

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

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## ♦ OBJECTIVES

Multiannual fluctuations in population density ("cycles") of small rodents have been known since antiquity (Elton 1942). Numerous hypotheses have been proposed to explain this phenomenon (for reviews see Finerty 1980, Taitt and Krebs 1985). However, none of these hypotheses, alone or in combination, has been able to explain the causality of cycles, although recently removal of parasites was shown to prevent population cycles in the red grouse, *Lagopus lagopus scoticus* (Hudson et al. 1998).

The objectives of this long-term study are to determine whether environmental variables, possibly acting through reproductive responses, contribute to the multiannual fluctuations of the montane vole, *Microtus montanus*.

## ♦ METHODS

*Microtus montanus* were live trapped 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. Animals were aged using weight, total length and pelage characteristics. The digestive tract and the liver were examined for the presence of parasites. Reproductive organs, the spleen and the adrenal glands were collected from all animals and preserved in Lillie's buffered neutral formalin for further histological study. Flat skins were prepared from all animals.

Population density was estimated on the basis of the 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 livetrapp was set at each station. Additional trapping was carried out in nearby meadows to obtain additional females for litter size determination. In these areas, traps were not set in a regular pattern; rather, they were placed only in locations showing recent vole activity (cuttings, droppings).

During the spring study period trapping was carried out in a number of sites, all well removed from the permanent grid. The objective of trapping during the spring study period was to determine (on the basis of embryo size) the onset of reproduction on a population-wide basis. The reason for not trapping the grid during the spring study period was to leave the site as undisturbed as possible since the grid is the major source of information on population density. In order to ascertain the effects of habitat/density on population dynamics of *M. montanus* in Grand Teton National Park, populations of these rodents were monitored in both, optimal and marginal habitats.

## ♦ RESULTS

As predicted at the end of the 1997 field season, a very large population of *Microtus montanus* had, indeed, overwintered in 1997-1998. This was evidenced by the presence of unusually large numbers

of well-worn runways at the beginning of the spring study period. Reproduction had begun in late April. Every female trapped was pregnant with her first litter. An exception to this was a population from a warmer microenvironment where all females already were pregnant with their second litter. All second litters were approximately 30% larger than the first litter. This is a well-known phenomenon. In *Microtus montanus* the first litter is the smallest. Litter size then increases with each successive litter, up to the fifth litter (Negus and Pinter 1965). Although such laboratory findings hint at the reproductive potential of *Microtus montanus*, under natural conditions a given female rarely, if ever, produces five litters in her lifetime. However, the production of large litters early in the breeding season has significant repercussions on population dynamics since females from early litters breed in the year of their birth (Pinter 1986, 1988; Negus, Berger and Pinter 1992). Furthermore, during the spring study period of 1998, after meltwater had receded, there was no reflooding of the study areas, suggesting the potential for a high survival rate of all early litters. Consequently, the combination of early widespread breeding and the persistently well-drained habitats presaged a significant increase in population density for the remainder of the 1998 breeding season.

As expected, during the summer study period population densities of *Microtus montanus* had risen dramatically above those observed in 1997. In the summer of 1998 the population density in the permanent grid was almost twice that of 1997. Litter sizes were smaller than those in 1997; however, the breeding population was much larger than in the previous year. A similar increase in density was found in the other study areas - with one notable exception. Whereas, the 1998 population density had essentially doubled over that found in 1997 at all sites, one of the populations exhibited a dramatic decline in density. Indeed, the numbers were the lowest ever recorded at this site, although the population remained reproductively active, with litter sizes larger than those at any of the other locations.

At the present there is no explanation for the apparent collapse of this population. Recently, parasites have been implicated as causative agents of population cycles (Hudson et al. 1998). There was, however, absolutely no difference in the extent of endoparasitism in *M. montanus* among the different study sites in 1998. There was also no apparent difference among the sites with respect to the abundance of predators. The asynchrony observed

here is an excellent example of the variability in population dynamics at specific locations. Fluctuations in population density of *M. montanus* are generally synchronous over a wide geographic region. However, within a region of synchrony there exist populations that exhibit varying degrees of asynchrony with neighboring populations. The frequency and extent of such asynchronies becomes apparent only as a result of long-term observations. Furthermore, such asynchronous populations can be extremely valuable because any features that are not shared with their synchronous neighbors may hold clues to the causes underlying population fluctuations.

The disappearance of *M. montanus* from this study area was accompanied by an invasion of *Microtus pennsylvanicus*. Ordinarily *M. pennsylvanicus* are uncommon at this site. However, in 1998 the numbers of *M. montanus* and of *M. pennsylvanicus* were virtually identical. It is impossible to say whether the invasion of *M. pennsylvanicus* is related to the decline in population density of *M. montanus*. The *M. pennsylvanicus* had not taken over the entire area occupied by *M. montanus*; rather, they had expanded from their preferred habitat fairly uniformly into one third of the study area along one edge only. In this region the two species retained symmetry, although the *M. pennsylvanicus* outnumbered the *M. montanus* by a ratio of 2:1.

Another noteworthy aspect during the 1998 study period was the absence of parasitism by cuterebrid flies. Infestations of *M. microtus* by *Cuterebra* usually occur during the second half of the summer study period. The incidence is usually most severe in the driest study areas. During 1998, however, there was no evidence of either current or past cuterebrid parasitism at any of the locations, although by the end of the summer study period the vegetation was fruiting and drying at some of the sites.

## ◆ CONCLUSIONS

For the first time since this study began, a population of *M. montanus* at one of the study sites exhibited complete asynchrony with populations at all other sites. The crash of this population (in what is probably optimal *M. montanus* habitat) occurred at a time when all other populations in the region increased in density. Such asynchrony within a very



small region is an extremely valuable finding because a comparison with synchronous populations should hold clues to the causes underlying population cycles of small rodents.

#### ◆ ACKNOWLEDGEMENTS

I gratefully acknowledge the availability of the facilities at the University of Wyoming-National Park Service Research Center and the enthusiastic support of the Research Center staff without which it would have been impossible to accomplish this work.

I am particularly grateful to the Steering Committee of the UW-NPS Research Center and to the National Park Service for their cognizance of the fact that the understanding of microtine cycles can be gained only from long-term studies.

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