Breeding performance in captivity of meadow voles (*Microtus pennsylvanicus*) from decline- and increase-phase populations

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A major enigma in understanding microtine cycles is the failure of decline-phase animals to increase. We compared the performance of wild-caught meadow voles and their progeny from Pinawa, Manitoba, collected from a decline year (1985) with that of animals from an increase year (1986) by breeding them in the laboratory in Pinawa (animals from both years) and in the field and laboratory in Toronto (only F_1 and F_2 animals from 1985). Overall only 35% of the 1985 females or their progeny bred in the laboratory in Pinawa compared with 100% of the 1986 females. The interval between pairing with a male and birth of litters was 2–7 months for the 1985 females compared with 3–4 weeks for the 1986 females. The poor breeding performance of 1985 females occurred only in the laboratory; in small field enclosures in Toronto all F_1 and F_2 females conceived and had litters within 3–4 weeks. In contrast, 1985 males readily sired litters either with 1986 females in the laboratory or with Toronto females in the field. We conclude that the prior experience of decline-phase females had long-term detrimental consequences for the performance of the first two generations under laboratory conditions.

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L'une des principales énigmes reliées aux cycles des microtinés est de comprendre pourquoi une population en déclin ne réussit pas à reprendre sa croissance. Nous avons comparé la performance de Campagnols des champs et de leur progéniture capturés à Pinawa, Manitoba, en nature, au cours d'une année de déclin (1985) avec celle d'animaux d'une année de recrudescence (1986) en les gardant en laboratoire à Pinawa (animaux des 2 années) ainsi qu'en nature et en laboratoire à Toronto (seulement des animaux de F_1 et de F_2 de 1985). En tout, seulement 35% des femelles de 1985 ou de leur progéniture se sont reproduites en laboratoire à Pinawa, alors que 100% des femelles de 1986 se sont reproduites. L'intervalle entre l'accouplement avec un mâle et la naissance des portées était de 2–7 mois chez les femelles de 1985, alors qu'il n'était que de 3–4 semaines chez les femelles de 1986. La mauvaise performance reproductrice des femelles de 1985 ne s'est produite qu'en laboratoire; dans de petites enceintes en nature à Toronto, toutes les femelles de F_1 et de F_2 ont conçu et mis bas en moins de 3–4 semaines. En revanche, les mâles de 1985 se sont reproduits avec succès avec les femelles de 1986 en laboratoire ou avec les femelles de Toronto en nature. Nous concluons que l'expérience antérieure des femelles de la phase de déclin a entraîné des conséquences néfastes à long terme sur la performance des deux premières générations dans des conditions de laboratoire.

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Introduction

The failure of low-phase populations of voles and lemmings to increase following population declines has puzzled biologists for many years. Attempts to explain this phenomenon by means of field data have rarely been successful (Mihok et al. 1985). Similar difficulties have been encountered in setting up and interpreting relevant field experiments (Chitty 1987). Hence, many of our insights have been obtained from opportunistic monitoring of field populations at the time of major declines (Mihok et al. 1988).

In Scandinavia, researchers have compared populations of the same species that display different patterns of demography in a geographic gradient (Gustafsson et al. 1983; Gustafsson and Batzli 1985; Hansson and Henttonen 1985; Hansson 1987, 1990). A few experiments have also been conducted in the laboratory to differentiate between genetic and environmental factors that influence the characteristics of individuals (Boon-

stra and Boag 1987; Spears and Clarke 1988). Although various insights have been gained, there is still no consensus on the mechanism(s) responsible for maintaining the extended low phase in microtine populations.

Population declines and extended lows during the breeding season are often characterized by poor juvenile survival and growth (see Krebs and Myers 1974 for a review). Poor maternal condition has been suggested as a cause for this poor juvenile performance (Chitty 1952; Hansson 1984; Boonstra 1985). Recent field studies in other mammals have provided considerable support for the idea that maternal condition can have permanent repercussions on the total fitness of offspring, overriding genetic contributions to individual differences (Albon et al. 1987; Mech et al. 1987, 1991; Fryxell et al. 1991). In this study we were able to examine the long-term reproductive performance of animals from different phases of a population fluctuation under standardized conditions in the laboratory.

At the end of a long-term study of the biology of meadow voles (*Microtus pennsylvanicus*) we observed a sharp contrast in population dynamics between 1985 and 1986 (Mihok et al.

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1988). In the 1985 breeding season, the vole population remained stationary at an extremely low density; in 1986 it expanded at a phenomenal rate. In 1985 we initiated a breeding colony from these decline-low-phase animals for unrelated research in immunology (Mihok and Schwartz 1991a, 1991b) and added to it with increase-phase animals caught in 1986. We therefore were able to compare the breeding performance of animals coming from populations in which the demography was radically different. Though these differences have been observed just as dramatically in previous field studies (Krebs and Myers 1974), this is the first time they have been documented thoroughly in the laboratory. Hence, though these contrasts were not planned, we have analyzed data from this colony to gain insight into the mechanisms that might account for the population phenomena observed in the field.

Materials and methods

Source populations

Decline-phase voles were obtained by livetrapping in eight meadows near Pinawa, Manitoba, in early June and July 1985. The meadow vole population had experienced a severe winter decline followed by a 1-year period of extreme scarcity throughout 1985. A similar period of low density last occurred in 1971–1972 (Mihok et al. 1985). During the 1985 breeding season, the population increased only 3-fold, from a spring density of 3.9 ± 1.2 (SE) voles/ha to an autumn density of 10.2 ± 1.5 voles/ha (Mihok et al. 1988). Increase-phase voles were obtained at the start of breeding in May 1986. The 1986 population increased 56-fold from a similarly low spring density of 3.6 ± 0.7 voles/ha to an autumn density of 201.7 ± 22.0 voles/ha (Mihok et al. 1988).

Animal husbandry

Wild-caught females were transferred to the animal care facilities at the Whiteshell Nuclear Research Establishment, Pinawa, and before being paired with a male were allowed to wean litters conceived in the wild. Breeding pairs were maintained in large opaque plastic cages ($38 \times 48 \times 20$ cm) on a 16 h L : 8 h D cycle in a brightly lit room (daylight spectrum fluorescent light) with a high rate of air exchange. Temperatures were maintained between 16 and 22°C, at about 40–80% relative humidity, depending on the season.

Hardwood shavings were used as a bedding material, and Purina 5321 rabbit pellets were provided for food, along with a weekly supplement of carrots. Initially, we used Terylene fibre as a nesting material. This was discontinued in October 1985 in an attempt to improve breeding performance. As a substitute nesting material, and as a supplemental source of food and cover, we filled cages with large amounts of alfalfa hay. In December 1985, we also began a weekly supplement of sprouted wheat, in addition to carrots. This regimen was maintained until the colony was closed in October 1986.

Cages of breeding pairs were cleaned every 3–4 weeks, or at the time that litters were weaned. Voles were weaned mostly at 3 weeks of age. At weaning, they were isolated in medium-sized cages. New pairs were established in large cages as required, usually when voles were about 6–10 weeks old. As much as possible, pairs were established from voles originating from the same generation, but from different parental lineages. Initially, breeding pairs were disturbed as little as possible. When pairs failed to produce litters after 1–2 months, we weighed and examined the female every 1–2 weeks to ensure that litters were not being cannibalized and therefore going undetected. Once producing, pairs were disturbed as little as possible. Hence, we rarely counted young at birth.

On 10 May 1986, 40 voles (20 males, 20 females) from the 1985 F₁ and F₂ generations were sent to the University of Toronto for a comparative breeding study (P. T. Boag and R. Boonstra, unpublished data). Initially, pairs were set up in the laboratory, but because of poor breeding performance many were transferred to small outdoor breeding enclosures with natural turf (see Boonstra and Boag

1987 for details of these enclosures). Pinawa females were bred to either Pinawa males or to males from the Toronto area. When pregnant, the females were returned to the laboratory to litter and rear their young in conditions similar to those found at Pinawa.

Results

Fate of the wild voles

The decline-phase parental generation from June–July 1985 consisted of 17 wild females and 14 wild males. Judged by their body weights, about half of these individuals had overwintered. Although voles were surviving poorly in the field (21%/4 weeks; Mihok et al. 1988), they survived moderately well in captivity (80%/4 weeks). Two productive females and a few males were kept until October 1986; most of the remainder were killed for DNA studies in October 1985 (Plante et al. 1987). Decline-phase individuals were bred through to the fourth generation, but sufficient sample sizes for statistical analysis were obtained only for the first two generations.

The increase-phase parental generation from May 1986 consisted of 14 wild females and 7 wild males. All of these voles had overwintered. One male died within the first month; most of the remaining voles survived until they were killed in October 1986. No data were obtained on field survival rates, but these must have been excellent given the phenomenal rate of population growth. Once they had littered, females were paired with either increase-phase wild males (1986) or decline-phase laboratory-born males (1985). Only a few pairings were made between offspring of the 1986 wild stock.

Breeding performance of wild voles

Only 3 of the 12 wild 1985 females that survived in captivity produced litters after being paired with a male in the laboratory (Table 1). Five of the nine “nonbreeding” females had already successfully weaned a litter conceived in the wild. These nonbreeders were paired for an average of 14 weeks before being killed. The two long-lived females produced only 13 litters with 49 weaned young in 1 year (average interlitter interval of about 2 months); the other female produced only 1 litter.

Ten of the 14 wild-caught females from 1986 were pregnant at capture; all weaned their litters. Eleven females were subsequently paired with males from 1985 or 1986. All 11 bred prolifically, with fertile matings occurring mostly within the first week, followed by litters at 3- to 4-week intervals. Overall, they produced 122 young from 26 litters with a mean pairing time of only 9 weeks (Table 1). Output of weaned young was 1.29 per female-week (Table 1). This was close to the maximum possible for meadow voles (1.86 per female-week, assuming an average litter size of 5.57 (from the mean of all wild conceived litters, Table 2), 21-day gestation, and postpartum insemination).

Breeding performance of laboratory-born voles

In total, 443 young were weaned from 105 litters during the lifetime of the laboratory colony: 287 young were used in experiments (Mihok and Schwartz 1989, 1991a, 1991b), 28 young died soon after weaning, and the rest were used for breeding. Breeding was attempted with half of the voles descended from the 1985 decline-phase population. Altogether, 54 females were paired for an average of 31 (F₁), 34 (F₂), or 15 (F₃) weeks. Only 20 females produced litters (37%), and only 17 (31%) weaned any young (Table 1). In all but a few individuals,

TABLE 1. Breeding performance in captivity of female meadow voles (*Microtus pennsylvanicus*) originating from decline- and increase-phase populations at Pinawa, Manitoba

	No. of females not breeding	No. of females breeding		No. of litters surviving to weaning	Total no. of young weaned	Mean time of pairing (weeks)	Mean no. of young weaned per female-week*
		Not weaning litters	Weaning litters				
Decline phase (1985)							
Wild	9†	0	3	14	54	36	0.50
F ₁	20	0	9	26	96	31	0.34
F ₂	14	3	7	13	53	34	0.24
F ₃	0	0	1	3	5	15	0.33
Increase phase (1986)							
Wild	0	0	11	26	122	9	1.29
F ₁	0	2	2	4	14	9	0.78

NOTE: Breeding performance was assessed only for pairs kept together for at least 10 weeks; litters conceived in the wild were not tabulated for wild voles.

*Total no. of young weaned divided by cumulative time (in weeks) that all females weaning litters were paired with males.

†Five of these had been pregnant in the wild.

TABLE 2. Litter sizes at weaning in captivity of meadow voles (*Microtus pennsylvanicus*) originating from decline- and increase-phase populations at Pinawa, Manitoba and data from previous laboratory colonies from the same area

	Mean $\pm$ SE	Sample size	Source
Litters conceived in captivity			
1969	4.77 $\pm$ 0.34	30	S. L. Iverson, unpublished data
1972	3.57 $\pm$ 0.17	143	
1985–1986			
All	3.95 $\pm$ 0.16	88	Present study
1985			
Wild	3.86 $\pm$ 0.38	14	
F ₁	3.69 $\pm$ 0.26	26	
F ₂	4.08 $\pm$ 0.61	13	
1986			
Wild $\times$ 1986 male	4.50 $\pm$ 0.33	8	
Wild $\times$ 1985 male	4.68 $\pm$ 0.27	19	
Litters conceived in the wild			
1985, decline phase	4.14 $\pm$ 0.68	7	
1986, increase phase	6.60 $\pm$ 0.43	10	

NOTE: Four pregnant overwintered females captured in May 1985 had embryo counts of 5, 5, 5, and 6. Mean litter size at birth was 3.82 $\pm$ 0.15 in Iverson's 1972 colony.

production was sporadic, with long delays between litters. Some females produced 1 litter only, at an age of 6–7 months.

A small increase in the percentage of breeding occurred between the F₁ and F₂ generations (31 to 42%), but this difference was not significant. Given the relatively small numbers of females breeding, we were surprised to find that female lineages of the most prolific mothers did not dominate successive generations. The 7 granddaughters producing the F₃ generation (Table 1) could be tracked back to 3 daughters of 2 of the original 8 wild females that weaned litters. One of these came from a prolific mother and two came from a mother that did not breed in the laboratory. In contrast, males contributing to the F₃ generation came from diverse backgrounds, with most of the original voles represented.

Virtually every male produced in the colony became sexually mature at 1–2 months of age. However, owing to poor female productivity, few of the 1985 F₁ and F₂ males (36%) sired litters with 1985 females. When paired with 1986 wild females, all 9 males sired litters; 4 of these males had not sired litters previously.

Owing to the prolific output of the 1986 wild voles, we bred

few of the increase-phase offspring. In the F₁ generation, 4 females were paired with males for an average of 9 weeks. Two pairs produced 6 litters and two produced 1 litter each.

Owing to initially poor breeding of the 1985 voles, the majority of the breeding data were collected from December 1985 onwards (Fig. 1). The poor breeding of 1985 F₂ females occurred at roughly the same time, and under the same conditions of animal care, as the prolific breeding of 1986 wild-caught females (Fig. 1). If the percentage of 1985 F₂ females producing litters (42%) is compared with that of 1986 wild-caught females (100%), the differences are highly significant (Table 1, $\chi^2 = 8.4$, $P < 0.004$).

Litter sizes

Litter sizes at weaning for all litters conceived in the laboratory did not differ significantly from previous experience with captive breeding of voles from our study area (Table 2). We also found no significant differences in litter sizes based on the phase of the original population, the generation of the mother, or the parity of the mother (ANOVAS). However, the first litters of the 1986 increase-phase voles that were conceived in the

FIG. 1. Dates of birth of litters born in captivity to meadow voles (*Microtus pennsylvanicus*) originating from decline-phase (1985) and increase-phase (1986) populations at Pinawa, Manitoba.

wild but born in captivity were roughly 2 individuals larger than subsequent litters sired in captivity by 1985 or 1986 males (Table 2, $F = 10.2$, $P < 0.001$, $df = 2, 34$).

The large, wild-conceived litters of increase-phase voles in 1986 contained an excess of males (40 males vs. 26 females), in contrast to a slight excess of females in wild-conceived litters of decline-phase 1985 voles (12 males vs. 17 females). Differences between 1985 and 1986 wild-conceived sex ratios of litters were not significant ($X^2 = 2.3$, $P = 0.13$). Subsequent litters conceived in captivity had unbiased sex ratios (total of 170 females and 161 males), with no significant trends relating to phase of the original population, generation, or parity.

Breeding performance of laboratory-born voles in Toronto

Initially 10 pairs of F_1 and F_2 progeny from 1985 wild-caught mothers were set up for 38 days in the laboratory in Toronto, but only 2 produced litters (1 F_1 and 1 F_2 female; mean time between introduction of male and parturition was 33 ± 2 days). Thirteen females and their mates (five bred to Pinawa males and eight to males from the Toronto area) were then placed into field enclosures for 19 days, retrapped, and allowed to litter in the laboratory. Ten (two F_1 s and eight F_2 s) were recovered from the enclosures, and all produced litters in the laboratory. They bred within 2 or 3 days, as the mean time between being put with a male in the enclosure and parturition was 24.2 ± 1.3 days. Therefore, significantly more females bred in the field enclosures than in the laboratory ($X^2 = 10.2$, $P \leq 0.001$). Males also readily sired litters in the field. Of the 8 males whose females were recovered from the enclosures (4 bred to Pinawa females and 4 bred to Toronto females), all sired litters. Thus, these Pinawa animals bred much more readily in the field than in the laboratory.

Litter size at birth was marginally higher in F_2 females (5.5 ± 0.56 , $N = 10$; 1 female gave birth to 2 litters) than in F_1 females (3.33 ± 0.33 , $N = 3$) ($t = 2.02$, $P = 0.07$). We could not compare litter size at weaning with that in Table 2, as litters were reduced to 6 at birth because of the research carried out in Toronto. The sex ratio was similar for litters con-

ceived in the laboratory (7 males, 9 females) and in the field enclosures (21 males, 26 females).

Discussion

This study conducted predominantly in the laboratory highlights the poor reproductive performance of females during decline years in contrast to that of females from increase years. In the laboratory, this was reflected in the poor breeding performance of the decline-phase 1985 females and their progeny relative to that of the increase-phase 1986 females. The decline-phase females had many fewer litters over time than the increase-phase females (Table 1). In contrast, breeding performance of male offspring of decline-phase females was good, being hampered only by the poor breeding performance of decline-phase females. Growth of progeny also declines during population declines (Krebs and Myers 1974) but because we did not weigh animals regularly in the laboratory, especially at young ages, we were unable to quantify differences between decline- and increase-phase animals.

This poor breeding performance of decline-phase females occurred despite supplementation of their diet with wheat sprouts from December 1985 onwards, when most of the litters in the study were produced (Fig. 1). Consumption of wheat sprouts is known to result in production of 6-methoxybenzoxaolone, a secondary plant compound that stimulates reproductive activity in herbivorous rodents, including microtines, in both the laboratory and field (reviewed in Korn 1989). Thus, the decline-phase females showed little if any response to this compound and the differences we observed between years cannot have been due to a difference in food supplements.

In the field, poor juvenile survival characterizes years of population decline in microtines (Krebs and Myers 1974). Population growth is directly tied to juvenile survival (Krebs 1971; Gaines and Rose 1976; Gaines et al. 1977). Although the breeding season may be shortened in decline years (Krebs and Myers 1974), female microtines do appear to breed regularly, but young do not survive well. Evidence during the decline suggests that lactation and maternal condition have deteriorated and that these have their impact at weaning (Godfrey 1955; Hoffmann 1958; Chitty and Phipps 1966; Boonstra 1985; Bondrup-Nielsen and Ims 1988). Thus, poor juvenile survival and growth is a key determinant of the decline low phase in microtines and appears to be related to maternal condition.

The contrast in breeding performance in the laboratory between the 1985 and 1986 females indicates that the 1985 females were much more sensitive to the conditions of the laboratory. The 1985 females and their progeny bred poorly in the laboratory in both Pinawa and Toronto, but when they were taken to small field enclosures with natural grass in Toronto, they bred immediately. The laboratory imposes some negative conditions on breeding animals, such as a common olfactory environment; this is obviously one variable we were eliminating or reducing out-of-doors. Space is also presumably a critical constraint in a laboratory cage, but we see no reason why increase- and decline-phase voles would react differently to this feature of the laboratory setting. In both cases, these 1985 and 1986 voles originated from very low density populations, and hence should have reacted in a similar fashion to space constraints.

Pheromones play a central role in the prevention or induc-

tion of estrus and in the maintenance of pregnancy in a number of rodent species (Bronson 1989), including *M. pennsylvanicus* (Baddaloo and Clulow 1981). Getz et al. (1983) found that reproductive development of young females was inhibited by primer urinary pheromones produced by other voles. Primer pheromones from male voles are known to have at least two effects: to elicit LH and estradiol secretion to prepare the female for ovulation following copulation (Dluzen et al. 1981; Carter et al. 1986) and to block pregnancy when a female is exposed to the odor of a strange male (Stehn and Richmond 1975). It is possible that 1985 females and their progeny were more vulnerable than the 1986 females to the mix of olfactory signals from adjacent cages of males and females in the laboratory and that this blocked estrus or interfered with the normal hormonal balance required to maintain pregnancy.

The ultimate cause for the differential response of 1985 and 1986 females and their progeny in the laboratory is unknown. The original 1985 females were survivors and first-generation progeny of a population that had just experienced a severe overwinter decline (Mihok et al. 1988); the 1986 females were a number of generations removed from the 1985 field generations, but were somehow capable of initiating a rapid increase. There is a great deal of laboratory evidence with rats and mice that stress occurring during pregnancy can have long-term, irreversible consequences for progeny behavior and reproductive performance (e.g., Ward and Reed 1985; Fride et al. 1986; Crump and Chevins 1989; Takahashi et al. 1990) and that these effects can last for at least two generations (Pollard 1986). Stresses occurring prior to pregnancy can also affect offspring performance (Christian and LeMunyan 1958). In our case, conditions experienced by the females prior to pregnancy may have made them more susceptible to laboratory conditions (differential reactions to space, handling, odors, etc.) and less able to breed. The importance of maternal, non-genetic effects was highlighted in the study of Boonstra and Boag (1987) on *M. pennsylvanicus*, in which females obtained during the spring of an increase-phase population produced slower growing young in the optimal conditions of the laboratory than did females obtained from the spring of a peak-phase population.

In the past, there has been some criticism of the ideas and methodologies of Christian (1980) concerning the role of stress in population regulation (summarized in Lee and McDonald 1985). Nevertheless, recent evidence obtained by measuring hormone levels in breeding field populations of *M. pennsylvanicus* with radioimmunoassay supports some of Christian's hypothesis. Specifically, in populations at high density, males and females had higher total corticosterone levels, lower levels of corticosterone binding globulin (the protein that normally binds corticosterone and prevents it from being active), and higher free corticosterone levels than populations at low density (Boonstra and Boag 1992). Whether these hormonal differences between females at low and high densities translate into differences in survival, growth, and reproduction of their progeny remains to be determined. The high-density conditions experienced by half of the original 1985 females in the year of their birth (1984) may have had long-term consequences for their progeny, in spite of the fact that the latter were born under low-density conditions.

Our results clearly call into question the necessity of extrinsic agents in population declines and periods of low numbers. Factors such as predation, which has been invoked as the

cause of declines in northern Scandinavia (e.g., Erlinge et al. 1984; Henttonen et al. 1985), and lack of food, which is still regarded as an explanation by some (Hestbeck 1982; Ford and Pitelka 1984), cannot explain the poor reproductive performance of the 1985 females and their progeny under benign conditions in the laboratory. Similarly, our success in breeding decline-phase males with increase-phase females and with Toronto females suggests that genetic explanations for the decline (Chitty 1987) are unlikely.

One of the great puzzles of microtine fluctuations is the nature of the factors that permit the population to recover from the decline. If the 1985 animals and their progeny were indeed less fit than those from 1986, how did 1985 animals eventually give rise to 1986 animals and the period of rapid increase? Perhaps the negative maternal environment is gradually eliminated in successive pregnancies by succeeding cohorts in what is essentially an optimal, uncrowded environment.

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