Infanticide in Microtines: Importance in Natural Populations

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Summary. To test the hypothesis that the incidence of infanticide should increase as population density increases in microtines (Mallory and Brooks, 1978), an index of pregnancy success was developed. There was no negative correlation between population density and pregnancy success in four species of *Microtus* and thus the hypothesis is refuted. There was a positive correlation between instantaneous growth rate and pregnancy success in *M. pennsylvanicus* and *M. townsendii*.

Introduction

In natural populations of lions (Bertram 1975) and langurs (Hrdy 1974), strange males, when taking over female groups from resident males, often destroy the young in those groups. By such infanticide, these incoming males destroy potential competitors of their own offspring and ensure that the females quickly come into estrus. From a laboratory study on the collared lemming, *Dicrostonyx groenlandicus*, Mallory and Brooks (1978) found that a large percentage of strange males destroyed the young of females which had just given birth. They hypothesize that strange males, in causing both infanticide and pregnancy blockage (Bruce 1959), play a significant role in causing microtine cycles, and that these males gain a similar advantage to that found with lions and langurs. At low densities, these effects would be infrequent, since females would seldom encounter a new adult male; at high densities, both effects would increase. I use field data from four species of *Microtus* to examine whether infanticide increases with density.

Materials and Methods

The basic technique involved mark-and-recapture of field populations by live-trapping with Longworth live-traps for 2 days every second week throughout the year. Details of the areas trapped and the trapping techniques, which differ only slightly from one species to the next, are described in Krebs (1966), Krebs et al. (1969), and LeDuc and Krebs (1975). Obvious pregnancies and lactations were recorded. Pregnancy is relatively easy to detect from about the ninth day, after which the female gains over 50% of her non-pregnant weight (Innes 1978). Since the trapping interval was 2 weeks and age at weaning is about 18 days (Innes 1978), any female classed as obviously pregnant in one trapping session should be suckling her litter by the next. Therefore any female not lactating 2 weeks after being detected as pregnant has lost

her litter. Some females will have lost their litter but may still appear to be lactating when trapped. From lactating females removed from the field and kept in the lab until they stopped lactating and from lactating females in the lab from which their litters had been removed, I found that females retain nipples indicating lactation for only 3.33 days (95% confidence limits: 2.91–3.76 days). Therefore, since the lag time between loss of the litter and cessation of lactation is short and the variance is small, this factor should not affect the analysis. Using only females caught at both t and $t+2$ weeks, I define percent pregnancy success as:

$$\text{Percent Pregnancy Success} = \left[\frac{\text{number of these females known to be lactating at time } t+2 \text{ weeks}}{\text{females obviously pregnant at time } t} \right] \times 100$$

The analysis was carried out for the main breeding periods only. Because the number of obviously pregnant females caught during any trapping session was small, the data were pooled over the entire breeding period. Periods in which the total number of obviously pregnant females detected was less than 5 were eliminated from the analysis. Population density was arithmetically averaged over each period. Population growth rate was calculated as the average instantaneous rate of population growth per week over the period. I used all data except those for *M. townsendii* after July. After July the annual botfly infestation (*Cuterebra grisea*) affects female survival in this species (Boonstra, Krebs and Beaucham, 1980).

Results

The hypothesis predicts that there should be a negative relationship between density and pregnancy success. In none of the four species are population density negatively related to pregnancy success (Table 1); all show nonsignificant positive correlations. I therefore conclude that infanticide does not increase at higher densities. Moreover, pregnancy success in *M. pennsylvanicus* and in *M. townsendii* is positively related to population growth (Table 1 and Fig. 1). Survival of the litter past parturition may therefore be higher when the population is growing than when it is stationary or declining. The reason that the other 2 species did not show this effect is unknown, but may partly be related to small sample size.

Confinement of pregnant females in live-traps may cause abortions or resorptions of the litter. However, since the trapping technique remained constant, this effect is expected to remain constant as well. Pregnancy success differs markedly in the four

Table 1. Percent pregnancy success in four species of *Microtus* as a function of population density and population growth rate. Percent pregnancy success is defined in the text

Species	Number of periods	Percent pregnancy success		Total number of pregnant females pooled over all periods	Population density on 0.7 ha grids		Partial correlation of percent pregnancy success vs.	
		$\bar{x}$	SE		$\bar{x}$	Range	Population density	Population growth rate
<i>M. californicus</i>	7	81.0	4.9	276	110.5	27.4-221.1	+0.40	+0.19
<i>M. ochrogaster</i>	9	79.8	5.4	361	48.7	13.3-183.7	+0.09	+0.41
<i>M. pennsylvanicus</i>	15	39.6	5.0	299	59.8	7.0-211.0	+0.17	+0.65**
<i>M. townsendii</i>	15	46.4	4.7	455	100.2	23.0-294.1	+0.46	+0.52*

* $P < 0.05$; ** $P < 0.01$

Fig. 1. The relationship between percent pregnancy success and the instantaneous rate of population increase in *M. pennsylvanicus*

species: approximately 80% in *M. californicus* and *M. ochrogaster* and approximately 40% in *M. pennsylvanicus* and *M. townsendii*. Since the percentage of adult females lactating seldom falls as low as 40% in natural populations of the latter two species (Krebs et al. 1969; Tamarin 1977a; LeDuc and Krebs 1975; Anderson and Boonstra 1979), they may suffer more than the former from trap confinement.

Discussion

The expectation that pregnancy blockage and infanticide should be greater at high densities is based on the belief that females would be more likely to encounter strange males at this time. However, at high densities, adults of both sexes move less so that the number of contacts between them may be smaller (Getz 1961; Krebs 1966). Little information is available on the amount of immigration into a vole population, but what evidence there is suggests that high density populations are almost closed to immigration (Boonstra and Krebs 1978; Beacham 1979) and that those animals that do enter or are introduced are subordinate to those already present (Andrzejewski and Rajska 1972; Boonstra and Krebs 1978). Emigration rates have been measured in microtine populations (Myers and Krebs 1971; Kozakiewicz 1976; Krebs et al. 1976; Tamarin 1977b; Gaines et al. 1979), and if the assumption is made that emigration rates are equal to immigration rates (Krebs and Boonstra 1978), one would expect to see the highest immigration rates during the increase phase of the cycle and the lowest during the peak and decline phases. Therefore the largest number of strange males should be entering a popula-

tion during the increase phase; yet it is at this time when the rates of reproduction are also the highest (Krebs and Myers 1974).

There is extensive laboratory evidence in microtines that disruption of pregnancy by exposure of the female to a strange male can occur both before implantation (Clulow and Clarke 1968; Clulow and Langford 1971; Clarke et al. 1970; Mallory and Clulow 1977) and after it (Stehn and Richmond 1975; Kenny et al. 1977). In natural field populations, some evidence has been found in *M. pennsylvanicus* (Mallory and Clulow 1977). However, in *M. montanus*, Hoffmann (1958) felt that this loss was insignificant. Extensive autopsy has been collected on a number of microtine species (Hoffmann 1958; Keller and Krebs 1970; Tamarin 1977c; Rose and Gaines 1978), but with the techniques used to count corpora lutea (a dissecting microscope), it is difficult to detect whether total loss of the litter has occurred. In situations in which only one set of corpora lutea are present, one can not determine whether only one set of embryos are developing but have not yet implanted or whether they will fail to implant for reasons such as pregnancy blockage. In situations where multiple sets of corpora lutea are present, such as those which can be produced by a series of copulations by strange males (Clarke and Clulow 1973; Mallory and Clulow 1977), it should be possible to detect the loss of a set of embryos. Situations such as this are expected to occur in nature, yet in no study except that of Greenwald (1956) report cases such as this. The absence of this phenomenon suggests that pregnancy blockage prior to implantation may be infrequent. If pregnancy blockage occurs after implantation, the ability to detect it will depend on how soon after implantation it occurs and how rapidly it proceeds. However, since blockage in the lab can occur up to day 17 of the pregnancy (Kenny et al. 1977), and since autolysis and resorption of the embryos is the result of blockage (Brambell 1948; Stehn and Richmond 1975) and, as resorptions start, can take up to 3 days (Stehn and Richmond 1975), a portion of the entire litter loss should be detectable macroscopically. If it is important to microtine cycles at all, it should be reasonably frequent, especially at high densities. Hoffmann (1958) reports only 2 cases of resorption of the entire litter in *M. montanus* and 1 case in *M. californicus*. Rose (pers. comm.) reports finding no more than 2 cases of embryo resorption of the entire litter in about 1,500 autopsies of *M. pennsylvanicus* and *M. ochrogaster*. Pelikan (1970) estimates the loss of entire sets of embryos to be 4.7% in *M. arvalis*. This evidence suggests that the rates of postimplantation mortality are low. These low rates of postimplantation loss plus the high rates of pregnancy seen during the breeding season (often approaching the theoretical maximum detectable level of 71%) (Hoffmann 1958; Keller and Krebs 1970; Tamarin 1977c; Rose and Gaines 1978; Anderson and Boonstra 1979), indicates that this loss, if it does occur, plays only an insignificant or minor role in microtine population cycles.

In addition, there is evidence that pregnancy blockage does not occur while lactation is occurring (Mallory and Clulow 1977) and in natural breeding populations, the percentage of adult females lactating is also high (Krebs 1966; Krebs et al. 1969; LeDuc and Krebs 1975; Tamarin 1977c).

Poor survival of young voles is a major depressant of population growth in microtines (Krebs and Myers 1974). Death of the young may occur before or after weaning. Evidence indicates that preweaning survival is high and independent of the phase of the cycle (Hoffmann 1958; Boonstra and Krebs 1978; Beacham 1979), whereas postweaning survival is low and dependent on the phase of the cycle (Krebs and Myers 1974). Adult females rather than males may be responsible for these poor postweaning survival rates (Boonstra 1978).

I conclude that infanticide by strange males, though it may occur in microtines, plays a very minor role in causing population cycles. Pregnancy blockage by strange males at either the preimplantation or postimplantation stage, though it is more difficult to detect, is also not likely to be a major factor causing the demographic changes accompanying microtine cycles. Two significant aspects of reproduction which play a much greater role in influencing the total reproductive output of the population are changes in the length of the breeding season and changes in the age at sexual maturity, both of which vary as a function of the population cycle (Krebs and Myers 1974). The cause of the former remains to be determined and that of the latter appears to be density-dependent (Krebs and Myers 1974; Boonstra 1978).

The potential for pregnancy blockage and infanticide to occur may have influenced the social organization of microtines. Infanticide appears to offer no benefits to the female and pregnancy blockage may be beneficial under certain conditions (for a review see Schwagmeyer 1979). The relatively short life expectancy of reproductive females (probably less than 3 to 4 months) means that any loss due to either of these processes could greatly reduce their contribution to future generations. Females should therefore restrict their movements to the home range of the male that mated them and show strong site attachment when pregnant. In males, there is both a benefit and a cost involved in the ability to affect female reproduction in these ways. Males, which appear to be polygamous, benefit by being able to breed with as many females as they come into contact with. However, other males are engaged in similar endeavors, so that unless the original male protects his reproductive investment by excluding strange males, he gains little in long-term reproductive advantage. Males should therefore also show strong site attachment if females that they have mated with are present. It is to the male's advantage to have as many females within his home range as possible, but the number obtained will depend on the number and quality of other males competing for the same resource.

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