abundance (Table 2). Fifteen of these correlations, 12 positive and three negative, were statistically significant ($P<0.05$, not corrected for experiment-wise error rate). Among 45 comparisons, one would expect two to three comparisons to be statistically significant by chance alone. If we were to correct for experiment-wise error rate, there would be no significant comparisons. Nevertheless, we believe these results demonstrate a logical, nonrandom pattern. A generally positive association was observed among a murid group consisting of deer mice, white-footed mice, pinyon mice, and western harvest mice. A separate positive association was observed among a mostly

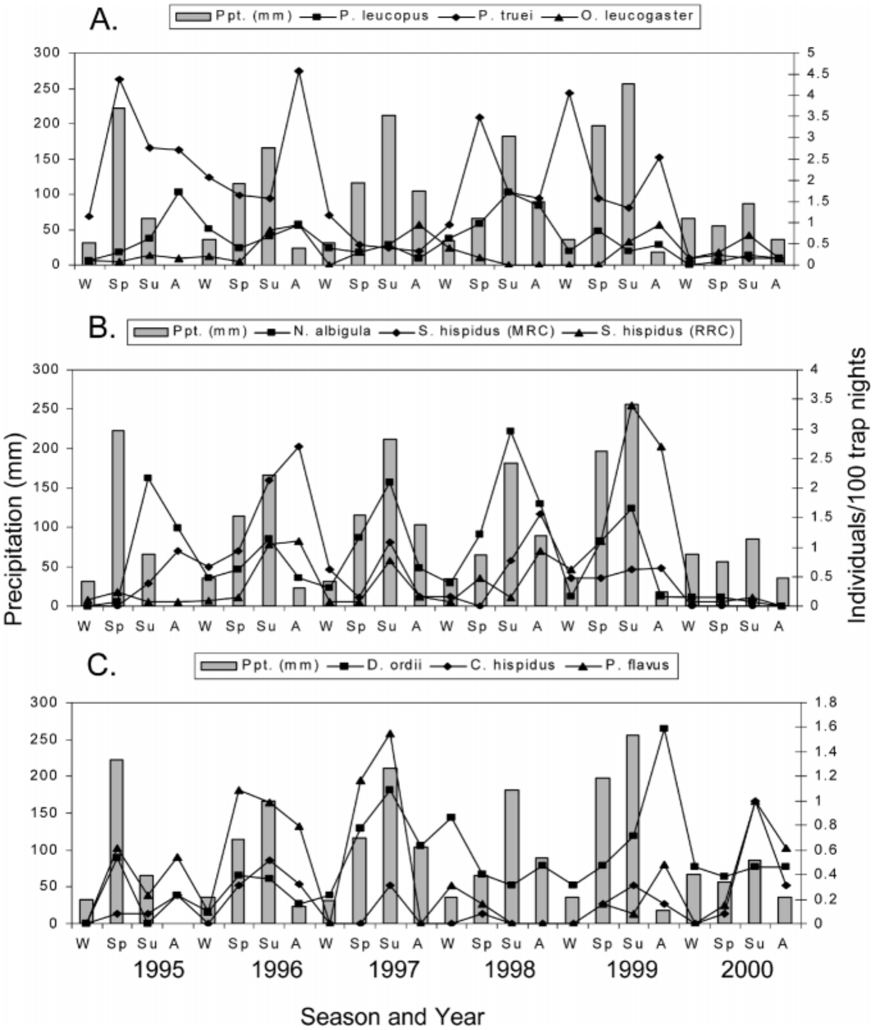

FIGURE 5. Quarterly trap success for white-footed mice and pinyon mice (*Peromyscus leucopus*, *Peromyscus truei*) and northern grasshopper mice (*Onychomys leucogaster*) (A); white-throated woodrats (*Neotoma albigula*) and hispid cotton rats (*Sigmodon hispidus*) at MRC, and hispid cotton rats at RRC (B); Ord's kangaroo rats (*Dipodomys ordii*), hispid pocket mice (*Chaetodipus hispidus*), and silky pocket mice (*Perognathus flavus*) (C), at two mark-recapture sites in southeastern Colorado, 1995–2000.

heteromyid group consisting of Ord's kangaroo rats, hispid and silky pocket mice, and grasshopper mice. Finally, cotton rats and white-throated woodrats might represent a third positive association. Negative associations were observed among some members of the heteromyid and murid groups (e.g., between Ord's kangaroo rats and white-footed and pinyon mice).

Recaptured rodents

Most rodents were not recaptured; the majority of those recaptured were recaptured only once, 4–6 wk after first capture. Mean minimum longevities for recaptured rodent species ranged from 6 to 38 wk (Table 3).

Of 786 deer mice (four mice of undetermined sex and 22 with missing tag numbers are not included), 277 (35.2%) were recaptured, but few (1.0%) were recaptured >42 wk after they were first captured. This pattern held true for western harvest mice (26.2%; 0%); pinyon mice (40.6%; 2.2%); hispid cotton rats (19.8%;

TABLE 2. Matrix of correlation coefficients for time series of monthly trap success (number of individuals captured per 100 trap nights) for 10 common rodent species at Pinyon Canyon Maneuver Site, southeastern Colorado, 1995–2000.[a]

	PM	RM	SH	PT	PL	OL	DO	CH	PF	NA
PM	1	0.357*[b]	0.371*	0.409**[c]	0.365*	−0.091	−0.410	−0.213	−0.199	−0.068
RM		1	−0.049	0.032	−0.142	−0.215	0.258	−0.181	0.071	−0.333*
SH			1	0.184	0.238	0.512**	0.263	0.226	0.180	0.390*
PT				1	0.506**	−0.072	−0.310*	−0.207	−0.152	0.025
PL					1	−0.008	−0.306*	−0.108	−0.034	0.489*
OL						1	0.272	0.452**	0406**	0.091
DO							1	0.098	0.437**	0.068
CH								1	0.525**	0.027
PF									1	0.262
NA										1

[a] PM = *Peromyscus maniculatus*; RM = *Reithrodontomys megalotis*; SH = *Sigmodon hispidus*; PT = *Peromyscus truei*; OL = *Onychomys leucogaster*; DO = *Dipodomys ordii*; CH = *Chaetodipus hispidus*; PF = *Perognathus flavus*; NA = *Neotoma albigula.*

[b] * = Correlation significant at P=0.05 (two-tailed).

[c] ** = Correlation significant at P=0.01 (two-tailed).

1.3%); silky pocket mice (5.6%, 0.5%); and northern grasshopper mice (36.9%, 3.0%). A higher proportion of other species were recaptured >42 wk after they were first captured: white-throated woodrats (36.2%, 10.8%); white-footed mice (38.0%, 7.6%); Ord's kangaroo rats (37.9%, 7.6%); and northern rock mice (*P. nasutus*; 36.8%, 10.5%). The eight most commonly captured species were compared using survival analysis. There were highly significant differences among survivorship curves (P<0.0001, Kaplan-Meier log-rank test). Significance of pairwise comparisons is shown in Table 4. Because of space limitations, survival analysis was not conducted for all species, but such analysis could be performed using the data in Table 3. Of the commonly captured species, white-throated woodrats, white-footed mice, and Ord's kangaroo rats had the highest survivorship; silky pocket mice had the lowest (Fig. 6). Deer mice had a relatively high short-term survivorship but did not survive well after about 30 wk. Although pinyon mice had high short-term survivorship (6–18 wk), white-throated woodrats did better in the longer term. Meadow voles, the Mexican vole, least chipmunks, and rock squirrels were not recaptured.

Breeding condition in deer mice and western harvest mice

We monitored breeding condition of rodents by determining whether adult females had perforate vaginal orifices or enlarged or lactating nipples or whether adult males had descended (scrotal) testes. Except for the unusually warm winter of 1998 (mean maximum temperature >3 C above 18-yr mean), breeding was strongly seasonal. The percent of adult (>18 g) deer mice in breeding condition was highest in spring and summer, usually decreasing to very low levels in autumn and winter (Fig. 3B). The only exception was in the wet autumn of 1997, when the percent of adults in breeding condition did not decrease. Although the seasonal pattern is not as clear, the same general trend is seen for adult (>8 g) western harvest mice (Fig. 4B). The proportion in breeding condition did, however, decrease sharply in the autumn of 1997.

Recruitment

Analysis of the proportion of the deer mouse population consisting of subadults (Fig. 3B) indicates that some recruitment took place throughout the year. The seasonal pattern was variable, but the highest

TABLE 3. Rodents recaptured by species, sex, and number of weeks between first and last capture, Pinyon Canyon Maneuver Site, southeastern Colorado, 1995–2000.

Species	Sex	Total captured[a]	4–6	7–18	19–30	31–42	43–54	55–66	67[b]	Mean
Chaetodipus hispidus	F	20	1	0	0	0	0	0	0	5.7
	M	19	4	0	0	0	0	0	0	5.8
Dipodomys ordii	F	37	1	7	2	0	3	0	2	29.7
	M	29	5	2	2	1	0	0	0	15.0
Neotoma albigula	F	106	14	12	4	4	8	3	2	25.9
	M	51	1	6	0	1	2	1	1	29.3
Neotoma mexicana	F	14	1	1	1	1	0	0	0	21.0
	M	12	1	0	0	0	1	0	0	29.5
Neotoma micropus	F	7	0	0	1	0	0	0	0	29.9
	M	3	0	1	0	0	0	0	0	13.3
Onychomys leucogaster	F	31	3	5	1	0	1	0	0	14.7
	M	35	7	4	0	0	1	0	0	12.2
Perognathus flavus	F	129	3	2	1	0	0	0	0	10.2
	M	66	3	0	1	0	1	0	0	19.0
Peromyscus boylii	F	2	0	0	1	0	0	0	0	30.1
	M	1	0	0	0	1	0	0	0	36.0
Peromyscus leucopus	F	46	1	6	6	1	4	1	0	27.4
	M	46	6	4	3	1	0	2	0	19.4
Peromyscus maniculatus	F	316	26	53	20	9	3	1	0	17.4
	M	470	41	63	45	12	2	1	1	17.6
Peromyscus nasutus	F	26	0	3	3	0	0	1	0	23.3
	M	31	4	2	3	0	2	1	2	38.1
Peromyscus truei	F	191	29	19	17	5	4	0	0	16.5
	M	218	26	39	16	6	1	0	4	17.5
Reithrodontomys megalotis	F	255	25	20	7	8	0	0	0	14.6
	M	249	24	31	12	5	0	0	0	14.0
Sigmodon hispidus	F	121	11	9	4	0	0	1	0	13.2
	M	111	10	5	3	1	2	0	0	14.7
Tamias quadrivattatus	F	10	1	0	0	0	0	0	0	6.4
	M	4	0	0	0	0	0	0	0	0

[a] Ninety-one animals deleted because of missing tag number.

[b] Rodents captured more than 66 weeks after they were first captured (number of weeks between first and last capture): *D. ordii* F (74 and 87), *N. albigula* F (73 and 101), *N. albigula* M (87), *P. maniculatus* M (81), *P. nasutus* M (106 and 125), *P. truei* M (69, 69, 70, and 75).

TABLE 4. Kaplan-Meier log rank statistic for significance of differences in pairwise comparisons among survivorship curves for eight commonly captured species at a mark–recapture site in southwestern Colorado, 1995–2000.[a]

	DO	NA	PL	PM	PT	PF	RM
NA	0.03						
PL	0.00	0.13					
PM	3.47	10.93*[a]	5.94				
PT	1.02	3.43	1.77	1.31			
PF	37.10*	57.35*	47.30*	63.47*	70.68*		
RM	12.47*	29.30*	19.76*	17.58*	20.99*	30.73*	
SH	14.13*	25.98*	19.44*	21.14*	25.75*	14.11*	2.26

[a] NA = *Neotoma albigula*; PL = *Peromyscus leucopus*; PM = *Peromyscus maniculatus*; PT = *Peromyscus truei*; PF = *Perognathus flavus*; RM = *Reithrodontomys megalotis*; SH = *Sigmodon hispidus*; DO = *Dipodomys ordii.*

* Alpha set to $P=0.002$ to provide for experiment-wise error rate of 0.05.

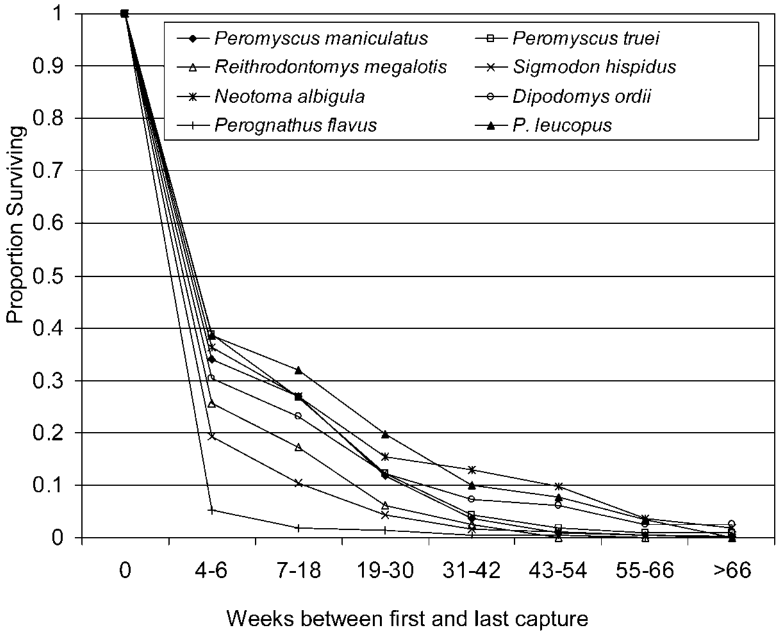

FIGURE 6. Survivorship curves for seven common species of rodents in a mark-recapture study at Pinyon Canyon Maneuver Site, Southeastern Colorado, 1995–2000.

percentage of subadults generally occurred in fall or winter. The most notable exception was the wet autumn of 1997; this was the only point when the percentage of subadults was zero. The harvest mouse population also showed a low level of recruitment throughout the year. No clear seasonal pattern was evident (Fig. 4B).

DISCUSSION

We followed seasonal and year-to-year population dynamics for a diverse rodent assemblage in southeastern Colorado for 6 yr. Patterns in population dynamics differed among species but shared some common characteristics. Seasonal trends were generally evident, and three primary patterns were discernable by visual inspection. The two most common species, deer mice and western harvest mice, showed high populations in winter and nadirs in summer. Other sigmodontine species (white-footed mice, pinyon mice, and grasshopper mice) generally had highest relative abundances in autumn and lowest numbers in spring. White-throated woodrat and hispid cotton rat populations generally peaked in summer and were lowest in winter.

Superimposed upon these seasonal trends was clear interannual variation, sometimes associated with meteorologic conditions that affected most species similarly. These results indicate that "typical" seasonal population dynamics may occur only under "average" conditions, and departures from these average conditions may occur frequently and result in distinct changes in rodent population dynamics. Cold, wet fall/winter conditions and hot, dry spring/summer conditions were associated with negative effects on populations of most species. The cold, wet autumn of 1997 was coincident with an El Niño event that brought high winter precipitation to the Southwest and, at our study site, was associated with abrupt declines in relative abundances of rodents. The abrupt decline in populations of many species in winter 2000 is not easily explained by meteorologic conditions. Although precipitation was 40% above normal during the winter, much of that rainfall occurred in March. The population crash was first observed in January, when rainfall was not higher than normal and the temperatures were about 2 C warmer than normal. It is possible that our meteorologic monitoring at Rocky Ford did not detect local unfavorable conditions at PCMS, or other factors may have been responsible. Because populations of most species declined simultaneously, competition is unlikely to have been a factor. Other extrinsic factors that may have adversely affected rodent populations were not monitored in our study. These include food resources, disease, and predation. Although expensive and labor intensive, studies that monitor all of these factors have the best chance of identifying the factor or combination of factors responsible for population phenomena.

Our results emphasize the importance of long-term studies in understanding the dynamics of small-mammal populations. Conclusions based on 1 yr or 2 yr worth of data may be inaccurate or misleading. Similarly, we caution that our conclusions are based on two trapping arrays at a single location. Extrapolation of the patterns we observed to other geographic areas, habitats, or climatic conditions may not be appropriate.

The apparent interaction between precipitation and temperature indicates that these variables must be considered simultaneously when attempting to understand or predict changes in relative abundance of rodents. Precipitation during a period of cold temperature was associated with negative effects on rodent populations (autumn 1997). Conversely, the lack of rainfall during a period of warm temperature (spring–summer, 2000) was associated with negative effects on populations of all species except those that do not require free water (heteromyids). The timing of precipitation events will also be important in its effect on the vegetation resource base that supports animal populations. The positive effects of rainfall during the growing season may be much more important than they are during quiescent periods, and frequent and evenly distributed rains will be much more beneficial than occasional downpours that result in large amounts of runoff.

Favorable environmental conditions, such as higher summer rainfall and mild winters, have been associated with increases in rodent population densities (Beatley, 1969; Meserve et al., 1995; Brown and Ernest, 2002; Yates et al., 2002). These increases result from improvement in survival, reproductive success, and recruitment and therefore frequently involve a time lag that may be as great as a year. Some investigators, however, have observed effects of weather on population growth with little or no time delay (Llewellen and Vessey, 1998). Two notable departures from normal population dynamics observed in this study were not periods of population growth but rather periods of abrupt population declines. One of these declines appeared to be associated with high rainfall during a cold period and involved no temporal lag (occurred within the same 3-mo period). This indicates that these unfavorable climatic conditions not only adversely affect reproduction but may result in the death of individual rodents through exposure or denial of food and shelter. The hot, dry conditions during the spring and summer of 2000 were associated with an apparently very low level of recruitment in the following autumn, probably indicating unfavorable conditions during the spring-summer breeding season and very low reproductive success. Both direct and indirect (through vegetation) effects of unfavorable weather conditions, especially hot, dry summers and cold, wet winters, have been observed in temperate ecosystems in both North (Garsd and Howard, 1981, 1982) and South America (Crespo, 1944; de Villafane and Bonaventura, 1987; Mills et al., 1992).

Not all species were affected similarly by environmental conditions. Hispid pocket mice and silky pocket mice were not negatively affected by the drought in spring-summer 2000. In fact, populations of each species reached very high relative abundances during summer 2000. It is not clear if they simply thrived because of their lack of dependence on free water or if their populations were enhanced because of a release from competitive pressures by other species whose populations remained low during this period.

The degree of correlation in abundance between species pairs is another way to look for commonalities in patterns of population dynamics that consider both seasonal and interannual trends simultaneously. These analyses have been used as an indication of the extent to which sympatric species are limited by common resources. A positive correlation between species pairs may indicate that those species pairs respond similarly to, and are limited by, fluctuating common resources. A negative correlation may indicate that those species avoid competition by responding differently to resource variation (Valone and Brown, 1996). The results of our correlation analyses indicate that murids such as *Peromyscus* species share a generally common pattern of population dynamics and may respond similarly to limiting environmental resources. Heteromyid species and grasshopper mice share a separate pattern. We cannot say whether these different patterns in sympatric species evolved to minimize interspecific competition or as specializations for different resources independent of competitive pressures. Our results differ from those seen by Valone and Brown (1996) and Brown and Heske (1990) for many of the same species. Those authors found most associations to be positive, even among murid and heteromyid species, and concluded that general environmental conditions (as opposed to interspecific interactions) were of overriding importance in determining population dynamics. A possible explanation for the different results may be that the former studies took place in a more xeric, water-restricted, desert environment than is PCMS. Thus, the rodent assemblage at PCMS may be controlled by a combination of overriding abiotic environmental factors during harsh conditions and a mix of environmental and competitive factors during more benign conditions.

The dynamics of breeding and juvenile recruitment add to the interpretation of seasonal and multiyear population dynamics for deer mice and western harvest mice. The percent juvenile generally paralleled the overall relative abundance, while percent in breeding condition varied inversely with relative abundance. These trends probably reflect not only cessation of breeding but also the dilution of the breeding population by the new, sexually immature cohort in the postbreeding season (autumn–winter). An exception to the pattern is clearly seen for deer mice in the fall of 1997, when the percent sexually mature remained high and the percent juvenile decreased to zero, indicating the complete absence of recruitment during that unfavorable period.

Populations of hispid cotton rats at MRC and RRC increased abruptly at the end of the summer of 1996 (Fig. 5B), declining just as precipitously thereafter. In summer 1999, cotton rats increased abruptly at RRC (but not at MRC), and again decreased precipitously. Fleharty et al. (1972) have described "crashes" of hispid cotton rat populations. Hispid cotton rats are a southern species that are near the limit of their distribution at PCMS, and they would be expected to be sensitive to harsh, wintry conditions. We do not know the explanation for the striking difference between cotton rat population dynamics between MRC and RRC in summer–autumn 1999. However, these patterns emphasize the importance of continuity and replication when attempting to describe general patterns of population dynamics for any species.

Based on low recapture rates for rodent reservoirs of hantaviruses and commensurately low prevalence of these viruses at another site at PCMS, we have inferred that long-lived mice infected with a hantavirus are crucial to the trans-seasonal persistence of these viruses (Calisher et al., 2001b). Given that most rodents were adults when first captured, the mean number of weeks between first and last captures is a minimum estimate of longevity and at least 1 mo less than the actual longevity. Also, failure to recapture an animal may represent emigration, not death. The majority of rodents were captured only once. Either they survived only a short period or, perhaps more likely, they were transients. Larger-bodied rodents (e.g., woodrats) generally had higher survivorship than smaller-bodied rodents, but some *Peromyscus* species (brush mice, rock mice, white-footed mice) had much longer survivorship compared to deer mice and pinyon mice. Whether such persistence at these sites was dependent on the presence or absence of competing species, predators, available nutrients, other components of the environment, or species-specific trapping responses is unknown.

On the basis of our relatively short study period, we observed a trend toward warmer, wetter conditions in southeastern Colorado. If these conditions continue, they may result in changing species compositions in the rodent assemblages at PCMS. Possible changes could include increasing dominance by warm-adapted species, such as hispid cotton rats, and decreasing representation by some more dry-adapted species, such as the heteromyids.

Our results have important implications for those attempting to develop predictive models of rodent population dynamics. To the extent that they were associated with abiotic causes, the population crashes we observed and the subsequent extended effects on some populations could not have been predicted using models based on vegetative greenness indices. This implies that 1) models that do not incorporate temperature and precipitation may fail to predict population changes such as the general decline we observed in autumn 1997, and 2) it may be very difficult to predict populations for more than a few months in advance whenever such overriding extrinsic abiotic environmental factors are involved. Our results may be generalized to some other temperate ecosystems. Cold, wet winters and hot, dry summers were found to be detrimental to rodent populations inhabiting the temperate Argentine Pampa (Crespo, 1944; Mills et al., 1992). However, increased winter precipitation may be advantageous to murid rodents inhabiting the desert Southwest (Brown and Ernest, 2002; Yates et al., 2002), and increased winter precipitation in the form of snowfall may be advantageous to some species in high-altitude or boreal areas (Merritt et al., 2001). Thus, a given model may be useful only for a specific region and a specific range of elevations.

During this nearly 6-yr study, we were able to discern at least three patterns of population dynamics for suites of rodent species in southwestern Colorado. We also identified specific abiotic environmental (meteorologic) phenomena that were associated with dramatic changes in population dynamics. These meteorologic phenomena affected different species in different ways and had enduring effects for some species. Typical seasonal population cycles, which may be controlled within certain limits by the interaction of a suite of biotic and abiotic environmental factors, are subject to disruption by periodic overriding abiotic phenomena. Such unusual conditions are likely to be those associated with population irruptions and outbreaks of zoonotic diseases. In our study, we were fortunate to witness several events that were associated with apparent perturbations of normal population cycles. Nevertheless, much longer term studies will be required to discern the effects of truly rare phenomena or to identify trends or cycles that have a multiyear periodicity, such as the El Niño southern oscillation.

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