CLIMATIC FACTORS, REPRODUCTIVE SUCCESS AND POPULATION DYNAMICS IN THE MONTANE VOLE, *MICROTUS MONTANUS*



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✦ OBJECTIVES

A variety of hypotheses has been proposed to explain multiannual fluctuations in population density ("cycles") of small rodents (for reviews see Finerty 1980, Taitt and Krebs 1985). Doubtless, such cycles – known since antiquity (Elton 1942) - result from an interaction of a multitude of factors. However, the inability of extant hypotheses, alone or in combination, to explain the causality of cycles rests in no small measure with the fact that long-term studies of the phenomenon are notoriously uncommon.

The objectives of this project are to continue the long-term study of population dynamics of the montane vole, *Microtus montanus*, in Grand Teton National Park. Earlier observations (Pinter 1986, 1988) indicate that environmental variables might contribute to the population density cycles of these rodents, possibly by influencing their growth and various aspects of their reproduction.

✦ Methods

In 2004 *Microtus montanus* were livetrapped at two times of the year: the second half of May (spring study period) and mid-July to mid-August (summer study period). Animals were killed with an overdose of Metofane as soon as possible after capture. They were aged using weight, total length and pelage characteristics. Reproductive organs, the spleen and the adrenal glands were collected from all animals and preserved in Lillie's neutral buffered formalin for further histological study. Flat skins were prepared from all animals.

Population density was estimated on the basis of trapping success in a permanent grid (established in 1970). The grid consists of 121 stations placed in a square, 5 m apart, 11 stations (50 m) on a side. Each station is marked with a stake. Trapping in this grid was performed only during the summer study period. One unbaited Sherman livetrap was set at each station. Additional trapping was carried out in nearby meadows away from the grid to obtain additional females for litter size determination.

During the spring study period trapping was carried out at a number of sites, all of them well removed from the permanent grid. The purpose of this was to leave the grid site as undisturbed as possible since the grid was the major source of information on population density. The main objective of the spring study period was to determine (on the basis of embryo size) the onset of reproduction on a population-wide basis. This information is very important for two major reasons: (1) onset of reproduction in *M. montanus* in Grand Teton National Park can vary by as much as 40 days among years, and (2) the time at which reproduction begins has significant repercussions on the productivity of the population for the year.

Weather data were obtained from records at the Jackson Lake Dam. Although Moran 5WNW is not a Class A weather station, it is located less than 2 km

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from the permanent grid. Data collected included temperature, precipitation, and the date of complete spring melt-off.

✦ RESULTS AND DISCUSSION

At the onset of the spring study period it became apparent almost immediately that populations of montane voles in GTNP were headed for a significant increase in density in 2004. The overwintering population of voles (i.e., the initial breeding population) was remarkably high as indicated by extensive sign (droppings, cuttings, numerous heavily used runways). In 2004 reproduction on a population-wide basis began early (i.e., in April). Not only were all trapped females pregnant - 50% were already pregnant with their second litter. Mean litter sizes were larger than those seen in the spring of 2003 - a year already characterized by a rise in population density over that seen in 2002. Furthermore, as a result of the continuing drought the meadows were well drained so that May precipitation did not result in flooding of these meadows and the consequent danger of drowning of many of the first litters in their natal burrows (Pinter 1988).

Data from the spring study period turned out to be an accurate presager of the population dynamics of M. montanus in the summer of 2004: conditions favorable for spring reproduction had, indeed, resulted in a spectacular increase in the population density of these rodents. Until now the highest population density recorded in this 35-year study had been in 1969. The density recorded for 2004 exceeded, albeit slightly, the 1969 levels, leaving 2004 as the year with the highest population density recorded for M. montanus in GTNP in the past 35 years. Furthermore, the percent of females in the population was 15% greater in 2004 than that observed in 2003. During the first half of the summer study period all females (with the exception of those that had been weaned recently) were reproductively active. During the second half of the summer study period, in spite of the drought and the rapid drying of the herbaceous vegetation, females born before the first week in July were still either reproductively active or maturing rapidly. However, by the middle of August reproduction had slowed dramatically, litter sizes were 30% smaller than those recorded at the beginning of the summer.

The factors that underlie the multi-annual fluctuation in vole population density remain a mystery. There are environmental factors that

correlate fairly predictably with population processes of voles. The difficulty in deciphering the causes of vole cycles is due to the number of variables that contribute to this phenomenon. For example, the onset of spring, specifically, the onset of the growth of herbaceous vegetation can be linked reliably with the onset of reproduction in M. montanus. The time at which *M. montanus* begin to reproduce in the spring has profound consequences for their population dynamics. In M. montanus the first litter of the year invariably reproduces in the year of its birth, the females attaining puberty at approximately 5 weeks of age. The second litter matures at 8-10 weeks of age, the third - depending on its date of birth - may or may not mature in the year of its birth (Negus, Berger and Pinter 1992). Consequently, the earlyborn young of he year do not merely represent an addition of individuals - they represent the addition of breeders. Thus, an early increase in the number of reproductively active individuals results in rapid population growth. The earlier the young breeders can be produced the greater their contribution to that year's population numbers. However, an early onset of reproduction does not always guarantee rapid population growth, essentially because of the dramatic phenotypic plasticity exhibited by M. montanus in response to environmental variables (Negus, Berger and Pinter 1992). Such was the case in the summer Of 2004. As the drought intensified throughout the summer, the preferred food plants of M. montanus began to senesce and dry out. As was the case in 1987-88 (Negus, Berger and Pinter 1992), in 2004 environmental vicissitudes significantly impacted population processes in M. montanus. By the middle of August 2004 the drought had slowed the growth and maturation of the young of the year and suppressed reproduction in the population as a whole. Nevertheless, the record high vole population density in 2004 was attained because of the stunning coincidence of a number of factors, all favorable for rapid population growth. In the spring these favorable factors consisted of an inordinately early spring with a consequent early onset of reproduction by an exceptionally large surviving population of breeders. The continuing drought had resulted in a rapid draining of the meltwater, thereby permitting a rapid drainage of any additional May precipitation and preventing the drowning of the first litter of the year in their natal burrows. The summer populations continued to grow rapidly because of the large number of breeders produced in the spring and the extraordinarily high percentage of females in the population. Furthermore, since there was a very low population density of weasels (Mustela erminea and M. frenata) there must have been a significant reduction in predation pressure.

CONCLUSIONS

The data collected in the 2004 field season exemplify the extreme sensitivity of *M. montanus* to environmental vicissitudes and reinforce the point that climatic variables play an extremely important role in their reproductive processes. Furthermore, these data also demonstrate the surprising speed with which climatic change can shape the population dynamics of these animals. In turn, population dynamics of voles result in major consequences for the ecosystem. Montane voles constitute a major prey base for a variety of predators. Unexpected shifts in the reproductive responses and population dynamics of these rodents must therefore also have significant repercussions on population parameters of their predators.

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