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Aelita J. Pinter

University of New Orleans

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EFFECTS OF ENVIRONMENTAL VARIABLES ON SOME PHYSIOLOGICAL RESPONSES OF MICROTUS MONTANUS UNDER NATURAL CONDITIONS
(summary for 1976)

Aelita J. Pinter
Department of Biological Sciences
University of New Orleans

Introduction

Multiannual cycles in population density are known for a number of micro­
tine rodents. However, factors that govern various phases of the cycle are poorly understood. In other words, little is known to what degree environmental factors and physiological responses of the animals contribute to such cyclicity. The purpose of the present study was essentially four­fold:

A. Characterization of environmental variables that might affect Microtus populations at three or four different times of the year.

B. Investigation of growth, maturation, and reproductive activity of Microtus montanus under natural conditions.

C. Study of maturation molts and seasonal pelage changes in Microtus montanus in relation to sex, age, and reproductive status.

D. A correlation of the information obtained in #1-3 above. It is hoped that the results will help to elucidate causes underlying the multiannual fluctuations in population density of microtine rodents.

Materials and Methods

Microtus montanus were livetrapped and sacrificed as soon as possible after capture. Age estimation for all animals was based on weight, total length, and pelage characteristics.

Reproductive organs, the spleen, and the adrenal glands were collected and preserved in Lillie's buffered neutral formalin for future histological study. Flat skins were prepared from all animals. All tissues are currently being processed at the Department of Biological Sciences, University of New Orleans.

Field Observations

In 1976 field observations were carried out at the Research Station over two study periods: spring (16-21 May), and summer (11 July - 11 August). The fall study period, planned for the first two weeks in October, had to be cancelled when the principal investigator had to be scheduled for major surgery at a directly conflicting time.
Spring and summer study period

During spring melt off many of the meadows in the study area become temporarily flooded. Since Microtus must therefore also retreat to higher ground, they tend to become concentrated only in small pockets throughout their habitat. Consequently, trapping success in the spring is probably more a measure of the success with which these pockets can be located rather than a measure of the true population density.

In 1976 spring began relatively early. Sixty percent of the females trapped at this time were pregnant with their first litter. Backdating (on the basis of embryo size) revealed that breeding on a population-wide basis began during the second week in May. This is a significant fact in terms of the population growth of Microtus. Data from previous years indicate that any voles born after approximately the first week in July will not reach sexual maturity in the year of their birth. Rather, they would have to overwinter, and then become a part of the breeding population the following spring. Microtus have a gestation period of 21 days; females can remate in post partum estrus. Consequently, if a female were to be capable of producing three litters before the first week in July, she would have to start spring breeding no later than the first week in May. In the spring of 1976 Microtus started breeding on a population-wide basis early enough to permit the production of two litters that would mature in 1976. Isolated animals might have been breeding even early enough to permit the production of three such litters. This is in sharp contrast with the exceptionally late spring of 1975. At that time Microtus started breeding very late. Most of the females probably succeeded in producing only one litter (some, at the very most, two) before the first week in July. The timing of the onset of spring breeding affects the Microtus population density in three ways. First, if three, rather than two, litters are produced, there is the sheer increase in numbers within that time span. Second, the ability to produce a third litter before early July does not merely represent the addition of just a litter. Laboratory data have revealed that litter size in Microtus increases with each successive litter, up to the fifth litter (Negus and Pinter 1965). Consequently, the addition of a second or of a third litter represents the addition of a litter that is larger than the one immediately preceding it. Third, and most significant, is the fact that the production of litters before the first week in July does not merely represent the addition of numbers. Rather, this represents the addition of breeders - these are young that will become breeders in the year of their own birth; they will contribute offspring to the population in the year of their birth. Therefore, to reiterate: the number of Microtus born before the first week in July represents not only an increase in the absolute numbers of voles for that year; it represents an increase in the size of the breeding population for that year. Furthermore, based on laboratory and field observations it is known that a female Microtus can conceive her first litter when she is between four and five weeks of age. It is also known that mean litter sizes will probably range between three and five. Assuming a 50:50 sex ratio, it is possible, with the help of rather simple arithmetic to project the numbers that could be attained if a breeding population produced one,
two, or three litters that would enter the breeding population in the year of their birth. A case in point is the outcome of the 1975 breeding season. Due to the abnormally late onset of that spring, only one, and certainly no more than two, litters matured and bred in the year of their birth. The result was rather dramatic. In the fall of 1974 there had been every indication that in 1975 there would be an increase in the population density (especially since a decrease in density—not a true "crash"—had occurred from 1973 to 1974). Because of the late spring and the consequent delay in the onset of breeding, the population density turned out to be lower in 1975 than it had been in 1974. Conversely, the early onset of breeding in the spring of 1976 resulted in a population density that by the end of the summer readily exceeded the density of 1974 (although it never reached that of 1973). This increase took place despite the fact that whereas the mean litter size for subadult females was 5.6, for adult females it was only 5.5. However, the adult females made up 75% of the breeding female population. It also indicated that these were animals that had been contributing to the population since the beginning of the breeding season.

Doubtless the fluctuations in the population density of Microtus are affected by numerous variables. Nevertheless, it has become quite apparent that it is the reproductive success that will, in a large measure, determine the dynamics of the multiannual cycle of population density of microtines. Furthermore, it is also clear that the reproductive responses of these rodents are basically a reflection of their environment. In other words, environmental variables exert a profound effect on microtine population dynamics by governing the reproductive responses of the animals.

Probably two of the most important environmental variables known to affect reproduction and sexual maturation in Microtus are photoperiod and diet (Negus and Pinter 1966; Pinter and Negus 1965; Pinter 1968; 1968a). The seasonal changes in the reproductive responses of these rodents under natural conditions, as observed during the course of the present study, can be explained on the basis of such laboratory findings. Gonadal recrudescence in the spring probably occurs in response to the lengthening photoperiod.

However, it is not until the appearance of the first vegetative growth that reproduction begins on a population wide basis. This explains the variability in the onset of breeding from one year to the next. As yet unidentified substances in new green plants have a stimulating effect on the reproductive responses (including sexual maturation) in Microtus. It is also the interaction of photoperiod and of nutrition that may explain the failure of young, born after the first week in July, to mature in the year of their birth. Such young are growing up at a time of decreasing photoperiod. Green plant food is still plentiful. As some of the preferred plant foods of Microtus reach their fruiting stage and begin to dry, the substances in these plants that exert a stimulating effect on the reproductive system are known to disappear from these plants. However, Microtus are opportunists when it comes to food selection. They continue to select whatever green vegetation may be available, for as long as it
it remains available. It is noteworthy that if breeding occurs during the fall, it is confined only to full adult animals. It would seem, therefore, that once the reproductive system has been activated by photoperiod (and by tropic substances in green plants), it is not readily suppressed by shortening daylength and a decrease in the availability of green plant food. On the other hand, a decreasing photoperiod and the drying of vegetation effectively delays or even totally prevents sexual maturation of voles born and reared under these conditions.

It is not difficult to envision the adaptive significance of the reproductive responses of Microtus. One might view the variables, photoperiod and nutrition (say, in the spring), as being the coarse and the fine adjustment, respectively, on the microscope. In the spring it is photoperiod (actually, the increase in daylength) that initiates gonadal recrudescence of the reproductive system, very much the same as the coarse adjustment on the microscope brings a slide into general focus. However, photoperiod is a "constant" variable - at a given geographical point, on a given date, there will always be the same number of hours of light and of darkness. On the other hand, local climatic conditions are far more variable from year to year. It is obvious that a reliance strictly on photoperiod as a cue for the initiation of reproduction might have disastrous repercussions on the outcome of the reproductive effort (although a tiny proportion of the animals may achieve gonadal competence and actually begin breeding solely in response to photoperiod). Consequently, Microtus have evolved the capability of using a second cue - the onset of spring vegetative growth - as the ultimate signal. As a result, reproduction on a population-wide basis is triggered by the availability of green plant food, the same as the fine adjustment on a microscope brings the slide into ultimate sharp focus. As a result, young will be produced as soon as - or, only when - conditions are optimal for their survival, growth and maturation (indeed, laboratory studies have demonstrated that young born under a long photoperiod and provided with new green vegetation in their diet, will grow and mature significantly more rapidly than those young which lack one or both of these environmental resources, Pinter and Negus 1965; Pinter 1968). Consequently, by utilizing a coarse adjustment (photoperiod), and the ultimate fine adjustment (diet) Microtus have evolved a highly effective mechanism that permits them a very fine degree of adaptation to a changing environment.

Conversely, the failure of late born young to mature in the year of their birth prevents the production of large numbers of further young just before winter, when food and suitable habitat may become a severe limiting factor. Incidentally, laboratory studies have also shown that a winter pelage can be produced only by sexually quiescent individuals - another adaptive advantage for the cessation of reproductive activity in the fall (Pinter 1968a).
All of the above is not to say, however, that multiannual cycles in population density of microtine rodents are governed solely by environmental variables acting on the reproductive performance of these animals. Clearly there are other means whereby the environment can and does act on a population, affecting both, the length as well as the amplitude of a given cycle. Furthermore, environmental variables may be superimposed on something far more basic - that is, the genetic quality of the individual. In other words, it is quite conceivable that there is a genetic difference between animals that constitute the population during different phases of the cycle.

Next year (1977) should prove extremely interesting. For the first time since 1969 the potential exists for the Microtus to achieve a high peak in population density. However, this potential at the moment resides solely in the number of animals. It will be realized only if it is combined with the appropriate set of climatic circumstances. In 1977 these should include an early spring, and abundant rainfall during June and the first part of July (a drought during these months in the summer, as in 1973 and 1974, severely depresses the growth of the herbaceous vegetation and, in turn, causes a similarly severe inhibition of reproduction). There should also be no catastrophic climatic conditions that might decimate the numbers of Microtus before the onset of the breeding season (as in later winter - early spring of 1972, when an unseasonable "heat wave" caused extensive melt off and subnivean flooding, followed by a hard freeze; there is evidence that large numbers of Microtus probably died from exposure). Consequently, once again it will be the environmental variables, acting principally through the reproductive response of Microtus, that will be the main factor in determining the amplitude and the length of the multiannual cycle currently under investigation.

The views expressed in this report have been presented in sections earlier, as data became available during the course of this study, and gradually permitted their formulation (Pinter 1974; 1976; 1976a).
LITERATURE CITED


Pinter, Aelita J. 1974 Some aspects of population dynamics in the montane vole, Microtus montanus (Rodentia). First International Theriological Congress, Moscow, USSR, 6-12 June 1974 (abstract).

