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Analysis of spacing behaviour of females from a live-trapping study of *Clethrionomys gapperi*

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A live-trapping study was conducted near Lesser Slave Lake, Alberta, Canada to examine space use and spacing behaviour of female *Clethrionomys gapperi*. Voles were censused over three breeding periods in 1980 to 1982 on three 4-ha grids in different habitat types. The home ranges of females were exclusive at low density but overlapped slightly at high density and home range size was larger in the coniferous habitat than in deciduous vegetation. Sexually mature females, once settled on a home range, appeared to show only minor shifts. Further, the home range size of females was not a function of density. In 1982, in deciduous habitat the number of mature females remained constant for the last six weeks of the breeding season at the density predicted from home range size and effective sampling area of the grid. Spacing behaviour appeared to limit the breeding density of females in this species. However, in order to test this, experiments will have to be performed.

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1. Introduction

Sexual maturation may be regulated through social dominance (Gustafsson et al. 1980, 1983) or through spacing behaviour (Watson & Moss 1970). Spacing behaviour has been invoked as a density regulating mechanism of mature female *C. glareolus* (Bujalska 1970, 1973) and *C. rufocanus* (Kalela 1957, Viitala 1977, Saitoh 1981). Both of these species have cyclic and non-cyclic populations (Hansson and Henttonen 1985). *C. gapperi* appears to be non-cyclic (Fuller 1985, Hansson & Henttonen 1985). Mihok (1979) and Perrin (1979) have shown that mature female *C. gapperi* have exclusive home ranges. However, Fuller (1979) and Mihok (1979) both showed that maturation of females was not a function of the density of mature females. Does this then mean that spacing behaviour did not limit breeding density or that the density at the time of their studies was too low to reveal the effect of spacing behaviour?

For a constant resource level, spacing behaviour may limit the density of breeding individuals in a density dependent or in a density independent manner. If the space required by an animal is fixed and exclusive then spacing behaviour will limit the density of breeding individuals in a density-independent manner. However, if the space required shows an increasing degree of overlap or is compressed with increasing density up to a limit, then spacing behaviour will operate in a density-dependent manner.

In this paper I will try to answer, from live-trapping results, the following questions about space use and spacing behaviour in *C. gapperi* from central Alberta, Canada: 1) Are the home ranges of mature females exclusive? 2) Do home ranges shift with time? 3) Does home range size change with density? 4) Is there an upper limit to the number of home ranges of mature females for a given area?

2. Methods

This study was carried out 25 km SE of Lesser Slave Lake, Alberta, Canada in 1980 to 1982. The study area was situated in a mixed boreal forest of mainly trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) and has been described in detail by Bondrup-Nielsen (1986a). The data for this article were collected from animals live-trapped on three 4-ha grids: traps (Longworth) were spaced at 20 m. Two grids, A1 and A2, were in predominantly deciduous forests and grid B1 was located in a predominantly coniferous forest. In 1982 Grid

A2 was not trapped and grid B1 was enlarged to a 12×13 grid with 20-metre spacing (6.2 ha). Voles on the grids were enumerated (five trap-checks over three days) every 2 weeks (called a rota) starting in early May and ending in late August to early September. Standard live-trapping procedure was followed (Bondrup-Nielsen 1986a). I define a mature female as a sexually mature female that is pregnant and/or is lactating. A mature male is a male with scrotal testes.

Estimates of home range size (range length technique, Abramsky & Tracy 1980; exclusive boundary strip method, Stickel 1954) are based only on animals caught at least five times (during the period they were present on the grid) and for which 80 % of the capture points occurred inside the perimeter traps on the live-trapping grids, i.e., animals usually caught on the edge of the grid are excluded.

3. Results

3.1. Density

The live-trapping results are based on approximately 37 000 trap-nights and a total of 861 captured individuals of *C. gapperi*. The average trapability (Boonstra & Krebs 1978) was always higher than 80 %. After a slight decrease in numbers during the early rotas, especially in 1980 and 1981, the increase in numbers was generally exponential, with similar rates of increase on most grids in most years (Fig. 1). I consider 1982 the year with a high density of voles (Fig. 1).

3.2. Capture overlap

The maximum percentage of captures of two or more mature individuals at one trapstation during a rota was 11.2 % for females and 27.6 % for males (Table 1). Mature males were always caught more often at the same trapsite during a rota than females but the difference was only significant in the deciduous habitat in the high density year, 1982 (Table 1). The percentage of captures of different individuals of either sex at the same trapsite during a particular rota increased significantly with density, except for females in the coniferous vegetation type (Table 1). Only mature males and only in the high density year (1982) were different individuals caught more often at the same trapsite in the deciduous than in the coniferous habitat (Table 1).

Captures of mature males revealed extensive overlaping. When different mature females were caught at the same trapstation, that trap station was always peripheral to both.

3.3. Home range shift

For two out of 13 females and five out of 10 males that were caught on six consecutive rotas the mean "home range centre" (Hayne

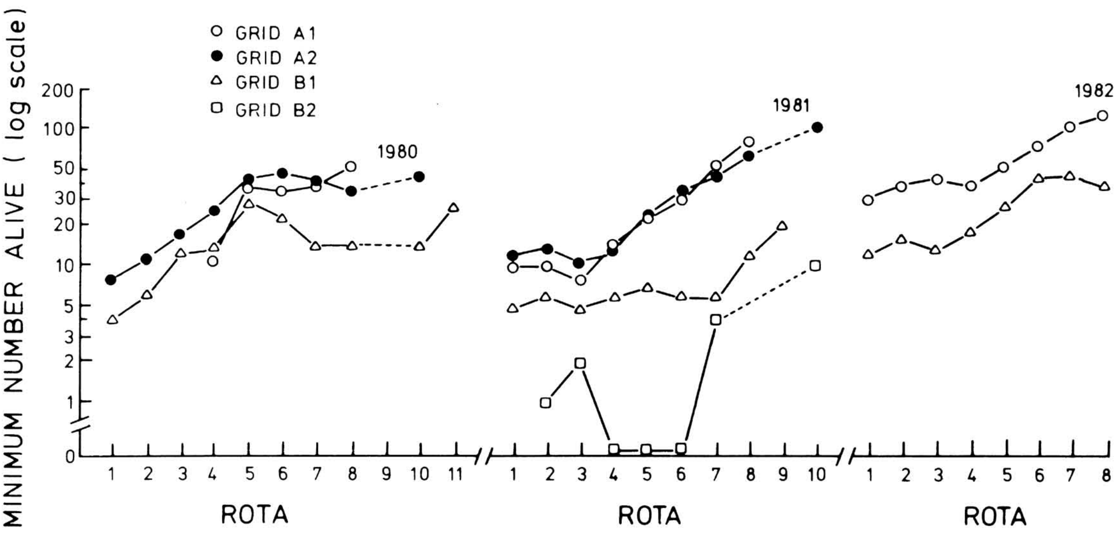

Fig. 1. Minimum number of *Clethrionomys gapperi* known to be alive on live-trapping grids in 1980, 1981 and 1982.

Table 1. Comparison of the percentage of trapstations at which two or more mature males or females were caught during any rota, (sample size in parenthesis, *G*-test Sokal & Rohlf 1969:575).

Habitat		Males	Females	*G*	*P*
Coniferous	1980	5.0^1(60)	4.5^3(67)	0.08	NS
	1982	15.4^2(156)	10.3^4(117)	1.21	NS
	G	4.05	1.06		
	P	< 0.05	NS		
Deciduous	1980	10.8^1(148)	4.6^3(110)	3.03	NS
	1982	27.6^2(340)	11.2^4(214)	15.29	<0.001
	G	12.44	3.75		
	P	< 0.001	< 0.05		

[1] $G=1.64$, NS [2] $G=6.01$, $P<0.05$ [3] $G=0.12$, NS [4] $G=0.06$, NS

1949) between the first set of three rotas and the second set of three rotas was significantly different. However, this did not result in a significant shift of home range.

3.4. Home range size

The mean range length (Abramsky & Tracy 1980) was not a function of density of mature females in either the deciduous habitat or the coniferous habitat (Fig. 2). However, home range size as measured by the exclusive boundary strip method (Stickel 1954) was a function of habitat (Table 2).

3.5. Density of breeding females

If spacing behaviour of mature female voles limits the density of breeding individuals, one would expect the number of mature females to reach a plateau. This plateau should occur before rota 8 since no females became sexually mature after this rota during any of the three years of the study. In 1980 total density, especially on grids A1 and B1, decreased after rota 5. Density then increased again after rota 7 on grid A1 and after rota 9 on grids A2 and B1 (Fig. 1). The same density trend was observed for mature and immature females on all three grids (Fig. 3). In 1981 there was an indication that the density of mature females was starting to level off at about 22 individuals on grid A1 and 19 on grid A2 (Fig. 4). However, the clearest expression of the prediction occurred on grid A1 in 1982 (Fig. 5), when the number of mature females stabilized at about 26, beginning at rota 5. On grid B1 in 1982 the density of mature females levelled off and showed a slight drop between rotas 7 and 8 but this trend was observed in the total density as well (Fig. 5). The density of mature females on grid B1 in 1982 did not show a substantial increase

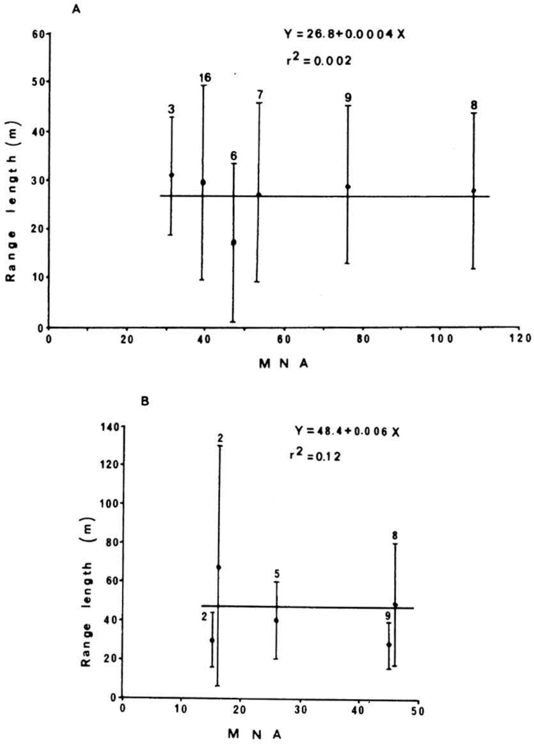

Fig. 2. Regression of mean (±*SD*) range length (m) of mature females on grid A1 in 1982 (A) and on grid B1 in 1982 (B) caught at least five times and with 80 % or more of captures occurring inside the perimeter traps against MNA (Minimum Numer Alive).

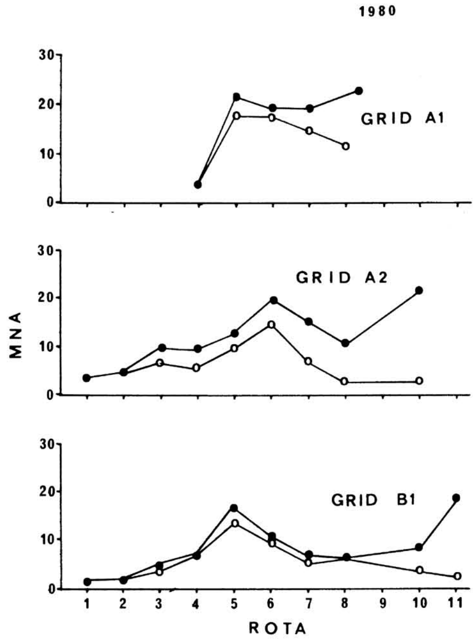

Fig. 3. Density change of total number of female and mature female *Clethrionomys gapperi* on three grids in 1980 (MNA, Minimum Number Alive; filled circles, total number of females; open circles, total number of mature females).

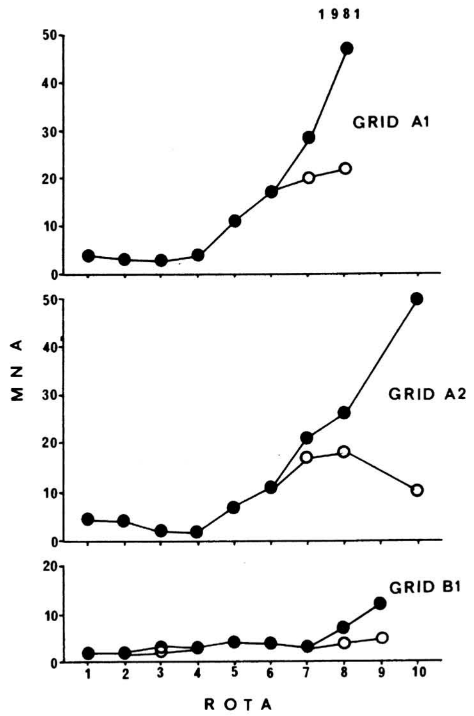

Fig. 4. Density change of total number of female and mature female *Clethrionomys gapperi* on three grids in 1981 (MNA, Minimum Number Alive; filled circles, total number of females; open circles, total number of mature females).

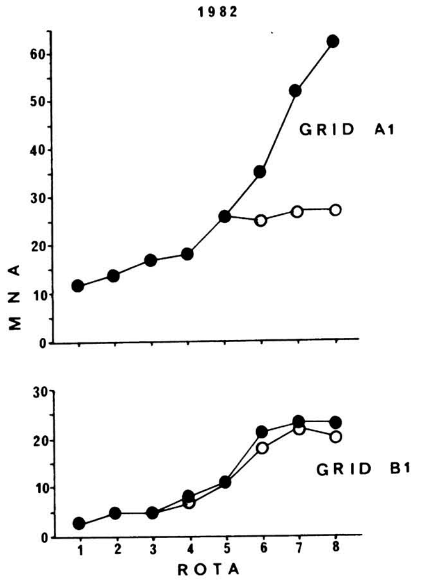

Fig. 5. Density change of total number of female and mature female *Clethrionomys gapperi* on three grids in 1982 (MNA, Minimum Number Alive; filled circles, total number of females; open circles, total number of mature females).

until rota 5, the period when the density of mature females stabilized in the deciduous habitat (grid A1).

Apparently only in 1982 and only in the deciduous habitat did the density of mature females reach a saturation level of approximately 26 animals on the 4-ha grid.

A second estimate of carrying capacity for breeding females can be obtained by estimating home range size and determining the number of home ranges on a 4-ha grid. The home range size of mature females as calculated by the exclusive boundary strip method was 0.26 ha in the deciduous habitat (Table 2). The number of female home ranges in 4 ha should therefore be between 15 and 16; but the number of mature females stabilized at about 26. When the ratio of grid size to home range size is 16 the animals on the grid are over-estimated by a factor of 1.6 (Bondrup-Nielsen 1983). Therefore, the true number of mature females on grid A1 is 26/1.6, which is approximately equal to 16. On grid B1 where the

Table 2. Estimate of home range size (for all years) of female *Clethrionomys gapperi* based on the exclusive boundary strip method (Stickel 1954).

Grid	Trap stations	*N*	Area (ha)
A1	6.40±2.72	31	0.26
A2	6.60±2.97	10	0.26
B1	8.18±3.79	17	0.33

home range size for mature females was 0.33 ha (Table 2) one would have expected approximately 21 mature females when that grid was 4 ha in size, and approximately 28 mature females when it was 6.2 ha in size. In 1982 the maximum density of mature females on grid B1 was 22 which was well below the predicted saturation level of 28.

4. Discussion

My analysis mainly concerns female voles since females have been implicated in density regulation in *Clethrionomys* (Kalela 1957, Koshkina 1965, Bujalska 1970, 1973, Mihok 1979), and have also been shown to maintain exclusive home ranges. The results from this study suggest that there was some overlap of mature female home ranges, especially at high density. Bujalska (1970, 1971, 1973), working with *C. glareolus* on a 4-ha island in Poland, also found that the overlap of mature female home ranges increased with the density of mature females. However, the density of mature females on the island levelled off during each year of her study at about 60 individuals, which is far more than the maximum number of mature females in my study.

There is confusion in the literature concerning mature female microtines changing their nest site within the home range as a means of weaning litters and changing home range as a strategy to increase fitness in temporary environments (Bondrup-Nielsen 1985). Only two out of 13 mature females, in this study, changed their activity centres over a 12-week period, but this did not result in a change of home range location. One would not expect a mature female *C. gapperi* to change its home range since it lives in a stable environment. *M. oeconomus* females, for example, living in wet and unstable meadows do change home ranges (Tast 1966). I do not have any information on nest placement and mature female *C. gapperi* may indeed change nest sites with each litter.

The mean range length of female voles in this study was not a function of density as has been found to be the case with some other small mammals (Forsyth & Smith 1973, Maza et al. 1973, O'Farrell et al. 1975). Where the home range approaches the status of a territory, i.e. is exclusive, size should be partly a function of food quality and quantity (Smith 1968, Mares et a. 1982). The differences in mature female home range sizes in different habitats may reflect this.

Only in 1982 and only on grid A1 did the number of mature females stabilize. This density corresponded to the number one would have expected based on home range size, grid size and an allowance for edge effect. Only the deciduous habitat became saturated with breeding females and one would therefore not expect to catch subadult females (after Myllymäki 1977) in that habitat owing to the dispersal of subadult females to unsaturated habitats (Bondrup-Nielsen & Ims 1986).

Why did Fuller (1979) and Mihok (1979) not find that the maturation rate of females was affected by the density of mature female *C. gapperi*? Density regulation in *C. gapperi* has been studied extensively at Heart Lake (Fuller 1969, 1977a, 1977b, 1979, Fuller et al. 1969, Mihok 1979). The home range of mature females at Heart Lake was approximately 0.3 ha (Fuller pers. comm.). A density high was recorded in 1974, when, in early August, there were 40 individuals on a 2.25 ha grid, of which 13 were mature females (Fuller 1977a). The ratio of grid size to home range size for mature females was 7.2 and mature females were consequently overestimated by a factor of about 2.5 (Bondrup-Nielsen 1983). This means that the true number of mature females on 2.25 ha was 5.2. With a mature female home range size of 0.3 ha one would expect approximately 7.5 mature females on 2.25 ha. Consequently the grid was not saturated with mature females. There was another peak in the population of *C. gapperi* at Heart Lake in 1976 (Fuller pers. comm.). In late July 26 mature females were caught on a 6 ha grid. Following the same logic as above the corrected density of mature females on 6 ha was 17.4 and the expected was 20; density was again below the saturation level. Regulation through spacing behaviour would therefore not be apparent and consequently it is no surprise to find that there was no relationship between the maturation rate of females and density (Fuller 1979). It should of course be kept in mind that the home range sizes are estimates.

It appears then that under circumstances of relatively high density, the limitation of the density of mature females, through spacing behaviour, is the same as described for *C. glareolus* (Bujalska 1970). Furthermore, it appears that spacing behaviour in *C. gapperi* is density-independent; that is, home range size is not a function of density and home range overlap was minor, with only about 10 % sharing of adjacent trapstations between females at high density. Experiments confirming that spacing behaviour limits the breeding density of female *C. gapperi* have been performed (see Bondrup-Nielsen 1986b).

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