

Tracking or Delay Effects in Microtine Reproduction?

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HANSSON L., 1989: Tracking or delay effects in microtine reproduction? Acta theriol., 34, 8: 125—132, [With 2 Tables].

Onset and duration of microtine reproduction varies with the cycle phase in cyclic populations and is temporally stable in non-cyclic populations. This reproductive variation has been related to annually more or less varying growth rates, including varying contents of chemical stimuli of food plants, or to effects of maternal condition, especially nutrition, on the reproductive performance of the succeeding generation. To distinguish between these two explanations, immatures of *Microtus agrestis* were caught at annual density peaks in south Sweden and were kept under constant laboratory conditions but natural light and on a simplified food with stable composition for one year or until reproduction ended. Their young were kept in exactly the same way. The second generation animals showed a two month earlier start of reproduction and common winter breeding but not higher reproductive output than their mothers. Neither start nor end of breeding in these animals could have been due to chemical cues alone. It is concluded that delay effects will be especially important in cyclic populations but that at present we are unable to evaluate the varying effects of delay, tracking and social influences on the overridingly important photoperiodic regulation of reproduction.

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1. INTRODUCTION

Microtine populations often fluctuate strongly in numbers and concurrently timing of and output from reproduction varies considerably (Krebs & Myers, 1974; Hansson & Henttonen, 1985a; Stenseth *et al.*, 1985). There are, however, many stable microtine populations, with only seasonal variations in numbers, and reproduction is also a more stable process under such circumstances (Nyholm & Meurling, 1979). Negus *et al.*, (1986) have recently argued that stable reproductive and, as a suggested consequence, demographic conditions arise in environments which are climatically or hydrologically/edaphically stable. The food plants there always start growing at the same time of the year and microtines track plant growth by reacting to cueing chemicals in the plants, perhaps especially 6-MBOA.

Such conditions were suggested for spring-fed grasslands and humic islands and were assumed to be applicable to microtines mainly eating monocotyledons. In climatically more variable areas such microtines

should respond to the phenology of their preferred food plants and the consequent varying beginning of reproduction should cause "pseudo-cyclic" population performance and dynamics due to varying cohort production.

Reproduction is consistently starting late, and is of short duration, in peak compared to increase cyclic populations (Hansson & Henttonen, 1985a). Increasing populations often show winter reproduction (Hansson, 1984a). From such observations of regular reproductive changes in vole cycles, Hansson (1984b) suggested that maternal conditions influence thus difficult to distinguish between the hypotheses offered by Hansson mothers in early increase years were supposed to be in good nutritional condition and should reproduce early independent of plant phenological states, and females in presumably bad shape, from late increase to peak cyclic densities, should not become mature until late in the following spring-summer independent of external conditions. From these ideas it was also predicted that numerically stable populations should show regular breeding seasons and a recurrent cohort pattern. It seems thus difficult to distinguish between the hypotheses offered by Hansson (1984b) and Negus *et al.* (1986) by field observations, at least on stable microtine populations. However, breeding of young from mothers in different nutritional states under constant laboratory conditions, including the same food, should disclose the most important factor.

The field vole *Microtus agrestis* (Linnaeus, 1761) occurs in noncyclic populations in south Sweden but in strongly cyclic ones in north Scandinavia (Hansson & Henttonen, 1985b). Immature animals from a south Swedish population were caught at autumn seasonal density peaks and kept under constant conditions for one year or until reproduction ended. Their young, born in the laboratory in late summer-early autumn next year, were treated in the same way, with the only difference that the second group had well-nourished mothers with a constant food surplus. Differences in reproduction between these two groups would thus demonstrate delay effects while food tracking should not provide any significant variation but presumably a seasonally very even pattern of reproduction.

2. METHODS

The voles were caught in their preferred grassland habitat (mesic abandoned fields) at Revinge (56° N) in south Sweden in the early autumns of 1980-83 and were kept as monogamous pairs in laboratory mouse cages on only laboratory mouse pellets and water at 20°C and in natural light. Laboratory mouse pellets consist mainly of cereals and do not contain any green vegetation or hay but

wheat sprouts instead. The chemical composition included 22% protein, 52% digestible carbohydrates and 4% crude fibres and mineral and vitamin supplements.

The animals were monitored continuously by daily inspection of the cages. The maturation of the females, *i.e.* vaginal opening, was observed during a regular weighing program (Hansson, 1987). The date of birth of the first litter was recorded for each animal as were the dates and number of succeeding litters and litter sizes at birth. The litters were weaned at 15 days of age (*cf.* Myllymäki, 1977).

3. RESULTS

In wild-caught animals, 63% out of 27 pairs produced young, while 81% of 26 laboratory-born pairs reproduced. This difference is not significant.

Both maturation and birth of the first litter were much earlier in spring in laboratory-born than in wild-caught animals (Table 1). No significant difference appeared in the length of the breeding period, in part due to fairly variable breeding seasons which even included winter. Winter breeding (December-February) was very rare in wild-caught animals. It increased significantly among laboratory-born animals. Breeding ended usually at the beginning of September in both groups.

There were no significant differences in either number of litters, litter sizes or total number of young produced between wild-caught and laboratory-bred animals (Table 2). However, the number of litters was, as a mean, larger in the laboratory-born animals.

Table 1
Breeding phenology of wild-caught (wild) and
laboratory-born (bred) female *Microtus agrestis*.

Variables	Type	N	Date, days or %	SD
Sexual maturation, date	Wild	23	3.4	27
	Bred	26	9.2	53
Significance			$p < 0.001$	
First litter, date	Wild	17	9.6	49
	Bred	21	2.4	52
Significance			$p < 0.001$	
Breeding period, days	Wild	17	105	75
	Bred	21	155	102
Significance			NS	
Winter breeding, %	Wild	17	6	
	Bred	21	38	
Significance			$p < 0.05$	

Table 2
Reproductive output in wild-caught (wild) and
laboratory-born (bred) *Microtus agrestis*.

Variables	Type	N	\bar{x}	SD
Number of litters	Wild	17	5.1	2.9
	Bred	21	6.8	4.2
Significance			NS	
Litter size	Wild	88	4.5	1.6
	Bred	141	4.4	2.0
Significance			NS	
Young produced	Wild	17	23	13
	Bred	21	30	21
Significance			NS	

4. DISCUSSION

Laboratory breeding may select for special genotypes. However, both reproductive frequency and rates were high in wild-caught animals and did not differ significantly compared with the second generation in the laboratory so such a bias was small or non-existent in the present study. Already in the wild-caught animals the production of young was close to the maximum in natural population (*e. g.* Myllymäki, 1977).

Differences in reproduction between laboratory-born and wild-caught animals should thus only depend on the conditions before the capture of the wild-born mothers. At capture most of these animals still had remnants of juvenile pelage and the decisive factor must have operated perinatally, during the embryo stage, during lactation and just after weaning. Here, this factor complex is termed "maternal" even if it is recognized that nutrition shortly after weaning might also have been involved. However, time of weaning may depend on the mother's condition. Boonstra & Boag (1987) and Hansson (1987) found evidence of maternal effects on other aspects of the development and sexual maturation of *Microtus voles* and Green (1967) provided similar evidence for the laboratory mouse.

6-MBOA, stimulating onset of reproduction, was isolated from sprouted wheat (Sanders *et al.*, 1981). Thus, it should have been present all the year round for the voles examined and, had it been very efficient, reproduction should have been aseasonal. However, reproduction was very seasonal in wild-caught animals and agreed in timing well with the local natural population (Erlinge *et al.*, 1983). Thus, the photoperiod is of overriding importance in deciding the normal start of reproduction. Still, laboratory-born females with mothers on good food started reproduction two months earlier, sometimes even in mid-winter, than the

wild-caught females. In this study, chemical plant stimuli thus seemed to be of considerably less importance than maternal condition for the timing of reproduction. The number of offspring did not appear to be affected by maternal state but it should be observed that the production by wild-caught animals already agreed with or surpassed normal production in nature. The ending of the reproductive season of microtines has been suggested to depend on certain phenolic substances developing in senescing grasses (Berger *et al.*, 1977). However, the laboratory food did not contain any grass or hay and the regular ending of reproduction in early September was obviously also set by the photoperiod.

Still, chemical stimuli such as 6-MBOA have been clearly shown to affect the start of reproduction (Korn & Taitt, 1987). Possibly, temporary access to 6-MBOA might have narrowed down the dispersion around the mean start of reproduction in Table 1. Obviously, many factors can affect sexual maturation of microtine rodents. For example, in *Clethrionomys* voles ownership of a territory and social dominance seems also to be a prerequisite for physiological maturation and reproductive performance (Bujalska, 1973; Saitoh, 1981; Bondrup-Nielsen & Ims, 1986). Obviously, we are still ignorant of the relative quantitative impact of the many other influencing factors besides photoperiod.

Many North American and Central European *Microtus* populations do not show any clear pattern in cyclicity (Taitt & Krebs, 1985, Hansson & Henttonen, 1985b). *Microtus montanus* (Peale), which was examined in detail by Negus *et al.* (1986) regarding reproduction in relation to population dynamics, seems to be particularly poorly known in this respect (Taitt & Krebs, 1985, Table 7). However, cycles in north Fennoscandian *Microtus* and *Clethrionomys* species are very clearcut (Hansson & Henttonen 1985b). Possible relations between weather and vole cycles were analysed for Norwegian conditions by Myrberget (1974, 1986) who found these relationships to be ambiguous for, among others, *M. agrestis*. Neither did Fuller (1985) find any consistent effect of spring temperature on spring or late summer numbers of an irregularly fluctuating *Clethrionomys gapperi* (Vigors) population. Thus, there is hardly any evidence, apart from certain *M. montanus* populations, that the timing of microtine spring reproduction and the consequent population development is due to a tracking of food resources or stimuli.

Early maturation confers an individual fitness advantage (Pianka & Parker, 1975; Stearns, 1976) and should be favoured by selection. At early maturation young born before mid summer will mature in the year of birth and get own young the same year. Late spring maturation causes a disproportionately low production of offspring. Thus, delay

effects due to maternal condition may have profound effects on population dynamics. Even if such effects do not generate the rodent cycles, they will amplify fluctuation amplitudes (Hansson, 1987).

Acknowledgements: I am grateful to H. Henttonen and N. C. Stenseth for comments on an earlier version of this paper. The study was supported by the Swedish Natural Science Research Council.

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Received 28 August 1988, Accepted 22 November 1988.

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ROZRÓD NORNIKÓW — REAKCJA NA ZMIANY SKŁADU POKARMU CZY
EFEKT MATCZYNY?

Streszczenie

Początek i długość rozrodu u norników zmieniają się wraz z fazą cyklu w populacjach cyklicznych, są natomiast dość stałe w populacjach nie cyklicznych. Tę zmienność próbowano wyjaśnić dwoma czynnikami: (1) mniej lub bardziej zmiennym między poszczególnymi latami tempem wzrostu roślin pokarmowych oraz zawartości w nich substancji chemicznych stymulujących rozród norników, lub (2) wpływem kondycji fizycznej matki na sukces rozrodczy jej potomstwa (tzw. efekt matczyny). W niniejszej pracy starano się rozróżnić wpływ obu tych czynników na rozród nornika burego *Microtus agrestis*. Młode norniki odłowione w południowej Szwecji w czasie sezonowego szczytu liczebności trzymano w laboratorium w standardowych warunkach, lecz przy naturalnych warunkach świetlnych i żywiono według uproszczonej formuły pokarmowej, takiej samej przez cały rok bądź do zakończenia rozrodu.

W drugim pokoleniu norniki rozpoczęły rozród o 2 miesiące wcześniej niż w pierwszym i intensywniej rozmnażały się zimą (Tabela 1). Jednak całkowity wy-

siłek reprodukcyjny samic nie był większy, niż w pokoleniu ich matek (Tabela 2). Wobec tego ani rozpoczęcie ani zakończenie rozrodu nie mogło być spowodowane samymi tylko bodźcami chemicznymi. Autor wnioskuje, że wpływ kondycji matki na rozród jej potomstwa jest szczególnie istotny w populacjach cyklicznych, jednak nie jesteśmy jeszcze w stanie ocenić, jak się mają efekt matczyny, wpływ pokarmu i zawartych w nim stymulatorów chemicznych oraz zmiany socjalności norników do sezonowych zmian warunków świetlnych, które najsilniej regulują okres rozrodu norników.