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Notes and Discussion

Vole Population Dynamics: Influence of Weather Extremes on Stoppage of Population Growth

Abstract.—Effects of 74 episodes of extreme weather on stoppage of population growth and resulting amplitudes of annual population fluctuation of 39 fluctuations of *Microtus ochrogaster* and 20 fluctuations of *M. pennsylvanicus* were studied over a 25 y period in east-central Illinois. Episodes of extreme weather may have stopped population growth of only six *M. ochrogaster* fluctuations and of two *M. pennsylvanicus* fluctuations. Cessation of growth of only one population fluctuation (*M. pennsylvanicus*) could be attributable solely to an episode of extreme weather. Episodes of extreme weather occurred during 62% of the increase phases of *M. ochrogaster* population fluctuations and 75% of those of *M. pennsylvanicus*, with no associated cessation of population growth. We conclude that episodes of extreme weather were not a primary factor responsible for cessation of population growth or variation in amplitudes of population fluctuations of either *M. ochrogaster* or *M. pennsylvanicus*.

Introduction

Populations of many arvicoline rodents undergo large fluctuations in numbers. Some population fluctuations are short-term, occurring over a few months (Krebs and Myers, 1974; Taitt and Krebs, 1985), whereas others may take 2–3 y to run their course (Oksanen and Henttonen, 1996). Population fluctuations may be annual or erratic or may occur periodically at 2–5 y intervals (Krebs *et al.*, 1969; Krebs and Myers, 1974; Taitt and Krebs, 1985; Krebs, 1996; Bjørnstad *et al.*, 1998). An understanding of factors responsible for high-amplitude population fluctuations, irrespective of their periodicity, is necessary to evaluate patterns of fluctuation of arvicoline populations.

Populations of small mammals in temperate and high latitude regions often display annual fluctuations in population density. Population densities increase rapidly during the growing season (typically spring-early autumn) when food availability is high and decline during late autumn-winter because of reduced reproduction and survival in response to lesser food quality and quantity (Batzli, 1992). Episodes of unusually extreme weather conditions (*i.e.*, high and low temperatures and high or low precipitation) may result in sudden high mortality or reduced reproduction, producing multiannual fluctuations in population density that obscure annual fluctuations (Batzli, 1992). Although it has been shown that weather conditions may influence population densities of small mammals, mainly through effects on food supplies (Drabeck, 1977; Lewellen and Vessey, 1998a, b; White, 2004), there is little evidence for episodes of adverse weather having direct effects on survival and reproduction (Pinter, 1988) or resulting in cessation of population growth (Getz *et al.*, 1987; Batzli, 1992).

Getz *et al.* (2006) concluded that increased mortality was the main factor involved in cessation of population growth of the prairie vole, *Microtus ochrogaster*. The time at which such increased mortality occurred appeared to be the primary determinant of peak densities and amplitudes of population fluctuations. Predation from generalist predators was presumed to be the most likely source of mortality. Reduced survival also was most commonly associated with cessation of population growth of the meadow vole, *M. pennsylvanicus* (Getz *et al.*, *in press*); however, a winter decline in reproduction was associated with cessation of growth of population fluctuations that peaked in late autumn-winter. Neither of these papers addressed the potential for episodes of extreme weather to stop population growth through effects on survival and reproduction and to influence the peak densities and amplitudes of population fluctuation. In the present paper we address the question of whether episodes of extreme weather may be involved in cessation of population growth of arvicoline rodents.

We used the results of a 25-y study (Getz *et al.*, 2001) of sympatric populations of *Microtus ochrogaster* and *M. pennsylvanicus* in alfalfa (*Medicago sativa*), bluegrass (*Poa pratensis*) and tallgrass prairie (a mixture of big bluestem, *Andropogon gerardii*; Indian grass, *Sorghastrum nutans*; and switch grass, *Panicum* spp.) to examine the influence of episodes of extreme weather on cessation of population growth of the two species in east-central Illinois. Our data included 30 population fluctuations of *M. ochrogaster* and 14 of *M. pennsylvanicus* in our long-term study sites. Another nine population fluctuations of *M. ochrogaster* and six of *M. pennsylvanicus* were observed in other sites monitored for shorter periods during manipulative studies (Getz *et al.*, 1987). We test the hypothesis that episodes of extreme weather stopped population growth through reduced survival and reproduction, resulting in variation in peak densities and amplitudes of population fluctuations across years.

METHODS

STUDY SITES

The study sites were located in the University of Illinois Biological Research Area (''Phillips Tract'') and Trelease Prairie, 6 km NE of Urbana, Illinois (40°15′N, 88°28′W). We trapped 0.5–2.0 ha sites in two restored tallgrass prairies, Trelease Prairie and a prairie in Phillips Tract from Mar. 1972 through May 1997 (Getz *et al.*, 2001). Study sites (0.8–2.0 ha) established within a former bluegrass pasture located in Phillips Tract that had been released from grazing in spring 1971 were trapped Jan. 1972–May 1997. Two adjacent 1.0–1.4 ha sites in Phillips Tract planted with alfalfa were alternately trapped May 1972–May 1997. The study sites are described in detail by Getz *et al.* (1979, 1987, 2001).

TRAPPING PROTOCOL

A grid system with 10 m intervals was established on all study sites. One wooden multiple-capture live-trap (Burt, 1940) was placed at each station. Each month a 2-d prebaiting period was followed by a 3-d trapping session; traps were set about 1500 h and checked at 0800 h and 1500 h for the next 3 d. All animals were toe-clipped at first capture for individual identification (≤2 toes/foot). All procedures were approved by the University of Illinois Laboratory Animal Resource Committee and meet the guidelines recommended by the American Society of Mammalogists (Animal Care and Use Committee, 1998). At each capture we recorded species, grid station, individual identification, sex, reproductive condition (males: testes abdominal or scrotal; females: vagina open or closed, pregnant as determined by palpation, or lactating) and body mass to the nearest 1 g. For analysis, we grouped voles as adult (≥30 g) or young (≤29 g; Hasler, 1975). We obtained climatological records from a National Weather Station maintained by the Illinois State Water Survey on the campus of the University of Illinois, 6.6 km from the study sites.

DATA ANALYSIS

Voles occurred at low densities for extended periods of time (Getz *et al.*, 2001). Consequently, attempts to apply capture-mark-recapture models to our data to estimate population size and survival rates (Pollock *et al.*, 1990; Lebreton *et al.*, 1992) did not succeed because of the inability to estimate time-specific parameters resulting from small sample sizes for the majority of capture occasions. Thus, we used estimates of population size reported by Getz *et al.* (2001) to identify population fluctuations and estimate survival.

All fluctuations were less than one year in duration. Population fluctuations of *Microtus ochrogaster* with at least the following peak densities (most peaks were well in excess of these minimal densities; Getz *et al.*, 2001) were used in the analyses: alfalfa, 75 voles/ha; bluegrass, 25 voles/ha; tallgrass, 20 voles/ha. These fluctuations stood out as conspicuous events that were > twice the highest densities of non-fluctuation years in each habitat (Getz *et al.*, 2001). All fluctuations displayed typical phases (trough, increase, peak, decline) characteristic of population fluctuations of arvicoline rodents (Krebs and Myers, 1974)

We examined weather data for evidence of episodes of extreme weather sufficiently close to the peak (the month of the peak or the month before or after the peak, *i.e.*, before the next trapping session) that may have contributed to cessation of population growth and initiation of population declines. Because there is no good evidence as to magnitude of episodes of extreme weather necessary to adversely affect individual voles, we examined the weather records for 1972–1997 to identify the most likely episodes that would adversely affect survival and reproduction of individuals and result in stoppage of population growth. We arbitrarily defined the following as episodes of extreme weather as most likely to stop population growth. In so doing, we attempted to error on the side of being overly inclusive as to what conditions might stop population growth. For temperature stresses, we used five continuous days of mean daily temperatures 10 C below the 30-year mean for the months of Dec., Jan.

and Feb. and 10 C above the 30-year mean for Jun., Jul. and Aug. Precipitation episodes included only rain and a total of ≥5 cm during two consecutive days or ≥10 cm during five consecutive days. The rationale for such amounts of precipitation was that, from field observations, this amount of rain in such short periods of time had the potential to flood underground nests of *Microtus ochrogaster* and the surface nests of *M. pennsylvanicus* that might be in low depressions, forcing the voles to disperse to new sites, thus exposing them to increased mortality. We also included periods during which there was less than 0.5 cm of precipitation for 60 d preceding stoppage of growth as an episode of extreme weather. For each episode of extreme weather, temperature or precipitation, we recorded the magnitude of the other variable for comparison. We used Mantel-Haenszel chi-square test (M-H χ^2) (Agresti, 2002) to test for association of episodes of weather extremes with cessation of population growth.

For potential effects of episodes of extreme weather on survival, we compared monthly survival the month before the episode with survival the month after the episode. Because females more accurately determined when reproduction starts or ends, we used the proportion of the adult females that were reproductively active (vagina open, pregnant or lactating) as an index of reproductive activity of the population the month before and after the episodes of extreme weather. We also calculated survival and the proportion of reproductively active females the three months before and after the peak (Getz *et al.*, 2006) to compare changes of these two variables during the increase and decline phases associated with cessation of population growth. From these we estimated the potential impact of the episodes of extreme weather on survival and reproduction and in turn cessation of population growth.

We further compiled the incidents of episodes of extreme weather that occurred during an increase phase in which the population increase continued for at least 2 mo, *i.e.*, population growth did not stop. We used a 2 × 2 contingency table (Zar, 1999) to test significance of differences between when cessation of population growth did and did not occur.

RESULTS

During the 304 mo of the study there were 74 episodes of extreme weather (23 involving temperature episodes and 51, precipitation) and 59 population fluctuations of the two species of voles. Only 11 episodes of extreme weather coincided with cessation of population growth (*Microtus ochrogaster*, 7; *M. pennsylvanicus*, 4; Table 1). A period of low temperature or heavy rain coincided with cessation of growth for 2 of 13 population fluctuations of *M. ochrogaster* in alfalfa, one of 12 fluctuations in bluegrass, and four of eight fluctuations in tallgrass (Table 1). An episode of extreme weather was not associated with cessation of growth of any of the five population fluctuations of *M. pennsylvanicus* in alfalfa and of only four of the 20 fluctuations in bluegrass (Table 1). Episodes of extreme weather were not correlated with cessation of population growth of the two species (*M. ochrogaster*: M-H $\chi^2 = 0.0034$, $p = 0.95$; *M. pennsylvanicus*: M-H $\chi^2 = 0.3556$, $p = 0.55$; two species combined: M-H $\chi^2 = 0.0878$, $p = 0.78$).

Eight episodes of extreme weather involved a ≥20% decline in survival or reproduction (*Microtus ochrogaster*, 6; *M. pennsylvanicus*, 2) the month after the episode. Reduced survival of *M. ochrogaster* was associated with two episodes of low temperatures in Jan. 1985 in alfalfa and bluegrass and one episode of high rainfall in May 1973 in tallgrass (Table 1). A decline of ≥20% in the proportion of reproductively active female *M. ochrogaster* in bluegrass was associated with the 1985 Jan. low temperature episode and in tallgrass with two episodes of low temperatures, Jan. 1988 and Dec. 1989, and in alfalfa with one episode of high precipitation, Nov. 1985 (Table 1). Survival of *M. pennsylvanicus* in bluegrass declined by ≥20% during the month after a 2-wk period of high temperatures and no precipitation in Jul. 1980 (Table 1). The proportion of adult females that were reproductively active in bluegrass declined by ≥20% after a low temperature episode in Nov. 1977.

Survival the 3 mo after the peak was ≥20% lower than the 3 mo before the peak for all population fluctuations of *Microtus ochrogaster* associated with episodes of extreme weather, except for one fluctuation in tallgrass, Dec. 1989 (Table 1). The proportion of reproductively active females was ≥20% lower the three months after than the 3 mo before the peak, except for in tallgrass in May 1973 and Aug. 1985. Either survival or the proportion of reproductively active females was ≥20% lower the 3 mo after than before the peak of two of the four *M. pennsylvanicus* population fluctuations in bluegrass (Table 1).

TABLE 1.—Episodes of extreme weather coinciding with cessation of population growth of *Microtus ochrogaster* and *M. pennsylvanicus* and change in survival and reproduction (proportion of reproductively active adult females) associated with the episode of extreme weather. Duration, days; temperatures, mean daily deviation from the previous 30-y mean; precipitation, total precipitation during the episode; survival, change in the proportion of total population surviving the month after the episode; reproduction, change in the proportion of adult females reproductively active the month after the episode. Comparisons of change in survival and the proportion of reproductively active females the three months after the episode in comparison to the three months before to the episode are also included

Species/habitat	Month/year peak	Duration	Temperature (°C)	Precipitation (cm)	Survival 1 Mo	Survival 3 Mo	Reproduction 1 Mo	Reproduction 3 Mo
M. ochrogaster								
Alfalfa	Jan. 1985	5	−11.5	0.28	−0.39	−0.25	−0.12	−0.47
	Nov. 1985	2	+13.5	7.40	+0.03	−0.23	−0.44	−0.78
Bluegrass	Nov. 1985	2	+13.5	7.40	−0.45	−0.26	−0.46	−0.85
Tallgrass	May 1973	5	+17.8	9.60	−0.50	−0.30	+0.05	+0.11
	Aug. 1985	31	+26.3	7.50	+0.06	−0.34	0.08	+0.08
	Jan. 1988	7	−10.0	0.03	−0.12	−0.20	−0.60	−1.00
	Dec. 1989	11	−18.7	0.33	−0.18	−0.03	−0.28	−0.60
M. pennsylvanicus								
Bluegrass	Nov. 1977	6	−11.1	0.20	−0.08	−0.12	−0.69	−0.38
	Jan. 1980	6	−10.3	0.08	−0.16	−0.35	−0.18	−0.75
	Jul. 1980	14	+28.4	0	−0.44	+0.41	−0.20	+0.15
	Feb. 1986	6	−10.4	0.10	+0.05	−0.21	ND	+0.22

Episodes of extreme weather occurred during 24 of 39 increase phases of population fluctuations of *Microtus ochrogaster* and during 15 of 20 increase phases of *M. pennsylvanicus* fluctuations. Population growth of all these fluctuations continued for at least two months after the episodes of extreme weather. Association of episodes of extreme weather with the increase phase without cessation of growth was significantly greater than those associated with cessation of growth ($\chi^2 = 26.19$, df = 1, $p < 0.01$).

DISCUSSION

Results of the present study indicated that cessation of population growth of neither *Microtus ochrogaster* nor *M. pennsylvanicus* was associated with episodes of extreme weather. We observed potential for such an influence in only seven of 39 (18%) population fluctuations of *M. ochrogaster* and four of 20 (20%) fluctuations of *M. pennsylvanicus*. Further, the month after an episode of extreme weather, a ≥20% decline in either survival or proportion of reproductively active females was associated with cessation of growth of six of the seven *M. ochrogaster* and two of four *M. pennsylvanicus* population fluctuations. Thus, in only 14% of the 59 cessations of population growth of the two voles was there a decline in survival or the proportion of reproductively active females associated with an episode of extreme weather.

The proportion of reproductively active adult females of both *Microtus ochrogaster* and *M. pennsylvanicus* was significantly lower (36% and 47%, respectively) during winter than other seasons, irrespective of population fluctuations (Getz *et al.*, 2005). Although a winter decline in reproduction may have enhanced effects of declines in survival in stopping growth of populations peaking in late autumn and winter, a decline in reproduction did not appear to be the primary determinant of cessation of population growth of either species (Getz *et al.*, 2005, *in press*). Those fluctuations for which cessation of population growth was associated with a decline in reproduction during late autumn or winter may, therefore, have done so irrespective of an episode of extreme weather.

For the three fluctuations in which a decline in survival was associated with the episode of extreme weather, the 3-mo mean decline in survival following the extreme weather episode was ≥20%. Further, for all three fluctuations of *Microtus ochrogaster* in which the proportion of reproductively active females declined following the extreme weather episode, the 3-mo mean decline was much greater than that for the first month after the decline. The cessation of population growth of *M. pennsylvanicus* in bluegrass involving a decline in the proportion of reproductively active female occurred in Nov. when there was a typical winter decline in reproduction. Thus, cessation of population growth of only one of the 59 fluctuations, that of *M. pennsylvanicus* in bluegrass in Jul. 1980, appeared to be attributed only to an episode of extreme weather.

Episodes of extreme weather with no associated cessation of population growth for at least the next two months occurred during 62% of the 39 population increases of *Microtus ochrogaster* and of 75% of the 20 increases of *M. pennsylvanicus.* This is further evidence that episodes of extreme weather were not the primary factor stopping population growth and affecting amplitudes of fluctuation of the vole populations in our study area.

Getz (2005) has shown that temperatures recorded at the National Weather Station from which the episodes of extreme weather were defined in this analysis were much more extreme than those actually encountered by the voles within their surface runways under the vegetation. We conclude, therefore, that stoppage of population growth and variation in amplitudes of population fluctuations of neither *Microtus ochrogaster* nor *M. pennsylvanicus* may be attributed to effects of episodes of extreme weather.

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