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Influence of female relatedness on the demography of Townsend's vole populations in spring

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Summary

1. The relatedness of individuals can influence their behaviour and changes in the degree of female relatedness in spring may influence the demography of vole populations (Lambin & Krebs 1991a). Here we report on an experiment testing the effect of relatedness on the demography of Townsend's vole (*Microtus townsendii*) populations (kin and non-kin treatments) over three consecutive springs.

2. Most nestlings were marked before weaning such that we knew which recruits were related to one another and to which adult female. The average size of matrilineal groups was experimentally manipulated by selectively removing voles of known origin and by preventing predation by birds of prey.

3. Nearest neighbours had their nests closer to one another on the kin treatment, but there were no differences in home range size between treatments. Home-ranges of females present on both treatments were smaller in a spring of high density than in the springs with lower density.

4. Female survival was better on the kin treatment. Within the kin treatment, females with at least one first degree relative as a neighbour survived better than females without such a relative. No such difference was observed within the non-kin treatment.

5. Females in the kin treatment gave birth to their first spring litter 5–7 days later than females in the non-kin treatment, possibly as a consequence of space sharing with related neighbours. The weaning success of the first spring litter was significantly higher on the kin tratment than on the non-kin treatment, but there were no differences in the weaning success of females with and without related neighbours within treatments. The presence of immigrant females on the non-kin treatment and not on the kin treatment may have caused the difference in weaning success between the treatments.

6. We conclude that female relatedness influences the pattern of space use and the survival of females in spring. The presence of immigrant females attempting to establish in the population has a pronounced effect on the weaning success of residents.

Key-words: kin-selection, natal philopatry, population cycles, spacing behaviour, *Microtus townsendii*.

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Introduction

For many years population biologists have attempted to demonstrate an unambiguous link between population dynamics and changes in social behaviour (Chitty & Phipps 1966; Chitty 1967; Christian 1970; Charnov & Finerty 1980; Krebs 1985). In voles and lemmings changes in behaviour have been postulated to cause the dramatic fluctuations in numbers typical of these species. Changes in behaviour have been thought to result in and to cause changes in the genetic make-up of individuals (Chitty 1967), changes in the level of stress experienced by individuals (Christian 1970), and to be due to changes in the degree of relatedness of the members of populations (Charnov & Finerty 1980; Kawata 1990).

There is good evidence that spacing behaviour

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(Watson & Moss 1970) limits population numbers of several microtine species (review in Lambin & Krebs 1991a) and at least one grouse species (Watson & Moss 1985). Spacing behaviour in spring limits the number of individuals able to reproduce (Taitt & Krebs 1985) and aggressiveness of adults influences juvenile survival and recruitment (Boonstra 1978). Territoriality of one or both sexes is a cause of spring declines in voles and, therefore, strongly influences demography (Krebs & Boonstra 1978; Boonstra & Rodd 1983; Taitt & Krebs 1983; 1985; Gipps *et al.* 1985; Lambin & Krebs 1991b). Taitt & Krebs (1985) have argued that in years of outbreak of the non-cyclic Townsend's vole (*Microtus townsendii*, Bachman), spring declines are absent or present only among males. Population eruptions of this species are accompanied by changes in adult body mass, length of the breeding season and juvenile survival typical of species with periodic fluctuations in population size (Krebs 1979) and are, therefore, considered as equivalent to cyclic population peaks. As spacing behaviour in spring limits population size, it is important to know what changes in spacing behaviour allow populations to reach peak densities in some years. In red grouse (*Lagopus lagopus scoticus* Lath.), changes in the size of cock territories and cock aggressiveness with density limit population size, and changes in the relatedness of cocks might be linked to changes in aggressiveness (Mountford *et al.* 1990; Moss & Watson 1991). In 1980, Charnov & Finerty proposed that kin selection, as evidenced by aggression between individuals with a low coefficient of relatedness, may be a significant contributing factor in vole population cycles. Their hypothesis assumes that the degree of relatedness is high in sparse populations of voles and that kin-selection favours amicable behaviour between related individuals. The degree of kinship is assumed to be inversely related to population density, and individuals living at high density are assumed to experience high dispersal rates and low reproductive success as a result of their interactions with unrelated neighbours. However, in a recent review Kawata (1990) concluded that the assumptions of the Charnov and Finerty hypothesis are inadequate, and that its predictions are not supported by the available evidence. There is no convincing evidence that relatedness is lower at high density than at low density (Frank 1957; Jannet 1978; Jones *et al.* 1988; Pugh & Tamarin 1990) and experimental evidence available to date on the effect of kin interaction on demography is conflicting (Kawata 1987; Boonstra & Hogg 1988; Ylönen Mappes & Viitala 1990). Recently we have outlined the conditions under which changes in female relatedness are likely to influence microtine demography (Lambin & Krebs 1991a) and measured the benefits accruing to voles interacting with their kin (Lambin, 1993, and submitted). Specifically, we predicted that (i) female relatedness influences the intensity of the spring decline in vole populations because this is when social interactions determine breeding population size; (ii) competition for space is relaxed among related females in spring, and this enables more females to remain and reproduce in the summer; (iii) there is no simple relationship between density and relatedness, but the degree of female relatedness is higher before the beginning of the breeding season of outbreak or peak density years than in the spring of lower density years; (iv) the effects of extrinsic factors such as predation and parasitism on population density are amplified through the disruption of relatedness among females. This amplification occurs because mortality not only reduces density, but causes a reduction in the size of matrilineal families and creates vacancies for immigrants. Conversely, high overwinter survival or winter breeding not only keeps vole numbers high, but also maintains or increases the size of matrilineal vole families. Female philopatry and the lack of successful immigration are the factors bringing about increases in the degree of female relatedness in populations.

In this paper, we present the results of a field experiment testing the prediction that the degree of female relatedness influences the demographic parameters of Townsend's vole populations during the spring decline. We also compared the reproductive success of females living with and without related neighbours in the spring. We manipulated the degree of relatedness in natural populations of Townsend's vole (*M. townsendii*) by means of selective removal and predator exclosures. The experiment was designed to measure the influence of female relatedness on adult and juvenile survival rather than on population numbers *per se*.

Methods

STUDY AREA AND CENSUS TECHNIQUES

The study took place between 15 January 1989 and 15 September 1991 near Boundary Bay, Ladner, 35 km south of Vancouver, British Columbia, Canada (49°04′N, 123°00′W). Two 0·5-ha grids (G1, G2) were trapped in a grassland that had been left undisturbed for more than 40 years. G1 had been trapped at least bimonthly since February 1988 (Lambin & Krebs 1991b), whereas G2 was established in December 1988. Both grids had an heterogeneous plant cover and were characterized by a gradient in wetness. G2 is wetter than G1 in winter and spring, but both grids are otherwise similar. The two grids were 125 m apart and were both bounded by a 7-m wide ditch on the south side and by a gravel road on the east side. A 2-m wide grass strip was mown regularly in summer on the west and north sides of the grids in order to delineate further the grid edges and distinguish between voles living within the trapping grids from those living outside the grids. Longworth traps were placed at 5-m intervals under 20 cm × 20 cm plywood boards at each of 170 points in a grid pattern. Longworth traps were left locked open between trapping sessions and were intensively used by voles as part of their runway system. An additional line of Longworth traps with 10-m spacing was added beyond the ditches and the mowed strip in order to census the individuals living on the outer edge of the grid. Pitfall live-traps were used in addition to Longworth starting in May when the water table receded sufficiently. Trapping was performed weekly in spring and summer, and bimonthly when voles were not breeding. Before each sampling period, traps were checked for proper functioning and were generally set in the morning, and checked between three and six times at 2-hour intervals. In winters when the voles were not breeding we checked traps every 5 hours during the day and traps were left set overnight. Field procedures are further detailed in Lambin (submitted).

DETERMINING RELATEDNESS AND IDENTIFYING IMMIGRANTS

Matrilines were determined by marking pups in the nests of radio-collared lactating females (68% of all recruits) and assigning young from unmarked litters to the female most likely to have produced them (32% of all recruits, see below and Lambin, submitted, for details). Radio-transmitters (SS-1, Biotrack, Dorset, England) were attached to females with tie-grip collars as soon as possible *after* parturition. Transmitters weighed 2·85 g, which represents 3·5–7·9% (mean 5·17%) of the mass of the vole to which they were attached. Active nests were located by repeatedly locating collared females by means of a probe antenna. Located nests were opened and pups were marked by toe-clipping with microscissors (maximum one toe per foot); age was based on stage of development. Pups were returned to the nest within 2 minutes of removal. Females typically moved the pups to another nest within 30 min after marking and invariably abandoned the previous nest. Upon first capture, we checked all voles for clipped toes and assigned them to the appropriate dam if they had been marked in the nest. Juveniles 32 g or less when caught for the first time that had not been marked in their mother's nest were assigned a mother by mapping the position of mothers of all unmarked litters of appropriate age and assuming that juveniles were caught close to their natal nest (details in Lambin, submitted). The number of young weaned per litter is defined as the number of juveniles from a litter caught in traps at least once. Radio-tagging mothers and marking young in the nest did not affect the success of litters (Lambin, submitted).

THE EXPERIMENT

We applied two treatments to the trappings grids in the springs of three successive years to assess the effects of female relatedness on the intensity of the spring decline in *M. townsendii*. On the non-kin grid treatment (NK: G1 1989, G2 1990, G1 1991), we attempted to keep the size of vole matrilines low by removing females known to have close female relatives as neighbour. We removed all but one randomly chosen adult female per group of close relatives. However, some females with relatives were left untouched to avoid inducing significant differences in density between the two treatments. In the kin treatment (K: G2 1989, G1 1990, G2 1991), we attempted to increase the proportion of females having at least one female relative as a neighbour. To do so, we removed all female immigrants upon first capture and we attempted to reduce predation by birds of prey and great blue herons (*Ardea herodias* L.) by covering the grids with fishing nets during the winters of 1989–1990 and 1990–1991. In this manner, it was hoped to prevent any dilution of families by immigrants and to improve over-winter survival of members of existing families. Fish nets were laid between trap lines directly on the vegetation, 40–120 cm above ground level. They covered approximately 90% of the grid. Nets were left on the kin grids between December (1/12/89, 13/12/90) and mid-February (22/02/90, 22/02/91), and were thus removed before signs of reproductive activity were observed. Therefore, the two treatments experienced identical conditions during the onset of reproduction, and differed only in their recent history and in the average relatedness of the voles inhabiting them. Nets were not used on the kin grid in 1988–1989, as G2 was not established until the end of December 1988. Also, during the winter of 1988–1989 immigrants were not removed from this kin grid, as we could not distinguish them from site-born voles until the whole resident population had been marked. Three females with relatives could be identified from previous trapping on G1 and were removed before the onset of reproduction. Thus, in 1989, female relatedness was reduced by selective removal in the non-kin treatment and was higher, but not quantifiable in the kin treatment. Owing to the logistical difficulties of running intensive trapping programmes and determining relatedness in more than two populations simultaneously, treatments were replicated between years and not within them.

DATA ANALYSIS

We analysed adult vole survival before and after the onset of reproduction with the Cormack (1964)–Jolly (1965)–Seber (1965) method recently extended by Clobert, Lebreton & Allaine (1987) and detailed in Lebreton *et al.* (1992). The method used is based on the philosophy of generalized linear models (Pradel, Clobert & Lebreton 1990). It involves selecting models that adequately describe the probabilities of recapture and survival of members of the study population. Models may include dependance of survival and trappability upon external variables or be partitioned by sex, cohort or experimental treatment. A biologically meaningful model that explains the variability of the data, but excludes unnecessary parameters is selected by comparing the fit of a specific model to a more parsimonious model which is a general case of the previous one. Differences in the adjustment of competing models can be tested by means of likelihood-ratio tests (see Lebreton *et al.* 1992, for a comprehensive review on modelling survival).

For 1989 and 1990, we considered the survival of males and females separately during the 2 weeks before and after the week of the first births of the breeding season. For the purpose of this paper we refer to this period as the spring decline even though populations declined during a longer time interval. Due to the presence of a long-tailed weasel (*Mustela frenata*) on the non-kin grid during the 2 weeks after the birth of the first spring litter in 1991, we chose to consider the survival over the 4 weeks before the birth of the first litter for both grids in this year. The weasel is known to have killed at least four radio-collared females in 1991 and its influence on survival could not be separated from any influence of the treatment. In all years and treatments, voles born in the previous year or of those that immigrated before the onset of reproduction were included in the survival analysis. Because females migrating into the kin treatment area were removed, the survival of immigrant females on the non-kin treatment area is not considerd in this analysis. The survival of winter born voles is not considered as they were not competing for territories in spring.

For comparing survival rates in different treatments, we first tested the constancy of survival rates and trappability over the 4-week period for each repetition of each treatment separately. We then tested the constancy of trappability across treatments by comparing a model specifying a different trappability for each repetition of each treatment to a model with a single estimate of trappability. Our initial survival model included a log-linear relationship between survival and the treatment effect (Kin vs. Non-Kin), the year of experimentation effect (1989, 1990, 1991) and an interaction between these two variables. We first tested the significance of the interaction between year and treatments, and for an effect of the year of experimentation on survival. According to the result of these comparisons, we finally analysed the effect of the treatments on survival with the model of greatest parsimony.

Because of the lack of formal control treatment in the present study, we further investigated the effect of female relatedness on survival using the data from the 2 years for which genetical relationships between females were known precisely (1990, 1991). We distinguished between females that had at least one first degree relative as neighbour and those that were surrounded only by unrelated females, and included this additional criterion in the survival models. The death of three females in trapping accidents was taken into account in the survival analysis. All computations were performed using the package SURGE 4·0 (Clobert *et al.* 1987; Pradel *et al.* 1990).

Results

VOLE NUMBERS BEFORE THE SPRING DECLINE

Townsend's vole populations in and around the study area fluctuated greatly in size over the 3 years of study (Fig. 1). As we used unenclosed populations, we did not attempt to control for these changes and try to maintain similar densities between years. Also, as emigration was not restricted, we focussed our analysis on comparison of survival and recruitment rates between treatments rather than on vole numbers. Overall, spring numbers were highest in the spring of 1990 and lowest in the spring of 1991. There were no systematic differences in vole numbers between treatments before the onset of reproduction (Table 1). Nevertheless, there was a deficit of males in the kin treatment in 1991 and a larger number of females in the kin treatment than in the non-kin treatment in 1990 despite the removal of 17 immigrant females during February and March from the kin treatment.

To ensure that the manipulation carried out during the winter did not cause differences between treatments other than changes in the degree of relatedness, the mean body mass, age distribution and parity of the overwintered female voles present before the onset of reproduction on the two grids were compared. There were no significant differences in average body mass or mean age of females or males between treatments. However, males were on average significantly lighter in 1989 than in other years and females were significantly heavier in 1990 than in 1991. The mean age of the overwintered females present before the spring decline was similar in the two treatments in 1990 and 1991, and not known in 1989 (Mann-Whitney *U*-test, $P > 0{\cdot}5$ in both years). However, a significantly higher proportion of the females present on the non-kin grid in the spring of 1990 had previously immigrated from outside the study area and their age was not known (Table 1, $\chi^2_{\text{adj}} = 14{\cdot}07$, df = 1, $P < 0{\cdot}01$). In 1991, the proportion of immigrant females was identical on both grids and lower than in 1990. Under the assumption that immigrant females had not reproduced elsewhere, similar proportions

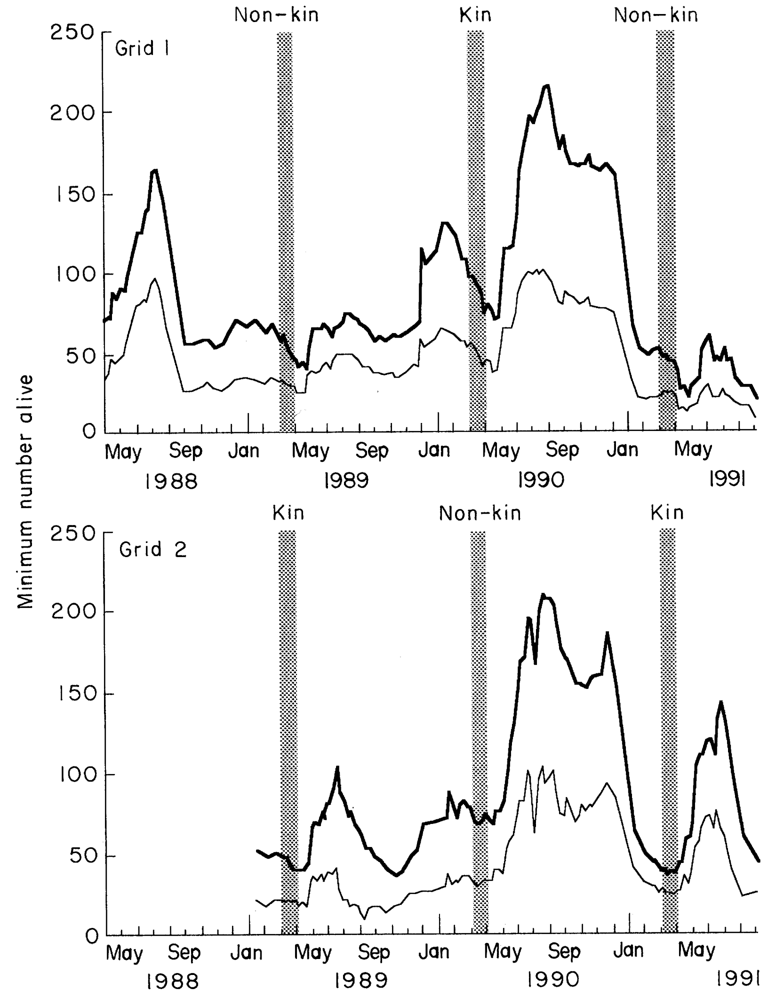

Fig. 1. Changes in female number on Grid one and two at Boundary Bay between 1989 and 1991. Shaded areas are centred on the birth date of the first spring litters. The thick line represents the number of males and females combined, and the thin line represent the number of females.

Table 1. Number (MNA) of adult voles present on G1 and G2 2 weeks (1989, 1990) or 4 weeks (1991) before the birth of the first spring litters and considered for the survival analysis (see text for justification)

	Kin treatment			Non-kin treatment		
Year	1989	1990	1991	1989	1990	1991
Grid	G2	G1	G2	G1	G2	G1
Spring decline	21/3–21/4	1/3–1/4	1/3–1/4	21/3–21/4	1/3–1/4	1/3–1/4
Number of overwintered females before decline	21	49	27	28	32	22
Number of overwintered males before decline	21	45	10	23	41	23
Number of females with related neighbours	>5 >25%	38 77·5%	13 48·1%	?	6 18·7%	5 22·7%
Number of established immigrants among overwintered females	?	4	5	?	15	4
Number of female immigrants						
before decline	11	8*	7*	9	5	0
during decline	4*	9*	4*	1	13	11
Female body mass before decline (g ± SE)	45·0 ± 1·24 (21)	46·7 ± 1·0 (49)	43·9 ± 1·0 (27)	46·9 ± 1·4 (28)	50·5 ± 2·3 (32)	44·8 ± 1·1 (22)

* Removed upon first capture.

of females were nulliparous in both treatments (1990: 62·7%; 1991: 60·4%; χ^2_{adj}, $P > 0·5$). Therefore, except for there being more established immigrant females among the overwintered cohort in the non-kin treatment in 1990 and an unbalanced sex ratio in two replicates (non-kin treatment 1990, kin treatment 1991), the two populations were quite similar.

During the three spring declines, a total of 17 females immigrated into and were removed from the kin treatments (1989:4; 1990:9; 1991:4) and 25 females immigrated into the non-kin treatments (1989:1; 1990:13; 1991:11). Five newly immigrant females gave birth to a litter during the spring decline on the non-kin treatment (1989:1; 1990:2; 1991:2).

THE DEGREE OF FEMALE RELATEDNESS IN SPRING

Our manipulation of the degree of female relatedness in spring through the combined use of fish nets and selective removal succeeded in producing contrasting treatments (Table 2). However, the average relatedness was lower in 1991 than in 1990 in the kin treatment owing to catastrophic mortality in January 1991 on both trapping grids and to the lack of fall or winter reproduction during the previous winter. In 1989, the degree of relatedness was not known exactly nor increased experimentally in the kin treatment grid (G2) which had not been established until December 1988. However, two young females caught as juveniles in December 1988 were living near their mother and two other putative sisters were also living in overlapping home-ranges. Therefore, a minimum of five females had a first-degree relative (FDR: mother, daughter or littermate sister) as neighbours. On the kin treatment grid (G2) in 1989, 13 females out of 21 had their home-range overlapping with the home-range of another female, as related females often do (Lambin & Krebs 1991b, see below). No female was known to have a related female neighbour on G1 in 1989 following the removal of three females. Thus, the degree of relatedness was probably higher in the kin treatment than in the non-kin treatment in 1989.

In 1990, eight matrilines including 43 females were present on the kin treatment grid (G1). Thirty-eight adult females out of 49 (77·5%) had at least one FDR (33) or second-degree relative (5, SDR: non-littermate sister, aunt, niece) as a neighbour at the beginning of the spring decline. Six females were immigrants without female offspring. On the non-kin treatment grid (G2), 10 females out of 32 (31%) had a FDR female as a neighbour and 21 (65·6%) females were surrounded by unrelated females. In 1991, six matrilines comprising 15 females were present on the kin treatment grid (G2). Thirteen females out of 27 (48.1%) had at least one FDR (10) or SDR (3) relative as a female neighbour. On the non-kin treatment grid (G1), eight females out of 22 (36%) had a FDR or SDR neighbour and 14 females (64%) had no related female neighbour.

HOME RANGE SIZE AND OVERLAP

To estimate the extent of space-sharing in spring between females of different degrees of relatedness, we calculated the distance between the location of the nest or centre of activity of all females during the spring decline (Fig. 2). First-degree relatives were closer to each other than other pairs of females and had their nest 16·6 (±1·82, $n = 65$) meters apart from each other. Forty-nine per cent of the pairs of FDR, 22·2% of the pairs of SDR or third-degree relatives and 7% of the pairs of unrelated females had the nest or activity centres closer to each other than the diameter of an average home range (12·2 m). Females were significantly closer to their nearest neighbour in the kin treatment than in the non-kin treatment and in 1990 than in other years (two-way ANOVA, Year effect F 1,126 = 5·70, $P < 0·02$; Treatment effect F 1,126 = 5·72, $P < 0·02$; Interaction F 1,126 = 2·73 $P > 0·1$).

We measured the home-range sizes of females

Table 2. Number of female Townsend's vole that have at least one first degree relative (FDR) or second degree relative (SDR: non-littermate sister, aunt, niece) as a neighbour at the beginning of the spring decline

	Kin treatment			Non-kin treatment		
	1989	1990	1991	1989	1990	1991
Number of females	21	49	27	28	32	22
Number of females with related neighbour						
with FDR		34	10		6	5
with SDR only		4	3		0	0
all	>5	38	13	?	6	5
%	>25	77·5	48·1	?	18·7	22·7

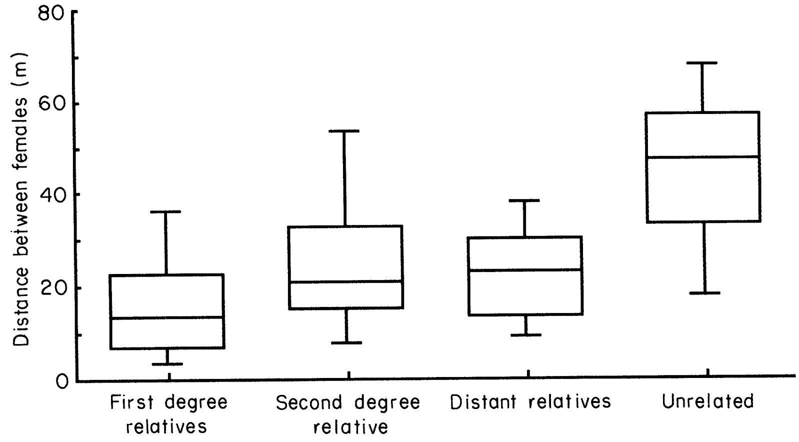

Fig. 2. Distance between nest or centre of activity of females of different degree of relatedness in the spring of 1990 and 1991. First-degree relatives are mother–daughters, littermate sisters. Second-degree relatives are non-littermate sisters, aunt-nieces. Distant relatives are cousins, grandcousins, grandnieces and aunts. Boxplots give the median, interquartile ranges and the 95% confidence intervals of the parameter.

that gave birth during the spring decline as polygons centred on the nest-site encompassing 95% of all capture locations during this 5-week period. When the nest of a female had not been located, polygons were centred on the recalculated arithmetic mean (Kenward 1987). Home range size was similar within both treatments in all three years, but was approximately 35% smaller in the spring of 1990 when female density was higher (two-way ANOVA, Year effect, F 2,105 = 5·82, $P < 0·01$; Treatment effect F 1,105 = 1·52, $P > 0·2$; Interaction F 2,105 = 1·60, Tukey's HSD 1990 < 1989 1990 < 1991, $P < 0·05$, Table 3).

CHANGES IN SURVIVAL IN SPRING

For females, models assuming that trappability and survival were constant over the 4 weeks of the spring decline fitted the data equally well as models allowing for variation in either survival or trappability over the spring decline (all six P values >0·1). This was expected as the trapping sessions were only one week apart from each other and trappability was extremely high. We could, therefore, assume the survival and trappability were constant over the 4 weeks considered. In males, survival and trappability were constant in all samples except for a sharp decline in the last period of sampling of one of the six replicates (G2 1989) for a reason unknown to us. The survival and capture rates are not separately identifiable for the last period of sampling. As a result, we allowed for a distinct estimate of the probability of survival and capture for the last occasion of capture of this replicate in all later models.

Our initial survival model included a log-linear

Table 3. Characteristics and success of the first spring litter born during the spring decline. Sample sizes are in parentheses

	Kin treatment			Non-kin treatment		
Year	1989	1990	1991	1989	1990	1991
Grid	G2	G1	G2	G1	G2	G1
Birthdate of first spring	07/04	27/03	09/04	09/04	22/03	02/04
litter of resident females	(20)	(29)	(22)	(24)	(22)	(14)
Litter size (±SE) of	5·8 ± 0·9	4·6 ± 0·3	5·2 ± 0·2	5·0 ± 0·4	5·5 ± 0·3	3·9 ± 0·6
resident females (nest found)	(5)	(19)	(17)	(4)	(15)	(8)
Weaning rate of marked	79 ± 11	39 ± 7	66 ± 8	63 ± 24	16 ± 8	27 ± 15
litters (% ± SE)	(5)	(19)	(16#)	(4)	(15)	(8)
Number of young	2·7 ± 0·6	1·6 ± 0·3	3·0 ± 0·5	2·0 ± 0·4	0·6 ± 0·3	0·8 ± 0·4
weaned per litter (±SE)	(19*)	(29)	(20#*)	(24)	(21*)	(14)
Proportion of litters	31·6	41·3	20·0	41·6	80·9	71·4
with no young weaned (%)	(19)	(29)	(20)	(24)	(21)	(14)
Age of young when first	25·0 ± 0·8	33·0 ± 1·5	27·7 ± 0·8	29·6 ± 1·4	28·6 ± 3·0	28·5 ± 2·9
caught (days ± SE)	(52)	(47)	(61)	(49)	(13)	(11)
Home-range of females	170 ± 25	86 ± 12	168 ± 23	120 ± 21	102 ± 16	144 ± 19
with litter in spring (m2 ± SE)	(19)	(19)	(21)	(21)	(19)	(12)
if number capture > 10						

Differences in sample size are because one litter was accidentally destroyed (#) and three females died in trapping accidents (*). These are excluded from the analysis.

relationship between survival and the treatment effect (e), the year of experimentation effect (y) and an interaction between these two variables (e^*y). For females and males, we were able to simplify the model, successively dropping dependency of trappability on year and on treatment, the interaction term between year and treatment on survival, and the year effect on survival (Table 4). Thus, trappability was constant over the 3 years of experimentation and over the two treatments, and survival did not differ between years of experimentation. The overall trappability estimate was 0·975 for females (lower 95% confidence limit = 0·954; upper 95% Cl = 0·986), and 0·973 for males (lower 95% Cl = 0·951; upper 95% Cl = 0·986). We tested the effect of relatedness treatment (S_eP) against a model including a single survival estimate for the six samples ($S\ P$). For females, a significant difference in deviance ($P = 0{\cdot}04$ one-tailed) between the two models indicates that survival was higher in the kin treatments than in the non-kin treatment (Table 4, Fig. 3). The use of one-tailed probabilities is applicable here as we predicted that females on the kin-treatment would survive better than females on the non-kin treatment. Thus, the most parsimonious model that fits the female survival data includes a distinct survival probability for the females living on either treatments (S_eP). Females in the kin treatment had a weekly survival rate 3·36% higher than females in the non-kin treatments. This translates into a survival rate of 72·5% (lower 95% confidence limit = 61·2, upper 95% confidence limit = 81·3) over 4 weeks in the non-kin treatments, and 83·8% (lower 95% Cl = 74·5, upper 95% Cl = 89·9) in the kin treatment. For males, there was no difference in survival between the treatments and the common estimator of weekly survival is 88·0%, which translates into a rate of 60·0% survival (lower 95% Cl = 52·0, upper 95% Cl = 67·1) over 4 weeks. Thus, the most parsimonious model that fits the male survival data includes a single survival probability ($S\ P$), except for the last trapping period of one of the six samples (G2 1989). Male survival and trappability estimates for this sample are 62·9%. Thus, overall male survival is lower than female survival (Fig. 3) and female, but not male survival is higher where average female relatedness is higher.

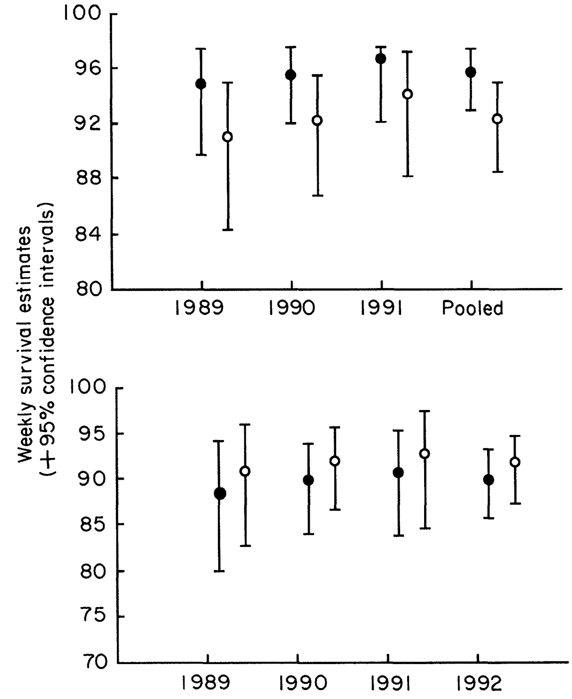

Fig. 3. Weekly survival estimates (±95% confidence interval) of overwintered females (top) and males (bottom) during the spring decline. Data from the kin treatment are empty circles and data from the non-kin treatment are filled circles.

To acertain that the differences in female survival

Table 4. Values of deviance of survival models of increasing parsimony (with fewer dependent variables). The deviance measures the fit of the model to the data. The number of free parameters represents the number of different survival probabilities estimated under each model. The statistical significance of the difference in deviance of successive models is distributed as a Chi-square. The degrees of freedom is given by the difference of parameters estimated under each model. The most parsimonious model that fits the data is in bold characters. S = survival, P = trappability, y = dependence of S or P upon year effect, e = dependence of S or P upon treatment effect, y^*e = interaction between year and treatment effect

Models	Deviance	Number of free parameters	Difference in deviance	df	One-tailed probability
Females					
S_{y*e} P_{y*e}	397·08	12			
S_{y*e} P	403·29	7	6·21	5	NS
S_{y+e} P	403·41	5	0·12	2	NS
S_e P	**404·37**	**3**	**0·96**	**2**	**NS**
S P	407·12	2	3·05	1	$P = 0{\cdot}04$
Males					
S_{y*e} P_{y*e}	500·88	13			
S_{y*e} P	506·81	8	5·93	5	NS
S_{y+e} P	507·70	6	0·24	2	NS
S_e P	507·29	4	0·23	2	NS
S P	**507·75**	**3**	**0·45**	**1**	**NS**

observed between treatments resulted from social factors and not simply from the use of fishing nets in winter, we considered the presence of at least one FDR female as a neighbour and included this new variable in survival models. Data from the two years for which this information was available were considered together to obtain adequate sample size in each subgroup. The initial model included the treatment (e), the presence of a related neighbour (n) and the interaction term (n^*e) (Table 5). Dropping the interaction increased the deviance of the model relative to a model including the treatment and neighbour effects alone (S_{e+n} P, $P = 0{\cdot}09$). We tested the effect of the treatment against models including only the neighbour effect (S_n P vs. S_{e+n} P) and against a model including both the neighbour and the neighbour* treatment interaction ($S_{e+n+e*n}$ vs. S_{n+n*e}) without significantly decreasing the fit of the model ($P > 0{\cdot}1$). Finally, we tested the influence of the presence of FDR as neighbour on female survival by comparing models S_{n+e*n} P and S_n P to a model involving a single survival for the whole data set (S P). The deviance of the null model (S P) was significantly increased relative to models assuming that survival depended upon the presence of a related neighbour (both $P = 0{\cdot}04$, one-tailed). Comparing the Akaike information criteria (AIC) of model S_{n+e*n} P and S_n P, (see Lebreton *et al.* 1992, p. 111 for a discussion of the use of AIC in model selection) indicates that the former model is the most appropriate model that fits the data. Therefore, we concluded that female survival was influenced by the presence of a first degree relative, but this influence was not the same for both treatments (Fig. 4). A local test comparing the survival of females with and without related neighbours within the kin treatment confirmed that females with related neighbours had a higher survival probability during the period considered (difference in deviance 4·91, df = 1, $P = 0{\cdot}013$ one-tailed). This result indicates that the effect of treatment detected above clearly results from most, but not all, females living on the kin treatment having a FDR as a neighbour. However, the survival benefits accruing from interacting with close relatives are expressed when average relatedness is high, but not when average relatedness is lower and more immigrant females are present.

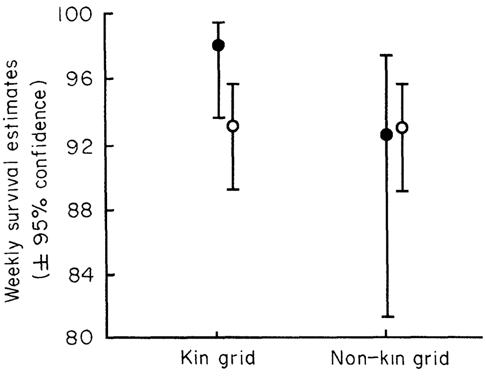

Fig. 4. Weekly survival estimates (±95% confidence interval) of overwintered females during the spring decline of 1990 and 1991. Survival of females with at least one first degree relative as neighbour are symbolized with empty circles and data from the non-kin treatment are filled circles.

Table 5. Values of deviance and Aikake's information criterion (AIC) of models of female survival in the springs of 1990 and 1991 including treatment (e) and the presence of at least one first degree relative as a neighbour (n) as dependent variables. The model that best fits the data has the lowest AIC. S = survival, P = trappability, n = dependence of S or P upon the neighbour effect, e = dependence of S or P upon treatment effect, $e*n$ = interaction between neighbour and treatment effect, $y + e$ = additivity of year and treatment effects

Models	Deviance	Number of free parameters	AIC
(1) $S_{e+n+e*n}$ P	247·05	5	257·05
(2) S_{e+n} P	249·88	4	257·08
(3) S_{n+e*n} P	**247·99**	**4**	**255·99**
(4) S_n P	250·14	3	256·14
(5) S P	253·03	2	257·03

REPRODUCTION AND WEANING SUCCESS

To examine whether living near a relative influences the timing of reproduction, we compared the mean date of birth of the first spring litter on each replicate (ANOVA, Year effect F 2,125 = 47·09, $P < 0{\cdot}01$, Treatment effect F 1,125 = 4·47, $P < 0{\cdot}04$, Year* Treatment F 2,125 = 3·54 $P < 0{\cdot}035$, Table 3). Females from the kin treatments gave birth to their first spring litters four to seven days later than those from the non-kin treatments in 1990 and 1991 (Fig. 5). There was no significant difference in the date of parturition in 1989. Overall, female on both treatments gave birth to their first spring litters earlier in 1990 than in other years (Contrast $P < 0{\cdot}01$). In addition, intermittent reproduction was

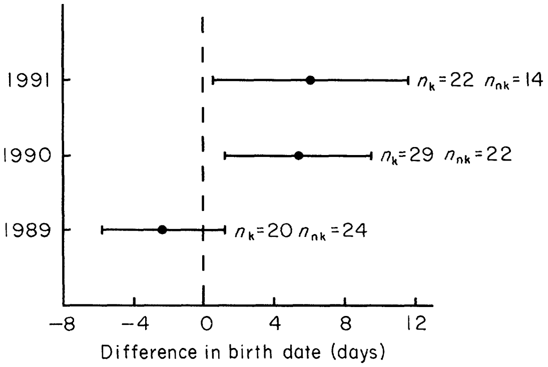

Fig. 5. Differences (95% confidence interval) in birth date of the first spring litter between the kin and non-kin treatments.

observed during the winter of 1989–1990, and 32 litters were born between 10 December 1989 and 15 February 1990.

The manipulation of female relatedness strongly influenced the success of the first spring litter. The proportion of first spring litters producing at least one weanling and the mean number of young weaned per litter born was consistently higher within the kin treatment than within the non-kin treatment for the three replicates (Table 3). Litter size at birth did not vary between years or between treatments (Table 3). As expected, the effect of the treatment on the number of young weaned per litter was less pronounced in 1989 when the extent of the experimental manipulation of female relatedness was lower. A log-linear model (Proc catmod, SAS Inc. Cary, North Carolina) indicated that the success of the first litters of the spring was contingent upon the year of birth and the treatment, but that there was no interaction between these two terms (Likelihood ratio $\chi^2 = 3{\cdot}81$, df $= 2$, $P = 0{\cdot}14$, treatment effect $\chi^2 = 13{\cdot}04$, df $= 1$, $P < 0{\cdot}001$, Year effect $\chi^2 = 6{\cdot}51$, df $= 2$, $P < 0{\cdot}04$). Mothers of spring litters living on the kin-treatment weaned significantly more young than mothers from the non-kin-treatment (ANOVA on ranks, Treatment F 1,121 $= 11{\cdot}15$, $P < 0{\cdot}001$, Year F 2,121 $= 1{\cdot}65$, $P > 0{\cdot}1$, Interaction F 2,121 $= 4{\cdot}2$, $P < 0{\cdot}02$, Table 3). On average, less young per litter were caught in traps in the kin treatment than in the non-kin treatment and the difference between treatments was less pronounced in 1989 than in other years. The effect of female relatedness on the proportion of successful litters and on the number of young weaned per litter are still significant even when data from the grid known to have experienced high weasel predation (G191) are excluded (both $P < 0{\cdot}02$). The weaning success of individual females with or without FDR as a neighbour were very similar on both treatments ($P < 0{\cdot}5$). This indicates that the influence of the treatment on weaning success affected all females independently of the relatedness of their neighbours. On the non-kin treatment, the success of the second litter was much improved relatively to the first litter such that there was no difference between treatments in the success of the second litter.

Discussion

In this experiment, we manipulated the degree of female relatedness by removing selected individuals and decreasing predation by aerial predators in unenclosed populations during three successive springs. Closely-related females lived closer to each other than more distantly related or unrelated females. We found that females living within populations of high average female relatedness survived better than those living in population of low average relatedness. Similarly to the results obtained by Kawata (1987) with *Clethrionomys rufocanus bedfordiae* (Thomas), individual females that had their mother, sisters or daughters as a neighbour were more likely to survive the spring decline and reproduce than females without close relatives as neighbour. By comparing the survival of females with and without a first degree relative as a neighbour within the kin-treatment, we were able to separate any influence of the use of fishing nets and the removal of immigrants from the influence of the presence of a relative as a neighbour on female survival. Only the latter influenced female survival during the spring decline. Immigration and emigration were not prevented in this study and this proved to be important. First, it is possible that the lower survival by females from the non-kin treatment stems partly from their increased dispersal tendency. These females might have settled in marginal, unoccupied habitat or died during dispersal. As we did not catch any adult female beyond the ditches or the mowed strips, we find this possibility unlikely. Secondly, females that had a related neighbour within a population of low average relatedness and were exposed to immigrant females did not survive better than females without relatives. The birth of the first spring litter was slightly delayed on the kin treatment in 2 years out of 3. The weaning success of the first spring litter was considerably higher on the kin treatment than on the non-kin treatment. No such difference was observed for the second litter. Because all females, with or without related neighbours, had their weaning success influenced by the treatment, we believe that immigrant females attempting to establish within the non-kin treatment depressed juvenile survival. This experiments was not designed to detect differences in vole abundance in populations of contrasting relatedness because we continually removed immigrants from the kin treatment and reduced family size on the non-kin treatment during the ensuing summers (see Lambin unpublished). We were interested in measuring adult and juvenile survival of voles from high and low average relatedness and we found that they were clearly superior when average relatedness is high. We do not know whether the differences in survival and weaning rate observed would induce pronounced differences in vole abundances in natural populations, but it is likely.

There are several reasons why our use of natural populations makes this experimental design superior to those used in previous similar studies. First, dispersal, which is central to all hypotheses linking demography to social factors was not restricted in our design. Secondly, we avoided making assumptions about the clues involved in kin discrimination (as in Boonstra & Hogg 1988; Ylönen *et al.* 1990; see Ferkin 1990; Ferkin *et al.* 1992) such that voles with related neighbours experienced normal conditions of mutual familiarity in this study. We also avoided problems associated with releasing individuals in enclosures and having to interpret demographic responses which do not become apparent until two months after the introduction (as in Ylönen *et al.* 1990). Our experiment focussed on the degree of female relatedness because the number of breeding females has the strongest influence on the demography of populations of *M. townsendii* (Redfield *et al.* 1978). The weakness of our design is that we were not able to measure numerical responses to our experiment as we only manipulated voles in a small fraction of the vole habitat available. Also, because we relied on recruitment and philopatry to increase female relatedness, not all females from the kin treatments had a relative as neighbour. Nevertheless, the conditions experimentally created in this study were closer to the condition occurring when the size of some, but not all families is maintained or restored by winter breeding or good overwinter survival. Finally, our experiment focusses on the spring, which is a period of low adult survival (e.g Krebs & Boonstra 1978) when spacing behaviour limits population size. Several detailed previous studies have identified this time as critical to the dynamics of vole populations (review in Taitt & Krebs 1985; Lambin & Krebs 1991a). Socially-induced mortality or dispersal resulting from female territoriality in spring limit the size of Townsend's vole population. Our study populations experienced pronounced declines at other times than spring, but these resulted from either botfly-induced mortality (July–Oct) or severe weather conditions (December 1990).

In this experiment, population numbers fluctuated between years and year effects had to be included in the data analysis. This reduced the number of degrees of freedom below that which is adequate for performing meaningful statistical analyses using populations as experimental units. Consequently, for analysing the effect of female relatedness on breeding performances, we first considered the pattern of variation and then considered individual females living on the two treatments as experimental units. As it is unlikely that members of a population are independent from each other, statistical tests of differences in weaning success are pseudo-replicated and associated probabilities should be considered only as indicative (Hurlbert 1984). Even though treatments were alternated between grids, we did not explicitly include potential differences in habitat quality between grids in our analysis. As the vegetation of the two grids was very similar and the pattern of variation between treatments was consistent on both grids, we do not believe that differences between grids influenced our conclusions.

FEMALE RELATEDNESS AND ADULT SURVIVAL

Both adult female survival during spring and the weaning rate of the first litter born in the spring varied in response to our manipulation of the degree of female relatedness. Such variation in female survival, although small on a weekly basis, could have important demographic and evolutionary consequences. Indeed, in Townsend's vole populations, overwintered females reproduce continuously until mid-summer and produce most of the recruits entering the population in summer (Lambin unpublished). As most overwintered females have not reproduced before the spring, those that fail to survive the spring decline leave no descendants at all at a time of intense population growth. It is, therefore, not surprising that behavioural adaptations improving the likelihood of surviving this critical period have evolved. As female Townsend's voles living in populations of high average relatedness or near their close relatives are more likely to enter the breeding population in the spring, natal philopatry of females born in late-summer or autumn can be viewed as such an adaptation. Frank (1957) suggested that the formation of 'great families' of female common voles (*Microtus arvalis* L.) was one of the behavioural adaptations that enabled populations of this species to reach abnormally high densities and caused their cyclic fluctuations. He found that at high population density, clusters of two to four sisters and their mother were formed. They would occupy a common territory and bring up their litter communally. The formation of extended families by addition of philopatric females is known from at least four other *Microtus* species (Jannet 1978; Myllymäki 1977; Heske 1987; Madison & McShea 1987; Lambin & Krebs 1991b) and is suspected to be the rule among microtines in summer (*Boonstra et al.* 1987; Lambin, Krebs & Scott 1992).

Most female Townsend's vole and other voles species are territorial or overdispersed in spring and defend space free of other females (Madison 1980; Bujalska 1973; Saitoh 1981; Boonstra & Rodd 1983; Bondrup-Nielsen 1986; Taitt and Krebs 1983; Boyce & Boyce 1988; Lambin & Krebs 1991b). Food addition experiments have demonstrated that female spacing in the spring results from the need by females to secure food resources critical for reproduction (Taitt & Krebs 1983; Ostfeld 1986; Ims 1987a). Female home ranges are larger and more exclusive in spring than in summer in Townsend's voles, probably in response to seasonal changes in resource availability and population density (Lambin & Krebs 1991b).

In the present study, groups of related females were present in the spring when resources are scare and exclusive use of space is the norm (Lambin & Krebs 1991b). Related females were closer to each other than other females. Females living in populations of high average relatedness interacting with their direct female relatives were more likely to survive the spring decline. As there were no differences in home-range size between treatments, females with relatives had to share limited resources. As food supplementation in the spring induces early reproduction (Andrzejewski 1975; Negus & Berger 1977; Taitt and Krebs 1983), variability in the onset of reproduction is likely to reflect differences in access to resources (Ims 1987c; Lambin 1993). The 4–7 days delay in parturition date observed on the kin treatment in 1990 and 1991 probably reflects a cost endured by females sharing resources with their close kin. In red-backed voles (*C. rufocanus bedfordiae*), females that do not have exclusive home-ranges showed similar delays in parturition (Kawata 1987). The total number of litters produced in a female's lifetime is an important determinant of her reproductive success relative to other variables (Ims 1987b; Lambin unpublished). Therefore, delaying reproduction by as little as 25% of the length of one gestation could represent a significant handicap for females sharing resources with relatives in spring.

FEMALE RELATEDNESS AND JUVENILE SURVIVAL

The large differences in all measures of success of the first spring litter observed between treatments is clearly a consequence of social factors influenced by the degree of relatedness. Several field experiments have demonstrated that adult females depress juvenile survival (Boonstra 1978; Redfield *et al.* 1978; Rodd & Boonstra 1988; Gilbert *et al.* 1986; Galindo & Krebs 1987). To date, however, it is not known whether females influence the survival of related and unrelated juveniles. Whereas selective removal experiments have shown that females reduce the recruitment and maturation rates of subadult females, few studies have explicitly measured the influence of survival before juveniles enter traps (see Galindo & Krebs 1987, for an exception). In this study, we found that juvenile survival was strongly depressed between the time they were marked in their mother's nest (mean age: 3·95 days) and their first capture in traps (mean age 28·5 ± 0·6 days, $n = 233$). In 3 years of marking litters in their mother's nest, we observed only six instances of apparent infanticide out of 448 litters. Even though two such instances were observed in spring, infanticide in the nest is too infrequent to account for the difference in weaning rate observed between treatments. Furthermore, contrary to nestling meadow voles *Microtus pennsylvanicus* Ord. (McShea & Madison 1987) there is not negative relationship between litter size and the age of litters when they were marked in their mother's nest ($rs = 0{\cdot}06$; age range: 1–11 days; litter size: 1–8; $n = 68$ litters marked in spring). It is, therefore, unlikely that mortality in the nest has a strong influence on weaning rates in the spring or at other times. It is possible, however, that young voles are exposed to infanticidal neighbour females when they first leave their mother's nest when they are 12 days old. In this study, juvenile survival was strongly influenced by the average degree of relatedness, but not by the presence of close relatives as neighbour. The factor responsible for this difference might be the presence of immigrant females on the non-kin treatment. We continually removed immigrant females from the kin treatment to maintain female relatedness and it is possible that immigrant females depressed juvenile survival on the non-kin. Dispersal by adults is common in spring (Beacham 1978) and immigrants are probably individuals in search of a breeding territory. One would expect immigrant females to behave aggressively towards potential competitors of their offspring. The absence of a treatment effect on the weaning success of the second spring litter is consistent with this, as most adult females have either succeeded or succumbed by then.

If Townsend's voles are unable to recognize their relatives without preweaning association, as meadow voles (*M. pennsylvanicus*) seem to (Ferkin 1990), there is little opportunity for adult females to recognize and influence the survival of their close-relatives' offspring. Related females occasionally raise their litter in the same nest, but most often in adjacent nests. It is possible that voles could recognize their sister's, mother's or daughter's offspring in those circumstances, but this needs to be documented.

DOES FEMALE RELATEDNESS INFLUENCE MICROTINE DEMOGRAPHY?

In this experiment, we found support for the main assumptions of our hypothesis linking microtine demography to female relatedness (Lambin & Krebs 1991a). Female survival was improved during spring in populations of high average degree of relatedness. Relatives had their home-ranges closer and more overlapping than did unrelated females. The large differences in weaning success were unexpected because we previously underestimated the disrupting effect of the presence of immigrant females on juvenile survival. Further experiments are needed to demonstrate whether these factors can cause outbreak densities in vole populations, but our data on demographic parameters allow us to predict that high degree female relatedness should lead to high population density. Changes in the degree of females relatedness in winter influenced adult and juvenile survival later in spring. Our vole populations showed a delayed demographic response to the experimental changes in family size. The influence of such factors modifying the degree of females relatedness are thus amplified through social behaviour as predicted by us (Lambin &

Krebs 1991a). We have suggested previously that predators such as weasels and parasites such as botflies have a delayed influence on population demography of microtines owing to the changes in female relatedness they induce (Lambin & Krebs 1991a). Experiments preventing infestation of Townsend's voles by botflies in summer would be a useful test of this prediction. The demographic consequences of the changes in the prevalence of winter reproduction hypothesized by Nelson (1987) could also be amplified by its effect on female relatedness.

We do not provide data on the relationship between the degree of female relatedness and density in this paper. Nevertheless, the proportion of females with a relatives as neighbour was highest in the year of high density owing to the occurrence of winter reproduction. Two characteristics of populations on their way to a cyclic peak were observed in the year of high density: reproduction started earlier and females were significantly heavier than in other years (Krebs & Myers 1974). Clearly, it is unlikely that high female relatedness alone caused the differences in vole density between years.

Our findings together with those from other studies are inconsistent with Charnov & Finerty's (1980) assumption that relatedness is highest at low density in small mammal populations. Pugh & Tamarin (1990) did not find lower levels of relatedness among adult residents of three enclosed meadow vole (*M. pennsylvanicus*) populations at low density than at moderate density. In a fourth, non-enclosed population, average relatedness between females was higher at moderate density than at low density. However, their populations did not reach high densities during their study and they did not distinguish between increase and decrease phases. In an elegant study of dispersal by banner-tailed kangaroo rats, *Dipodomys spectabilis* (Gray), Jones *et al.* (1988) found that effective dispersal was higher at lower density than at high density. This pattern of successful dispersal, completely opposite to that assumed by Charnov and Finerty's hypothesis, results from the saturation of available habitat leading to competition for breeding sites at high density. Danielson & Gaines (1987) have provided convincing evidence that resident prairie voles (*Microtus ochrogaster* Wagner) restrict the settlement of dispersers and it is therefore likely that the pattern described by Jones *et al.* (1988) will hold true for other territorial species.

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