Aggressive behavior of adult meadow voles (*Microtus pennsylvanicus*) towards young

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Summary. Field evidence indicates that adult microtines, especially females, may be a major cause of poor juvenile survival and this may be instrumental in their population regulation. This suggests that males and females behave differently towards young animals. To examine how adult males, nonlactating females, and lactating females behave towards strange young, I introduced young animals into the home cage of the adults. Lactating females were most aggressive towards young; most males investigated them; most nonlactating females ignored them. However, discriminant function analysis indicated a great deal of overlap in the behavior of the classes. None of the classes behaved differently towards young of either sex. Females did not vary their behavior during lactation. Behavior varied among lactating females, with 55% showing little aggression and 20% showing a great deal. Most lactating females showed similar behavior in each of their bouts: docile females remained docile, aggressive females remained aggressive. I conclude that lactating females are most aggressive towards strange young. These results are consistent with the field evidence, which suggests that adult females depress juvenile survival and recruitment and that the main culprits are breeding females.

Introduction

Juvenile microtines generally survive poorly. Variation in juvenile survival rate is a major determinant of population growth in a number of microtine species: *Microtus ochrogaster* (Krebs and Myers 1974; Gaines and Rose 1976), *M. pennsylvanicus* (Krebs and Myers 1974), and *Synaptomys cooperi* (Gaines et al. 1977). One of the causes of these low rates is postulated to be aggressive behavior by adults towards young (Chitty and Phipps 1966). Though the evidence initially suggested that adult males might be the causal agents, it is now becoming evident that adult females may be responsible for depressing juvenile survival (Boonstra 1978; Getz et al. 1979) and recruitment (Redfield et al. 1978). In addition, adults of both sexes may also inhibit juvenile growth and maturation (Bujalska 1973; Boonstra 1978; Saitoh 1981).

Pregnancy, parturition, and lactation in females complicate experiments designed to examine behavior. In all the studies of behavior in microtines, only Clarke (1956) men-

tions maternal aggression. (Mihok (1979) does briefly discuss this in his thesis). However, it is clear from the studies of house mice, rats, and hamsters that reproductive females, especially when lactating, can be particularly aggressive towards conspecifics (for reviews see Rosenblatt and Siegel 1981; and Svare 1981). Pregnant and lactating females obviously represent a major component of the social structure of any rodent population during the breeding season and cannot be ignored in any attempt to understand the population dynamics of this group. Since the secretive behavior of voles makes direct behavioral observations in the field difficult, yet aggression by adults towards young may have major demographic consequences, I have examined the behavior of adult males, lactating females, and nonlactating females towards strange young in the laboratory.

Materials and methods

Adult animals (> 33 g) were brought in from two field sites near Toronto, Ontario. Only breeding males (with scrotal testes) ($N=21$), pregnant females ($N=92$), and nonlactating, nonpregnant females ($N=47$) were used. All voles were habituated to the laboratory conditions for at least 5 days before being tested. Pregnant females were allowed to litter before being tested. I attempted to test each animal twice and tested lactating females during the nursing period from 0 to 13 days to examine whether behavior changed over lactation. Tests were separated by at least a two-day interval. All nonlactating females had littered in the laboratory. Some of these had been previously tested while lactating, whereas others had been used for breeding purposes only. At least eight days were allowed to elapse between the time their young were weaned at 21 days and the test.

In the laboratory, all animals were maintained on a 18L:6D light cycle. Water and food (Purina Lab Chow and Purina Rabbit Chow) were provided ad libitum, and lettuce was provided twice weekly. Adults were individually housed in 50 × 18 × 12 cm clear polycarbonate cages on a bedding of hardwood chips and given cotton nesting material. Young animals (mean weight = 21.06 ± 0.28 (SE), $N=284$, range 11–30 g) used as opponents were born in the laboratory, housed with up to four littermates in 48 × 27 × 16 cm polypropylene cages, and fed on a diet identical to that of the adults. None of the young males were mature; some of the young females were perforce. All animals were tagged with fingerling ear-tags.

Behavior tests were carried out in the adult home cage, which was fronted by a large one-way-view mirror. Constant lighting was provided by a 100-W incandescent bulb suspended 80 cm above the cage. All cotton nesting material was removed during the test so that the adult would readily detect the presence of the young intruder. In bouts involving lactating females, their litter remained in the cage. The cage lid was replaced by one of clear plexiglass, and in one corner of the cage a metal tube 7 cm in diameter protruded through the lid. The tube was closed at the bottom and had a gate that could be raised from outside the cage. A young vole was placed inside the tube and allowed 5 min to settle down before the gate was raised. If the young animal did not leave within 30 s, it was gently pushed out with a ruler and the gate was closed. The bout started as soon as the young animal left the tube.

The behaviors recorded were similar to those used by Turner and Iverson (1973) and Krebs et al. (1977). The bout lasted 10 min. When events were continuous, each type of behavior was recorded only once every 10 s. The following data were recorded: (1) time to first contact; (2) number of approaches (as defined by Krebs (1970)); (3) naso-nasal sniffing; (4) naso-anal sniffing; (5) vocalizations (number of squeals); (6) groom-self (wiping of the face, ears, and body fur); (7) groom-other (sniffing and pawing of the fur of the back of the opponents); (8) pounces (springing aggressively toward the opponent); (9) uprights (standing on the hind legs at the approach of the opponent); (10) avoidances (leaping sideways or fleeing rapidly, either in response to an approach, pounce, or fight); (11) follows (moving rapidly after the other vole); (12) fights (tumbling and wrestling; attempting to bite); (13) attacks ((number of pounces + number of fights)/number of approaches (after Krebs 1970)). In addition to these forms of behavior, submissions (Krebs 1970) and wounds were also recorded, but since these were always restricted to the young, they were not included in the analysis. The behavior variables were transformed by the $(x+0.5)^{1/2}$ transformation to attempt to normalize the distributions, and all analyses were carried out on these transformed values. However, in Fig. 1 the untransformed values are presented, as the observed frequency is more readily understood. I used the appropriate computer programs of the SPSS package (Nie et al. 1975) to carry out the analysis.

Results

Comparison among adult classes

To test the hypothesis that the three classes differed in their response to young animals, I first performed an analysis of variance on each behavioral variable for all the data combined. Time to first contact (in s), which is not presented in Fig. 1 and was not significant, had the following values for males, lactating females, and nonlactating females respectively: 81.10 ± 18.24 (SE), 100.15 ± 15.90 , and 77.01 ± 9.45 . Three major points can be made from Fig. 1. First, lactating females were more obviously aggressive (pounces and fights) than adult males or nonlactating females; they were also less ready to avoid an encounter and more ready to follow. The nature of the following by lactating females was different from that of males. In lactating females, it often came after a pounce or fight and therefore could perhaps be more properly called a pursuit. Second,

Fig. 1. Response of adult *Microtus pennsylvanicus* towards young intruders. All values are presented as untransformed means ($\pm$ SE) but the one-way analysis of variance of each behavioral variable was performed on the transformed means $(x+0.5)^{1/2}$. Samples sizes are as follows: adult males – 40, nonlactating females – 78, and lactating females – 166. Significance levels are * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

in males most of the behavior could be classed as investigatory – high frequencies of approaches, follows, naso-nasal and especially naso-anal sniffing. The latter was almost absent from the other two classes. Males were seldom aggressive. Third, nonlactating females seldom investigated or fought the young.

To test the hypothesis that the mean of all the behavioral variables differed among the three classes, I carried out discriminant function analyses: one involving the data in which each animal was included only once in a class (thus the values were independent of one another), and another involving all the data in which each animal may have been included more than once. In both cases, the discriminant functions were significant and similar and I therefore present only the analysis using all the available data (Table 1). The absolute values of the standardized canonical discriminant function coefficients indicate the relative contribution of that variable to the function. For function 1, two of the investigatory variables – naso-anal sniffing and approaches – rank the highest, followed by two of the aggressive variables – fights and pounces. In the classification of the animals into the three groups, the functions were able to classify 66.2% correctly. This relatively low success rate indicates that there was a great deal of overlap in the behavior among the groups.

The response of the adults may vary as a function of the sex of the young intruder. I tested this by examining each adult group separately and dividing the bouts into those against young males and those against young females. Pairwise comparisons of each of the behavioral variables separately and of all the behavior variables together by discriminant function analysis were performed. In none of the three groups was the discriminant function significant. Neither adult males nor lactating females showed any significant differences in any behavioral variable in response to the sex of the young intruder. Nonlactating females showed significantly different responses towards the two sexes with respect to naso-anal sniffing ($P < 0.05$) and number of groom-self periods ($P < 0.05$). However, in gen-

Table 1. Results of discriminant function analysis on the three adult groups

	Function 1	Function 2
Wilks' lambda	0.576***	0.835***
Eigenvalue	0.449	0.198
Canonical correlation	0.557	0.406
Percent variation explained	69.4	30.6
Standardized canonical discriminant function coefficients		
Time	0.101	-0.161
Approaches	0.625	0.349
Naso-nasals	-0.028	-0.760
Naso-anals	0.801	0.366
Vocalizations	-0.061	0.157
Groom-self	-0.043	-0.050
Groom-other	-0.405	-0.033
Pounces	-0.431	0.021
Uprights	-0.054	0.244
Avoidance	0.315	-0.275
Follows	-0.089	0.154
Fights	-0.468	0.036
Attacks	0.236	-0.089

Classification results

Actual group	Predicted group membership (percent)		
	Adult males	Nonlactating females	Lactating females
Adult males	17 (42.5)	5 (12.5)	18 (45.0)
Nonlactating females	2 (2.6)	24 (30.8)	52 (66.7)
Lactating females	5 (3.0)	14 (8.4)	147 (88.6)

*** $P < 0.001$

eral I conclude that the adults respond in a similar manner towards both sexes of young animals.

Lactating female behavior

Females at various stages of lactation may differ in their response to young animals. This is the reason that I tried to test each lactating female at least twice. A two-way analysis of variance was performed to test whether there was a difference in the behavior between a females' first and second bout (i.e. an experience effect) and whether there were differences between females. One behavioral variable was examined at a time. There was no effect of bout number for any of the variables, and thus I conclude that experience did not systematically influence behavior. However, there were differences among females in the following behaviors: approaches, groom-other, pounces, and fights (all $P < 0.001$); follows ($P < 0.005$); and attacks ($P < 0.01$). All these variables are investigatory or aggressive, and thus some females are more aggressive than others.

To test whether female behavior varied during lactation, I carried out two analyses. In the first, two groups were formed in which the young were 0-7 or 8-13 days old. In the second, three groups were formed in which the young were 0-3, 4-8, and 9-13 days old. The formation of these groups was entirely arbitrary, but in the last analysis, I tried to divide data into a postpartum period when mating could have occurred, a main lactating period, and a final

Fig. 2. Percentage of lactating females showing various levels of aggressiveness. See text for the definition of the aggressive index

period just prior to weaning. There were no significant differences in either of these two analyses, either when each variable was tested separately or when discriminant function analysis was performed to test for an overall effect. Thus, I conclude that female behavior did not vary over the lactational cycle.

Females varied greatly in aggressiveness. To obtain an index of aggression, I added together the number of pounces, uprights, follows, and fights. If females were tested more than once, they were given an average index per bout. The mean index of aggression for all lactating females was 6.15 ± 0.88 (SE) ($N=92$, range 0.0 to 45.0). Figure 2 shows that 55.4% of the females had an index of 4 or less which indicates that most females showed little or no response to a young intruder. However, over 20% had an index of greater than 9, indicating a high level of aggressiveness. Though wounding was difficult to detect in some of the young voles because of dense short hair, I did observe it occasionally. An example of a female showing a high degree of aggressiveness was female 5096 (average index of 21), who got into 8 fights with a 15 g female intruder and delivered 14 separate bite wounds. In a subsequent bout she got into 14 fights with a 25 g male intruder and delivered 12 wounds. Thus, though most females showed little aggression towards young intruders, a substantial proportion was highly aggressive.

To get an indication of the similarity of a female's behavior from one bout to the next, I correlated the aggressive index for the first bout with subsequent ones. For all lactating females tested twice, the correlation was poor ($r=0.24$, $df=55$). The correlation was improved when I eliminated 7 females which either had a zero or low aggressive index in one bout and a very high index in the other ($r=0.80$, $df=48$). For all lactating females tested three times, the correlation was good ($r=0.82$, $df=20$). Thus although some females were unpredictable in different bouts, most were very predictable: docile females remained docile; aggressive females remained aggressive.

Discussion

Aggression towards young *Microtus pennsylvanicus* was exhibited primarily by lactating females, not adult males or nonlactating females. This is consistent with the field evidence that juvenile survival (Boonstra 1978; Getz et al. 1979) and recruitment (Redfield et al. 1978) were inversely

correlated with female density. None of these studies reports a significant relationship between male density and juvenile survival or recruitment. Beacham (1979a) suggested that adult males were the culprits in causing poor juvenile survival because the only relationship he could find in his 3 year study was a negative one between the proportion of males in his populations and juvenile survival. However, this relationship is questionable since 4 of the 12 survival estimates used in his correlation came from the spring of 1978 when he stopped trapping in June and therefore he could not have known for certain the fate of these young, and when sample sizes ranged from 2 to 8 young, in comparison with estimates from previous years with sample size of from 114 to 695 young per year. Care must be taken in field experiments designed to test the role of adult males or females on juveniles. If spacing behavior varies over a microtine fluctuation and if it has a genetic basis as proposed by Chitty (1967; see Krebs 1978 for a review), then we cannot compare experiments done in different years unless it is known that the behavior of the animals is similar in both years (Krebs and Boonstra 1978). Similar densities in different years may produce different results. Thus any experiment designed to manipulate interaction rates between animals should be done within a year.

What is the function of maternal aggression in the meadow vole? The obvious answer seems to be to protect her young. This is probably reasonable when the intruder is a strange adult male or adult female and thus it functions to prevent infanticide (Mallory and Brooks 1978, 1980; Webster et al. 1981), and in the case of other adult females, competition for space. Unlike strange adults, however, young voles seldom harm the litter. In this study I never observed a young intruder biting or behaving aggressively towards members of a litter, though in another experiment (Boonstra, unpublished), I have observed some aggressive behavior by the young intruder. There are a number of possible reasons for maternal aggression towards a strange young animal. First, by attacking strange young, a female may increase her own fitness by decreasing that of others. Second, the female ensures that the space she defends will be available for the use of her offspring while they are young. Third, the female ensures that strange young will not be allowed to attempt to nurse from her and thus deprive her current litter. Members of a previous litter, if allowed to remain in the maternal cage, may continue to suckle after the birth of a new one. In a number of species of microtines, females avoid this problem by abandoning a litter at weaning and prior to the birth of the next litter (Brooks and Banks 1971; Jannett 1978; Madison 1978) (note that other reasons for nest abandonment, such as to avoid predation, may also be involved). Savidge's (1974a) observation that lactating *Peromyscus maniculatus bairdi* females were aggressive towards a previous litter may thus be a result of the mother's inability under laboratory conditions to move to a new nest site prior to the birth of the next litter.

The large degree of variation in aggressiveness found in lactating females (Fig. 2) occurs in other species as well (Savidge 1974b; Rowley and Christian 1976; Halpin 1981; Svare 1981). The consequences of this variation in aggressiveness on the fitness of the individual females and on population dynamics is unclear. Anderson (1975), from a study on *M. townsendii* in small outdoor breeding enclosures, found that female behavior could account for as much as

50% of the variance among mothers in the mean number of young offspring recruited per litter. Savidge (1974b) found evidence to suggest that in *P. m. bairdi* mothers with an intermediate level of aggressiveness were more successful in rearing the first litter, and that aggressive mothers with a subsequent litter increased the rate of departure of her previous litter (Savidge 1974a). Dispersal plays a fundamental role in the population fluctuations in microtines (for a review see Gaines and McClenaghan 1980). There is evidence for variation in dispersal tendency among litters (Hilborn 1975; Beacham 1979b), but its cause is not known. Therefore, future work should examine whether the young from aggressive females disperse more readily, whether there is a change in the proportion of aggressive lactating females over the course of a microtine population fluctuation, and, if possible, what advantages accrue to aggressive females at different times.

A second area of interest arising from this variation in aggressiveness among lactating females is the heritability of the trait. No one has looked at lactating females as such, but some have examined the problem in other classes of adults (e.g. Anderson 1975). However, if this is the time when the adult female is most aggressive and when it may be most relevant to the dynamics of the population, this period should be used for studies on the heritability of aggressiveness. I would expect that since in many species this behavior may be under hormonal control (Rosenblatt and Siegel 1981) or a response to suckling stimulation (Svare 1981), it might be less subject to the effects of previous experience (Bekoff 1977), and thus be easier to obtain and interpret.

My experiment does not address the crucial question of how adult microtines respond to their own young nor how this response varies as a function of the sexual maturity of the young. Only Halpin (1981) has compared adult behavior towards related and unrelated young in *P. m. austerus* and she found that neither adult males nor females were aggressive towards their own young, though she does not discuss the maturity of the young. In *M. pennsylvanicus* an experiment in which lactating females are exposed to their own weaned young is technically difficult to perform because of poor breeding success in the lab. It requires that two litters be produced sequentially, the second by postpartum insemination, so that the members of the first are still young enough and immature when the second is still in the nest. Alternate methods of producing two sequential litters, such as by small outdoor breeding enclosures (e.g. Anderson 1975) should be attempted.

Because *M. pennsylvanicus* has a polygamous mating system in which males compete for access to females while females compete for access to space to raise young (Boonstra and Rodd 1983), males have home ranges which overlap extensively while females occupy mutually exclusive home ranges (Madison 1980; Webster and Brooks 1981). Thus an adult male might not know for certain the relatedness between itself and a strange juvenile (note, however, that Grau (1982) reports that in *P. leucopus*, related animals appear to recognize each other even though they have never been in contact). Under this type of social system, an adult male should not be aggressive towards immature males and females, should be aggressive towards maturing young males independent of whether these young are related to him or not because the young males are a reproductive threat, and should not be aggressive towards maturing

young females independent of whether these young are related to him or not because these young are potential breeding partners. My results and that of Getz (1972), from a study with multiple capture traps, indicate that the first of these predictions is correct. The next two await further experimentation. The consequence of the second prediction is that adult males should largely be the cause of dispersal of maturing young males (Murray 1967; Gaines and McClenaghan 1980; Greenwood 1980).

An adult breeding female should be able to recognize her own young and therefore she should be aggressive towards strange immature females for reasons given above, should be aggressive towards strange maturing females because they would be potential competitors for space and at times towards strange maturing males depending on proximity of the male to her nest site and her own sexual receptivity, and should not be aggressive towards her own immature and perhaps maturing young, though the latter is not clear. Again, only the first of these predictions was tested in my experiment and appears generally correct. If females are not aggressive towards maturing daughters, this would allow daughters to settle near to their mothers. However, this may be possible mainly at low density. As density increases, the habit of females abandoning a litter at weaning and moving to a new nest site (Madison 1978) may expose the young to aggressive behavior by other females. This argument implies that the poor survival and perhaps high dispersal of young females (Gaines and McClenaghan 1980) is not due to maternal behavior but to that of other breeding females the young encounter.

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