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

AELITA J. PINTER DEPARTMENT OF BIOLOGICAL SCIENCES UNIVERSITY OF NEW ORLEANS New ORLEANS

♦ 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, have been able to explain the causality of cycles.

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

In 1992, *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. 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 livetrap 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 *A. montanus* in Grand Teton National Park, populations of these rodents were monitored in both optimal and marginal habitats.

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RESULTS

A dramatic decline in the population density of Microtus montanus occurred in 1993. Apparently the decline had occurred before the onset of the spring study period. There were few well defined runways at this time - a decided contrast with the spring of 1991 and 1992 (both were years of high density). Yet, spring trapping success in 1993 was not significantly lower than in the spring of 1991 and 1992, suggesting essentially comparable spring densities in 1991, 1992, and 1993. However, spring trapping success is not necessarily a reliable indicator of population density. This is prticularly true in springs with high precipitation - and 1993 was a wet spring. In a wet spring large portions of the voles' habitat can become flooded. Spring trapping success is, therefore, essentially a reflection of the success with which the trapper locates the temporary refugia to which the animals have retreated, rather than an indication of population density. Consequently, the severity of the decline was not readily apparent during the spring study period.

By the time the summer study period began the extent of the decline was unmistakable. Furthermore, several findings from the spring study period indicated that recovery from the crash would be limited during 1993:

- Precipitation in May 1993 was very high (95 mm); high precipitation in May is linked highly significantly with population declines in *M. montanus* (Pinter 1988).
- In the spring of 1993 the onset of breeding (2)was unusually late and the size of the first litter was very small. The first litter invariably becomes a part of the breeding population in the year of its birth (Pinter 1986; Negus, Berger and Pinter 1992). However, litters born in the second half of the summer usually do not reproduce in the year of their birth. Consequently, the later the onset of breeding - and the smaller the first litter - the smaller the addition of new breeders in a given year. The wet spring, the small initial breeding population, the late onset of breeding and the small litter sizes all pointed toward a low density for the summer of 1993.

The population decline in 1993 occurred in both optimal and marginal habitats. Population densities in optimal habitats can exceed densities in marginal habitats by a factor of five. Nevertheless, population dynamics in these two types of habitats parallel each other with exceptional fidelity, in spite of the highly significant differences in absolute density.

The different study sites within GTNP are as much as 18 km apart. Nevertheless, at all sites population dynamics followed an identical pattern. Furthermore, population dynamics of *M. montanus* at a study site on the upper Green River (Sublette Co., WY, 160 km southeast of the GTNP sites) exhibited the same profile as the GTNP populations. The concordance of population dynamics within a geographic region serves to reinforce the hypothesis that such population dynamics are cued to a significant degree by climatic factors (Pinter 1988).

Until recently, spring precipitation patterns in GTNP had exhibited 3-5 year cycles. The cycles in population density of M. montanus showed a highly significant correlation with these precipitation cycles (Pinter 1988). An examination of weather records from GTNP for the past 80 years reveals that cyclic patterns in spring precipitation (e.g., 1939-1946; 1960-1990) alternate with periods of no cyclicity (1946-1960; 1990-present). Since population cycles of voles are linked significantly with climatic cycles, would population dynamics of voles be altered in a series of years with no cycles in precipitation? The answer is a tentative "yes". Since 1990 wet springs have alternated with dry springs (rather than exhibit a gradual cycle from dry to wet springs over a period of 3-5 years). Since 1990 the population underwent a cycle in which it remained at peak densities for two consecutive years. It is the first time in this long-term study that such a phenomenon has been recorded. Once again, this anomaly was recorded at all study sites. Once again, the data are strongly suggestive of a climatic role in the generation of vole population dynamics.

CONCLUSIONS

In 1993 populations of *M. montanus* declined in all study areas. The decline was independent of population density and habitat. It was observed in

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populations as much as 160 km apart, at elevations ranging from 2057 to 2134 m. These results support the hypothesis that climatic factors contribute significantly to the fluctuations in population density of *M. montanus* in GTNP: cycles in spring precipitation show a significant correlation with population cycles of voles. This hypothesis has been strengthened recently by the finding that a departure from multiannual cycles in spring precipitation is associated with perturbations in the cyclic nature of vole populations. However, a more extensive series of years with an acyclic spring precipitation pattern is needed before the hypothesis can be confirmed or invalidated.

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