Journal of Animal Ecology (1987), **56,** 655–673

NATAL PHILOPATRY AND BREEDING SYSTEMS IN VOLES (*MICROTUS* SPP.)

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SUMMARY

(1) We tested the hypotheses of Greenwood (1980) and Dobson (1982) by examining natal philopatry in males and females of five species of *Microtus* from live-trapping data collected from seven areas in North America.

(2) In all species, similar or larger proportions of males than females remained near the natal site as immature animals and both sexes moved similar distances from the natal site if they remained immature.

(3) In the four mainland species of voles—*M. californicus*, *M. ochrogaster*, *M. pennsylvanicus*, and *M. townsendii*—about twice as many females as males matured near their natal site regardless of whether the mating system was monogamous or polygynous. This evidence is consistent with the Greenwood hypothesis and suggests that females in both monogamous and polygynous species primarily compete for resources, and males compete for access to females.

(4) In the island species, *M. breweri*, and in enclosed populations (some with and some without an opportunity to disperse) of *M. ochrogaster*, *M. pennsylvanicus*, and *M. townsendii*, similar proportions of males and females remained near the natal site as mature animals. Thus, preventing or reducing dispersal eliminated the bias towards female philopatry. Nevertheless, in all of these species, mature males still moved about twice as far from the natal sites as females.

(5) Males in polygynous species from control populations, if they did mature within the population, tended to move farther from the natal site than females; males in the one monogamous species showed no such difference.

(6) Thus, though male–male competition may be a primary cause of male dispersal, inbreeding avoidance may be a secondary cause. We suggest that the basic social organization in females all species is one based on female kin clusters.

INTRODUCTION

Dispersal plays a significant role in the regulation of small mammal populations (Lidicker 1975; Gaines & McClenaghan 1980), in the maintenance of genetic variability and in gene flow among subpopulations (Roff 1975; Spieth 1979), and has been implicated in rapid short-term evolutionary changes in response to density changes (Krebs 1978a; Tamarin 1980). In mammals, females tend to remain at or near the natal site and males to disperse from it. In birds, dispersal tends to be the other way round (Greenwood 1980).

Two major hypotheses have been proposed to account for this sex-biased dispersal in juveniles. Greenwood (1980) argued that dispersal depends on which sex competes for resources. If males compete for resources to attract females (as in most birds), males should be philopatric, and females should disperse, regardless of whether the mating system is monogamous or polygynous. If females compete for resources for reproduction (as in most mammals), they should be philopatric and males should disperse, regardless of the mating system. Dobson (1982) presented a second hypothesis that male-biased dispersal in mammals depends on mate competition by males. In polygynous mating systems (the majority in mammals), males should disperse and females should not; but in monogamous mating systems, similar numbers of males and females should disperse. Liberg & von Schantz (1985) proposed a slight variant of the above two hypotheses, in which they stress the importance of reproductive competition between parents and offspring and the costs of allowing young to stay. However, for the mammals we consider here, their predictions do not differ from those of Dobson (1982).

Microtines have a diversity of breeding patterns ranging from monogamy to various forms of polygyny (Table 1 and see Ostfeld 1985 for a review). Our principal objective in this study was to test the predictions of Greenwood and Dobson by examining the sex bias in philopatry in five species of voles (*Microtus*). Our second objective was to examine dispersal distances of young voles from the natal site to the site of settlement within the area trapped to obtain insights into the possible role of inbreeding avoidance as a consequence of sex-biased dispersal (Greenwood 1980; Dobson & Jones 1986).

METHODS

We analysed data from five species of *Microtus*. 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 differed only slightly from one species to the next are described in the references given in Table 1. Two studies, those of Beacham & Krebs (1980) on *M. townsendii* (Bachman) and Boonstra & Rodd (1984) on *M. pennsylvanicus* (Ord), also used pitfall traps, which are better at catching young voles. Tamarin, Reich & Moyer's (1984) study on *M. pennsylvanicus* used Ketch-all multiple capture traps.

Our analysis is based on the assumption that animals caught below a critical body weight have just emerged from the nest and entered the nearest trap. We recognize that the use of body weight to identify residents may introduce biases into the analysis (Dueser, Rose & Porter 1984; Tamarin 1984) if this assumption is not critically tested. Our weight cutoffs were extremely conservative and may have eliminated many animals that may actually have been born on the grid. However, we were interested more in obtaining a sample of relatively 'pure residents', rather than trying to identify all residents. As a result, our sample sizes are small relative to the total number of animals caught on the trapping grids in most populations. The weight below which young animals were included in this analysis was based on the criterion that less than 2% of the young males should have been judged reproductive at this weight. Sexual maturation has a major effect on movements in rodents, especially males (see Gaines & McClenaghan 1980 for a review), and the use of a greater weight would have included voles that had moved after they reached reproductive maturity. Females may mature at lower weights than males (see Keller 1985 for a review of reproduction) and our weight cutoffs may thus be more conservative for males than

TABLE 1. *Microtus* species used in the analysis

Species	Weight cutoff	No. of populations	Locations	References	Breeding system	References
M. breweri	≤ 31 g	2	Muskeget Island Massachusetts	Tamarin (1977)	?	
M. californicus	≤ 23 g	2	California	Krebs (1966)	polygynous (males territorial)	Ostfeld (1986)
M. ochrogaster	≤ 20 g	4	Indiana	Krebs, Keller & Tamarin (1969) Gaines & Krebs (1971)	monogamous (both sexes territorial)	Thomas & Birney (1979) Getz & Carter (1980)
		4	Kansas	Gaines & Rose (1976) Gaines, Vivas & Baker (1979)		
M. pennsylvanicus	≤ 22 g	3	Indiana	Krebs, Keller & Tamarin (1969)	polygynous (females territorial)	Madison (1980) Webster & Brooks (1981)
		5	Massachusetts	Tamarin (1977) Tamarin, Reich & Moyer (1984)		
		2	Ontario	Boonstra (1985) Boonstra & Rodd (1984)		
M. townsendii	≤ 26 g	7	British Columbia	Krebs *et al.* (1976) Krebs (1979) Beacham (1980)	polygynous ?	Boonstra (1977) Krebs (1978b)

females. However, our tests of the assumption indicate no differences in the recruitment of young males and females into our control populations (see below).

For *Microtus pennsylvanicus* we used three lines of evidence to test the critical assumption that the site of first capture is near the point of birth. First, in Ontario a removal grid (grid E) was trapped for 5 years near control grid A (see Boonstra & Hoyle 1986). We calculated the number of juveniles (≤ 22 g) entering the removal and control grids over the study. We expected the majority of recruits entering the removal grid to be above this weight, though some below it may have entered from immediately adjacent populations. In addition, we recognize that recruitment to a vacant area is likely to be easier than to an intact population. Second, to determine whether recruitment to an intact population is restricted, we examined dispersal into two control populations in Ontario. Control grids A and F were surrounded by a number of adjacent trapping grids and some animals from these grids dispersed onto the control grids (see Boonstra & Hoyle 1986 and Boonstra & Rood 1983 for pictures of grids A and F and adjacent grids, respectively, and for a description of the manipulations that were performed on these adjacent grids). We calculated the total number of animals that disappeared from the adjacent grids, the proportion of these that were ≤ 22 g when they disappeared, and the number and weight of these that subsequently recruited to the control grids. Third, we located nest sites in the field with a spool-and-line technique (Boonstra & Craine 1986), marked the young or removed pregnant females to the laboratory, allowed them to litter, and then reintroduced mother and marked young (< 5 days old) to the field to the same trap site at which the mother was first caught. We subsequently caught some of these young in live-traps. We then calculated the distance between the trap nearest the nest (or the trap to which the female and young were reintroduced) and that trap in which the young were first caught. This work was done at the Station for Atmospheric Experiments, just north of Toronto. In addition, McShea (1985 and personal communication) kindly made available similar data from New York. He used radiotelemetry to locate nests, marked the young, and recorded where they were first captured. His trap spacing was 10 m (ours was 7·6 m) and he calculated maternal home range by taking all the radio-locations where a female was found over a 10-h period, connecting the points, and adding two standard deviations (a conservative estimate of maternal home range—McShea personal communication). He recorded the number of trap stations from the maternal home range at which the young were caught. We expected that young entering traps below the cutoff weight should do so near the maternal home range.

Two analyses were carried out for each population of each species. First, to examine for sex-biased philopatry, we determined what percentage of males and females caught on the trapping grid became residents. Second, to examine for sex-biased dispersal distances within a population, we determined how far males and females moved from their natal site to their location of residence on the grid. An animal was classed as a resident in the population only if it was caught at least twice in a given reproductive class after its initial capture. Animals found dead in the traps were eliminated from this analysis. The initial place of capture is referred to as its natal trap site or *natal site*. Once an animal had reached the mature class, it was not again included in the immature class, even if it stopped breeding, for example at the end of the breeding season. The dispersal distance was defined as the movement distance from the natal trap site to the mean point of all captures within a trapping grid. We recognize that we can detect only a portion of all the dispersal movements because live-trapping constrains us to that portion of the vole habitat within the grid (i.e. the distribution of dispersal distances is truncated; N. Gilbert, pers. comm.).

However, from the standpoint of philopatry, we are interested only in the differences between those voles that remain near their natal site and those that do not. Voles were classed as immature if males had abdominal testes or if females had a non-perforate vagina, and were not pregnant or lactating. For mature animals, males had scrotal testes and females were either perforate, lactating, or pregnant.

We did not analyse for differences between areas or grids within a species. We recognize that such differences do occur and can be explained by variability in grid quality (percentage cover, plant species composition, soil type, etc.). For this analysis, we regarded these differences between areas as noise and instead are concerned with broad generalities between species.

RESULTS

Tests of the critical assumption

Three lines of evidence from *Microtus pennsylvanicus* support the assumption that most animals entering the traps below a critical weight are recruited near the natal site. First, we found only 10·6% ($N = 3807$) of the voles that entered removal grid E were ≤ 22 g, and only 16 of these were tagged on other grids. In contrast, 52·3% ($N = 3029$) of the voles on control grid A weighed ≤ 22 g when first caught. Clearly, small juvenile voles rarely colonize a vacant area of grassland. Second, of the 3242 animals that disappeared from grids B (1549), C (780), and D (913), 23·8% were ≤ 22 g the last time they were captured (B, 444; C, 99; D, 238). Only 47 (1·4%, 38 males and 9 females) of all tagged animals that disappeared from these three grids were subsequently caught on control grid A. Of these, ten were ≤ 22 g on last capture on their home grid and only one was subsequently trapped on control grid A at ≤ 22 g. Of the 2781 animals that disappeared from grids G (1501) and H (1280), 19·2% were ≤ 22 g the last time they were captured (G, 42; H, 492). Only 48 (1·7%; 39 males and 9 females) of all tagged animals that disappeared from these two grids were subsequently caught on control grid F. Of these, four were ≤ 22 g on last capture on their home grid and two of these were subsequently trapped on control grid F at ≤ 22 g. Clearly, dispersal of small juvenile voles into intact populations is negligible and that of larger voles is very rare. From the marking of nestlings in the field in southern Ontario, at least 95% of the young were recruited to traps within about two trap stations of the natal trap site (Table 2). W. J. McShea (unpublished data) in New York found 80% ($N = 125$) of young *M. pennsylvanicus* recruited at ≤ 22 g, did so within 10 m of the maternal home

TABLE 2. Distance moved by *Microtus pennsylvanicus* from the trap site nearest the natal nest to the first trap entered. Data from southern Ontario

Distance moved (m)	Cumulative percentage Grid A	Grid C
0	16	16
7·62	55	47
10·67	73	72
15·24	89	81
16·76	97	95
> 16·76	100	100
Total number caught	38	43
Sex ratio (males : females)	(17 : 17)	(22 : 21)
Mean distance	9·37	10·21
S.E.	0·92	1·05

range and 88·6% did so within 20 m. Finally, the sex ratios of the young (≤ 22 g) recruiting to control grids A (781 males: 802 females) and F (532 males: 543 females), and from the study of marked young in the field (Table 2) were not significantly different from 1 : 1, and since the sex ratio at birth is 1 : 1 (I. T. M. Craine, unpublished data), there appeared to be no sex bias in movement below the critical weight. This evidence indicates that the majority of young at or below the critical weight were first captured near the natal site.

Natal philopatry and dispersal patterns

Microtus breweri (Baird)

This species was the only one caught exclusively on an island and was trapped on two adjacent grids (Table 1). There was no effect of sex on the proportion of young recruited to the grids as immature animals (total chi-squared = 0·7, d.f. 2; chi-squared of totals = 0·4, d.f. 1; heterogeneity chi-squared = 0·3, d.f. 1) nor as mature animals (total chi-squared = 0·4, d.f. 2; chi-squared of totals = 0·1; heterogeneity chi-squared = 0·3, d.f. 1). Thus, within a grid, similar proportions of both sexes were recruited to the population irrespective of maturity class (Table 3).

The ANOVA analysis indicated that there were significant effects of sex and maturity on the dispersal distance from the natal trap site (Table 4). There was also a significant interaction effect between sex and maturity because mature males moved about twice as far as immature males, whereas mature and immature females moved a similar distance (Table 5).

Microtus californicus (Peale)

This species was trapped on a number of grids (Krebs 1966), but only two of the populations provided reasonable sample sizes for our analysis (Table 1). A significantly higher proportion of males than females remained on the grids as immature residents (total chi-squared = 43·3, d.f. 2, $P < 0{\cdot}001$; chi-squared of totals = 43·4, d.f. 1, $P < 0{\cdot}001$; heterogeneity chi-squared = 0·1, d.f. 1; Table 3). A significantly lower proportion of males than females remained on the grids as mature residents (total chi-squared = 22·6, d.f. 2, $P < 0{\cdot}001$; chi-squared of totals = 21·8; d.f. 1, $P < 0{\cdot}001$; heterogeneity chi-squared = 0·8, d.f. 1; (Table 3). Thus, young females had a higher probability of remaining in the population as mature animals, whereas if males remained in the population, they did so as immatures.

The ANOVA analysis (Table 4) indicated that the only significant effect was that mature animals moved farther than immatures from the natal trap site (Table 5). However, given that only 2 of the 248 young females caught remained on the area as immatures, this conclusion should be treated with caution.

Microtus ochrogaster (Wagner)

In comparing the proportion of males and females that remained on the grids for this species, we divided the analysis into control and enclosed populations (Table 3). A significantly higher proportion of males than females remained on the control grids as immature residents (total chi-squared = 17·3. d.f. 4, $P < 0{\cdot}001$; chi-squared of totals = 12·0, d.f. 1; heterogeneity chi-squared = 5·3, d.f. 3, N.S.). A significantly lower proportion of males than females remained on the control grids as mature residents, but the significant heterogeneity chi-squared indicated these differences were not equally large among all grids (total chi-squared = 27·9, d.f. 4, $P < 0{\cdot}001$; chi-squared of totals = 18·7, d.f. 1, $P < 0{\cdot}001$; heterogeneity chi-squared = 9·2, d.f. 3, $P < 0{\cdot}03$). The data obtained from

TABLE 3. Percentage of young animals caught on the trapping grids at or below the weight cutoffs that recruited to the grids as mature or immature animals. Chi-square comparisons were made within a maturity class between the sexes

	Mature		Immature		Total no. of young captured	
Species	Male	Female	Male	Female	Male	Female
Microtus breweri						
Grid A	15·0	14·0	20·0	25·6	60	86
Grid B	9·2	12·7	29·2	31·7	65	63
Means and totals	12·0	13·4	24·8	28·2	125	149
Microtus californicus						
RFS 6	8·9*	23·3	8·9*	3·8	79	120
Tilden control	8·6***	29·7	26·0***	0·0	104	128
Means and totals	8·7***	26·6	18·6***	0·8	183	248
Microtus ochrogaster						
Indiana Grid A	15·2	32·1	12·1	14·3	33	28
Grid H	22·6	36·2	11·3	12·8	53	47
Grid B†	41·0	44·0	25·6	16·0	39	25
Grid D†	76·9	67·9	20·5	25·0	39	56
Kansas Grid A	17·5**	33·9	14·0	6·8	143	118
Grid B	20·5	23·9	17·3*	8·5	156	201
Grid C	3·8*	20·0	5·8	6·7	52	45
Grid D	9·3*	20·4	11·6*	3·8	129	186
Means and totals						
Controls	15·5***	25·8	13·2***	7·2	566	625
Enclosures	59·0	60·5	23·1	22·2	78	81
Microtus pennsylvanicus						
Indiana Grid A	36·4*	49·6	33·2	25·3	184	194
Grid I	32·2	40·6	25·4	20·3	59	64
Grid B†	32·1	27·6	37·1	44·9	78	127
Mass. Grid D	11·1	20·7	15·3	9·8	72	82
Grid F	5·2*	17·7	10·4	10·1	77	79
Grid J	4·9	11·4	9·0	15·8	122	114
Grid K†	8·0	9·1	19·1	22·7	225	176
Grid L†	22·2	20·1	14·4	18·1	216	204
Ontario Grid A	9·5***	37·2	31·0***	22·0	739	760
Grid F	15·1***	30·8	53·6**	45·3	496	497
Means and totals						
Controls	14·2***	30·6	34·4***	27·3	1749	1790
Enclosures	17·9	18·1	19·8*	26·4	519	507
Microtus townsendii						
Grid C	17·1***	38·4	28·1	27·2	192	224
Grid E	14·0***	35·9	43·0	37·6	121	181
Grid I	13·5**	25·9	62·6*	51·4	155	255
Beacham A	19·9	26·3	40·9	43·0	171	186
Beacham B†	19·9	20·3	54·0*	43·9	326	297
Beacham C†	19·6	22·2	54·6	52·3	271	328
Beacham D	14·6	18·7	44·3	35·7	185	182
Means and totals						
Controls	16·0***	29·3	43·1	39·4	824	1028
Enclosures	19·8	21·3	54·3*	48·2	597	625

† Enclosed grids.
P<0·05, ***P*<0·01, ****P*<0·001.

the two enclosures were very different from those obained on the controls. There was no significant difference in the proportion of either sex remaining on the grids as immature residents (total chi-squared = 1·1, d.f. 2; chi-squared of totals = 1·1, d.f. 1; heterogeneity

TABLE 4. Analysis of variance tables to test for non-random movement from the natal trap site in *Microtus* species. Unless specifically indicated all analyses are for control grids

Microtus	Source	d.f.	Mean square	*F*	*P*
M. breweri	Maturity	1	32·6	5·28	*
	Sex	1	97·7	15·83	***
	M × S	1	50·1	8·13	**
	Error	104	6·2		
M. californicus	Maturity	1	54·3	8·76	**
	Sex	1	9·7	1·56	N.S.
	M × S	1	0·4	0·07	N.S.
	Error	114	6·2		
M. ochrogaster	Maturity	1	104·0	13·77	***
	Sex	1	5·2	0·68	N.S.
	M × S	1	9·3	1·24	N.S.
	Error	365	7·5		
Enclosures	Maturity	1	250·4	17·58	***
	Sex	1	16·2	1·24	N.S.
	M × S	1	66·9	5·11	*
	Error	127	13·1		
M. pennsylvanicus	Maturity	1	279·7	39·78	***
	Sex	1	253·4	36·04	***
	M × S	1	66·9	9·51	**
	Error	1880	7·0		
Enclosures	Maturity	1	278·2	35·05	***
	Sex	1	319·7	40·28	***
	M × S	1	181·6	22·89	***
	Error	489			
M. townsendii	Maturity	1	647·2	107·52	***
	Sex	1	25·7	4·26	*
	M × S	1	10·8	1·79	N.S.
	Error	1187	6·0		
Enclosures	Maturity	1	1093·6	192·70	***
	Sex	1	11·0	1·93	N.S.
	M × S	1	0·5	0·09	N.S.
	Error	872	5·7		

$*P < 0·05$, $**P < 0·01$, $***P < 0·001$.

chi-squared = 0·0, d.f. 1) or as mature residents (total chi-squared = 1·0, d.f. 2; chi-squared of totals = 0·0, d.f. 1; heterogeneity chi-squared = 1·0, d.f. 1). Thus, preventing dispersal in enclosed populations resulted in up to four times as many young males and up to twice as many young females remaining as mature residents as in control populations. (Note that there were differences between the two enclosures which may be related to the presence of *M. pennsylvanicus* on grid B, whereas grid D was a single-species grid.)

The ANOVA analysis for the control populations (Table 4) indicated that the only significant variable was that mature animals moved about twice as far as immature animals (Table 5) and that there were no differences between the sexes. Fig. 1 presents a frequency distribution of distance moved by voles from control grid B in Kansas, illustrating that within a maturity class both sexes moved similar distances, and that mature animals moved farther than immature animals. Mature males moved about one trap station farther from the natal trap site than did mature females (Table 5), though there was a great deal of variation among the grids. Immature resident males and females moved a similar distance from the natal trap site. In enclosures, maturity was again

Table 5. Distance (m ± 1 S.E.) moved by young animals from the natal trap site to their settlement location on the grid as either a mature or an immature resident. Animals were classed as residents if they were caught at least twice after their first capture in a given reproductive class. Sample sizes are given after the standard errors

	Mature						Immature					
	Males			Females			Males			Females		
Microtus breweri												
Grid A	30·6	(5·80)	9	15·2	(2·22)	12	15·4	(1·52)	12	19·0	(4·51)	22
Grid B	33·3	(9·39)	6	10·7	(2·00)	8	16·7	(2·14)	19	12·0	(2·29)	20
Pooled results	31·6	(4·92)	15	13·4	(1·60)	20	16·2	(1·42)	31	15·7	(2·63)	42
Microtus californicus												
Tilden Control	10·0	(1·63)	9	11·5	(2·12)	38	5·9	(0·95)	27			0
RFS 6	15·7	(5·49)	7	9·6	(1·33)	28	7·4	(3·78)	7	1·1	(1·14)	2
Pooled results	12·5	(2·56)	16	10·7	(1·34)	66	6·2	(1·06)	34	1·1	(1·14)	2
Microtus ochrogaster												
Indiana Grid A	23·1	(8·80)	5	32·7	(6·61)	9	13·6	(5·72)	4	14·3	(4·78)	4
Grid H	16·5	(4·01)	12	13·1	(2·24)	17	10·1	(2·39)	6	7·1	(2·28)	6
Grid B†	43·6	(5·98)	16	23·5	(5·71)	11	7·9	(2·81)	10	13·2	(6·37)	4
Grid D†	28·5	(4·00)	30	17·5	(2·87)	38	7·3	(1·71)	8	11·7	(3·58)	14
Kansas Grid A	28·3	(2·94)	25	14·7	(1·35)	40	14·0	(1·49)	20	11·1	(3·09)	8
Grid B	25·4	(2·77)	32	21·5	(2·41)	48	15·2	(1·64)	27	15·3	(1·96)	17
Grid C	7·3	(3·03)	2	20·2	(16·49)	9	21·0	(5·04)	3	9·1	(2·19)	3
Grid D	25·6	(6·25)	12	25·7	(2·84)	38	15·1	(2·77)	15	13·1	(1·61)	7
Controls pooled	24·6	(1·77)	88	20·4	(1·22)	161	14·6	(0·99)	75	12·61	(1·13)	45
Enclosures pooled	33·8	(3·47)	46	18·8	(2·56)	49	7·6	(1·70)	18	12·03	(3·04)	18
Microtus pennsylvanicus												
Indiana Grid A	28·4	(2·28)	67	13·8	(1·38)	91	12·3	(1·39)	61	10·0	(1·24)	49
Grid I	35·4	(5·35)	19	12·8	(1·63)	26	15·3	(3·05)	15	10·1	(2·08)	13
Grid B†	31·9	(3·93)	25	13·3	(1·91)	35	12·5	(2·98)	29	12·9	(1·54)	57
Mass. Grid D	35·0	(7·57)	8	10·6	(1·64)	17	17·0	(3·83)	11	11·5	(2·92)	8
Grid F	15·3	(6·41)	4	13·1	(3·59)	14	13·3	(2·10)	8	7·9	(1·85)	8
Grid J	15·0	(3·27)	6	20·3	(6·60)	13	12·0	(2·19)	11	14·9	(2·66)	18
Grid K†	29·7	(4·27)	18	15·9	(2·65)	16	17·0	(1·66)	42	16·6	(1·86)	40
Grid L†	27·4	(2·77)	48	12·7	(1·20)	41	14·6	(1·57)	31	12·2	(2·54)	37
Ontario Grid A	24·9	(1·91)	70	10·5	(0·61)	233	8·2	(0·47)	229	6·5	(0·50)	167
Grid F	17·8	(1·66)	75	10·2	(0·87)	153	7·2	(0·35)	266	6·6	(0·35)	225
Controls pooled	24·6	(1·13)	249	11·3	(0·48)	547	8·7	(0·31)	601	7·4	(0·30)	488
Enclosures pooled	29·1	(2·01)	91	13·7	(1·01)	92	15·0	(1·19)	102	13·8	(1·11)	134
Microtus townsendii												
Grid C	16·1	(2·26)	33	12·5	(1·15)	86	10·7	(1·25)	54	9·7	(1·21)	61
Grid E	17·6	(3·50)	17	12·1	(1·47)	65	8·2	(0·76)	52	8·1	(0·76)	68
Grid I	12·5	(2·72)	21	12·6	(1·36)	66	3·5	(0·44)	96	4·8	(0·58)	131
Beacham A	10·6	(1·58)	34	7·7	(1·07)	49	5·5	(0·56)	70	4·6	(0·45)	80
Beacham B†	13·5	(1·49)	65	12·1	(1·37)	60	4·8	(0·35)	176	4·9	(0·50)	130
Beacham C†	12·9	(1·52)	53	11·3	(1·26)	73	4·5	(0·47)	148	4·1	(0·35)	171
Beacham D	9·1	(0·96)	27	9·5	(1·37)	34	5·0	(0·52)	82	5·2	(0·62)	65
Controls pooled	12·9	(0·98)	132	11·3	(0·60)	300	6·0	(0·33)	354	6·1	(0·33)	405
Enclosures pooled	13·2	(1·06)	118	11·7	(0·92)	133	4·7	(0·29)	324	4·5	(0·30)	301

† Enclosed grids.

significant, but this time an interaction effect between sex and maturity occurred, largely as a result of mature males moving farther than mature females but immature males moving less than immature females.

Microtus pennsylvanicus

In this species as well, data from both control and enclosed populations were included in the analysis. A significantly higher proportion of males than females remained on the

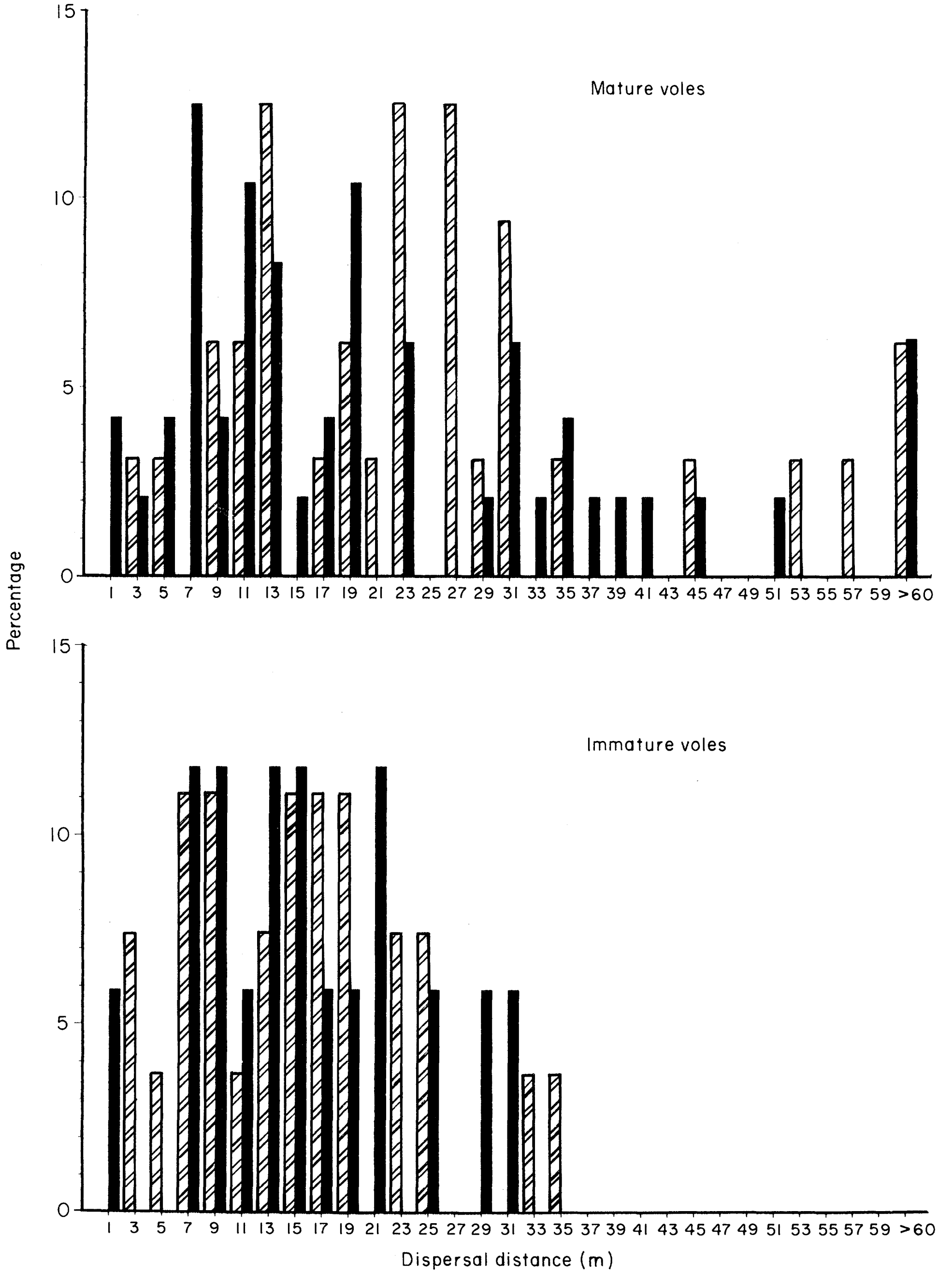

FIG. 1. Frequency distribution of dispersal distances from the natal trap site of *Microtus ochrogaster* caught on Grid B, Kansas when the young remained immature for at least two trapping sessions after first capture and when the young became mature and remained on the grid for at least two trapping sessions after first capture. Filled columns = females; hatched columns = males.

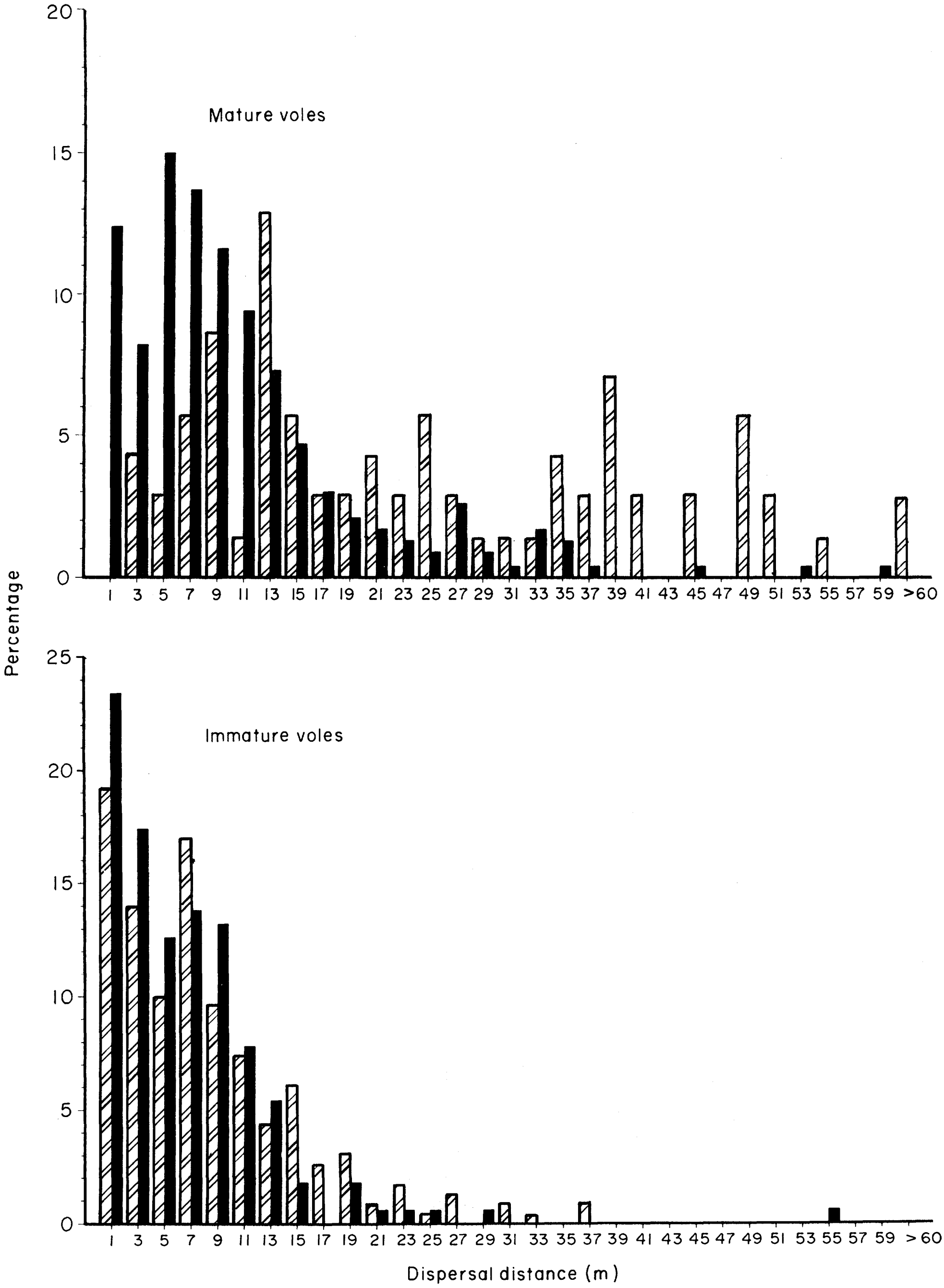

FIG. 2. Frequency distribution of dispersal distances from the natal trap site of *Microtus pennsylvanicus* caught on Grid A, Ontario. Conditions as in Fig. 1.

control grids as immature residents (total chi-squared = 29·5, d.f. 7, $P<0{\cdot}001$; chi-squared of totals = 20·9, d.f. 1, $P<0{\cdot}001$; heterogeneity chi-squared = 8·6, d.f. 6, N.S.; Table 3). A significantly lower proportion of males than females remained on the control grids as mature residents, but the significant heterogeneity chi-squared indicated that this difference was not equally large among all grids (total chi-squared = 155·9; d.f. 7, $P<0{\cdot}001$; chi-squared of totals = 35·2, d.f. 1, $P<0{\cdot}001$; heterogeneity chi-squared = 120·9, d.f. 6, $P<0{\cdot}001$). Among the enclosures, a significantly lower proportion of males than females remained on the grids as immatures though there were differences in magnitude between the areas (total chi-squared = 3·1, d.f. 3; chi-squared of totals = 6·3, d.f. 1, $P<0{\cdot}05$; heterogeneity chi-squared = 3·2, d.f. 2). There was no significant difference in the proportion of males and females that remained on the enclosed grids as mature residents (total chi-squared = 1·3, d.f. 3; chi-squared of totals = 0·0, d.f. 1; heterogeneity chi-squared = 1·3; d.f. 2).

The ANOVA analysis for both control and enclosed populations (Table 4) indicated that all sources of variation were significant. The significance of the interaction effect on both grid types was largely due to immature males and females moving similar distances, but mature males moving farther than mature females (Table 5). On control grids mature males moved about three times farther from the natal site than did immature males and about twice as far as mature females. Mature females moved about 50% farther from the natal site than did immature females. Fig. 2 presents a frequency distribution of distance moved for voles from grid A in Ontario, illustrating this conclusion. Enclosed populations showed much the same differences between the sexes. However, in these situations mature and immature females showed similar dispersal distances.

Microtus townsendii

This species was trapped at four sites in south-western British Columbia. In control populations there were no differences in the proportion of males and females that remained on the natal area as immature residents (total chi-squared = 8·8, d.f. 5, N.S.; chi-squared of totals = 2·6, d.f. 1, N.S.; heterogeneity chi-squared = 6·2, d.f. 4, N.S.), but a significantly lower proportion of males than females remained on the natal area as mature residents (total chi-squared = 52·2, d.f. 5, $P<0{\cdot}001$; chi-squared of totals = 44·3, d.f. 1, $P<0{\cdot}001$; heterogeneity chi-squared = 7·9, d.f. 4, N.S.; Table 3). In enclosed populations, a significantly higher proportion of males than females remained on the grids as immature residents (total chi-squared = 6·6, d.f. 2, $P<0{\cdot}05$; chi-squared of totals = 4·4, d.f. 1; $P<0{\cdot}05$; heterogeneity chi-squared = 2·2, d.f. 1), but a similar proportion of males and females remained as mature residents (total chi-squared = 0·7, d.f. 2; chi-squared of totals = 0·4, d.f. 1; heterogeneity chi-squared = 0·2, d.f. 1).

In the ANOVA analysis, maturity was the major significant factor in dispersal distance from the natal site in both control and enclosed populations, with sex being significant only on the control grids (Table 4). In both types of populations, mature animals moved about two to three times farther than immatures, and on control grids, mature males moved only about 1·6 m farther than females (Table 5).

DISCUSSION

The general pattern found in this analysis was that, on reaching sexual maturity, about twice as many females as males remained near their natal site in the four mainland species, irrespective of breeding system (Table 3). Thus, monogamy does not result in equal

Table 6. Predictions of the two major hypotheses which propose to explain female-biased philopatry in mammals. We assume in all cases that females compete for resources for reproduction

	Direction of the bias	
Breeding system	Greenwood hypothesis	Dobson hypothesis
Monogamous	Females ≫ Males	Females = Males
Polygynous	Females ≫ Males	Females ≫ Males

proportions of young males and females remaining, contrary to the predictions of Dobson (1982) and Liberg & von Schantz (1985) (see Table 6). Our study could have been strengthened if we had had other microtines which were monogamous. Such a study has recently been completed by Caley (1987) on the largest microtine, *Ondatra zibethicus*. He found that muskrats are monogamous and, by marking young in the nest and following subsequent settlement locations, that females are philopatric and males disperse from the natal site. Thus, this is the same pattern as we found in *M. ochrogaster*. The evidence is thus consistent with the Greenwood hypothesis (1980). Greenwood proposes that where male paternal investment is low and where females invest heavily in areas to provide adequate resources, female philopatry should be favoured, while dispersing males benefit through increased access to females. Our evidence suggests that the basic pattern in microtines is one in which females compete for breeding sites and males compete for females. The critical test to determine the object of male–male competition in monogamous species is to remove males from one area and females from another and observe which sex remains attached to the site. We predict that in monogamous voles females will stay in the absence of males, whereas males will leave in the absence of females.

Male defence of resources has been proposed for a number of species. Wolff (1980) speculated that *M. xanthognathus* (Leach) has a social system in which males are territorial and, in patchy environments, defend optimal resources which are needed by females. These highly productive locations provide adequate resources (food and nest sites) for several females, who have extensively overlapping home ranges. We would expect under these conditions and based on Greenwood's predictions, that sons would be more philopatric than daughters. Apparently, however, they are not, since late summer dispersal favours juvenile males. Hence, we hypothesize that these breeding males are really defending females, not resources, and that it is the females that defend these communal territories. Apparently, familiar females were not aggressive towards one another, while unfamiliar females were aggressive. *Microtus agrestis* (L.) (Myllymäki 1977a) and *M. californicus* (Ostfeld 1986) have polygynous mating systems which are similar to that of *M. xanthognathus*. By providing food, Ostfeld (1986) found that females shifted their home ranges to encompass more of it, but males did not. Thus, food was not the resource for which males were competing. From an experiment in which breeding male and female numbers were manipulated in *M. pennsylvanicus*, a species which is also polygynous but in which females are territorial and males have overlapping home ranges (Madison 1980; Webster & Brooks 1981), Boonstra & Rodd (1983) concluded that females were the resource for which males were competing. We suggest that for species such as *M. agrestis*, *M. californicus*, and *M. xanthognathus*, the mating system is a variant of female defence polygyny proposed for Emlen & Oring (1977) but, in this case, females compete for the resources for reproduction. To discriminate which resource each sex is competing for, breeding male and female numbers should be manipulated in these species. As with monogamous microtines, we predict that in polygynous microtines males would not remain on territories without females, whereas females would remain on areas without males.

Microtus breweri, the island-endemic species, does not fit the above pattern: similar proportions of young males and young females remain on the natal area as mature animals. If *M. breweri* is polygynous, then these results do not fit either Greenwood's or Dobson's hypotheses. This same pattern emerges for the other species when populations are enclosed (Table 3), irrespective of whether these populations are able to disperse (*M. pennsylvanicus*, grids K and L; *M. townsendii*, grids B and C) or not (*M. ochrogaster*, grids B and D; *M. pennsylvanicus*, grid B). Thus, preventing or reducing dispersal eliminates the bias towards female philopatry in mature animals. Simply providing an unoccupied area for potential dispersal within an enclosure will not be sufficient to produce an identical demography to that of the control. Tamarin, Reich & Moyer's (1984) enclosed populations had higher survival and apparently reduced dispersal from that found in the control population, though they did find overall density changes to be similar. Thus, our evidence suggests that though most males in unenclosed populations do not normally stay near the natal area when they reach maturity, if forced to remain by fencing them, a greater proportion do so. This lends support to the hypothesis by Howard (1960) that at least some of the dispersal by males is genetically motivated. Nevertheless, the males from the island *M. breweri*, the enclosed *M. ochrogaster*, and the enclosed *M. pennsylvanicus* still moved about twice as far from the natal site as did females (Table 5), which suggests that males are more strongly motivated than females to move away from the natal area. Enclosed *M. townsendii* males did not show this trend for reasons that are not clear. Evidence from other species (see below for references) suggests that at least part of the motivation for this movement pattern is inbreeding avoidance.

The generality of our findings should be tested in other microtine genera as well. A great deal of reasearch has been done on *Clethrionomys* species and it appears that all species have a social system of adult female territoriality and adult male home range overlap (for reviews see Alibhai & Gipps 1985; Bondrup-Nielson & Karlsson 1985; Gipps 1985). Differences in natal philopatry and dispersal patterns between the sexes have not been elucidated, but young females delay maturation if vacant breeding sites are not available (Bujalska 1973; Saitoh 1981; Gilbert *et al.* 1986). We would expect that females would be the philopatric sex in these species as well.

In microtines, one of the obvious consequences of male–male (including father–son) competition is avoidance of brother–sister and son–mother matings. Though inbreeding avoidance may not be a primary cause of differential dispersal, but rather an effect of male–male competition, the above discussion suggests that inbreeding avoidance may still operate to promote movement from the natal site by males (see Dobson & Jones 1986 for a discussion of multiple causation of dispersal). Although the importance of inbreeding avoidance as a significant factor in influencing dispersal patterns has been questioned (Moore & Ali 1984; Shields 1983), it has been difficult to tease out cause and effect in small mammals, in part because they are small, secretive and difficult to observe. As a consequence, the genetic relatedness between individuals is, for the most part, unknown. However, in an elegant study by Cockburn, Scott & Scotts (1985) on the small dasyurid *Antechinus*, in which maternity could be established with certainty, male–male competition could be ruled out as a cause of dispersal in young males because the fathers were all dead by the time their sons were born. Mothers apparently drove their sons from their nests and allowed strange young males to live with them and their daughters. Thus, inbreeding avoidance was the only sufficient cause for the biased dispersal in this species. In microtines, because of differential dispersal of young males, the combination most likely to result in inbreeding is fathers mating daughters. Various mechanisms such as suppression of maturation and growth because of familiarity may all operate in some species to reduce the probability of inbreeding (Batzli, Getz & Hurley 1977; Hasler & Nalbandov 1974; McGuire & Getz 1981; Schadler 1983; Boyd & Blaustein 1985). Richmond & Stehn (1976) reported that in *M. ochrogaster*, a father would not normally induce oestrus in his daughters unless he was separated from them for at least 8 days and thus was seen as a 'stranger'. Caley (1987) found no evidence for close inbreeding in the muskrat. Whether fathers avoid mating with their daughters, as do blacktailed prairie dogs (Hoogland 1982), is unclear and must await a precise determination of relatedness in field populations. Techniques for nest site location such as radiotelemetry (McShea 1985) and a spool-and-line technique (Boonstra & Craine 1986) or for marking the young indirectly through the use of radionuclides (Tamarin, Sheridan & Levy 1983) will allow a precise determination of maternity. Paternity exclusion analysis involving electrophoresis (e.g. Foltz & Hoogland 1981) and recombinant DNA techniques (Y. Plante & P. T. Boag, personal communication) will permit a determination of paternity.

There are two possible criticisms of our analysis. The first is that some young animals may disperse from their site of birth before reaching the critical weight. However, this should not affect our conclusions so long as dispersers, if and when they recruit elsewhere, enter at a weight greater than the cutoff. Our evidence (on p. 659 and Table 2) supports this idea. In addition, numerous studies, including ours, have found that breeding populations in a variety of species are very impermeable to the addition of recruits from outside the social system (Andrzejewski, Petrusewicz & Walkowa 1963; Healey 1967; Joule & Cameron 1975; Krebs *et al.* 1976; Boonstra 1978; Redfield, Taitt & Krebs 1978; Baird & Birney 1982; Boonstra & Rodd 1983). The second criticism is that *in situ* mortality, not dispersal is responsible for the higher disappearance of mature males from the natal area. If this is so, then the philopatry-dispersal arguments we have put forward may not be relevant. There are two lines of evidence indicating that dispersal by maturing males is the major cause of the differences between the sexes. First, immature males have a similar or greater probability than females of remaining as immatures near the natal area (Table 3) and it is only in the mature phase that the bias favours females. Second, by enclosing populations and thereby eliminating dispersal, we have eliminated the bias (Table 3). Thus, the bias appears to be directly related to differential dispersal by maturing males. Numerous other studies have also indicated mature males tend to disperse more than females (for reviews see Gaines & McClenaghan 1980 and Lidicker 1985).

The main cause of juvenile male dispersal may be male–male competition in which subordinates are driven off. However, the *Antechinus* study (Cockburn, Scott & Scotts 1985) suggests that we should not ignore the potential role of mothers in driving their sons away. Breeding females are more aggressive to strange young than are breeding males (Boonstra 1984), but we do not know how they will respond to their own maturing sons. Breeding females may be responsible for depressing juvenile survival (Boonstra 1978; Getz *et al.* 1979), recruitment (Redfield, Taitt & Krebs 1978), and growth and maturation (Bujalska 1973; Boonstra 1978; Saitoh 1981).

Our evidence indicates that between 10 and 30% of the young females in all species mature near the natal area (Table 3). There is conflicting evidence and opinion as to whether young female *Microtus* can mature and breed in or adjacent to the home range of the mother. In *M. pennsylvanicus*, Madison (1980) found one instance in which two females (one 35 g and the other 51 g) had overlapping home ranges and from this he concluded that mother–daughter units may form, but that daughters, though they may occasionally be sexually active, do not become pregnant and are thus inhibited by their mothers. This conclusion is questionable, both because of the sample size and because the daughter was radiotracked for one week only (7 August–14 August) and not apparently thereafter. In contrast, Boonstra & Rodd (1983) and McShea & Madison (1984) report instances of at least two breeding females raising their young in the same nest. However, in neither of these studies could the genetic relatedness between the females be established. Both laboratory and field evidence support the notion that typically only one female *M. ochrogaster* in a group breeds (Thomas & Birney 1979; Getz & Carter 1980; Getz, Carter & Gavish 1981). Recent field evidence by Getz & Hofmann (1986) indicates that monogamy may not be absolute in this species, though it is the major form of breeding system. More complex associations occur but it is unclear whether these represent polygyny or some form of extended family breeding system. However, Getz & Carter (1980) indicate (citing unpublished data) that dispersal of young from the natal site is rare and that most young remain within 30 m. Lidicker (1979) reported that both young male and female. *M. californicus* will mature and reproduce in the presence of their parents in enclosures. Jannett (1978), from a study of autumn populations of *M. montanus* (Peale), found that both young males and females were inhibited from maturing, but that young females did mature if the mother abandoned them. Frank (1957) reported that the same thing occurs. In *M. arvalis* (Pallas), but only in autumn populations. In spring and summer, young females mate in the maternal home range. Myllymäki (1977b) reported that female *M. agrestis* from early litters mature 2–3 weeks before males and settle in or near the natal site. Finally, FitzGerald & Madison (1983) report that family units in *M. pinetorum* (Le Conte) often contain more than one adult female and suggest that these were related.

We suggest that both our evidence and that of others summarized above is consistent with a view that young females differentially mature on or near the natal home range, and that by so doing, they obtain the benefits of living near kin: improved survival and reproductive fitness. We suggest that this type of social organization amongst female voles is similar to that reported in many ground-dwelling squirrels, where adult females live in kin clusters and behave amicably towards kin and aggressively towards strangers (Armitage 1981; Michener 1983; Davis 1984). Charnov & Finerty (1980) have proposed that kin selection is involved in microtine cycles, and that declines are caused by aggression as a result of being surrounded by strangers.

Many voles can remain immature for a long time, especially if they are born near the end of the breeding season or if they are born in peak years (Krebs & Myers 1974). In our analysis, similar or larger proportions of males than females remained near their natal site as immatures in all species (Table 3), and these males and females moved similar distances from the natal site (Table 5). We suggest that immature males and females are treated the same by their parents. Anderson (1980) speculates that young males born early in the breeding season, by maturing more slowly than females, delay their own expulsion and maximize their chances of either inheriting the paternal range through their father's mortality or successfully establishing elsewhere. R. Boonstra (unpublished data) found that of all the young males born on the area, those born late in the breeding season and remaining as overwintering non-breeding animals, had the greatest probability of maturing near the natal site. Synchrony in onset of reproduction by all males at the start of the breeding season in spring (Boonstra & Rodd 1983) removes the disadvantage of lower body weight and inexperience that young males face when they mature at other times in the summer and autumn.

ACKNOWLEDGMENTS

We thank Bill McShea and Bob Tamarin for providing analysed data. We thank Barry Keller, Judy Myers, Bob Tamarin, Janice LeDuc, Jim Redfield, Robert Rose, Mary Taitt, Terry Beacham, Helen Rodd, and numerous technicians and students who helped to collect these data over 20 years. We are grateful to Drs Dennis Chitty, Bill McShea, Richard Ostfeld and Bob Tamarin for making constructive criticism on the manuscript. We thank the Natural Sciences and Engineering Research Council of Canada, the National Science Foundation of the U.S. and the National Institutes of Health of the U.S. for providing financial support.

REFERENCES

Alibhai, S. K. & Gipps, J. H. W. (1985). The population dynamics of bank voles. *Zoological Society of London Symposia*, **55**, 277–313.

Anderson, P. K. (1980). Evolutionary implications of microtine behavioral systems on the ecological stage. *Biologist*, **62**, 70–88.

Andrzejewski, R., Petrusewicz, K. & Walkowa, W. (1963). Absorption of newcomers by a population of white mice. *Ekologia Polska*, **11**, 223–240.

Armitage, K. G. (1981). Sociality as a life-history tactic of ground squirrels. *Oecologia*, **48**, 36–49.

Baird, D. D. & Birney, E. C. (1982). Pattern of colonization in *Microtus pennsylvanicus*. *Journal of Mammalogy*, **63**, 290–293.

Batzli, G. O., Getz, L. L. & Hurley, S. (1977). Suppression of growth and reproduction of microtine rodents by social factors. *Journal of Mammalogy*, **58**, 583–591.

Beacham, T. D. (1980). Demography of declining populations of the vole, *Microtus townsendii*. *Journal of Animal Ecology*, **49**, 453–464.

Beacham, T. D. & Krebs, C. J. (1980). Pitfall versus live-trap enumeration of fluctuating populations of *Microtus townsendii*. *Journal of Mammalogy*, **61**, 486–499.

Bondrup-Nielson, S. & Karlsson, F. (1985). Movements and spatial patterns in populations of *Clethrionomys* species: A Review. *Annales Zoologica Fennici*, **22**, 385–392.

Boonstra, R. (1977). Effect of conspecifics on survival during population declines in *Microtus townsendii*. *Journal of Animal Ecology*, **46**, 835–851.

Boonstra, R. (1978). Effect of adult Townsend voles (*Microtus townsendii*) on survival of young. *Ecology*, **59**, 242–248.

Boonstra, R. (1984). Aggressive behavior of adult meadow voles (*Microtus pennsylvanicus*) toward young. *Oecologia*, **62**, 126–131.

Boonstra, R. (1985). Demography of *Microtus pennsylvanicus* in Southern Ontario: enumeration versus Jolly-Seber compared. *Canadian Journal of Zoology*, **63**, 1174–1180.

Boonstra, R. & Craine, I. T. M. (1986). Natal nest location and small mammal tracking with a spool-and-line technique. *Canadian Journal of Zoology*, **64**, 1034–1036.

Boonstra, R. & Hoyle, J. A. (1986). Rarity and coexistence of a small hibernator, *Zapus hudsonius* with fluctuating populations of *Microtus pennsylvanicus* in the grasslands of Southern Ontario. *Journal of Animal Ecology*, **55**, 773–784.

Boonstra, R. & Rodd, F. H. (1983). Regulation of breeding density of *Microtus pennsylvanicus*. *Journal of Animal Ecology*, **52**, 757–780.

Boonstra, R. & Rodd, F. H. (1984). Efficiency of pitfalls versus live traps in enumeration of populations of *Microtus pennsylvanicus*. *Canadian Journal of Zoology*, **62**, 758–765.

Boyd, S. K. & Blaustein, A. R. (1985). Familiarity and inbreeding avoidance in the gray-tailed vole (*Microtus canicaudus*). *Journal of Mammalogy*, **66**, 348–352.

Bujalska, G. (1973). The role of spacing behavior among females in the regulation of reproduction in the bank vole. *Journal of Reproduction and Fertility* (Suppl.), **19**, 465–474.

Caley, M. J. (1987). Dispersal and inbreeding avoidance in muskrats. *Animal Behaviour*, **35**, (in press).

Charnov, E. L. & Finerty, J. P. (1980). Vole population cycles: a case for kin-selection. *Oecologia*, **45**, 1–2.

Cockburn, A., Scott, M. P. & Scotts, D. J. (1985). Inbreeding avoidance and male-biased natal dispersal in *Antechinus* spp. (Marsupialia: Dasyuridae). *Animal Behaviour*, **33,** 908–915.

Davis, L. L. (1984). Kin selection and adult female Richardson's ground squirrels: a test. *Canadian Journal of Zoology*, **62,** 2344–2348.

Dobson, F. S. (1982). Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour*, **30,** 1183–1192.

Dobson, F. S. & Jones, W. T. (1986). Multiple causes of dispersal. *American Naturalist*, **126,** 855–858.

Dueser, R. D., Rose, R. K. & Porter, J. H. (1984). A body-weight criterion to identify dispersing small mammals. *Journal of Mammalogy*, **65,** 727–729.

Emlen, S. T. & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, **197,** 215–223.

FitzGerald, R. W. & Madison, D. M. (1983). Social organization of a free-ranging population of pine voles, *Microtus pinetorum. Behavioral Ecology and Sociobiology*, **13,** 183–187.

Foltz, D. W. & Hoogland, J. L. (1981). Analysis of the mating system in the black-tailed prairie dog (*Cynomys ludovicianus*) by likelihood of paternity. *Journal of Mammalogy*, **62,** 706–712.

Frank, F. (1957). The causality of microtine cycles in Germany. *Journal of Wildlife Management*, **21,** 113–121.

Gaines, M. S. & Krebs, C. J. (1971). Genetic changes in fluctuating vole populations. *Evolution*, **25,** 702–723.

Gaines, M. S. & McClenaghan, L. R. Jr (1980). Dispersal in small mammals. *Annual Review of Ecology and Systematics*, **11,** 163–196.

Gaines, M. S. & Rose, R. K. (1976). Population dynamics of *Microtus ochrogaster* in eastern Kansas. *Ecology*, **57,** 1145–1161.

Gaines, M. S., Vivas, A. M. & Baker, C. L. (1979). An experimental analysis of dispersal in fluctuating vole populations: demographic parameters. *Ecology*, **60,** 814–828.

Getz, L. L. & Carter, C. S. (1980). Social organization in *Microtus ochrogaster* populations. *Biologist*, **62,** 56–69.

Getz L. L., Carter, C. S. & Gavish, L. (1981). The mating system of the prairie vole *Microtus ochrogaster*: field and laboratory evidence for pair bonding. *Behavioral Ecology and Sociobiology*, **8,** 189–194.

Getz, L. L. & Hofmann, J. E. (1986). Social organization in free-living prairie voles, *Microtus ochrogaster. Behavioral Ecology and Sociobiology*, **8,** 275–282.

Getz, L. L., Verner, L., Cole, F. R., Hofmann, J. E. & Avalos, D. E. (1979). Comparisons of population demography of *Microtus ochrogaster* and *M. pennsylvanicus: Acta Theriologica*, **24,** 319–349.

Gilbert, B. S., Krebs, C. J., Talarico, D. & Cichowski, D. B. (1986). Do *Clethrionomys rutilus* females suppress maturation of juvenile females? *Journal of Animal Ecology*, **55,** 543–552.

Gipps, J. H. W. (1985). The behaviour of bank voles. *Zoological Society of London Symposia*, **55,** 61–87.

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28,** 1140–1162.

Hasler, M. J. & Nalbandov, A. V. (1974). The effect of weanling and adult males on sexual maturation in female voles, *Microtus ochrogaster. General and Comparative Endocrinology*, **23,** 237–238.

Healey, M. C. (1967). Aggression and self-regulation of population size in deermice. *Ecology*, **48,** 377–392.

Hoogland, J. L. (1982). Prairie dogs avoid extreme inbreeding. *Science*, **251,** 1639–1641.

Howard, W. E. (1960). Innate and environmental dispersal of individual vertebrates. *American Midland Naturalist*, **63,** 151–161.

Jannett, F. J. (1978). The density-dependent formation of extended maternal families of the montane vole, *Microtus montanus nanus. Behavioral Ecology and Sociobiology*, **3,** 245–263.

Joule, J. & Cameron, G. N. (1975). Species removal studies. I. Dispersal strategies of sympatric *Sigmodon hispidus* and *Reithrodontomys fulvenscens* populations. *Journal of Mammalogy*, **56,** 378–396.

Keller, B. L. (1985). Reproductive patterns. *Biology of the New World* Microtus (Ed. by R. H. Tamarin), pp. 775–778. American Society of Mammalogists, Special Publication 8.

Krebs, C. J. (1966). Demographic changes in fluctuating populations of *Microtus californicus. Ecological Monographs*, **36,** 239–279.

Krebs, C. J. (1978a). A review of the Chitty Hypothesis of population regulation. *Canadian Journal of Zoology*, **56,** 2463–2480.

Krebs, C. J. (1978b). Aggression, dispersal, and cyclic changes in populations of small rodents. *Aggression, dominance, and individual spacing* (Ed. by L. Krames, P. Pliner & T. Alloway), pp. 49–60. Plenum, New York.

Krebs, C. J. (1979). Dispersal, spacing behaviour, and genetics in relation to population fluctuations in the vole *Microtus townsendii. Fortschritte der Zoologie*, **25,** 61–77.

Krebs, C. J., Keller, B. L. & Tamarin, R. H. (1969). *Microtus* population biology: demographic changes in fluctuating populations of *Microtus ochrogaster* and *M. pennsylvanicus* in southern Indiana. *Ecology*, **50,** 587–607.

Krebs, C. J. & Myers, J. H. (1974). Population cycles in small mammals. *Advances in Ecological Research*, **8,** 267–399.

Krebs, C. J., Wingate, I., LeDuc, J., Redfield, J. A., Taitt, M. & Hilborn, R. (1976). *Microtus* population biology: dispersal in fluctuating populations of *M. townsendii. Canadian Journal of Zoology*, **54,** 79–95.

Liberg, O. & von Schantz, T. (1985). Sex-biased philopatry and dispersal in birds and mammals: the Oedipus hypothesis. *American Naturalist*, **126,** 129–135.

Lidicker, W. Z. Jr (1975). The role of dispersal in the demography of small mammals. *Small Mammals: Productivity and Dynamics of Populations* (Ed. by F. B. Golley, K. Petrusewicz & L. Ryszkowski), pp. 103–128. Cambridge University Press, London.

Lidicker, W. Z. Jr (1979). Analysis of two freely growing enclosed populations of the California vole. *Journal of Mammalogy*, **60,** 447–466.

Lidicker, W. Z. Jr (1985). Dispersal. *Biology of New World* Microtus (Ed. by R. H. Tamarin), pp. 420–454. American Society of Mammalogists, Special Publication 8.

Madison, D. M. (1980). Space use and social structure in meadow voles, *Microtus pennsylvanicus*. *Behavioral Ecology and Sociobiology*, **7,** 65–71.

McGuire, M. R. & Getz, L. L. (1981). Incest taboo between sibling *Microtus ochrogaster*. *Journal of Mammalogy*, **62,** 213–215.

McShea, W. J. (1985). *Influences on the postpartum behavior of female meadow voles in a natural population.* Unpublished Ph.D. Thesis, State University of New York, Binghamton.

McShea, W. J. & Madison, D. M. (1984). Communal nesting between reproductively active females in a spring population of *Microtus pennsylvanicus*. *Canadian Journal of Zoology*, **62,** 344–346.

Michener, G. R. (1983). Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. *Advances in the Study of Mammalian Behavior* (Ed. by J. F. Eisenberg & D. G. Kleiman), pp. 528–572. American Society of Mammalogists. Special Publication 7.

Moore, J. & Ali, R. (1984). Are dispersal and inbreeding avoidance related? *Animal Behaviour*, **32,** 94–112.

Myllymäki, A. (1977a). Intraspecific competition and home range dynamics in the field vole *Microtus agrestis*. *Oikos*, **29,** 553–569.

Myllymäki, A. (1977b). Demographic mechanisms in the fluctuating populations of the field vole *Microtus agrestis*. *Oikos*, **29,** 468–493.

Ostfeld, R. S. (1985). Limiting resources and territoriality in microtine rodents. *American Naturalist*, **126,** 1–15.

Ostfeld, R. S. (1986). Territoriality and mating system of California voles. *Journal of Animal Ecology*, **55,** 691–706.

Redfield, J. A., Taitt, M. J. & Krebs, C. J. (1978). Experimental alteration of sex ratios in populations of *Microtus townsendii*, a field vole. *Canadian Journal of Zoology*, **56,** 17–27.

Richmond, M. & Stehn, R. (1976). Olfaction and reproductive behavior in microtine rodents. *Mammalian olfaction, reproductive processes, and behavior* (Ed. by R. L. Doty), pp. 197–217. Academic Press, New York.

Roff, D. A. (1975). Population stability and the evolution of dispersal in a heterogeneous environment. *Oecologia*, **19,** 217–237.

Saitoh, T. (1981). Control of female maturation in high density populations of the red-backed vole, *Clethrionomys rufocanus bedfordiae*. *Journal of Animal Ecology*, **50,** 79–87.

Schadler, M. H. (1983). Male siblings inhibit reproductive activity in female pine voles, *Microtus pinetorum*. *Biology of Reproduction*, **28,** 1137–1139.

Shields, W. M. (1983). Optimal inbreeding and the evolution of philopatry. *The Ecology of Animal Movement* (Ed. by I. R. Swingland & P. J. Greenwood), pp. 132–159. Clarendon Press, Oxford.

Spieth, P. T. (1979). Environmental heterogeneity: A problem of contradictory selection pressures, gene flow and local polymorphism. *American Naturalist*, **113,** 247–260.

Tamarin, R. H. (1977). Demography of the beach vole (*Microtus breweri*) and the meadow vole (*M. pennsylvanicus*) in southeastern Massachusetts. *Ecology*, **58,** 1310–1321.

Tamarin, R. H. (1980). Dispersal and population regulation in rodents. *Biosocial mechanisms of population regulation* (Ed. by M. N. Cohen, R. S. Malpass & H. G. Klein), pp. 117–133. Yale University Press, New Haven.

Tamarin, R. H. (1984). Body mass as a criterion of dispersal in voles, a critique. *Journal of Mammalogy*, **65,** 691–692.

Tamarin, R. H., Reich, L. M. & Moyer, C. A. (1984). Meadow vole cycles within fences. *Canadian Journal of Zoology*, **62,** 1796–1804.

Tamarin, R. H., Sheridan, M. & Levy, C. K. (1983). Determining matrilineal kinship in natural populations of rodents using radionuclides. *Canadian Journal of Zoology*, **61,** 271–274.

Thomas, J. A. & Birney, E. C. (1979). Parental care and mating system of the prairie vole, *Microtus ochrogaster*. *Behavioural Ecology and Sociobiology*, **5,** 171–186.

Webster, A. B. & Brooks, R. J. (1981). Social behavior of *Microtus pennsylvanicus* in relation to seasonal changes in demography. *Journal of Mammalogy*, **62,** 738–751.

Wolff, J. O. (1980). Social organization of the taiga vole (*Microtus xanthognathus*). *Biologist*, **62,** 34–45.

(*Received 16 June 1986*)