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BRUSH MOUSE (*PEROMYSCUS BOYLII*) POPULATION DYNAMICS AND HANTAVIRUS INFECTION DURING A WARM, DROUGHT PERIOD IN SOUTHERN ARIZONA

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ABSTRACT: We monitored Limestone Canyon hantavirus (LSCV) antibody prevalence, host (brush mouse, *Peromyscus boylii)* abundance, and environmental variables (temperature and rainfall) in brush mice captured on three trapping webs in southern Arizona for 5 yr. Although seasonal patterns were subtle, we observed large multiyear variation in population abundance and antibody prevalence. Limestone Canyon hantavirus infection in brush mouse populations varied over time with prevalence ranging from 0% to 33%. At all trapping webs, evidence of infection disappeared completely for an extended period (up to 2 yr) and eventually reappeared, suggesting that dispersal may play a role in maintaining infection in brush mouse metapopulations. Weather during the study period was drier and warmer than average and these conditions, especially during spring through fall, may have contributed to low brush mouse population density and the local extinction of LSCV during the second year of the study. Nevertheless, population growth was associated with relatively warm, dry conditions during winter periods and a cool, wet spring and summer period in the fifth year of the study. After prolonged absence, LSCV infection was consistently detected only when brush mouse population abundance reached relatively high levels during that fifth year. Comparison of our results to similar studies suggests that stochastic events resulting in the loss or survival of a few infected mice in low-density host populations may result in local extinction of virus; reestablishment of infection may occur via immigration of infected individuals from adjacent populations, but may be successful only when populations are of sufficient density to support frequent rodent-to-rodent interactions and virus transmission.

Key words: Brush mouse, epizootiology, hantavirus, Limestone Canyon virus, *Peromyscus boylii*, population dynamics.

INTRODUCTION

Hantaviruses (family *Bunyaviridae,* genus *Hantavirus*) are rodent-borne zoonotic agents that can be highly pathogenic to humans. Numerous hantaviruses are recognized throughout the world, with each virus usually restricted to a particular rodent host species in the superfamily Muroidea. In humans, distinct groups of hantaviruses are responsible for hemorrhagic fever with renal syndrome in Asia and Europe, and hantavirus pulmonary syndrome (HPS) in the Americas. The majority of HPS cases in the United States are caused by Sin Nombre virus (SNV), whose principal reservoir is the deer mouse (*Peromyscus maniculatus*; Nichol et al., 1993; Childs et al., 1994).

Other *Peromyscus* species have been shown to host distinct hantaviruses based on detection and sequencing of viral RNA. The brush mouse (*Peromyscus boylii)* is the host of Limestone Canyon virus (LSCV; Sanchez et al., 2001). Brush mice occur throughout much of the southwestern United States, from northern California to central Mexico. Although described as "common," the brush mouse is much less of a habitat generalist than the deer mouse, and prefers rock outcroppings and brushy areas with rock ledges, boulders, brush piles, and fallen trees (Bradley and Schmidly, 1999). Although LSCV is not demonstrated to be a human pathogen, the brush mouse occurs throughout much of the area with the highest density of

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human HPS cases (southwestern United States) and the specific hantavirus responsible for most HPS cases is not identified. Therefore, precautions are followed when sampling brush mice in the field (Mills et al., 1995a,b). The dynamics of LSCV infection in brush mice are similar to those for deer mice and SNV (Abbott et al., 1999; Kuenzi et al., 1999). Thus, we believe that lessons learned from studies of LSCV in brush mouse populations are applicable to other hantavirus–host systems, including SNV and the deer mouse.

Documenting hantavirus infection in rodent populations at one point in time, or over a short time, does not provide information on how the virus is maintained in those populations, or how prevalence of infection changes with population density or environmental factors. Long-term studies designed to monitor changes in rodent population abundances and the effects these changes have on the prevalence and incidence of hantavirus infection in these host populations are needed. The Centers for Disease Control and Prevention initiated long-term studies of hantavirus infection in *Peromyscus* populations in the southwestern United States and Montana in 1994 (Mills et al., 1999). During the first two and a half years of studies in southern Arizona, *P. boylii* and *Peromyscus eremicus* were the most common *Peromyscus* species captured (Kuenzi et al., 1999; Morrison et al., 2002), but hantavirus antibody was largely restricted to *P. boylii* (Kuenzi et al., 1999).

We investigated population dynamics and hantavirus (LSCV) antibody prevalence in brush mice captured on three trapping webs in southern Arizona from May 1995 through December 1999. We simultaneously examined temporal patterns of hantavirus antibody prevalence, host abundance, evidence of breeding, juvenile recruitment, and environmental variables (temperature and rainfall). We describe the dynamics of these variables and suggest potential cause-and-effect relationships that may help explain the complex interactions among these variables. We also compared hantavirus antibody prevalence between male and female brush mice.

METHODS

Study area

Our study was conducted on the Santa Rita Experimental Range (SRER), in the Santa Rita Mountains of southeastern Arizona (Pima County). The two major vegetation types are semidesert grassland in the upland areas and oak–riparian in drainage areas where water flow is seasonally intermittent. The semidesert grassland is characterized by Lehman lovegrass (*Eragrostis lehmanniana*), three-awn (*Aristida* spp.), prickly pear cactus (*Opuntia* spp.), and mesquite (*Prosopis velutina*). The oak–riparian is characterized by deciduous trees, including netleaf hackberry (*Celtis reticulata*) and Arizona white oak (*Quercus arizonica*), with an understory of mimosa (*Mimosa biuncifera*). Elevations range from 1250 m to 1370 m.

Trapping and processing procedures

In May 1995, we established three trapping webs (Anderson et al., 1983) at SRER. Each web was located in equal areas of semidesert grassland and oak–riparian vegetation. A trapping web consisted of 12 100-m transects radiating from the center (Mills et al., 1999). Along each transect were 12 Sherman live-traps (7.6 cm by 8.9 cm by 22.9 cm) placed 5 m apart for the first 20 m of the transect and 10 m apart for the remaining 80 m. Four additional traps were placed in the center of the web (148 total traps per web). Traps were baited with peanut butter and oatmeal and provided with polyester bedding. Trapping was conducted concurrently on all three webs for three consecutive nights each month from May 1995 through December 1999.

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Trapping was not conducted during October 1995 because of logistical constraints.

Animals were weighed, measured, and identified to species. Sex, age, and reproductive condition were recorded and individuals were uniquely marked by toe clipping and ear notching (rodent species <30 g) or ear tags (>30 g). Rodents were anesthetized using methoxyflurane (Metofane, Pitman-Moore, Inc., Washington Crossing, New Jersey, USA) and approximately 0.2 ml of blood was collected from the suborbital sinus using a heparinized microcapillary tube (Biven and Smith, 1984). Individuals were bled only once during each trapping session. All animals were released at their capture site. Blood samples were collected from individuals captured on two of the trapping webs for the entire study duration. Initially, the remaining web was a control web where animals were marked and processed but not bled. Because no difference was found in the survival rates of bled versus control animals (Swann et al., 1997), in November 1996 we began collecting blood samples on this web.

Blood samples were immediately frozen on dry ice and sent to the Centers for Disease Control and Prevention for testing for antibody reactive with SNV recombinant nucleocapsid protein by enzyme-linked immunosorbent assay (Feldmann et al., 1993; see Mills et al., 1999 for details).

Data analysis

We used the minimum number of mice known to be alive (MNA) during a 3-day trapping session as an index of population abundance. This index was calculated by taking the total number of individual mice captured during each 3-day trapping session and adding to that sum the number captured on at least one previous and one subsequent session, but not during the month of interest (Krebs, 1966). The minimum number of infected (hantavirus antibody-positive) brush mice (MNI) was calculated in the same way.

For the combined data from all three trapping webs, monthly data points were averaged to derive quarterly data. Quarters were designated as winter (January–March), spring (April–June), summer (July–September), and fall (October–December).

Brush mouse data: Adult *P. boylii* exhibiting at least one sign of breeding or breeding readiness (males: scrotal testes; females: perforate vaginal orifice, enlarged nipples, lactation, or pregnancy) were considered to be in breeding condition. Juvenile mice (<17 g) were excluded in quarterly calculations of percentage of mice in breeding condition.

Weather data: Santa Rita Experimental Range weather station data for 1951–2000 were downloaded from the National Oceanic and Atmospheric Administration's National Climatic Data Center website (National Oceanic and Atmospheric Administration, 2006). These data were in the form of daily values of minimum and maximum temperatures (°F) and precipitation (inches). Weather data from the trapping period were compared to the 50-yr mean for each quarter using z-scores (distance in standard deviations from the mean; Zar, 1984).

RESULTS

Environmental factors

Temperature: Temperatures varied seasonally at the Santa Rita weather station, with the coldest in winter (minimum: 4.27 C; maximum: 17.64 C) and the hottest 50-yr mean temperatures in summer (minimum: 18.36 C, maximum: 31.51 C). During the trapping period, no quarter's mean temperatures exceeded 2 standard deviations from the 50-yr quarterly mean (Fig. 1). However, four quarters had mean maximum temperatures in the uppermost 10th percentile (over the 50-yr period), and two quarters were in the lowest 10th percen-

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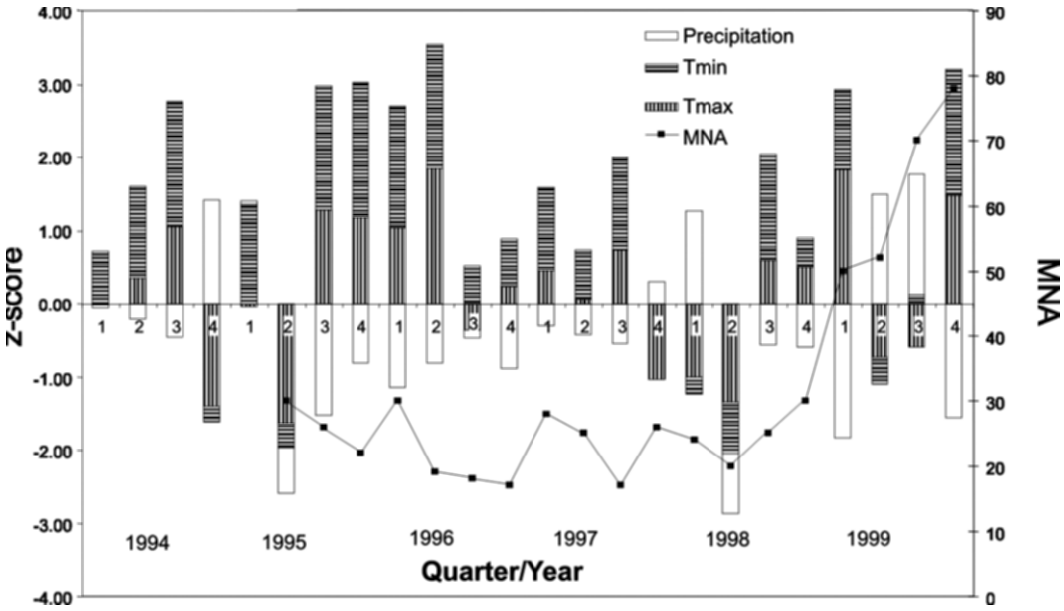

FIGURE 1. Quarterly values in minimum number of brush mice alive (MNA), and deviations of quarterly values in precipitation, minimum temperature (Tmin), and maximum temperature (Tmax) from the 50-yr mean values. Deviations are expressed as z-scores (Zar, 1984), and z-scores for precipitation, minimum temperature, and maximum temperature are stacked. Numbers in or below bars represent quarters: 1 (winter)=January–March, 2 (spring)=April–June, 3 (summer)=July–September, 4 (fall)=October–December.

tile. Six quarters were in the uppermost 10th percentile for mean minimum temperature and none were in the lowest 10th percentile. These data indicate that the trapping period was, on average, warmer than most of the 50-yr period.

Precipitation: Precipitation was lowest in spring and highest in summer. Five quarters during the trapping period exhibited mean precipitation values higher than the 50-yr mean, and 17 had below-average values (Fig. 1). Of these, four quarters were in the lowest 10th percentile rank and two were in the uppermost 10th percentile rank. Thus, the trapping period was, on average, drier than most of the 50-yr period.

Seasonal rodent population dynamics

Number of mice known to be alive: Brush mouse population dynamics and trends in antibody prevalence were similar among webs and the three webs were combined for analyses presented herein. Quarterly MNA generally remained stable throughout the year without noticeable peaks and troughs (i.e., little intra-annual fluctuation; Figs. 1, 2). The MNA remained below 30 brush mice from the beginning of the study until fall 1998, when the brush mouse population sharply increased, reaching a MNA near 80 by the end of the study in fall 1999.

Breeding condition: Although the percentage of adult mice in breeding condition peaked in the fall during 3 of 5 yr, the pattern was variable (Fig. 2) and brush mice continued to breed year-round. Breeding condition fluctuated widely from quarter to quarter, except for the period from spring 1997 to fall 1998, during which the percentage was consistently over 60%. This percentage greatly decreased during the warm, dry winter of 1999 (coinciding with the introduction of large numbers of nonreproductive young during a rapid population growth phase)

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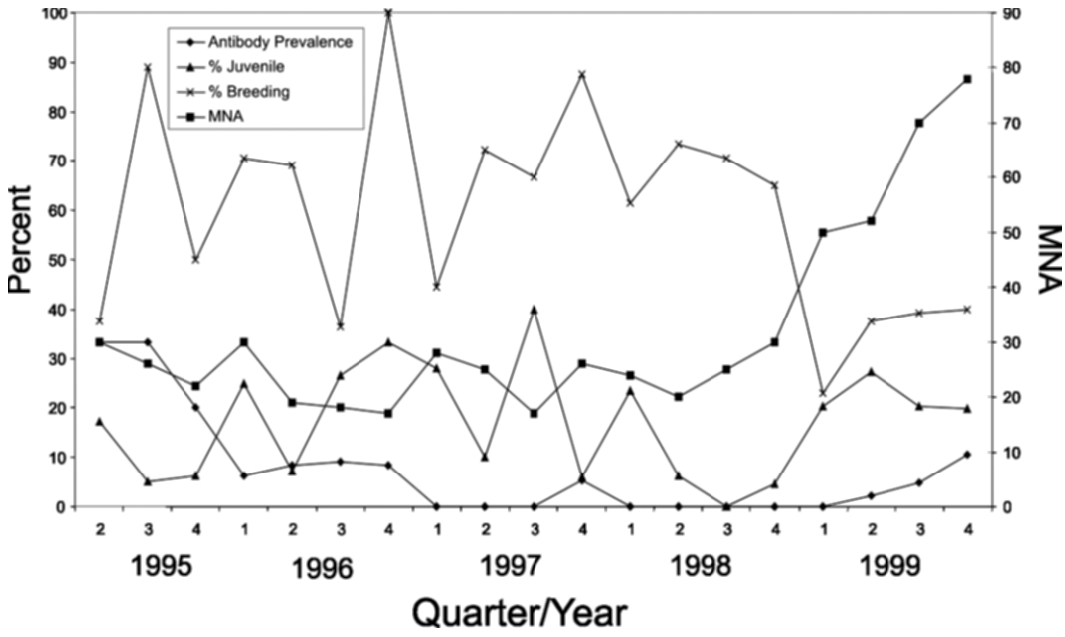

FIGURE 2. Quarterly values of minimum number of brush mice alive (MNA), percentage of adult mice in breeding condition (% breeding), percentage of juvenile mice, and prevalence of antibody reactive with Sin Nombre virus (SNV prevalence). Quarters are as follows: 1 (winter)=January–March, 2 (spring)=April–June, 3 (summer)=July–September, 4 (fall)=October–December.

and remained at 40% or below for the remainder of the study.

Recruitment: Recruitment was measured as proportion of the population consisting of juveniles. Recruitment fluctuated widely throughout the year, with no consistent patterns within a year (Fig. 2). The highest recruitment occurred in summer 1997, and the lowest recruitment (0% juveniles) occurred in summer 1998, summer 2000, and winter 2001. There was a period of sustained recruitment from winter through autumn, 1999, coinciding with the abrupt increase in MNA.

Antibody prevalence: We captured and took blood samples from 326 *P. boylii* captured 582 times (Table 1). Approximately 8% of these individuals had antibodies reactive with SNV. Web-specific antibody prevalence ranged from 6.2% on trapping web B to 10.4% on trapping web C. All antibody-positive mice were adults and the majority (88%) were males (χ^2 with Yates correction=10.77, P=0.001). The highest hantavirus infection prevalence among brush mice (33%; calculated as MNI/MNA) was observed at the beginning of the study (Fig. 2). Prevalence fell to 0% by winter 1996. Except for one antibody-positive brush mouse captured in fall 1997, antibody prevalence remained at 0% until spring 1999, when prevalence began increasing shortly after the increase in brush mouse MNA (Fig. 2).

DISCUSSION

Our enzyme immunoassay, based on SNV antigen, will detect, but not distinguish among, infections caused by all known New World hantaviruses (Mills et al., 1999). Nevertheless, hantaviruses are highly host-specific and, except under unusual circumstances, spillover infection into other rodent species is rare (Childs et al., 1994; Mills et al., 1998; Calisher et al., 2005a). Two other recognized hantavirus host species (*Peromyscus leucopus* and *P. maniculatus*) were present at SRER, but were rare (13 and three individuals,

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TABLE 1. Overall prevalence of antibodies reactive with Sin Nombre virus among *Peromyscus boylii* captured on three trapping webs in southeastern Arizona, May 1995–March 2001.

Location	Sex	No. individuals bled (total blood samples)	No. positive individuals (total no. positive blood samples)	Percentage of positive individuals
Web A	Male	78 (150)	9 (17)	12
	Female	68 (124)	2 (2)	3
	Both	146 (274)	11 (19)	8
Web B	Male	61 (106)	6 (16)	10
	Female	52 (87)	1 (1)	2
	Both	113 (193)	7 (17)	6
Web C	Male	39 (65)	7 (7)	18
	Female	28 (50)	0 (0)	0
	Both	67 (115)	7 (7)	10
All combined	Male	178 (321)	22 (40)	12
	Female	148 (261)	3 (3)	2
	Both	326 (582)	25 (43)	8

respectively). Thus we assume that hantavirus antibody detected in brush mice represented LSCV.

Hantavirus infection in brush mouse populations in southern Arizona was far more common in males than in females. Hantaviruses are transmitted horizontally within reservoir populations and infection appears to be associated with behavioral events surrounding maturation of animals, including aggressive encounters between males (Mills et al., 1999). The higher prevalence of infection in males is consistent with that hypothesis. The proportion of antibody-positive brush mice that were male (88%) is similar to that proportion of antibody-positive brush mice trapped in an ecologically distinct area in central Arizona (Abbott et al., 1999). This male bias in hantavirus infection is much higher than that demonstrated for deer mice and SNV (Mills et al., 1999; Calisher et al., 2007) and may suggest some differences in the mechanism of hantavirus transmission between the two species.

Precipitation during much of our study was below average and temperatures were generally higher than average. The exact effects of this combination of conditions on desert plant and animal populations are not well defined. It has been hypothesized that increased precipitation in the arid southwestern United States increases primary production, which then increases rodent populations (Yates et al., 2002). Increased rodent densities were associated with increased precipitation in some environments (Beatley, 1969; Meserve et al., 1995; Brown and Ernest, 2002). However, primary production does not always show a direct response to variations in precipitation. In a study also conducted on the SRER, Reynolds (1954) found that after prolonged dry periods, primary production did not increase for several years following increased rainfall. Although we did not measure primary production directly, large changes in vegetation productivity were not obvious during the course of the study.

The most salient feature of brush mouse population dynamics during our study was the abrupt increase in abundance in 1999. The relationship of this dynamic to associated environmental parameters is not clear. It may be significant that two of the three quarters with total rainfall in the uppermost 10th percentile of the 50-yr mean were associated with this population growth spurt. The spring quarter immediately preceding the growth period was perhaps the coolest quarter during the study. However, the early part of the growth period was characterized by warm and dry conditions, especially winter 1999, which was the driest quarter during the

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study. This association is best interpreted when considering that the direction of effects of environmental variables on rodent populations may depend upon the season (Mills, 2005). Cold, wet conditions are detrimental (and warmer, drier conditions are favorable) to rodent populations during the winter in temperate ecosystems (Mills et al., 1991; Calisher et al., 2005b). The warm, dry winters in 1996 and 1997 were also accompanied by a small spike in MNA, whereas the wetter winter in 1998 was not. Spring and summer 1999 were wetter and cooler than normal and were associated with continued population growth. Suggesting that these associations represent cause-and-effect relationships between environmental variables and rodent populations is speculative; such relationships are complex, involve multiple interactions, vary on multiple spatial and temporal scales, and may involve variable time lags. Only data from long-term studies with abundant replication are likely to demonstrate the relationship between environmental variation and rodent population dynamics (Mills, 2005).

Deciphering patterns of viral dynamics in host populations presupposes the presence of virus in the population. However, when host population density drops to very low levels (as in the first half of our study), transmission rates decrease, numbers of infected animals decrease, and transmission dynamics become more susceptible to stochastic events. The choice of our sampling sites was based, in part, on relatively high densities of *Peromyscus* and prevalence of hantavirus antibody during preliminary sampling in 1994. However, following the 1993 El Niño southern oscillation event, the associated high-density rodent populations, and the outbreak of HPS in the Four Corners area, rodent populations decreased throughout much of the southwestern United States. Data from multiple sites demonstrate that this decline produced two contrasting patterns in hantavirus-host dynamics, which may have been largely determined by chance events in low-density populations. As brush mouse populations declined in central Arizona in 1996, hantavirus infection was maintained in a few long-lived individuals, resulting in antibody prevalence as high as 75% (Abbott et al., 1999). In contrast, low density of brush mouse populations at our study sites appears to have led to the local extinction of LSCV from our webs for up to 2 yr (it is possible but unlikely that the virus was present on our webs in a few individuals that were never captured). Similarly, very low population densities were accompanied by the local extinction of SNV from deer mouse populations in southeastern Colorado in 1996, and again in 2000 (Calisher et al., 2005b). Such large differences in prevalence (75% vs. 0%) and the maintenance or extinction of virus in local populations may depend on the survival of very few individual mice, and may be determined largely by chance events.

A single antibody-positive brush mouse was captured in November, 1997, 12 mo after we last detected LSCV at our study sites. This individual was never captured again, was presumably a transient, and apparently did not transmit LSCV to resident mice. Reestablishment of LSCV into our study populations occurred only after a large increase in brush mouse population density in the fifth year of our study. Given the hypothesized primary mode of transmission of hantaviruses in host populations (aggressive encounters among adult males; Mills et al., 1999) it is likely that a threshold population density was necessary for successful introduction and maintenance of LSCV in our brush mouse populations.

In summary, hotter and drier than normal conditions in 1995–1998 were associated with low brush mouse abundance and, we believe, the extinction of LSCV at our study site. Abrupt and continued population growth was associated with a cool, dry winter; wet, cool spring and summer; and warm, dry autumn. After an absence of approximately 2 yr, LSCV

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became reestablished after population abundance reached a relatively high level. Although questions remain, we feel that these described associations may be causally related. We believe these explanations of relationships between environment, rodent population dynamics, and viral extinction and reintroduction represent the most likely (but not the only) interpretation of our data. Nevertheless, we emphasize that our interpretations are based on small sample sizes and are, necessarily, speculative. Even though we have five consecutive years of data, dynamics of host and virus populations occur in multiyear cycles, and each cycle is likely unique. Our explanations for the relationships among environment, host population dynamics, and hantavirus infection should more appropriately be viewed as hypotheses subject to additional testing, rather than as explanations.

Sixteen of the 24 quarters for which we analyzed climatic data had mean temperatures above the 50-yr mean; 17 quarters had rainfall below the 50-yr mean. Thus our study does not represent typical environmental conditions at the study site. On the other hand, these conditions may be an indicator of ongoing climate change in the study area. Either way, we urge caution in using short-term studies to extrapolate to temporally generalized conclusions. A 1- or 2-yr study at Santa Rita would have encompassed only a small part of the multiyear cycle that we observed and might have provided misleading results. We join others (Cody, 1996; Mills, 2005; Calisher et al., 2007) in calling for greater emphasis on long-term studies of ecological systems.

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