Spacing system of the tundra vole (*Microtus oeconomus*) during the breeding season in Canada's western Arctic

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We studied the spacing system of a population of tundra voles, *Microtus oeconomus*, living in wet meadows near Pearce Point, Northwest Territories, using both radiotelemetry and live trapping. The home ranges of sexually active males were larger than female home ranges and males had no spatial overlap with each other. Most females overlapped with other females but with only one male. The mating system was therefore probably polygynous. We suggest that the mating and spacing systems of this species in summer are a consequence of the differences in natal philopatry between females and males.

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Nous décrivons le mode d'utilisation de l'espace chez les membres d'une population de Campagnols nordiques, *Microtus oeconomus*, vivant dans des prairies humides près de Pearce Point, Territoires du Nord-Ouest. Une étude par radiotélémétrie et par capture-recapture a révelé que les domaines vitaux des mâles reproducteurs sont plus grands que ceux des femelles et que les mâles sont territoriaux. La plupart des femelles partagent leurs domaines vitaux avec d'autres femelles mais avec un seul mâle. Le système d'accouplement est donc probablement polygyne. Nous suggérons que le mode d'utilisation de l'espace et la nature du système d'accouplement résultent de la philopatrie plus prononcée des femelles par rapport à celle des mâles.

Introduction

Behavioural traits are of special interest to ecologists, as they are highly flexible and reflect differences in environmental conditions experienced by individuals of various species. Among microtine rodents, a wide array of spacing systems has been found (Wolff 1985; Cockburn 1988), some species showing strict female territoriality whereas others have females that do not defend territories and share space with other females. Male microtines can either defend one or more breeding females or they can share space with other males and compete for access to reproducing females within a common home range. Ostfeld (1985) hypothesized that interspecific differences in the pattern of space use and territoriality among microtines reflect differences in the renewability and hence the defensibility of food resources by females. Specifically he predicted that among microtine species feeding on fast-growing renewable herbs, females would not exhibit territoriality but males would defend territories including clumped females. Females of species using mostly dicots in their diet, would defend territories containing their food resource and males would use overlapping ranges, as dispersed females are not defensible. While Ostfeld's predictions seem to hold in general for interspecific variability in spacing systems, there is a great deal of intraspecific variability in the patterns of space use both between and within populations of the same species (Ims 1987; Madison 1991; Ostfeld and Klosterman 1991). It is not clear whether this variability can be explained by variation in resource defensibility. Other sources of intraspecific variation in space-use pattern have been proposed and they include differences in genetic relatedness between neighbours (Lambin and Krebs 1991*a*) and genetically based (Krebs 1985) or maternally induced (Ims 1989) differences in the sociability of individuals.

To understand the causes of intraspecific variability in space use among microtines, it is useful to compare the space-use patterns of the same species in different habitats and to consider the effects of habitat heterogeneity and genetic relationship of individuals while interpreting space-use patterns within populations. In this paper we present the results of a short-term trapping and telemetry study of the spacing system of two subpopulations of the tundra voles inhabiting tundra meadows located north of the tree line in Canada's western Arctic. We also compare our finding with those of Tast (1966), who documented the spacing system of the species in seasonally flooded meadows in the taiga forest of northern Finland.

Study animal

The tundra vole is a medium-sized microtine (40–50 g) with a Holartic distribution. In Canada, its distribution is limited to the Yukon territory, the northwest corner of British Columbia, and the Mackenzie District of the Northwest Territories eastward along the arctic coastal tundra to Bathurst Inlet (Banfield 1974). The tundra

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TABLE 1. Demographic traits of the *M. oeconomus* populations studied at Pearce Point

	Males	Females	Test[a]	H_0: males = females
Number present on June 25	9	19	Binomial test	$0.1 > P(\text{sex ratio} = 0.5) > 0.05$
Number reproductive on July 25	4	16	Binomial test	$P(\text{sex ratio} = 0.5) < 0.05$
Body mass of overwintering voles at first capture[b,c] (g)	48.6±3.5 ($n = 9$)	37.6±4.9 ($n = 16$)	*t*-test	$P < 0.01$
Home-range size of reproductive individuals 15 July – 10 August[b] (m^2)	3896±2044 ($n = 3$)	1087±327 ($n = 12$)	ANOVA	$P = 0.04$
Proportion of spring-born individuals maturing within the natal grid[b] (%)	14 (1:7)	62.5 (5:8)	*G*-test	$P < 0.05$

[a] H_0: number of males = number of females.

[b] Values are given as the mean ± SE.

[c] Females that were obviously pregnant at first capture were not used for body mass calculations.

vole inhabits wet sedge meadows or cotton-grass marshes around tundra lakes or along stream banks. The breeding season extends from May to early September. To date, the mating system of this species in North America has not been described, but Tast (1966) reported that in northern Finland breeding females shift their home ranges between successive litters as new habitat becomes available after the spring melt, and male movements are about twice as large as those of females.

Methods

The study took place between June 13 and August 10, 1991, near Pearce Point along the northwest coast of mainland Canada (69°49′N, 122°41′E). The demography of two populations inhabiting sedge meadows separated by a river and its gravelly banks was monitored by weekly livetrapping. The spacing behaviour of all reproductively active individuals was studied using radiotelemetry during the second half of the breeding season. For livetrapping, 62 Longworth traps were placed in an irregular pattern along runways showing signs of recent vole activity. We ensured that all parts of the meadow that had signs of activity had at least one trap. Traps were baited with a piece of apple and a handful of whole oats and were checked twice during each 14-h weekly trapping session. Reproductive condition was assessed using standard techniques (Krebs et al. 1976). The two grids encompassed 4.0 ha (0.5 ha in the Cariboo valley, 3.5 ha in Potentilla) of suitable vole habitat. The grids covered the totality of the vole habitat and were surrounded by drier grassy areas, dry tundra, or boulders. The vegetation of the meadows was dominated by *Carex membranacea*, *C. misandra*, *C. stans*, *C. atrofusca*, *C. petricosa*, *Juncus articus*, *Eriophorum angustofolium*, and *Equisetum arvense*. Collared lemmings (*Dicrostonyx kilangmiutak*) were found in the dry tundra surrounding the meadows but were rarely caught in the wet habitat.

Between July 18 and August 10, 1991, all reproductively active voles on the grids were fitted with a radio transmitter attached to a tie-grip collar (Biotrack, Wareham, Dorset, England). The transmitter package weighed 2.9 g, which was between 5.3 and 8.5% of the body mass of the study animals. Subsequently, voles were located approximately once daily by walking slowly in the direction of the strongest radio signal. The vole's coordinates were recorded in a 10 × 10 m block within the grid system. When locating a radio signal, the observers avoided walking directly towards the vole, to prevent it from leaving its home range. The observer usually stopped approximately 3–5 m from the location of the vole.

Home-range size and configuration were calculated using the computer package Ranges IV (Kenward 1987). Home ranges were measured as the smallest convex polygon encompassing 90% of the telemetry and capture locations available. Individuals (7) whose home range had not reached its asymptotic size, owing to the small number of available locations, were excluded from the home range size analysis but were included in the analysis of interindividual overlap. On average, 19 locations were available per individual used for estimating home-range size. Unless specified otherwise, data from the two meadows are presented together.

Results

Over the course of the livetrapping study, 53 tundra voles were caught 197 times. The vole population of the Cariboo valley fluctuated between 5 and 11 individuals, whereas between 11 and 14 voles were present on the Potentilla grid. Trappability was high throughout the study and averaged 96% per weekly session. Males constituted only 32% ($n = 9$) of the resident overwintering population (Table 1) and the operational sex ratio varied from 38% males in spring to 12% males in mid-August. In contrast, there was no bias in the sex ratio of the juveniles from the first and second litters that entered traps (Table 1). However, a higher proportion of spring-born females than males recruited in the breeding population (Table 1). Only one spring-born male out of 7 attained reproductive status before disappearing from the study area, whereas 5 spring-born females out of 8 reproduced on the grid where they were caught the first time.

Starting on July 18, all reproductively active voles were fitted with a radio transmitter. Overall, 4 overwintering males, 1 spring-born male, 11 overwintering females, and 5 spring-born females were radio-tracked. Nine individuals out of 21 were preyed upon while carrying a transmitter (4 by short-tailed weasels, *Mustela ermina*, 2 by a grizzly bear *Ursus arctos*, 1 by a red fox, *Vulpes vulpes*, 1 by a rough-legged hawk, *Buteo lagopus*, and 1 by an unidentified predator). At least 6 nests containing unweaned voles were excavated by arctic ground squirrels (*Spermophilus parryii*) or grizzly bears. These extremely high predation rates observed on both grids are representative of those observed near Pearce Point in previous years (C. J. Krebs, R. Boonstra, and D. Reid, unpublished data).

A two-way analysis of variance including sex and grid as classification criteria revealed that male home ranges (3896 m^2, $n = 3$) are larger than those of females (1100 m^2, $n = 11$, $P = 0.04$) and that home ranges were larger on the Potentilla grid than in the Cariboo valley ($P = 0.03$). There was absolutely no spatial overlap between male ranges, but the ranges of most females overlapped with those of one or several other females ($\bar{x} = 1.7 \pm 0.38$, $n = 17$) (Fig. 1). Whereas all spring-born reproducing females had a home range overlap-

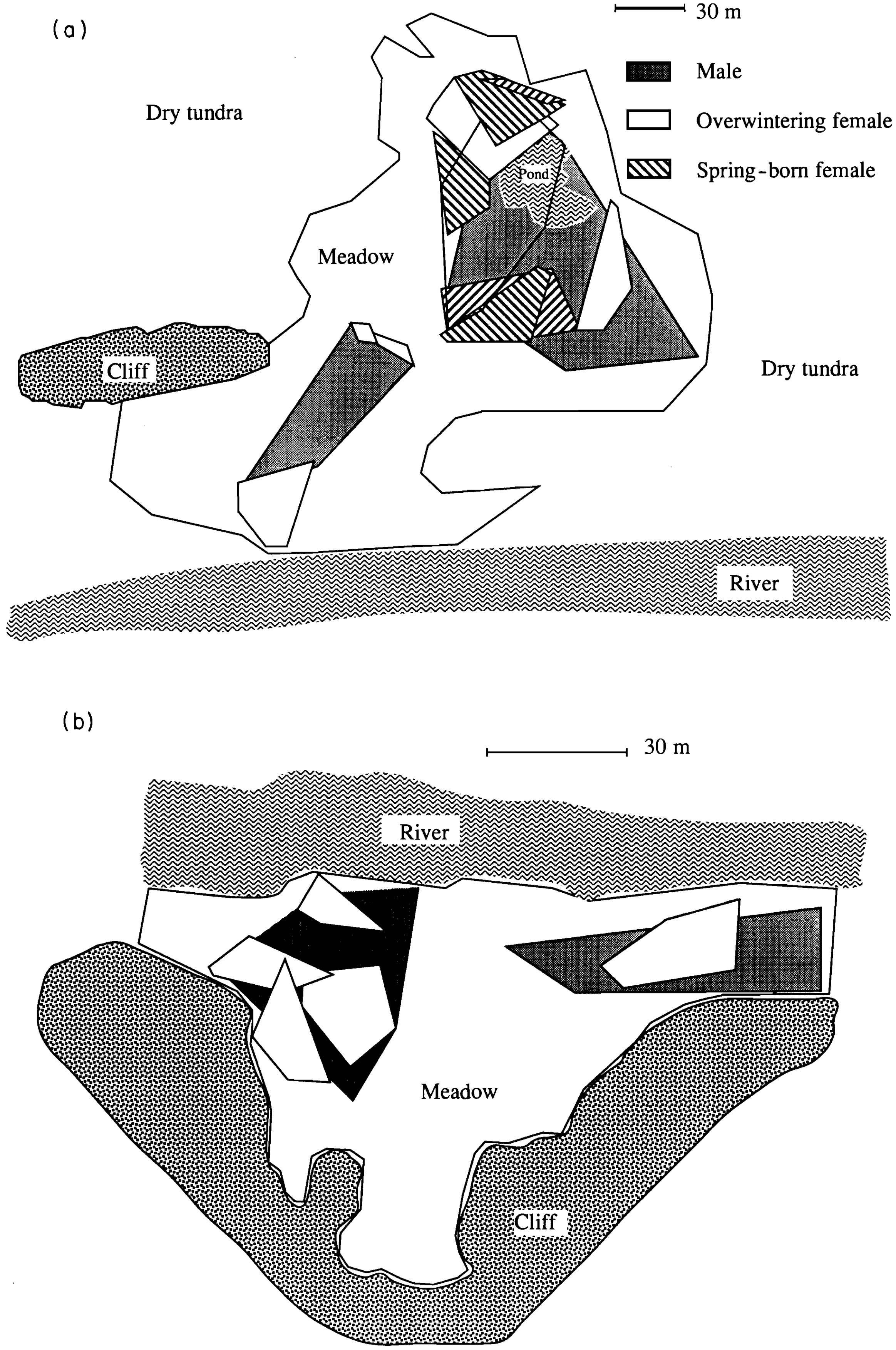

FIG. 1. Home ranges of all the sexually active voles living on the Potentilla (*a*) and Cariboo (*b*) grids between July 15 and August 10. The polygons encompass 90% of all locations and are centered on the recalculated arithmetic mean.

ping that of at least one female ($\bar{x} = 2.4 \pm 0.24$, $n = 5$), 7 overwintering females out of 11 had no female overlapper and were thus using exclusive home ranges. Male home ranges encompassed the range of several females ($\bar{x} = 4.0 \pm 1.5$, $n = 4$). On the other hand, no female had her range overlapped by more than one male.

Discussion

In this short-term study of the spatial organization of *M. oeconomus* in tundra habitat, we found that males had larger home ranges than females. We also found that there was no overlap between male home ranges, whereas the home ranges of some females substantially overlapped one another. Three males out of 4 had their home range overlapping that of several females and the operational sex ratio was strongly skewed in favour of females. These observations suggest that the mating system of the tundra vole is polygynous, as has been found in several other *Microtus* species (Madison 1980; Myllymäki 1977; Ostfeld 1986; Lambin and Kreb 1991*a*). Three of the 4 scrotal males present in our study area overlapped with up to 7 breeding females. As there was absolutely no overlap between males, those males likely had exclusive access to those females and can be considered polygynous. However, this conclusion is based on space-use patterns and not on actual mating patterns. Furthermore, our radiotelemetry study covered only the second half of the breeding season and we only provide an instantaneous picture of the spacing system of the breeding portion of the population. Because of the habitat of *M. oeconomus* is often patchy meadows surrounded by dry tundra, it is possible that facultative monogamy also occurs at low density or in small habitat patches. Between 1987 and 1990, males represented 43% ($n = 44$, $P(\text{sex ratio} = 0.5) > 0.5$) of all voles caught on three different grids in early June (C. J. Krebs, R. Boonstra, and D. Reid, unpublished data). Our data suggest that male tundra voles are territorial during the breeding season but this needs to be confirmed at higher male densities. In Townsend's vole (*Microtus townsendii*) the spacing system changes seasonally from a system based on strict territoriality of both sexes in spring to one in which territorial males overlap with several breeding females using overlapping home ranges (Lambin and Krebs 1991*a*). These groups of overlapping females are often composed of an overwintering female and her female offspring that reached sexual maturity near their birth site. Similar seasonal changes in spacing systems due to differential recruitment of males and females in the breeding population appear to exist in at least two other *Microtus* species (for *M. agrestis* compare Myllymäki 1977 with Erlinge et al. 1990, for *M. californicus* compare Ostfeld 1986 with Salvioni and Lidicker 1989).

Even though we do not know the genealogy of the individuals caught for the first time as juveniles at the beginning of the breeding season, it is reasonable to assume that they were caught in proximity to their birth site. Thus, it appears that, like most *Microtus* species (Boonstra et al. 1987; Sandell et al. 1990; Lambin and Krebs 1991*a*), female tundra voles are more philopatric than males and that sexual maturation of spring-born females is not inhibited by the presence of overwintering females. Unlike Tast (1966), we find no indication that females shift the position of their home range between successive litters, so their daughters inherit it when they mature. Furthermore, as all breeding spring-born females overlapped with one overwintering female and one or more spring-born females, it is likely that daughters share their mother's home range when reproducing during the second half of the breeding season. Tast (1966) reported that "although most females keep alone in summer, they sometimes inhabit a common area and form small colonies." Our data suggest that such clusters of reproducing females are matrilines, as first proposed by Frank (1957) for *M. arvalis* and documented for other species by Boonstra et al. (1987) and Lambin and Krebs (1991*a*).

The data presented here are consistent with the suggestion that much of the variability in space-use pattern among breeding females is a consequence of the variability in the weaning success of overwintering females, and that female philopatry leads to heterogeneity in the genetic structure of the population (Lambin and Krebs 1991*b*; Boonstra et al. 1987). If, like females of other *Microtus* species (references in Lambin and Krebs 1991*b*), most female tundra voles maintain exclusive use of space at the onset of the breeding season, those overwintering females using exclusive home ranges during the second half of the breeding season could be females that failed to produce any philopatric female offspring, as females living in the Cariboo valley seemingly did. Overwintering females who share space with younger females would be females that successfully weaned one or more female offspring from their spring litters and allowed them to settle in proximity to their birth site.

The monocot species present in the habitat used by *M. oeconomus* clearly fall in the renewable plants category of Ostfeld (1985). Thus, the presence of extensive overlap between the ranges of some breeding females apparently fits Ostfeld's prediction regarding the lack of female territoriality in species feeding upon monocots. However, we believe that the type of food resource used by a species only sets the *potential* for overlap among breeding females. If overwintering females are competitively superior to younger females seeking establishment in their home range, they should only tolerate the settlement of their relatives. At low density, the long-term benefit of maintaining an exclusive home range where future female offspring can settle should be higher than the short-term cost of territorial defense.

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Developmental abnormalities in triploid hybrids between tetraploid and diploid tree frogs (genus *Hyla*)

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Crosses between tetraploid female grey tree frogs, *Hyla versicolor*, and diploid males of the same genus may provide information on developmental differences between the parental species. Crosses with *Hyla cinerea* males in 1988 produced a large number of vigorous offspring, but abnormalities in eye development indicated some incompatibility of the parental genomes. The degree of eye development of the hybrids varied, ranging from completely absent to fully functional. Repetition of this cross combination in 1989 resulted in similar variation in eye formation. Histological sections through developing eyes indicated that the abnormalities may be related to improper formation of the cornea, improper orientation of the lens, or lack of lens induction. This may reflect differences in the timing of development between the two parental species.

MABLE, B. K., et RYE, L. A. 1992. Developmental abnormalities in triploid hybrids between tetraploid and diploid tree frogs (genus *Hyla*). Can. J. Zool. **70** : 2072–2076.

Des croisements entre des femelles tétraploïdes d'*Hyla versicolor* et des mâles diploïdes du même genre peuvent jeter de la lumière sur les différences dans le développement des espèces parentales. Des croissements opérés en 1988 avec des mâles d'*Hyla cinerea* ont donné naissance à un grand nombre de rejetons vigoureux, mais des anomalies dans le développement oculaire de cette progéniture indiquent un certain degré d'incompatibilité entre les génomes parentaux. Les hybrides n'avaient pas tous les yeux développés au même degré, certains n'avaient pas d'yeux, alors que d'autres avaient des yeux parfaitement fonctionnels. La répétition de ces croisements en 1989 a donné lieu à la même variation dans la formation dex yeux. Des coupes histologiques des yeux en développement ont indiqué que ces problèmes sont reliés à une formation imparfaite de la cornée, à une orientation faussée du cristallin ou à une défaillance de l'induction du cristallin. Ces phénomènes reflètent peut-être des différences dans le synchronisme du développement entre les deux espèces parentales.

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