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Spatial organization and mating system of *Microtus townsendii*

Xavier Lambin[1, 2] **and Charles J. Krebs**[2]

[1] Unité d'écologie et de biogéographie, Université Catholique de Louvain, Place Croix du Sud, 5, B-1348 Louvain-la-Neuve, Belgium
[2] The Ecology Group, Department of Zoology, The University of British Columbia, 2204 Main Mall, Vancouver B.C., V6R 1W5 Canada

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Summary. Space use by individual Townsend's voles, *Microtus townsendii*, was investigated in spring and summer by means of radiotelemetry and intensive live trapping in undisturbed grasslands near Vancouver, British Columbia. Home ranges of males were larger than those of females; females had significantly larger ranges in spring than in summer. Most males and females maintained territories free of individuals of the same sex in spring. Male-female pairs had their exclusive territories closely overlapping each other. The 1:1 operational sex ratio and the spatial association of pairs of males and females suggest that the voles were monogamous in the spring of 1988 and that 50% of the males were monogamous in the spring of 1989. In summer, there was more intrasexual overlap between home ranges of males and females and female ranges were considerably smaller than those of males. Females were more philopatric than males and females thought to be members of the same family group lived adjacent to each other or had overlapping home ranges. Males overlapped with more than one female in summer, but most females still overlapped with only one male, which suggests that the mating system is polygynous in summer. Thirty-five percent of the philopatric females became pregnant for the first time when the male spatially associated with their mother in the spring was still alive and thus could potentially have mated with their fathers. Male and female territoriality in spring is the proximate mechanism for the limitation of breeding density by spacing behaviour.

Introduction

Spacing behaviour of individuals is central to recent models of population regulation of small mammals (Hestbeck 1982; Charnov and Finerty 1980; Krebs 1985; Taitt and Krebs 1985). It has been postulated to contribute to population regulation through changes in aggressiveness (Charnov and Finerty 1980; Krebs 1985), limitation of the number of individuals gaining breeding status (Taitt and Krebs 1985), or by restricting dispersal of surplus individuals (Hestbeck 1982). In several microtine species, female territoriality seems to play an important role in limiting the size of breeding populations (i.e. Bujalska 1973; Madison 1980; Boonstra and Rodd 1983), but in other species females are thought to be non-territorial and their home ranges overlap with other females (Myllymäki 1977; Ostfeld 1986). A wide variety of social and mating systems has been identified among microtines (Wolff 1985; Cockburn 1988), and there have been several recent attempts to identify the factors that lead to the evolution of such a variety of social systems within an otherwise ecologically homogeneous group (Ostfeld 1985; Ims 1987a; Cockburn 1988). Ostfeld (1985) considered the importance of the renewal of the food resources in the evolution of space use by female voles, and Ims (1987a) pointed out that as well as the spatial distribution of females, the temporal distribution of receptive females influences the defensibility of females by males and therefore the mating system.

Although the dynamics of populations of Townsend's vole (*Microtus townsendii*) have been intensively studied (Krebs 1979; Krebs et al. 1978; Krebs and Boonstra 1978), the spatial organization and the mating system have not been documented. Previous studies indicate that populations of Townsend's vole are limited by spacing behaviour (Krebs et al. 1976; Boonstra and Krebs 1977; Krebs et al. 1978) or spacing behaviour and food (Taitt and Krebs 1981, 1983, 1985). When aggression was increased with implants of testosterone, females having larger home ranges suffered more wounds and had lower survival than control females during the spring decline in numbers (Taitt and Krebs 1982). Male survival was improved when females were made anoestrus with mestranol implants (Taitt and Krebs 1982). Taitt and Krebs (1983) found that females had smaller ranges when food was added. They suggested that females are responsible for part of the spring decline (Krebs and Boonstra 1978; Taitt and Krebs 1983), and

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Offprint requests to: C.J. Krebs

they hypothesized that *M. townsendii* females could be territorial, as are meadow voles (*Microtus pennsylvanicus*; Madison 1980; Boonstra and Rodd 1983) and *Clethrionomys sp.* (Bujalska 1973; Bondrup-Nielsen and Karlsson 1985). There have been no specific predictions about the spacing of male *M. townsendii*, but it has been repeatedly suggested that males space themselves in relation to oestrus females (Taitt and Krebs 1981; Ostfeld 1985; Ims 1988).

In this paper, we present the results of a descriptive study of spatial organization and the mating system of *M. townsendii* as revealed by telemetry and intensive live-trapping. We found that in spring, males and females are territorial and the mating system is monogamous. In summer males overlap with several females and the mating system is polygynous.

Methods

Census techniques. An intensive live trapping study was conducted from 15 February 1988 until 30 April 1989 at Boundary Bay airport near Ladner, 35 km south of Vancouver, British Columbia. The area had been studied previously by Krebs et al. (1978). As well as Townsend's voles, the area sustains a small number of deer mice (*Peromyscus maniculatus*). Although creeping voles (*Microtus oregoni*) were formerly in this area (Redfield et al. 1978a), none were captured during this study.

A 0.8-ha trapping grid was established in a grassland left undisturbed for more than 25 years. The grid was bounded on the south and west sides by ditches and on the east side by a gravel road. Neither of the ditches nor the gravel road were crossed routinely by voles. This reduced the potential edge effect on the estimates of the number of resident voles.

Longworth traps were placed at 5-m intervals under 20 × 20 cm plywood boards at each of 160 points in a grid pattern. Between 4 June 1988 and 1 November 1988, an additional Longworth trap was added at each station. Traps were left locked open between trapping sessions and were intensively used by voles as part of their runway system. During the breeding season, trapping was performed weekly for 30 h over 2 days. Before each sampling period, traps were checked for proper functioning and were usually set in the morning, checked four times (every 3 h) on the first day and 3 times on the second day of sampling. Since traps were left unlocked during the night, voles were also captured at this time. When no breeding occurred, trapping was performed biweekly for 2 days and 2 nights. The distance between traps was smaller than in previous studies of this species, and the traps were checked more often, so that the movements of voles were not restricted for more than 3 h at a time when they were caught during the day. Voles were rarely caught repeatedly in one trap during a trapping session and more than 50 captules were commonly available for each breeding resident. The trapping procedures were otherwise identical to those described by Krebs et al. (1976).

Radiotelemetry techniques. Radiotelemetry was used to study the pattern of space use in the spring of 1988. "Mouse type" radiotransmitters (Holohil, Canada) with tie-grip collars were used. Radios had an internal loop antenna and were tuned to separate frequencies near 151 Mhz. Radiotransmitter packages weighed 2.43 ± 0.01 g, which represented 3.0 to 5.7% of the mass of the vole to which they were attached. Transmitters were fitted without anesthesia in the field during weekly trapping sessions. All adult individuals using the southern half of the grid close to the south and east ditches were fitted with transmitters. Fourteen overwintering breeding females, 1 immigrant female, 5 females born on the site, 14 overwintering males, 1 male born on the site and 2 immigrant males were radio-tagged between 19 April and 6 June. All voles but the male born on site were reproductively active when fitted with transmitters. Owing to the limited availability of transmitters, male voles were radio-collared later than females (7 May), Radio-collared voles were located by means of a probe antenna (Ostfeld 1986). Since continuous trapping revealed that Townsend's voles are active throughout the day and are less active in the middle of the night (personal observation), radio-tracking was performed opportunistically during the daylight hours or at dusk. The interval between each reading was never less than 2 h, and each vole was located at least every third day. The method of radio-tracking is otherwise similar to that described by Ostfeld (1986). When the signal of an individual could not be heard through the probe antenna, a hand-held H antenna was used and the vicinity of the grid was searched until a signal was heard. During the telemetry study, 1 male and 6 females disappeared from the grid while carrying transmitters. The transmitters of 1 male and 4 females were found in the vicinity of the grid, indicating that these animals had been killed by predators. One of them was found in an underground runway, suggesting predation by a long-tailed weasel (*Mustela frenata*). Another transmitter was found under a crow's (*Corvus caurinus*) nest. Three transmitters were found lying on the grass. One male was found dead in an underground runway and had its radiocollar entangled in roots.

As the transmitter package could have influenced the survival of tagged voles, the rate of disappearance of the overwintering females carrying transmitters was compared with that of other females of the same mass class during the telemetry study. No significant difference in the weekly disappearance rate was found (14 females with transmitters: weekly survival 0.93; 18 females without transmitters: weekly survival 0.95, $\chi^2 = 0.218$, $df = 1$, $P > 0.5$).

Data analysis. Because telemetry was used only in spring, the locations provided by live trapping were also used to study space use. To test whether home ranges based on live trapping differed from home ranges based on telemetry, home range sizes computed using only trapping data and only telemetry data were compared for 11 females in the spring of 1988 (paired t test, $t = 1.51$, $df = 10$, $P > 0.10$). There was no significant difference between the two techniques. Therefore, trapping and telemetry data were combined to study spatial patterns. Heske (1987) and Desy et al. (1989) also found that when a sufficient number of captures is available over a short time, trapping and telemetry reveal similar patterns of space use.

Home range analyses were performed using the computer package Ranges IV (Kenward 1987). Home ranges were computed as 90% Probability Convex Polygons centered on the recalculated arithmetic mean. Home range size was not correlated with the number of locations (February–May: $r = 0.10$, $P > 0.5$, $n = 36$, range of number of captures = 8–55, May–July: $r < 0.01$, $P > 0.8$, $n = 45$). Percentage overlap between ranges was computed with the routine in the Ranges IV package. A frequency distribution of percentage overlap between adjacent individuals was calculated for quantifying spacing patterns. Because adjacent individuals with no home range overlap are not included in the distribution (see Fig. 3), the true overlap can be overestimated by this method. Individuals that have substantial (20% or more) portions of their ranges overlapping with each other are assumed to be socially associated.

Upon first capture, each vole was assigned to one of the following cohorts. All voles caught for the first time during the first month of study (15 February–15 March) were considered as "overwintering residents". Voles caught thereafter could either be "site born juveniles" if their mass at first capture was equal to or less than 32 g (equal to or less than 30 g for the juveniles that entered the trappable population after 15 May), "dispersing subadults" if their mass was between 33 and 42 g, and as "overwintering immigrants" if they weighed more than 42 g at first capture and were caught between 16 March and 12 May. By that time, the voles from the first litters could have reached 42 g; consequently, subadults could not be distinguished from overwintering adults. Juveniles of similar size were sometimes caught in the same or adjacent traps during the same trapping session. If the female using the home range where those juveniles were captured had given birth at a time consistent with their size, she was assumed to be the mother of that litter. Birth dates of juveniles were estimated from their mass at first capture. Mass categories have often been used to classify young voles as either site born or immigrant (e.g. Dueser et al. 1984; Boonstra et al. 1987); however, mass is not totally reliable (Tamarin 1984; Tamarin and Sheridan 1987; Danielson et al. 1986). Although we use more conservative mass cutoffs than those used in previous studies (Beacham 1979; Hilborn 1975), some individuals thought to be immigrants may have been born on the grid and escaped capture for a month. We have independently checked the validity of these criteria in another study [89% of the juveniles marked in the nest that later entered traps did so before reaching 32 g (Lambin, unpublished work)]. Thus, we believe that our classifying criteria are reasonably reliable for this species.

Voles first caught as juveniles were classified as having reached sexual maturity if males had scrotal testes for at least 2 consecutive weeks or if females were caught while pregnant or lactating. The effect of birth date on the probability of being recruited into the breeding population was examined using logistic regression between birth date and maturation. Maturation was treated as a binary variable (0 = disappeared before maturing; 1 = matured on the trapping grid). Maximum likelihood ratios were used as the criteria for goodness of fit of the factor.

Throughout, means ± SE are given unless stated otherwise. All statistical analyses were performed using procedures available from SAS (Cary, North Carolina).

Results

Demography

Although trappability was low during the first weeks of the study and not all voles present on the study site were caught at this time, minimum survival estimates suggest that vole numbers were declining from the beginning of the study until the beginning of April 1988. Vole numbers reached a peak of 235 voles ha^{-1} in July (Table 1) before a botfly (*Cutebra griseus*) infestation began. Numbers declined sharply in the second half of August when the intensity of the parasite infestation reached its maximum (42% of the voles trapped were infested by at least one larva). Even though botfly larvae seem to affect the survival of Townsend's voles (Boonstra et al. 1980), the percent of voles killed by these parasites is not known. After the summer decline, vole numbers remained fairly stable during the autumn and winter with a few females conceiving litters until December. Numbers declined again in spring of 1989, and the spring density was lower (60 voles ha^{-1} in March) than in 1988 (Table 1). Trappability per week was high, averaging 89.5% through the study. In a previous study, vole numbers fluctuated between 15 and 525 voles ha^{-1} between 1971 and 1976 (Taitt and Krebs 1985); thus, the population in this study was at intermediate density.

In 1988 breeding began in February, and 26 of 32 females gave birth to their first spring litter synchronously in mid-March. These females apparently mated postpartum. Juvenile recruits entered the trappable population starting on 1 April. The number of females known to have given birth each week between 15 February and 5 August as well as the number of juveniles entering the trappable population during this period differ significantly from a uniform distribution (number of births: $\chi^2 = 42.81$, $df = 19$, $P < 0.01$; number of recruits: $\chi^2 = 82.41$, $df = 18$, $P < 0.01$). Three pulses of juvenile recruits could be identified, indicating partly synchronous breeding. The first spring-born females started producing their first litters at the beginning of May. In 1989, 19 of 28 females gave birth to their first spring litter between 8 and 16 April.

Table 1. Summary of seasonal fluctuations in the minimum number of males and females alive (MNA), sex-ratio (proportion of males), number of scrotal males and reproductively active females and the operational sex ratio

	Number of males	Number of females	Sex ratio	Number of scrotal males	Number of breeding females	Operational sex ratio
March 1988	42	32	0.56	20	26	0.43
April	37	37	0.50	35	26	0.57
May	48	56	0.46	32	38	0.46
June	53	82	0.39*	32	48	0.40
July	89	99	0.47	32	53	0.37*
August	77	70	0.52	12	19	0.39
September	36	30	0.54	2	0	1.00
October	35	33	0.51	1	5	0.16
November	35	30	0.54	4	8	0.33
December	43	36	0.54	0	5	0.00
January 1989	42	36	0.54	0	12	0.00
February	37	35	0.51	0	3	0.00
March	33	37	0.47	0	6	0.00
April	20	28	0.41	16	25	0.39*

* $P < 0.05$, Yates corrected likelihood ratio test

The sex ratio did not differ significantly from 1:1 at the beginning of the study (Table 1). From May 1988 until July, the proportion of females gradually increased, but the sex ratio differed significantly from 1:1 only in June (Table 1). The operational sex ratio (Emlen and Oring 1977) followed the same trend in summer, with more breeding females than scrotal males present in June and July. The departure from a 1:1 ratio neared statistical significance in June and was highly significant in July (Table 1). In April 1989, the operational sex ratio significantly differed from 1:1 with a deficit of reproductively active males.

Philopatry and dispersal tendency of juveniles

More females than males reached maturity close to their birth site (Table 2, continuity-adjusted chi-square $\chi^2 = 15.97$, $df = 1$, $P < 0.001$). Thirty-nine females born on the study site ($n = 115$, 34%) reached sexual maturity near their birthsite. Thirty females became pregnant before the summer population crash (45 ± 2.8 days after estimated birth) while 9 females matured more than 6 months after their birth, during the winter of 1988 ($n = 4$) or in the spring of 1989 ($n = 5$). Nine juvenile males ($n =$

Table 2. Number, mean residency and natal dispersal distance of all males and females first caught as juveniles. For classification as an established mature individual, males must have had scrotal testes for at least 2 weeks and females had to be caught while pregnant or lactating. Natal dispersal is calculated as the distance between the location of first capture and the location where first caught as scrotal or pregnant

	Males		Females	
	Matured	Disappeared	Matured	Disappeared
Number	9	85	39	76
Natal dispersal (in meters)	30.6±9.3	–	12.6±2	–
Residency (in days)	131±11	71±24	126±16	58±11

94, 9.5%) became reproductively active (i.e. had scrotal testes for at least 2 weeks) before disappearing. The probability of juvenile males and females (that were trapped at least once as juveniles) being recruited into the breeding population within the year of their birth decreased significantly through the breeding season (logistic regression, maturation vs birth date, females $P<0.0001$, males $P=0.005$, Fig. 1). When the juvenile voles born after the summer population decline were excluded from the regression, the seasonal decline in the probability of recruitment were still highly significant for both sexes (females $P=0.0012$, males $P=0.013$).

The natal dispersal distance of juveniles (calculated as the distance between the trap where a juvenile was first caught and the trap where it was caught for the first time while sexually mature) was smaller for females (12.7 ± 2.0 m, $n=39$) than for males (30.6 ± 9.3 m, $n=9$; t-test, $t=2.95$; $df=1$; $P<0.005$). The dispersal distance of 66% of the young females and of 90.5% of the young males is not known since they disappeared from the trapping grid or died before reaching sexual maturity.

The average age at first conception of the philopatric females (100 ± 12 days, $n=39$) exceeds the average residency of all reproductively active males (59 ± 5 days, $n=55$; Mann Whitney U test, $P<0.001$). However, 14 philopatric females of 39 could have mated with their fathers; they first conceived while the male with which their mothers were spatially associated was still alive on the study site.

Home range size

Home range estimates were derived for all breeding males and females except those captured near the grid edges not bordered by ditches whose home ranges could have overlapped the grid limits. Home ranges were computed based on trapping and telemetry locations during the first breeding season and on trapping locations thereafter. We performed a two-way analysis of variance to investigate the effect of season and sex on home range size of reproductively active voles (Table 3). Home ranges of breeding males were significantly larger than

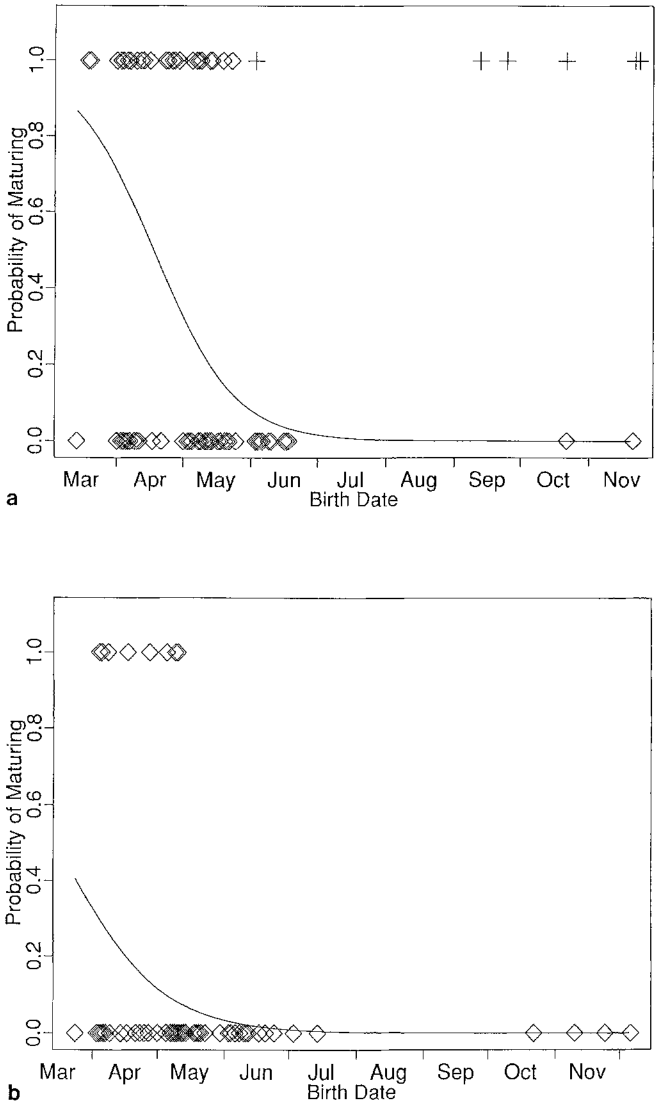

Fig. 1 a, b. Expected probability of being recruited into the breeding population as a function of birth date. The *regression line* was predicted by logistic regression. *Points* at the *top* of the graph represent individuals that matured, and *lower points* are juveniles that disappeared. *Diamonds* are for juveniles that matured before the population crash in August, and *crosses* are for voles that matured the year following their birth and that are *not* included in the regression; **a** shows the relationship for females, and **b** the relationship for males

Table 3. Mean (±SE) home range sizes (m^2) based on trapping and telemetry for reproductively active males and females in spring (22 February–15 April 1988, 1 March–30 April 1989) and summer (15 May–15 July 1988). Two-way ANOVA with three seasons; sex effect, $P<0.001$; season effect, $P=0.136$; sex vs season interaction, $P=0.17$. Means with the same superscript are not significantly different (orthogonal contrasts $P<0.05$)

	Males	Females
Spring 1988	198 ± 16 (24)^a	141 ± 12 (22)^b
Spring 1989	237 ± 47 (12)^a	152 ± 27 (18)^b
Summer 1988	219 ± 26 (28)^a	94 ± 8 (45)^c

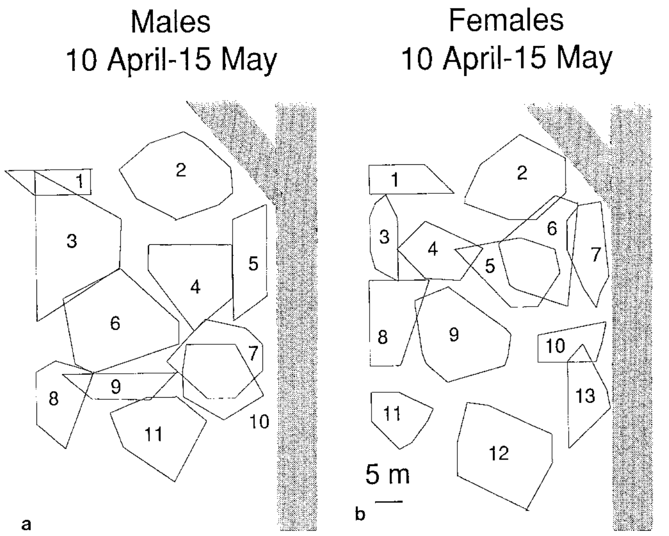

Fig. 2. **a** Home ranges of 11 male voles and **b** 14 female voles in the portion of the study area adjacent to the south ditch. Ranges are 90% polygons based on telemetry and trapping locations collected between 10 April and 15 May 1988. The spatial association between males and females can be visualized by superimposing the contour of the ditches. The numbers refer to the text

those of females ($P < 0.001$), but there was no significant variation with season. The Sex versus Season interaction was not significant. Orthogonal contrast revealed that male home ranges showed no significant variation in size with season but home ranges of breeding females were significantly smaller in summer 1988 than in spring of 1988 and 1989 ($P < 0.015$). Most voles showed a strong site fidelity and only two males shifted their home ranges from one part of the grid to another. Some short term excursions out of the usual home range were detected by trapping for both males and females, but in all cases, the voles had returned to their usual range or disappeared within a week.

Intrasexual spacing in spring

In 1988, home ranges of reproductively active males and females showed little intrasexual overlap (Fig. 2), and the whole study area was occupied by reproductively active voles. On average, a male's home range overlapped those of 1.39 ± 0.24 ($n = 18$) other males. The mean percentage overlap between males that had any overlap with other males was $11.03 \pm 3.05\%$ ($n = 29$ pairs). In most cases (22 of 29), the area shared by 2 males was less that 20% of a male's range. Male 7 and 10 (Fig. 2a), which overlapped substantially, were heavily scarred, and it is possible that they were fighting with each other for the exclusive use of the area. In the spring of 1989, even though only 16 scrotal males were present on the area, males had more male neighbours overlapping their ranges than in 1988 (Table 4). This is mostly due to the presence of 2 individuals whose ranges were exceptionally large and were overlapping large portions of the ranges of 3 and 2 other males. The number of males with 20% or more of their home ranges overlapping with those of other males was not larger in 1989 than in 1988, and most males (9 of 16) had no male neighbour overlapping 20% or more of their ranges.

The overlap between female ranges was slightly greater than between male ranges (Table 4). On average, females shared portions of their home range with 2.27 ± 0.28 ($n = 22$) females but 14 of 22 shared less than 20% of their range with an adjacent female. Females that had any overlap with other females shared $10.4 \pm 2.9\%$ ($n = 50$ pairs) of their range with a female neighbour (Fig. 3). As with males, 2 pairs of females had largely overlapping ranges (vole 10 and 13; 52% and 61%, Fig. 2b; another pair in the northern half of the grid not shown, 100% and 82% overlap). In 1989 the pattern of space use by females was very similar to that observed in 1988. Even though 3 females that shared an area with their sisters were removed for an experiment, 3 other females had largely overlapping home ranges in the same area as females 10 and 13 in 1988. Because these females were first caught as subadults during the winter, it is unlikely that they were related to each other unless they dispersed together from their natal area.

Males and females responded to the disappearance of neighbouring voles of the same sex and often expanded their home ranges in the direction of any vacant area. Figure 4a shows the expansion of the ranges of males 5 and 7 following the disappearance of male 1,

Table 4. Top: mean number of home ranges overlapped by an individual; bottom: mean number of neighbours with at least 20% of their range overlapped by an individual; (±SE; sample size in parenthesis)

Overlapper/ Overlapped	Spring 1988	Spring 1989	Summer 1988
Male/Male	$1.39 \pm 0.24(18)^{a}$	$2.50 \pm 0.34(16)^{b}$	$3.54 \pm 0.38(28)^{b**}$
Female/Female	$2.27 \pm 0.28(22)^{a}$	$1.67 \pm 0.32(21)^{ab}$	$3.02 \pm 0.28(45)^{b**}$
Male/Female	$2.11 \pm 0.23(18)^{a}$	$3.31 \pm 0.38(16)^{a}$	$5.36 \pm 0.47(28)^{b**}$
Female/Male	$1.95 \pm 0.21(22)^{a}$	$2.38 \pm 0.21(21)^{a}$	$3.40 \pm 0.22(45)^{b**}$
Male/Male	$0.33 \pm 0.11(18)^{a}$	$0.63 \pm 0.22(16)^{a}$	$1.25 \pm 0.19(28)^{b**}$
Female/Female	$0.36 \pm 0.10(22)^{a}$	$0.57 \pm 0.16(21)^{ab}$	$1.04 \pm 0.18(45)^{a**}$
Male/Female	$1.22 \pm 0.21(18)^{a}$	$2.19 \pm 0.39(16)^{ab}$	$2.96 \pm 0.34(28)^{b**}$
Female/Male	$1.05 \pm 0.08(22)^{a}$	$1.14 \pm 0.21(21)^{a}$	$1.27 \pm 0.14(45)^{a}$

** $P < 0.01$ one-way ANOVA

^{a,b,ab} Within each row, means with the same superscript are not significantly different (one-way Anova, followed by Student-Newman-Keuls test, $P < 0.05$)

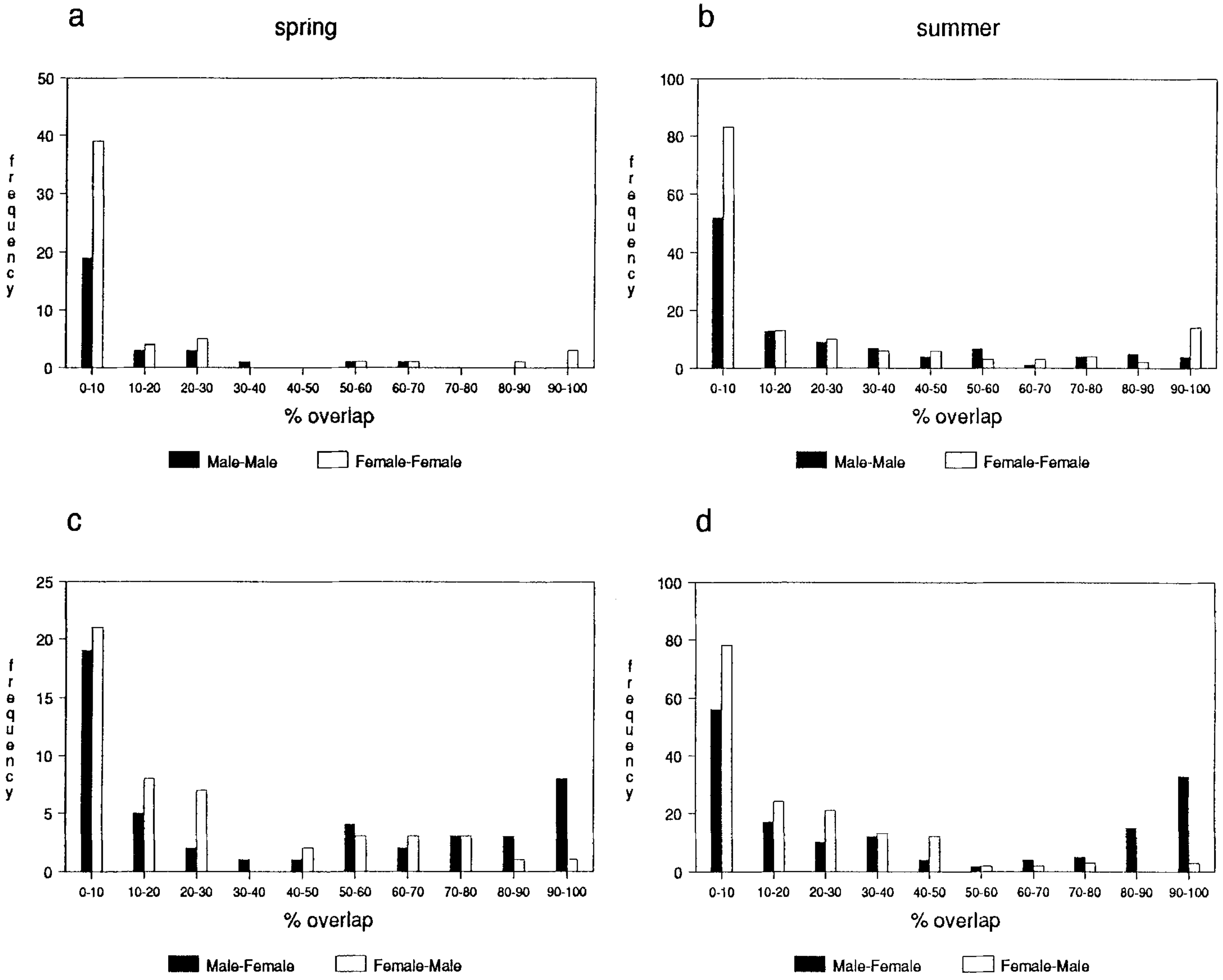

Fig. 3a–d. Distribution of the overlap percentages between 90% polygon home ranges of males and females in spring and summer 1988; **a** and **b** are intrasexual comparisons; **c** and **d** are intersexual comparisons

and the movement of males 3, 4, 7 and 9 following the disappearance of male 5. A subadult male (no. 10) settled in the middle of the former home range of male 5. Even though he became severely wounded and was observed being chased by male 7 during two telemetry checks, he successfully established residence in that area. Figure 4b shows a similar range dynamic after the disappearance of a female, with female 3 expanding her home range after the disappearance of female 1. These expansions typically occurred within a few hours of the disappearance of a resident vole.

Intersexual spacing in spring

Comparison of the relative position of males and females in April and May 1988, reveals that male-female pairs of voles have their ranges almost completely overlapping (male 2 and female 2, male 5 and female 7, male 6 and female 9, male 8 and female 11, male 11 and female 12; Fig. 2). One male (no. 3) overlapped with 3 females (no. 3, 4, 8) and 1 male (no. 4) had its range overlapping with that of 2 females that were overlapping with each other (male 4 and females 4 and 6). Both the frequency distribution of percentage area of female ranges overlapped by a male (43.1 ± 5.9%, $n = 42$ pairs) and the distribution of percentage area of male ranges overlapped by a female (27.2 ± 4.3%, $n = 44$ pairs) appear to be bimodal (Fig. 3c). Pairs of males and females either have very little overlap or are largely overlapping. Most males overlap 20% or more of the home range of 1 female (10 out of 18) while some males overlap the range of 2 (3 out 18), or 3 (2 out 18) females. Three males did not substantially overlap any female between 10 April and 15 May. As with males, most females had 20% or more of their range overlapping that of only 1 male (19 of 23). Two females (nos. 10, 13; Fig. 2a, b) had their ranges overlapped by 2 males (nos. 10, 7), themselves overlapping with each other. One female had no male substantially overlapping her range. On aver-

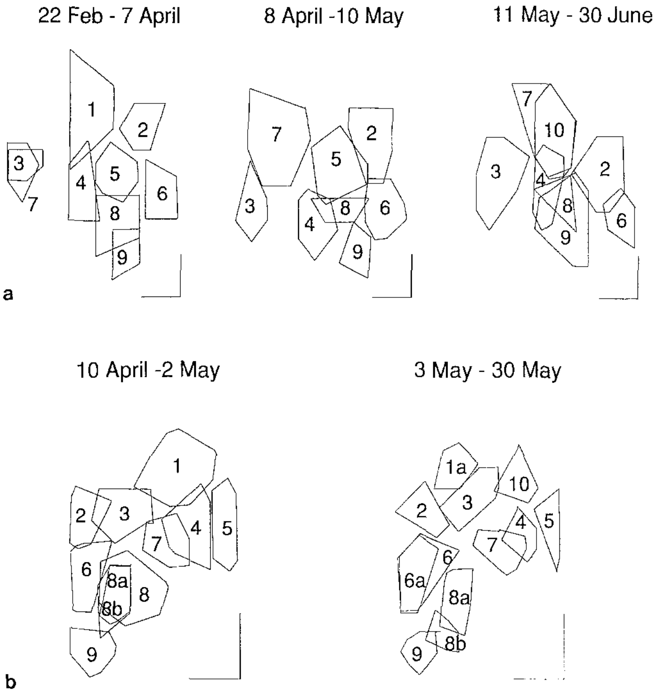

Fig. 4. **a** Dynamic of space use by adjacent males and **b** adjacent females in spring 1988. Home ranges are computed based on fewer locations than in Fig. 2. They only reflect the relative positions of the different individuals. **a**: Male 1 died between period 1 and period 2; male 5 disappeared between period 2 and 3; male vole 10 is an immigrant subadult, heavily scarred. **b**: Female 1 and female 8 disappeared between period 1 and period 2: females 8a, 8b, 1a and 6a are juvenile females, putative daughters of the females with the same number

age, a male was substantially overlapping with 1.22 ± 0.21 ($n=18$) females, while females were overlapping with 1.05 ± 0.08 ($n=22$) males. In 1989, males overlapped the home ranges of more females than in 1988, but this difference was not statistically significant (Table 4). This was because two males, with exceptionally large home ranges (627 m^2 and 427 m^2), were overlapping with 20% or more of the ranges of 6 and 4 breeding females, respectively. Seven males of 16 were overlapping 20% or more of the home range of only 1 female. Most females (17 of 21) had only 1 male overlapping 20% or more of their ranges. Because most individual voles tended to show strong site fidelity, no male-female spatial association disbanded without the disappearance of one of the partners, suggesting that males and females were truly associated in monogamous pairs. Further, on two occasions male 5 was located in the nest where female 7 was nursing a litter while that female was outside of the nest. Possibly this male was attending the litter of its probable mate. Thus, it appears that most males and females are spatially associated in monogamous pairs.

Intrasexual spacing in summer

A consequence of the natal philopatry of young females and the lack of recruitment of reproductively active males is that the breeding density of females increased considerably over the summer, while the number of scrotal males changed little (Table 1). The number of neighbouring breeding females with whom a female had her home range overlapping as well as the number of females with more than 20% of their range overlapping increased significantly as the summer progressed (Table 4). Many breeding females (17 of 45) did not overlap more than 20% of the range of their female neighbours, but other females were overlapping a significant portion of 1 ($n=19$), 2 ($n=3$) of 4 ($n=4$) breeding females. Relatively more females have large values of overlap in summer than in spring (Fib. 3b). Because young females showed little dispersal, genetically related breeding females tended to have home ranges adjacent and more overlapping than unrelated females (mean percentage overlap between unrelated females = 12.9 ± 2.5%, $n=90$ pairs; mean percentage overlap between related females = 45.6 ± 5.3%, $n=46$ pairs; $P<0.001$, Mann Whitney *U* test with normal approximation). Groups of related breeding females used adjacent and partly overlapping ranges.

Although the number of males increased dramatically during the breeding season, the number of males with scrotal testes stayed constant (Table 1). By mid-June, of the 32 scrotal males present on the grid, 15 were overwintering individuals, 7 were site born and had matured on the grid and 10 others were immigrants. Seven immigrants were caught first as subadults, while 3 others were likely overwintering individuals. As with females, the overlap between breeding males was higher in summer than in spring. Both the number of males overlapped by another male and the number of neighbours with more than 20% of their ranges overlapped increased significantly (Table 4). However, most males had relatively exclusive ranges (i.e. ≤20% overlap), and only 9 males (out of 28) had ranges largely overlapping (i.e. ≥20% overlap) with those of 2 or 3 other males. Two site born males had ranges totally overlapping with a male that was spatially associated with their mothers in the spring. It is thus possible that these 2 males shared the ranges of their fathers. Two other males, apparently littermates, had totally overlapping ranges as adults.

Intersexual spacing in summer

More breeding females than scrotal males were present in summer, when female home ranges were much smaller than those of males. Male ranges overlapped 20% or more of the range of 2.96 ± 0.34 ($n=28$) females, significantly more than they did in the spring of 1988 (Table 4). In contrast, although females overlapped with significantly more males than they did in the spring, no significant differences were found between the number of males with 20% or more of their range overlapped by a female in summer and in spring (Table 4). However, unlike in spring, several females had 20% or more of their ranges overlapped by 2 ($n=9$), 3 ($n=2$) or four ($n=2$) males in June 1988. The frequency distribution of the percentage overlap of female ranges by males was similar in the spring and summer but few females were overlapping a large portion of a male's home range (Fig. 3d).

Discussion

This study has shown that in spring male-female pairs have their intrasexual territories highly overlapping with each other. The 1:1 operational sex ratio and the spatial association of pairs of males and females suggest that a monogamous mating system was prevalent in the spring of 1988 and that 50% of the males were monogamous in the spring of 1989. In summer, home ranges of males and females were less exclusive, and female ranges were considerably smaller than those of males. Females were more philopatric than males, and few reproductively active males were recruited. This caused the mating system to change in summer. Females thought to be members of family groups lived adjacent to each other and had overlapping home ranges. Males overlapped with more than one female in summer but most females still overlapped with only one male, which suggests that the mating system is polygynous at this time.

In this study, we used both trapping and telemetry to study patterns of space use and to make inferences about the social and mating systems. Further, we used probabilistic polygons as a measure of home range and assumed that males and females spatially associated are likely to be mates. However, it is not known whether there is a good correlation between the actual mating system and the observed spacing system. For instance, in *Clethrionomys rufocanus*, the sire of a female's offspring often has it home range overlapping with that of the female (Kawata 1985), while in other species, females are known to mate with males other than those with whom they are socially associated (Ågren et al. 1989). Social monogamy does not necessarily imply sexual monogamy and all inferences on the mating system of microtine rodents based on spatial patterns alone should be tentative until actual mating patterns are documented.

Spatial organization and mating system

The spacing system of *M. townsendii* is based on territoriality of both males and females. The social system seems to be primarily monogamy at the beginning of the breeding season, but some social units are composed of one male and two or three females. Because of the higher philopatry of juvenile females than males, the mating system seems to change and polygynous groups become more prevalent in summer. But in the spring of 1989, when vole density was lower and most females used intrasexual territories, more were associated with multiple males and four males (25%) overlapped with several females. Polygyny in spring can thus result from three situations: the operational sex ratio can be skewed in favor of females owing to higher survival of females than males; related females can be overlapping home ranges (e.g. females 5 and 6, Fig. 2; see also McShea and Madison 1984); or males can have unusually large home ranges (e.g. male 3, Fig. 2).

Monogamy is rare among mammals (Kleiman 1977). Ims (1987a) predicted that monogamy should be the mating system of microtines when females are territorial and are sexually receptive in synchrony. He also pointed out that polygyny should be prevalent when spatially clumped females are sexually receptive in synchrony. Female *M. townsendii* are synchronous at the onset of breeding in spring, and the prevalence of monogamy at the beginning of the breeding season is consistent with Ims's (1987a) hypothesis. The overall breeding synchrony seems to dissipate in summer, and one would then expect to observe a promiscuous mating system at this time (Ims 1987a; Ims et al. 1988). Male *M. townsendii* did not increase their territories greatly in summer, and they overlapped one to four breeding females. Most males did not have largely overlapping home ranges, unlike promiscuous microtines (e.g. *Clethrionomys sp.*, Bondrup-Nielsen and Karlsson 1985). Based on spacing patterns, the mating system of Townsend's vole in summer appears polygynous rather than promiscuous as predicted by Ims (1987a). If adjacent, related females are breeding in synchrony in summer, they can represent a defendable resource for a male and territoriality and polygyny should be more advantageous for males than non-territoriality.

Monogamy is the main type of social system in *Microtus ochrogaster* (Thomas and Birney 1979; Getz and Hofmann 1986; Getz et al. 1987), *Microtus pinetorum* (Fitzgerald and Madison 1983) and *Pitymys multiplex* (Salvioni 1988). It also occurs at low vole density in other species [facultative monogamy: *Microtus montanus* (Jannett 1978)]. In *M. ochrogaster*, 50% of the breeding units are monogamous year round, both at low and at high density (Getz and Hofmann 1986). In this species, young females remaining in the natal nest do not become reproductive (McGuire and Getz 1981). because a chemical signal present in the urine of females suppresses the reproductive activation of young females (Getz et al. 1983). In *M. townsendii*, there was no suppression of reproductive activity of young females at the beginning of the breeding season, and up to 30% of the young females born in summer matured close to their birthsite. Few reproductively active males were recruited, and the sex ratio became skewed in favor of females. The mating system of *M. townsendii* is not as rigid as that of *M. ochrogaster* and changes seasonally from a predominantly monogamous system to a mostly polygynous or promiscuous system.

Female philopatry and social organization in summer

As observed in other microtines (e.g. Boonstra et al. 1987), female Townsend's voles are more philopatric than males. In the present study, we also observed a marked decrease in the probability of recruitment into the breeding population for both males and females during the breeding season. As the breeding season progresses, female dispersal increases and the maturation of some females is apparently suppressed by other females, possibly their mothers (Lambin, unpublished data). A decrease in resource availability to resident breeding females could make it uneconomical for a mother to allow her female offspring to reach sexual maturity. This can lead to either forced emigration of juvenile females or suppression of maturity by parental pheromones (Anderson 1989).

One consequence of the philopatry of young females is that clusters of related females living close to each other are formed as young females are recruited into the breeding population. These related females share home ranges more than unrelated females. Groups of females breeding close to each other and sharing space have been found among several other microtine species, and it has often been speculated that these were related females (Frank 1957; Fitzgerald and Madison 1983; Thomas and Birney 1979; Getz et al. 1987; Madison 1980; McShea and Madison 1984; Heske 1987; Chitty 1987), but no firm evidence has been available. In this study, we followed each individual for a long period; thus, we could infer the relationship of the breeding females. In a separate study, we confirmed the validity of this method by marking unweaned voles in their mother's nest (Lambin, unpublished work).

Boonstra et al. (1987) suggested that the basic social organization in all female *Microtus* may be one based on female kin clusters, and Frank (1957) suggested that space-sharing between related *Microtus arvalis* females allows populations of this species to reach extremely high densities. In our study, the increase in density of breeding female corresponds to a decrease of female home range sizes and an increase in the amount of overlap between females. Because related philopatric females are neighbours, they can maintain the social bonds developed before weaning through familiarity later in their lives. Living close to an amicable related female neighbour would be advantageous for a female if her offspring were immune from aggression from unrelated voles and thus experienced better survival. The spacing system of *M. californicus* and *M. agrestis* is based on highly overlapped female home ranges (Myllymäki 1977; Heske 1987; Ostfeld 1985). However, females of both species are territorial at the beginning of the breeding season and, as in Townsend's vole, female home ranges overlap later in the breeding season (Salvioni and Lidicker 1989; Erlinge et al. 1989). Thus, Boonstra et al.'s (1987) suggestion may be supported for many *Microtus* species.

The reason why maturation of philopatric females is suppressed in some species (*M. ochrogaster*, McGuire and Getz 1981; *M. montanus*, Jannett 1978, *M. pennsylvanicus*, Madison 1980, but see Boonstra et al. 1987; *Clethrionomys*, Bujalska 1973; Saitoh 1981; Bondrup-Nielsen 1986; Gilbert et al. 1986; but see Gliwicz 1989 for an exception in *Clethrionomys glareolus*), but not in others, could be related to the food resources (Ostfeld 1985) or the potential for inbreeding. In monogamous and polygynous species, inbreeding can occur through father-daughter mating if a female matures in her mother's home range.

Clutton-Brock (1989) found that among 27 species of social mammals, the average age at first conception of the females that do breed in their natal groups exceeds the average period of residence of breeding males. He argued that this indicates that inbreeding avoidance is the cause of dispersal between groups. Our data are consistent with Clutton-Brock's (1989) observation: mean residency of scrotal males is shorter than age at conception of philopatric *M. townsendii* female. However, up to 36% of these females conceived their first litter when the male spatially associated with their mother was still alive. If no incest avoidance mechanism has evolved, this could lead to frequent father-daughter matings. Pugh and Tamarin (1988) found that 4 out of 11 matings of meadow vole (*M. pennsylvanicus*) were inbred. One of these was a father-daughter mating, but there was no evidence that the voles seek out or avoid inbred matings.

Territoriality and density limitation

M. townsendii showed little intrasexual overlap at the beginning of the breeding season and occupied new areas following the disappearance of adjacent individuals. The high rate of wounding of males and the observation of a male chasing an intruder indicate that male Townsend's voles defend their home ranges aggressively and are truly territorial (*sensu* Kaufmann 1983). Although females are territorial, they are not wounded as often or severely as males and, as suggested by Taitt and Krebs (1982), they might not rely on overt aggression to defend their territories. Male and female territoriality appears to be the proximate mechanism for the limitation of breeding density by spacing behaviour, as demonstrated by Taitt and Krebs (1983). The sex-specific territoriality reported here is consistent with the failure of sex ratio manipulation to affect the demography of *M. townsendii* populations (Redfield et al. 1978b). When the whole habitat is saturated with territories, competition for space occurs between same sex individuals. This results in excess voles being driven out of breeding territories by established individuals in spring and contributes to the spring decline. The number of voles expelled depends on the density as well as on territory size prior to the onset of breeding activity in spring. Taitt and Krebs (1981) and Ims (1987b with *C. rufocanus*) found that when food was supplemented, female home range size decreased and populations with extra food increased in density.

The degree of relatedness could influence the density of breeding females in the spring. Both in 1988 (one case) and in 1989 (four cases on two trapping grids), pairs of females shared space in spring while most other females were territorial. In 1989, trapping records suggested that these were mother-daughter (two cases) or sister associations (two cases). If groups of related females were common before the onset of breeding and if such females were sharing home ranges, competition for space between females would be less severe and the density of breeding females would be higher. Winter breeding or increased survival of voles living in kin groups could influence the number of kin groups present at the end of the winter. The effects of fluctuations in the degree of female relatedness on breeding success and on the demography of Townsend's vole populations are currently being investigated.

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References

Ågren G, Zhou Q, Zhong W (1989) Ecology and social behaviour of the Mongolian gerbils, *Meriones unguiculatus*, at Xilinhot, Inner Mongolia, China. Anim Behav 37:11–27

Anderson PK (1989) Dispersal in rodents: a resident fitness hypothesis. Spec Publ Am Soc Mammal 9:1–141

Beacham TD (1979) Dispersal tendency and duration of life of littermates during population fluctuations of the vole *Microtus townsendii*. Oecologia (Berlin) 42:11–21

Bondrup-Nielsen S (1986) Investigation of spacing behaviour of *Clethrionomys gapperi* by experimentation. J Anim Ecol 55:269–279

Bondrup-Nielsen S, Karlsson F (1985) Movements and spatial patterns in populations of *Clethrionomys* species: a review. Ann Zool Fenn 22:385–392

Boonstra R, Krebs CJ (1977) A fencing experiment on a high-density population of *Microtus townsendii*. Can J Zool 55:1166–1175

Boonstra R, Rodd FH (1983) Regulation of breeding density in *Microtus pennsylvanicus*. J Anim Ecol 52:757–780

Boonstra R, Krebs CJ, Beacham TD (1980) Impact of botfly parasitism on *Microtus townsendii* populations. Can J Zool 58:1683–1692

Boonstra R, Krebs CJ, Gaines MS, Johnson ML, Craine ITM (1987) Natal philopatry and breeding systems in voles (*Microtus spp.*). J Anim Ecol 56:655–673

Bujalska G (1973) The role of spacing behavior among females in the regulation of reproduction in the bank vole. J Reprod Fertil Suppl 19:465–474

Charnov EL, Finerty JP (1980) Vole population cycles: a case for kin-selection. Oecologia 45:1–2

Chitty D (1987) Social and local environments of the vole *Microtus townsendii*. Can J Zool 65:2555–2566

Clutton-Brock TH (1989) Female transfer and inbreeding avoidance in social mammals. Nature 337:70–71

Cockburn A (1988) Social organization in fluctuating populations. Croon Helm, London

Danielson BJ, Johnson ML, Gaines MS (1986) An analysis of a method for comparing residents and colonists in a natural population of *Microtus ochrogaster*. J Mammal 67:733–736

Desy EA, Batzli GO, Jike L (1989) Comparison of vole movements assessed by live trapping and radiotracking. J Mammal 70:652–656

Dueser RD, Rose RK, Porter JH (1984) A body-weight criterion to identify dispersing small mammals. J Mammal 65:727–729

Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223

Erlinge S, Agrell J, Nelson J, Sandell M (1989) Social organization and population dynamics in a field vole (*Microtus agrestis*) population in southern Sweden. Abstract of papers and posters, vol 1:78. Fifth International Theriological Congress Rome 1989

Fitzgerald RW, Madison DM (1983) Social organization of a free-ranging population of pine voles. *Microtus pinetorum*. Behav Ecol Sociobiol 13:183–187

Frank F (1957) The causality of microtine cycles in Germany. J Wildl Manage 21:113–121

Getz LL, Hofmann JE (1986) Social organization in free living prairie voles *Microtus ochrogaster*. Behav Ecol Sociobiol 18:275–282

Getz LL, Dluzen D, McDermott JL (1983) Suppression of reproductive maturation in male-stimulated virgin female *Microtus* by a urinary chemosignal. Behav Processes 8:59–64

Getz LL, Hofmann JE, Carter CS (1987) Mating system and population fluctuations in the prairie vole *Microtus ochrogaster*. Am Zool 27:909–920

Gilbert BS, Krebs CJ, Talarico D, Cichowski DB (1986) Do *Clethrionomys rutilus* females suppress maturation of juvenile females? J Anim Ecol 55:543–552

Gliwicz J (1989) Individuals and populations of the bank vole in optimal, suboptimal and insular habitats. J Anim Ecol 58:237–247

Hestbeck JB (1982) Population regulation of cyclic mammals: the social fence hypothesis. Oikos 39:157–163

Heske EJ (1987) Spatial structuring and dispersal in a high density population of the California vole, *Microtus californicus*. Holarctic Ecol 10:137–148

Hilborn R (1975) Similarities in dispersal tendency among siblings in four species of voles (*Microtus*). Ecology 56:1221–1225

Ims RA (1987a) Male spacing systems in microtine rodents. Am Nat 130:475–484

Ims RA (1987b) Responses in spatial organization and behaviour to manipulations of the food resource in the vole *Clethrionomys rufocanus*. J Anim Ecol 56:585–596

Ims RA (1988) Spatial clumping of sexually receptive females induces space sharing among male voles. Nature 335:541–543

Ims RA, Bondrup-Nielsen S, Stenseth NC (1988) Temporal patterns of breeding events in small rodent populations. Oikos 53:229–234

Jannett FJ (1978) The density-dependent formation of extended maternal families of the montane vole, *Microtus montanus nanus*. Behav Ecol Sociobiol 3:245–263

Kaufmann JH (1983) On the definitions and functions of dominance and territoriality. Biol Rev 58:1–20

Kawata M (1985) Mating system and reproductive success in a spring population of the red-backed vole *Clethrionomys rufocanus bedfordiae*. Oikos 45:181–190

Kenward RE (1987) Wildlife radio tagging. Academic Press, London

Kleiman D (1977) Monogamy in mammals. Q Rev Biol 52:39–69

Krebs CJ (1979) Dispersal, spacing behaviour, and genetics in relation to population fluctuations in the vole *Microtus townsendii*. Fortschr Zool 25:61–77

Krebs CJ (1985) Do changes in spacing behaviour drive population cycles in small mammals? In: Sibly RM, Smith RH (eds) Behavioural ecology: ecological consequences of adaptive behaviour. Symp Br Ecol Soc 25:295–312

Krebs CJ, Boonstra R (1978) Demography of the spring decline in populations of the vole *Microtus townsendii*. J Anim Ecol 47:1007–1015

Krebs CJ, Wingate I, Leduc J, Redfield JA, Taitt M, Hilborn R (1976) *Microtus* population biology: dispersal in fluctuating populations of *M. townsendii*. Can J Zool 54:79–95

Krebs CJ, Redfield JA, Taitt M (1978) A pulsed-removal experiment on the vole *Microtus townsendii*. Can J Zool 56:2253–2262

Madison DM (1980) Space use and social structure in meadow voles, *Microtus pennsylvanicus*. Behav Ecol Sociobiol 7:65–71

McGuire MR, Getz LL (1981) Incest taboo between sibling *Microtus ochrogaster*. J Mammal 62:213–215

McShea WJ, Madison DM (1984) Communal nesting between reproductively active females in a spring population of *Microtus pennsylvanicus*. Can J Zool 62:344–346

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

Ostfeld RS (1985) Limiting resources and territoriality in microtine rodents. Am Nat 126:1–15

Ostfeld RS (1986) Territoriality and mating system of California voles. J Anim Ecol 55:691–706

Pugh SR, Tamarin RH(1988) Inbreeding in a population of meadow voles, *Microtus pennsylvanicus*. Can J Zool 66:1831–1834

Redfield JA, Taitt MJ, Krebs CJ (1978a) Experimental alterations of sex ratios in populations of *Microtus oregoni*, the creeping vole. J Anim Ecol 47:55–69

Redfield JA, Taitt MJ, Krebs CJ (1978b) Experimental alterations of sex ratios in populations of *Microtus townsendii*, a field vole. Can J Zool 56:17–27

Saitoh T (1981) Control of female maturation in high density populations of the red-backed vole *Clethrionomys rufocanus bedfordiae*. J Anim Ecol 50:79–87

Salvioni M (1988) Home range and social behavior of three species of European *Pitymys* (Mammalia, Rodentia). Behav Ecol Sociobiol 22:203–210

Salvioni M, Lidicker WZ (1989) Seasonal and sexual effects on territoriality in the California vole. Abstract of papers and posters, vol 1:99. Fifth International Theriological Congress, Rome 1989

Taitt MJ, Krebs CJ (1981) The effect of extra food on small rodent populations: II. Voles (*Microtus townsendii*). J Anim Ecol 50:125–137

Taitt MJ, Krebs CJ (1982) Manipulation of female behaviour in field populations of *Microtus townsendii*. J Anim Ecol 51:681–690

Taitt MJ, Krebs CJ (1983) Predation, cover, and food manipulations during a spring decline of *Microtus townsendii*. J Anim Ecol 52:837–848

Taitt MJ, Krebs CJ (1985) Population dynamics and cycles. Spec Publ Am Soc Mammal 8:567–620

Tamarin RH (1984) Body mass as a criterion of dispersal in voles: a critique. J Mammal 65:691–692

Tamarin RH, Sheridan M (1987) Sibship assignment and mass-defined recruitment in a population of meadow voles. Ecology 68:1102–1104

Thomas JA, Birney EC (1979) Parental care and mating system of the prairie vole *Microtus ochrogaster*. Behav Ecol Sociobiol 5:171–186

Wolff JO (1985) Behaviour. Spec Publ Am Soc Mammal 8:340–372