

Territorial behaviour and reproductive success of bank vole *Clethrionomys glareolus* females

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Summary

1. Although spacing behaviour in small mammals has been studied extensively, the ultimate function of territoriality in females is frequently under debate. Furthermore, almost no data exists on how territorial behaviour of females changes during reproductive cycles and how that affects their reproductive success. We studied these questions in large outdoor enclosures using the bank vole *Clethrionomys glareolus* as a study species.

2. Home range dynamics of females and behaviour of territory owners against intruder females were determined during four distinct periods of the reproductive cycle: (i) when females were non-pregnant, (ii) in early pregnancy, (iii) in late pregnancy and (iv) when females were lactating.

3. Home range size and home range overlap of females decreased from period (i) to period (iv) simultaneously when nearest neighbour distance increased. So, at the time of parturition female home range size (foraging area) was at its smallest but territory size (breeding area) at its largest.

4. Attacks of owner females increased and amicable behaviour decreased during the reproductive cycle. Attacks tended to correlate positively and amicable behaviour negatively with home range size.

5. The size of a female's home range significantly correlated with her litter size. However, the weight of females did not correlate with their home range size or litter size.

6. During lactation, nearest neighbour distance correlated negatively with the number of weanlings. Further, home range overlap did not have an effect on the number of weanlings. So, in contrast to an earlier study by Mappes et al. we did not find support for infanticide directly affecting reproductive success of females. That might be due to synchronous breeding in our study females in contrast to females in Mappes et al.

7. Our results indicate that space-resource (large home range) and thus probably food may be an important determinant of litter size in the bank voles. Aggressive defence of a territory may have a role in determining the amount of resources available for reproduction and thus the reproductive success.

8. Our study gives new evidence both for and against the two hypotheses for function of female territoriality and suggests that they are not necessarily mutually exclusive.

Key-words: home range, infanticide, reproductive cycle, space defence, spacing behaviour.

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Introduction

Territoriality of females in small mammals has been widely accepted as a means of defending a food resource (Ostfeld 1985, 1990; Ims 1987). According to this resource-defence hypothesis, food limits repro-

duction, and the distribution and type of food determines the spacing pattern of females. Thus, energy and nutrients are regarded as the most important determinants of female reproductive success, and defending a territory provides exclusive access to these resources (Ostfeld 1985). In contrast, the pup-defence

hypothesis (Wolff 1993) states that the ultimate function of territoriality is to defend a nest site aggressively and deter infanticide. Access to food may simply be a by-product of providing space exclusive from potentially infanticidal intruders.

Indirect evidence on the importance of food in spacing patterns comes both from comparative studies between populations (e.g. Andrzejewski & Mazurkiewicz 1976; Ylönen, Kojola & Viitala 1988) and field manipulations. Field studies, where access to food has been manipulated, have often shown that extra food decreases the size of the female home range and increases home range overlap between neighbouring females (e.g. Taitt & Krebs 1981; Ostfeld 1986; Ims 1987; Desy, Batzli & Liu 1990). Daily energy requirements of breeding mammals are much higher compared with non-reproductives (Gittleman & Thompson 1988). Pregnant bank voles *Clethrionomys glareolus* Schreber require an average 24% and lactating females even up to three times more energy than non-reproducing individuals (Kaczmarski 1966). So, if food is postulated as the most important resource of a territory, during a reproductive cycle (from sexual quiescence until the onset of lactation) a female should demand continually increasing food resources. That could lead to an increase in home range size and decrease in home range overlap with other individuals competing for the same resources. However, the relationship between the phase of female reproductive cycle and spacing behaviour in the field is largely unknown (Madison 1978; Gipps 1985). In fact, according to Wolff (1993) there is no evidence that female home range size during the reproductive season is based on energy demands.

Studies examining spacing behaviour of microtine females and threat of infanticide are quite rare. In our field observations and enclosure experiments (H. Ylönen, E. Koskela and T. Mappes, unpublished data) we have observed infanticide between *C. glareolus* females. As infanticide has sometimes been neglected as a phenomenon affecting spacing behaviour and reproductive success of reproducing females (Wolff 1993), it should receive more attention. Space resource can also mean (other than just food) an exclusive area to decrease the probability of intruders entering the nesting areas. Females should defend their territories most intensively when pups are present, and in that time females should have the largest amount of exclusive space from other females. So, also according to the pup-defence hypothesis, female spacing behaviour should change during the reproductive cycle.

Determinants of the reproductive success of female voles have seldom been studied. Breeding success has been estimated based on the number of pregnancies during the breeding season (e.g. Gliwicz 1990) or, more usually, by determining the number of weanlings (e.g. Mappes, Ylönen & Viitala 1995b). However, there is a shortage of data where the characteristics of

voles in a field population (e.g. age, reproductive status, density, kinship) are under control and the spacing behaviour and reproductive success of individuals can be determined.

In the *C. glareolus*, mature females have been observed to be territorial while male home ranges are larger and overlapping (Mazurkiewicz 1971; Bujalska 1973). Indeed, possession of a territory and thus of access to its space and nutrient resources is a prerequisite for breeding in *Clethrionomys* females (Kalela 1957; Viitala 1977; Saitoh 1981; Bujalska 1985; Kawata 1987). We used the bank vole as a study species to examine how female home range size, home range overlap and territorial behaviour change during the reproductive cycle, and how these factors affect the reproductive success of females. Further, we discuss our results with reference to the pup-defence hypotheses as explanations of female territoriality. In this paper we define home range as a foraging area, usually overlapping, whereas territory is part of home range and mutually exclusive apart from other females. Territory could also be considered as a breeding area. These definitions are in accordance with the general definition of female territoriality in small mammals (Kaufmann 1983) and that used in the bank vole (Bujalska 1991).

Methods

STUDY SITE AND ENCLOSURES

The study was conducted during July–August 1994 at Konnevesi, central Finland (62°37'N, 26°20'E). Vole populations were established on seven 0.25-ha enclosures in a homogeneous field abandoned from agriculture 10 years ago. The vegetation in the enclosures was typical for old fields: many grasses (e.g. *Alopecurus pratensis* L., *Phleum pratense* L., *Elymus repens* (L.) Gould, *Deschampsia* Beauv. spp., *Poa* L. spp.) and herbs (e.g. *Ranunculus acris* L., *Hypericum maculatum* Crantz, *Geum rivale* L., *Alchemilla* L. spp., *Trifolium* L. spp.) dominated the field layer. There were also some saplings of *Alnus incana* (L.) Moench and *Salix* L. spp.

The fences were constructed by embedding 1.5-m galvanized sheet metal into the ground to a depth of about 0.5 m, giving a wall height of 1 m. The fence prevented the movement of voles well, not a single vole immigrated into the enclosures from surrounding fields and forest during the study. For monitoring the voles 25 multiple-capture live traps were used in each enclosure with 10 m between the trap stations. Each trap was covered by a galvanized sheet metal chimney that reduced exposure to temperature extremes.

STUDY ANIMALS AND METHODS

Overwintered female *C. glareolus* ($n = 35$) at the same reproductive status (mature, non-pregnant but having

given birth once earlier in the summer) were used in the study. All voles for the study, caught from nearby forests in the early spring were randomly assigned to the seven enclosures taking into account that they originated from different areas to ensure that all individuals were unrelated and unfamiliar with each other. There were no differences in the weights of females in different enclosures at the beginning of the study (one-way ANOVA, $P > 0.9$). Five females (individually marked) were released simultaneously in the middle of each enclosure on day 1 of the study. This density is comparable to the highest breeding densities observed in earlier studies (Bujalska 1970; Ylönen *et al.* 1988). Three mature, randomly chosen males were introduced to each enclosure ($n = 21$) on day 11.

For monitoring the populations there were five trapping periods in relation to the reproductive state of females: (i) when non-pregnant; (ii) in early pregnancy; (iii) in late pregnancy; (iv) when lactating; (v) when weanlings were recruited to the population (Table 1). Each trapping period consisted of 10 trap checkings, twice a day (morning and evening) for 5 days except for the two last periods, when trap checkings were done three times a day. In this way we tried to minimize the possible harmful effects of longer trap-checking intervals for pups and/or lactating females. At each capture the following variables were recorded for an individual vole: identity, sex, trap location, weight and reproductive status. All voles were released at the point of capture. During the study some females disappeared from enclosures; they had most probably died. By immediately introducing new females in the same reproductive condition from laboratory stock (consisting of animals trapped from the same area as all the other study animals), it was ensured that there was always a constant density of females in each enclosure. However, only females who were present throughout the study and successfully gave birth ($n = 25$) were used in the analyses. These females were distributed in the seven enclosures as follows: 2, 4, 3, 3, 5, 5 females in enclosures 1–7, respectively.

After the third trapping period (late pregnancy) all females ($n = 35$) were removed from enclosures to standard breeding cages in the laboratory, where they gave birth. By inspecting females twice a day the actual litter size at parturition was determined. The breeding of females within each enclosure was in close synchrony: all gave birth within 2–3 days. Females and their litters (pups marked) were returned (still in breeding cages) to enclosures and placed in an activity centre, which should lie very near to their nests (Mironov 1990). Cages were left open so that the mothers could carry the pups back to the nests themselves. The advantages of this method are that actual time of parturition is known and the number of pups born can be compared with the number of weanlings.

Home range size, nearest neighbour distance and activity centre were estimated for individual females separately for each trapping period. Home ranges were calculated using two different methods: minimum convex polygon (MCP) and 80% mononuclear probability polygon centred on arithmetic mean (80% MPP) (Kenward 1987). This was to make comparisons of space use easier between different studies, as suggested for example in Andreassen *et al.* (1993). Both home range estimates are presented but only MCP is used in all analyses (except in Fig. 1). This was because we wanted to include all the possible areas in our home range estimates that females may have used for foraging. The number of captures per 10-trap checkings (trappability) differed between trapping periods (mean and variance for trapping periods 1–4: 7.8 (0.3), 8.6 (0.2), 8.1 (0.2) and 6.9 (0.2), repeated measures MANOVA; enclosure: $F = 0.6$, $P = 0.724$; female state: $F = 9.03$, $P = 0.001$). This was due to low trappability in daytime during the fourth trapping period (when traps were checked three times a day); trappability did not differ between first three trapping periods ($P = \text{NS}$). Home range size (MCP) was not correlated with the number of captures ($r_s = 0.09$, $P > 0.7$, $r_s = 0.32$, $P > 0.1$, $r_s = 0.07$, $P > 0.07$, $r_s = 0.20$, $P > 0.3$, trapping periods 1–4, respectively).

Table 1. Study design and reproductive cycle of females

Day	Study design	Reproductive cycle
1	Introduction of females	Habituation and occupation of territories
6–10	First trapping period First behavioural trials	Females not breeding
11	Introduction of males	Mating
15–19	Second trapping Second behavioural trials	Females in early pregnancy
24–28	Third trapping period Third behavioural trials	Females in late pregnancy
28–32	Determination of litter size	Parturition
42–45	Fourth trapping period Fourth behavioural trials	Females with litters, lactating
60–62	Fifth trapping period Determination of number of weanlings	Juveniles at the age of one month

The activity centre was calculated as the arithmetic mean point of each individual's capture coordinates (Hayne 1949). Nearest neighbour distance was calculated from distances between the activity centres of neighbouring females. Percentage home range overlap was measured as the proportion of total trap sites in the home range of each female also visited by other females (Ims 1987; Mappes *et al.* 1995b). This estimate does not take into account the frequency of use of space in the area of overlap, as does, for example Smith & Dobson's (1994) weighted overlap value. However, we suggest that the value we use is more appropriate for the purposes of the present study because it gives the accurate proportion of exclusiveness of a home range.

DETERMINATION OF TERRITORIAL BEHAVIOUR

The behaviour of owner females against intruder females was determined four times, once for each trapping period during the last 2 days of trapping (Table 1). Each owner was tested only once against an intruder during each reproductive phase. We used a total of 58 mature non-pregnant intruder females originating from field or laboratory stock. Every intruder was used only once in a trial with each owner and the same intruder was used only in one experiment per day. The weights of intruder females did not differ between trapping periods ($P > 0.10$). Behavioural trials lasted 10 min and were carried out in small arenas (50×60 cm) with wiremesh floors and Plexiglas front walls. These arenas were placed directly on the ground at the trap station nearest to the activity centre of the female, with the prerequisite that the owner female had visited that particular site during the trapping period. Both owner female and intruder were kept in separate tubes on opposite sides of the arena for 1–2 min before the start of the trial. We used the description of female behaviour following Ims (1987), where recorded variables were: amicable behaviour, approaching, freezing, avoidance, fleeing, threat and attacks. The frequencies of all mutually exclusive variables were counted continuously throughout the trial. Immediately after each trial the owner female was released at the place of capture and the intruder was returned to laboratory. These kinds of behavioural observations, which are based on the assumption that the owner female senses her situation in the territory by the means of olfactory cues from the surrounding environment, have been verified to operate well in previous studies (e.g. Wolff, Freeberg & Dueser 1983; Ims 1987).

DATA ANALYSIS

Because it could be expected that the change of variables (home range size, overlap, nearest neighbour distance, behaviour) is a function of female state, repeated measures MANOVA was used for making com-

parisons between different trapping periods. Enclosure was used as a separate factor in these analyses. Trappability was used as a varying covariate in repeated measures analyses of space use. Linear term of polynomial contrast was significant for all significant changes in behaviours (except for avoidance) and is reported. When analysing female behaviour, we used the relative proportion of different behavioural categories from the total behaviour of each female during that particular trial. These behavioural variables and overlap variable were arcsine square root transformed before analysis.

After females had given birth in the laboratory, their litter size was manipulated as a subject for a separate study (Mappes, Koskela & Ylönen 1995a). The only dependent variable used in the present study affected by the manipulation was the number of weanlings (when using $P = 0.10$ as a significance level). In correlation analyses concerning the number of weanlings, Kendall's partial correlations were used with manipulation as a controlling variable. For the other correlation analyses, Spearman rank correlations were used. The sample size was 25 in all analyses except when otherwise mentioned. All the tests are two-tailed. The statistical analyses were performed by using SPSS for Windows (SPSS Inc.; Norusis 1992).

Results

SPACE USE AND REPRODUCTIVE SUCCESS

The home range size of females decreased significantly during the reproductive cycle according to the MCP estimate, and tended to decrease according to the 80% MPP estimate (MCP: enclosure: $F = 0.76$, $P = 0.608$; covariate: $t = 0.582$, $P = 0.568$; female state: $F = 3.12$, $P = 0.034$; 80% MPP: enclosure: $F = 1.34$, $P = 0.293$; covariate: $t = 0.893$, $P = 0.385$; female state: $F = 2.41$, $P = 0.077$; Fig. 1). The home range overlap also decreased during the study (enclosure:

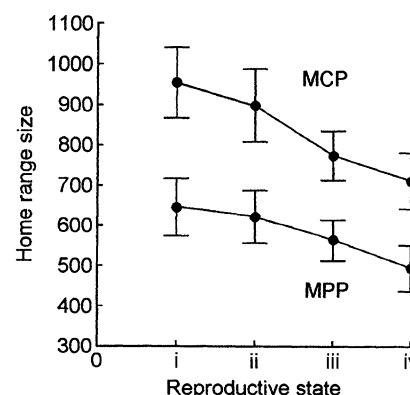


Fig. 1. Home range size (in m^2) of females calculated as minimum convex polygons (MCP) and 80% mononuclear probability polygons (MPP) in different reproductive states. (i) = non-pregnant; (ii) = early pregnancy; (iii) = late pregnancy; (iv) = lactating. Bars show the mean \pm standard error. For statistics see the Results.

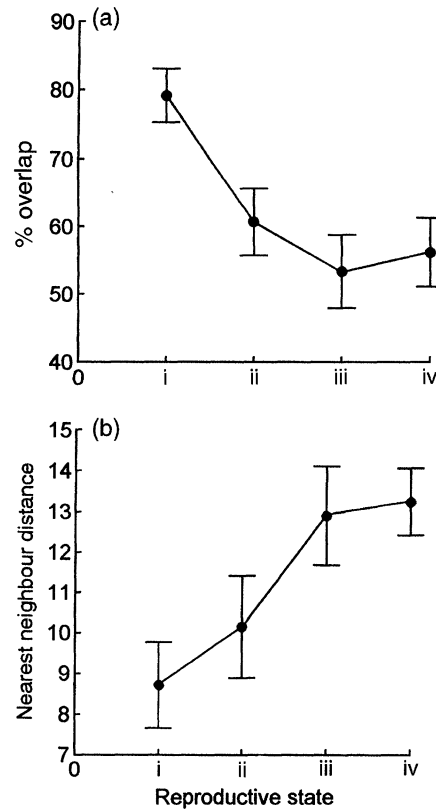


Fig. 2. Proportional home range overlap (a) and nearest neighbour distance (in m) (b) of females during reproductive cycle. See legend of Fig. 1 for details.

$F = 0.76$, $P = 0.608$; covariate: $t = -0.873$, $P = 0.395$; female state: $F = 7.58$, $P = 0.000$; Fig. 2a). Nearest neighbour distance increased as the study proceeded (enclosure: $F = 6.83$, $P = 0.001$; covariate: -1.236 , $P = 0.233$; female state: $F_{(3,16)} = 3.29$, $P = 0.048$; Fig. 2b).

Female weight at the beginning of the study or post-partum weight did not correlate significantly with home range size during any of the trapping periods (Fig. 3 for late pregnancy). The correlation coefficients between initial weight and post-partum weight of females with litter size were also non-significant (initial: $r_s = 0.269$, $P = 0.194$; post-partum:

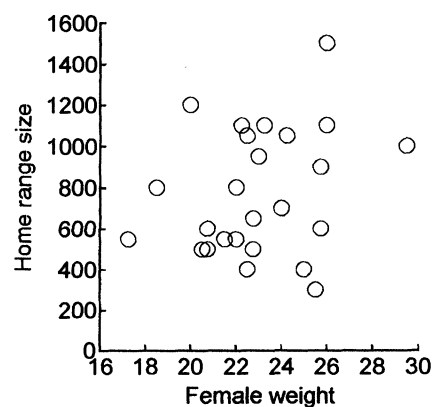


Fig. 3. The relationship between initial weight of female (in g) and home range size (in m^2) at late pregnancy ($r_s = 0.239$, $P = 0.249$).

$r_s = 0.194$, $P = 0.352$). The size of female home ranges at late pregnancy significantly explained the variation in litter size (Fig. 4). Litter size at birth correlated significantly with the number of weanlings ($r_k = 0.544$, $n = 24$, $P = 0.000$). Home range sizes at late pregnancy and at lactation also correlated significantly ($r_s = 0.699$, $P = 0.000$). This most probably leads to the result that when females were nursing their young, their home range size correlated positively with the number of weanlings ($r_k = 0.399$, $n = 24$, $P = 0.006$). However, the number of weanlings correlated negatively with nearest neighbour distance ($r_k = -0.343$, $n = 24$, $P = 0.019$). The home range overlap did not have an effect on the number of weanlings ($r_k = -0.079$, $n = 24$, $P = 0.588$).

BEHAVIOUR

When the time for parturition approached, females increased their attacks towards intruders significantly (Table 2). Simultaneously, the proportion of amicable behaviour decreased (Table 2). The linear term of the polynomial contrast was highly significant for both variables (attacks: $F_{(1,18)} = 14.01$, $P = 0.001$; amicable behaviour: $F_{(1,18)} = 49.54$, $P = 0.000$). Avoidance by owners also varied during the study (Table 2). Intruder behaviour did not change (in all cases $P > 0.05$) except for fleeing, which increased as the study proceeded (enclosure: $F_{(6,18)} = 2.23$, $P = 0.088$; female state: $F_{(3,16)} = 12.11$, $P = 0.000$; linear term: $F_{(1,18)} = 6.04$, $P = 0.024$). This change was most probably due to increased attacks of owners towards intruders.

Home range size at late pregnancy tended to correlate positively with attacks ($r_s = 0.374$, $P = 0.065$) and negatively with amicable behaviour ($r_s = -0.350$, $P = 0.087$). Threats had a negative correlation with home range size ($r_s = -0.466$, $P = 0.019$) when females were nursing their young. In the behavioural trials the threatening female was usually in the corner of the arena defending herself as another female tried

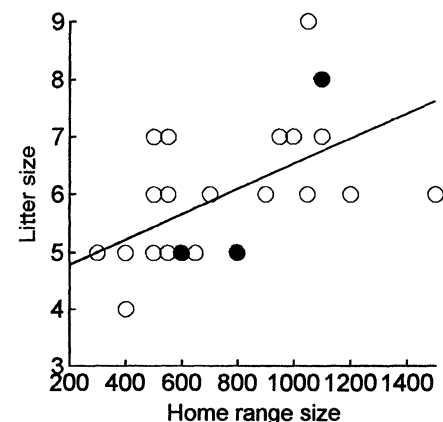


Fig. 4. Linear regression between female home range size (in m^2) at late pregnancy and litter size. Filled dots indicate two cases. $F = 10.02$, $n = 25$, $P = 0.004$; equation: litter size = $4.356 + 0.002 \times$ home range size.

Table 2. Observed proportion of different behaviours of owner females against intruder females in relation to reproductive cycle. First line of each variable gives statistics for female state, second for enclosure. Sample size is 25 for all behaviours. Values represent mean \pm standard error

	Non-pregnant	Early pregnancy	Late pregnancy	Lactation	<i>F</i> *	d.f.	<i>P</i>
Amicable behaviour	9.8 \pm 2.5	8.9 \pm 2.2	1.3 \pm 0.8	0.7 \pm 0.4	25.91	3,16	0.000
					2.50	6,18	0.062
Approach	42.9 \pm 4.6	53.3 \pm 5.1	62.1 \pm 7.0	57.1 \pm 5.4	1.71	3,16	0.206
					1.05	6,18	0.430
Freeze	1.1 \pm 0.8	1.9 \pm 1.4	0†	0†	0.00	1,18	0.983
					1.15	6,18	0.376
Avoid	22.3 \pm 4.9	16.7 \pm 4.4	7.4 \pm 2.3	14.5 \pm 4.6	3.74	3,16	0.033
					0.64	6,18	0.700
Flee	0.6 \pm 0.6	0.3 \pm 0.3	0†	0.0 \pm 0.0‡	0.04	2,17	0.959
					1.26	6,18	0.325
Threat	21.1 \pm 4.0	15.4 \pm 4.7	21.0 \pm 5.7	10.5 \pm 4.2	0.70	3,16	0.565
					0.63	6,18	0.708
Attack	2.2 \pm 1.0	3.6 \pm 1.9	8.3 \pm 4.4	16.9 \pm 4.9	5.03	3,16	0.012
					0.28	6,18	0.940

* Repeated measures MANOVA used.

† No cases for this variable.

‡ Proportion less than 0.0%.

to chase her away. That also indicates the result that threats correlated negatively with approaching ($r_s = -0.639$, $P = 0.001$). Female amicable behaviour at late pregnancy correlated negatively with their litter size ($r_s = -0.461$, $P = 0.021$).

Discussion

In comparative field studies of female territoriality there are usually many factors that make it difficult to interpret the results, e.g. density-dependent plasticity in spacing patterns and kin group effect (Wolff 1993). The former is caused by environmental conditions, mainly by variability in the food resource and in number and sexual status of individuals in a population. The effects of these factors on spacing systems are reported in several studies (reviewed in Bontrup-Nielsen & Karlsson 1985; Ylönen 1990). The latter, the kin group effect, is caused by greater overlapping of home ranges in related females compared with non-kin (Ims 1989; Lambin & Krebs 1993; Mappes *et al.* 1995b). Because the voles used in the present study were non-kin and unfamiliar to each other and the density in enclosures was the same during the study, these factors did not affect this study. Changing environment (seasonality) is one possible factor affecting our results. However, because changes in the spacing behaviour of females were so remarkable and were observed in midsummer during a rather short period (less than 40 days), we suggest seasonality as an unlikely cause of the observed changes in spacing behaviour of females. We cannot rule out the possible effect of changing food resources on our results. However, bank voles seem to have a rather continuous and stable availability of food. They use a varied range of food items from leaves, stems and seeds of plants to fungi, berries and invertebrates (e.g. Hansson 1971).

Because most of these are also highly renewable during the breeding season, we assume that food resources remained relatively constant during the study and that any possible changes were spatially quite similar.

SPACING BEHAVIOUR IN RELATION TO REPRODUCTIVE STATE

According to our study, female aggression increases significantly and amicable behaviour decreases as the time for parturition gets closer. These results agree with an earlier laboratory experiment with the bank voles (Rozenfeld & Denoël 1994) and the finding that aggressiveness increases at the onset of lactation in microtines (e.g. Ayer & Whitsett 1980; Mallory & Brooks 1980). At the same time, the size of home ranges gets smaller, the overlap between home ranges decreases and home range centres (activity centres) move further from each other. Clearly, the spacing pattern of females develops towards strict breeding territoriality. When studying home range oscillations in relation to female density in *Microtus pennsylvanicus*, McShea (1989) suggested that changes in home range size of females after parturition are more dependent on interactions with other individuals in the population than solely caused by mother-offspring interactions. Also, Korn (1982) failed to find a relationship between energetic requirements of bank vole females and the size of their home range and concluded that behavioural aspects seem to be a more important determinant of home range size. Our study, where individual females were followed throughout their reproductive cycle, gives support for these suggestions.

FEMALE BEHAVIOUR AND REPRODUCTIVE
SUCCESS

In our study female home range size at late pregnancy significantly correlated with her litter size. This result agrees with a recent experiment (E. Koskela, T. Mappes and H. Ylönen, unpublished data). One must remember that infanticide could not affect litter sizes because they were determined in the laboratory. Because the weights of females did not correlate with litter or home range size (even though considerable variation occurred in weights; Fig. 3), it seems that purely physiological properties (e.g. dominance status via large size) are not sufficient to explain our result. Furthermore, all the females were of the same age and sexual status, so the sizes of home ranges and litters seem to depend on other characteristics of females, behaviour being particularly important. According to the laboratory study of Rozenfeld & Denoël (1994), aggressiveness is a crucial part of the spacing behaviour of breeding females. It has been suggested that in the field scent marking by territory owners functions as a more usual form of territorial defence than aggression (Viitala & Hoffmeyer 1985). However, our behavioural trials revealed a positive correlation between aggressive behaviour (attacks) and home range size. Also, both threats (submissive act) and home range size, as well as amicable behaviour and litter size, correlated negatively. According to our results females who were aggressive towards intruders had larger home ranges. The larger home range may provide more food, which has been shown to affect litter sizes in many microtines (Hoffmann 1958; Batzli & Pitelka 1971; Cole & Batzli 1978). However, experiments are needed to certify the possible link between female behaviour, home range size and reproductive success.

INFANTICIDE AND REPRODUCTIVE SUCCESS

Infanticide is already known to occur in some microtines, and recent experimental studies (e.g. Cicirello & Wolff 1990; Wolff & Cicirello 1991; Mappes *et al.* 1995b) and theoretical papers (Wolff 1993) indicate that this phenomenon might also exist in the bank vole. In fact, in recent enclosure experiments (H. Ylönen, E. Koskela and T. Mappes, unpublished data) we have observed infanticide between female bank voles. So, as we now suggest that infantile behaviour exists in the bank vole, the remaining questions are (i) 'Does infanticide directly affect the reproductive success of females?' and (ii) 'Does threat of infanticide affect the spacing behaviour of females?' In the present study, we observed infanticide only indirectly, comparing the number of weanlings with the nearest neighbour distance and home range overlap among mothers. In the study by Mappes *et al.* (1995b) they found a significant positive correlation between nearest neighbour distance and number of weanlings. They

suggest that this might be due to neighbours killing each others' juveniles. However, in the present study, this correlation was negative, not supporting earlier results. Also, home range overlap did not affect the number of weanlings. Our findings suggest that, in the present study, reproductive success of females was not affected directly by infanticide. This difference between our results and those by Mappes *et al.* (1995b) may be due to the different timing of breeding in females. In the present study all females were breeding in synchrony and it might be possible that they had limited opportunity or potential for infanticide, as suggested in Lambin (1993). If, however, breeding is asynchronous (as in Mappes *et al.* 1995b), there are continuously females in different reproductive states and vulnerable pups in the population that may promote occurrence of infanticide.

Conclusions

Our study provides new data showing that the spacing behaviour of bank vole females is specific to the different phases of the reproductive cycle: at the same time as aggressive behaviour increases and amicable behaviour decreases, the spacing pattern of females develops towards strict breeding territoriality. At the time of parturition female home range size (foraging area) is at its smallest but territory size (breeding area) is at its largest. The ability to defend the territory aggressively may have an important role in determining the amount of resources available for reproduction (size of a home range) and is further reflected in the reproductive success. Infanticide did not seem to affect breeding success of females when they were breeding in synchrony. All these findings may also correspond to other small mammals, where females are territorial when breeding.

Our study provides new evidence both for and against the hypotheses of territoriality in female small mammals. On the one hand, that the size of home range, behavioural characteristics of females and their litter size seem to be linked emphasizes the importance of food as the cause of territoriality. However, the size of home range decreased during the reproductive cycle, in contradiction to the increased food demands of females. On the other hand, the finding that in territorially breeding voles like *Clethrionomys glareolus* the home range becomes more exclusive from other females when pups are present supports the pup-defence hypothesis (Bujalska 1991; Wolff 1993). Further support comes from the fact that females defend their territories most intensively when pups are present. However, that is also the time when food demands are greatest for mothers. We did not find evidence that infanticide affected the reproductive success of females in the present study. Our study suggests that food-defence and pup-defence hypotheses for female territoriality are not necessarily mutually

exclusive and demonstrates the need for experimental studies.

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References

- Andreassen, H.P., Ims, R.A., Stenseth, N.C. & Yoccoz, N.G. (1993) Investigating space use by means of radiotelemetry and other methods: a methodological guide. *The Biology of Lemmings* (eds N.C. Stenseth & R.A. Ims), pp. 589–618. Academic Press, London.
- Andrzejewski, R. & Mazurkiewicz, M. (1976) Abundance of food supply and size of the bank vole's home range. *Acta Theriologica*, **21**, 237–253.
- Ayer, M.L. & Whitsett, J.M. (1980) Aggressive behaviour of female prairie deer mice in laboratory populations. *Animal Behaviour*, **28**, 763–771.
- Batzli, G.O. & Pitelka, F.A. (1971) Condition and diet of cyclic populations of the California vole, *Microtus californicus*. *Journal of Mammalogy*, **52**, 141–163.
- Bondrup-Nielsen, S. & Karlsson, F. (1985) Movements and spatial patterns in populations of *Clethrionomys* species: a review. *Annales Zoologici Fennici*, **22**, 385–392.
- Bujalska, G. (1970) Reproduction stabilizing elements in an island population of *Chethrionomys glareolus* (Schreber, 1780). *Acta Theriologica*, **15**, 381–412.
- Bujalska, G. (1973) The role of spacing behaviour among females in the regulation of the reproduction in the bank vole. *Journal of Reproduction and Fertility*, **19**, 461–472.
- Bujalska, G. (1985) Regulation of female maturation in *Clethrionomys* species, with special reference to an island population of *C. glareolus*. *Annales Zoologici Fennici*, **22**, 331–342.
- Bujalska, G. (1991) The ecology of territoriality in bank voles. *Trends in Ecology and Evolution*, **6**, 300–301.
- Circirello, D.M. & Wolff, J.O. (1990) The effects of mating on infanticide and pup discrimination in white-footed mice. *Behavioral Ecology and Sociobiology*, **26**, 275–279.
- Cole, F.R. & Batzli G.O. (1978) Influence of supplemental feeding on a vole population. *Journal of Mammalogy*, **59**, 809–819.
- Desy, E.A., Batzli, G.O. & Liu, J. (1990) Effects of food and predation on behaviour of prairie voles: a field experiment. *Oikos*, **58**, 159–168.
- Gipps, J.H.W. (1985) The behaviour of bank voles. *Symposium of Zoological Society of London*, **55**, 56–87.
- Gittleman, J.L. & Thompson, S.D. (1988) Energy allocation in mammalian reproduction. *American Zoologist*, **28**, 863–875.
- Gliwicz, J. (1990) Habitat-dependent reproductive success in bank voles. *Social Systems and Population Cycles of Voles* (eds R.H. Tamarin, R.S. Ostfeld, S.R. Pugh & G. Bujalska), pp. 169–179. Birkhäuser Verlag, Basel.
- Hansson, L. (1971) Small rodent food, feeding and population dynamics: a comparison between granivorous and herbivorous species in Scandinavia. *Oikos*, **33**, 55–63.
- Hayne, D.W. (1949) Calculation of size of home range. *Journal of Mammalogy*, **30**, 1–18.
- Hoffmann, R.S. (1958) The role of reproduction and mortality in population fluctuations of voles (*Microtus*). *Ecological Monographs*, **29**, 79–109.
- Ims, R.A. (1987) Responses in spatial organization and behaviour to manipulations of the food resource in the vole *Clethrionomys rufocanus*. *Journal of Animal Ecology*, **56**, 585–596.
- Ims, R.A. (1989) Kinship and origin effects on dispersal and space sharing in *Clethrionomys rufocanus*. *Ecology*, **70**, 607–616.
- Kaczmarek, F. (1966) Bioenergetics of pregnancy and lactation in the bank vole. *Acta Theriologica*, **11**, 409–417.
- Kalela, O. (1957) Regulation of reproduction rate in sub-arctic populations of the vole *Clethrionomys rufocanus* (Sund.) *Annales Academiae Scientiarum Fennicae (AIV)*, **34**, 1–60.
- Kaufmann, J.H. (1983) On the definitions and functions of dominance and territoriality. *Biological Reviews*, **58**, 1–20.
- Kawata, M. (1987) Pregnancy failure and suppression by female-female interaction in enclosed populations of the red-backed vole, *Clethrionomys rufocanus bedfordiae*. *Behavioral Ecology and Sociobiology*, **20**, 89–97.
- Kenward, R.S. (1987) *Wildlife Radio Tagging*. Academic Press, London.
- Korn, H. (1982) Changes in home range size during growth and maturation of the wood mouse (*Apodemus sylvaticus*) and the bank vole (*Clethrionomys glareolus*). *Oecologia*, **68**, 623–628.
- Lambin X. (1993) Determinants of the synchrony of reproduction in Townsend's voles, *Microtus townsendii*. *Oikos*, **67**, 107–113.
- Lambin X. & Krebs, C.J. (1993) Influence of female relatedness on the demography of Townsend's vole populations in the spring. *Journal of Animal Ecology*, **62**, 536–550.
- McShea, W.J. (1989) Reproductive synchrony and home range size in a territorial microtine. *Oikos*, **56**, 182–186.
- Madison, D.M. (1978) Movement indicators of reproductive events among female meadow voles as revealed by radiotelemetry. *Journal of Mammalogy*, **59**, 835–843.
- Mallory, F.F. & Brooks, R.J. (1980) Infanticide and pregnancy failure: reproductive strategies in the female collared lemming (*Dicrostonyx groenlandicus*). *Biology of Reproduction*, **22**, 192–196.
- Mappes, T., Koskela, E. & Ylönen, H. (1995a) Reproductive costs and litter size in the bank vole. *Proceedings of the Royal Society, Biological Sciences*, **261**, 19–24.
- Mappes, T., Ylönen, H. & Viitala, J. (1995b) Higher reproductive success among kin groups of bank voles *Clethrionomys glareolus*. *Ecology*, **76**, 1276–1282.
- Mazurkiewicz, M. (1971) Shape, size and distribution of home ranges of *Clethrionomys glareolus* (Schreber, 1780). *Acta Theriologica*, **16**, 23–60.
- Mironov, A.D. (1990) Spatial and temporal organization of populations of the bank vole, *Clethrionomys glareolus*. *Social Systems and Population Cycles of Voles* (eds R.H. Tamarin, R.S. Ostfeld, S.R. Pugh & G. Bujalska), pp. 181–192. Birkhäuser Verlag, Basel.
- Norusis M.J. (1992) *SPSS for Windows. Advanced Statistics, Release 5*. SPSS Inc. Chicago.
- Ostfeld, R.S. (1985) Limited resources and territoriality in microtine rodents. *The American Naturalist*, **126**, 1–15.
- Ostfeld, R.S. (1986) Territoriality and mating system of California voles. *Journal of Animal Ecology*, **55**, 691–706.
- Ostfeld, R.S. (1990) The ecology of territoriality in small mammals. *Trends in Ecology and Evolution*, **5**, 411–415.
- Rozenfeld, F.M. & Denoël, A. (1994) Chemical signals

- involved in spacing behavior of breeding female bank voles (*Clethrionomys glareolus* Schreber 1780, *Microtidae*, *Rodentia*). *Journal of Chemical Ecology*, **20**, 803–813.
- Saitoh, T. (1981) Control of female maturation in high density populations of the red-backed vole, *Clethrionomys rufocanus bedfordiae*. *Journal of Animal Ecology*, **50**, 79–87.
- Smith, A.T. & Dobson, F.S. (1994) A technique for evaluation of spatial data using asymmetrical weighted overlap values. *Animal Behaviour*, **48**, 1285–1292.
- Taitt, M.J. & Krebs, C.J. (1981) The effect of extra food on small rodent populations. II. Voles (*Microtus townsendii*). *Journal of Animal Ecology*, **50**, 125–137.
- Viitala, J. (1977) Social organization in cyclic subarctic populations of the voles *Clethrionomys rufocanus* (Sund.) and *Microtus agrestis* (L.). *Annales Zoologici Fennici*, **14**, 53–93.
- Viitala, J. & Hoffmeyer, I. (1985) Social organization in *Clethrionomys* compared with *Microtus* and *Apodemus*: social odours, chemistry and biological effects. *Annales Zoologici Fennici*, **22**, 359–371.
- Wolff, J.O. (1993) Why are small mammals territorial? *Oikos*, **68**, 364–370.
- Wolff, J.O. & Cicirello, D.M. (1991) Comparative paternal and infanticidal behavior of sympatric white-footed mice (*Peromyscus leucopus noveboracensis*) and deermice (*P. maniculatus nubiterrae*). *Behavioral Ecology*, **2**, 38–45.
- Wolff, J.O., Freeberg, M.H. & Dueser, R.D. (1983) Interspecific territoriality in two sympatric species of *Peromyscus* (*Rodentia: Cricetidae*). *Behavioural Ecology and Sociobiology*, **12**, 237–242.
- Ylönen, H. (1990) Phenotypic flexibility in the social organization of *Clethrionomys*. *Social Systems and Population Cycles of Voles* (eds R.H. Tamarin, R.S. Ostfeld, S.R. Pugh & G. Bujalska), pp. 203–212. Birkhäuser Verlag, Basel.
- Ylönen, H., Kojola, T. & Viitala, J. (1988) Changing female spacing behaviour and demography in an enclosed breeding population of *Clethrionomys glareolus*. *Holarctic Ecology*, **11**, 286–292.

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