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Movements and spatial patterns in populations of *Clethrionomys* species: A review

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Domestic movement, home range size and dispersion, spacing behaviour, sexual maturation and dispersal in *Clethrionomys* species are reviewed. *Clethrionomys* species generally do not construct tunnels and their nocturnal to crepuscular activity in summer becomes diurnal in winter. The rhythm is 2 to 6 hours. Size of the home range varies with sex, age, habitat quality and season. Home ranges of males are overlapping and larger than those of females which do not overlap. Spacing behaviour limits the density of mature females and at high density maturation rate decreases. Dispersal among mature females, in particular, is very low while dispersal rate of immatures is high and occurs at puberty. When all space is occupied by mature females in high quality habitats, animals disperse to low quality habitats. Various comparisons are made with *Microtus*.

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1. Introduction

All microtines (Subfamily Microtinae) were for a long time assumed to cycle with a periodicity of 3 to 4 years (Elton 1942, Krebs & Myers 1974, Tamarin 1980). We now know that this was much too broad a generalization (Taitt & Krebs in press, Hansson & Henttonen 1985). The microtines include mainly lemmings, *Microtus* voles and *Clethrionomys* voles. However, most studies on cycles have been done on *Microtus* species and the findings often generalized to all microtines and to small mammals as a whole (Krebs & Myers 1974). We believe this generalization has led to much confusion in the study of microtine biology.

Microtines are found in three rather broadly defined areas — arctic tundra, forests, and meadows and grasslands. If we consider just *Clethrionomys* and *Microtus*, then a very obvious difference between them is that *Clethrionomys* lives mainly in forested areas while *Microtus* lives mainly in open areas — meadows, grasslands and arctic tundra (Krebs & Myers 1974, Batzli 1975). The genus *Clethrionomys* has a wide distribution in the northern hemisphere (Stenseth 1985). Some populations of *Clethrionomys* have multiannual cycles (Hörnfeldt 1978, Wiger 1979, Hansson & Henttonen 1985) while other populations have stable densities, i.e. annual cycles (Koshkina & Korotkov 1975, Bujalska 1970, Hansson & Henttonen 1985). Furthermore, within the same species (e.g., *C. glareolus*) there are populations that have multiannual cycles and populations that have annual cycles (Stenseth et al. 1985).

In recent years it has become increasingly obvious that if we wish to understand population dynamics of microtines we must acquire a thorough understanding of dispersal (Gadgil 1971, Krebs et al. 1973, Bekoff 1977, Gaines & McClenaghan 1980, Stenseth 1983, Vance 1984, Bondrup-Nielsen 1985). However, as pointed out by Bondrup-Nielsen (1985) the study of dispersal should be carried out with an emphasis on space use of a population as well as habitat configuration within which this population is found.

In this article we review movement, dispersal and space use in the genus *Clethrionomys*, and try to relate this to habitat patch configuration. Throughout we draw comparisons with the genus *Microtus*.

2. Definitions

2.1. Home range and domestic movement

Home range is usually defined as the area an individual occupies, exclusive of migrations or occasional sallies (Burt 1943, Jewell 1966). Burt (1943) considered the life-long home range, but this as Myllymäki (1977) has pointed out, is unrealistic for microtines. Individuals may be very mobile, and often change home ranges between litters. Bondrup-Nielsen (1985) defined the home range as a discrete area frequently traversed by an animal during its daily activity, producing a tight network of its life time track; occasional sallies outside this area are excluded. Bondrup-Nielsen (1985) further suggested three different types of home ranges — *natal, breeding* and *non-breeding home ranges.* Animals may possess more than one of these home range types including more than one breeding home range in its lifetime (Myllymäki 1977).

Domestic movement we define as all movement of an individual within its home range including occasional sallies outside this area.

2.2. Dispersal

Lidicker (1975) has defined three types of dispersal — *pre-saturation, saturation* and *frustrated.* Pre-saturation and saturation dispersal are defined in relation to carrying capacity. Pre-saturation dispersal takes place prior to the population reaching carrying capacity. These dispersers are generally in good condition and may include any sex and age group. Saturation dispersal takes place when the population has reached carrying capacity. These animals are generally forced out and represent social outcasts, juveniles and the very old individuals. Frustrated dispersal is a somewhat misleading term since dispersal is prevented such as might occur on islands and within enclosures.

Stenseth (1983) has proposed the terms *adaptive* and *non-adaptive dispersal.* In adaptive dispersal the individuals dispersing are successful at establishing and breeding, and dispersal is not dependent on density.

Non-adaptive dispersers are those forced to disperse. They represent the losers in intraspecific competition. They are in part equivalent to the saturation dispersers after Lidicker's terminology.

We will define dispersal according to Bondrup-Nielsen (1985) as movement in a random direction by an individual out of one home range for the purpose of establishment on a new home range. Dispersal mainly applies to young animals in search of a breeding home range but may also apply to mature animals in search of a new breeding home range (e.g., *Microtus agrestis*; see Myllymäki 1977).

3. Review

In Table 1 we have listed some of the features that seem to characterize *Clethrionomys* species. The four most studied species are listed and for each we have given the references that support the characteristic feature. We have divided the review into four sections: Domestic movements (3.1), Home range size and dispersion (3.2), Spacing behaviour and sexual maturation (3.3) and Dispersal (3.4).

3.1. Domestic movements

Throughout the year, *Clethrionomys* species exhibit a relatively constant rhythm of up to 7 periods daily, with each period consisting of 2 to 6 hours of activity (Kikkawa 1964, Karulin et al. 1973, Herman 1977). Nocturnal and crepuscular activity in summer shifts to diurnal activity in winter. Vicerky & Bider (1981) studied rodent activity in relation to the weather by recording the number of times rodents crossed sand transects per night. For *C. gapperi* activity was found to be correlated with relative humidity. Voles were most active when rain fell and temperatures were high. They also increased their activity on cloudy and moonless nights if rain had not fallen recently. However, weather only explained 8.3 % of the between-nights differences in the activity of *C. gapperi* (Vickery & Bider 1981).

Some populations of *Clethrionomys* are skilful climbers and make nests and store food several meters above ground (Vorontsov 1961). Approximately 17 % of the total captures of *C. glareolus* were in traps in trees 3 m above ground by Holisova (1969). Animals which feed on lichens in trees (Viro pers. comm.) are probably the most skilful climbers.

Table 1. Summary of space use and dispersal in the genus *Clethrionomys*.

Mature females have mutually exclusive home ranges
C. gapperi: Bondrup-Nielsen (1984), Perrin (1979, 1981), Mihok (1979)
C. glareolus: Bujalska (1970)
C. rufocanus: Kalela (1957)

Home range size for mature males larger than for mature females, sometimes by as much as a factor of two. Much overlap among home ranges of mature males
C. gapperi: Bondrup-Nielsen (1984), Perrin (1979, 1981), Mihok (1979)
C. glareolus: Mazurkiewicz (1971)
C. rufocanus: Kalela (1957)

Home range size for mature females constant or decrease with improved habitat quality or addition of food
C. gapperi: Bondrup-Nielsen (1984)
C. glareolus: Kutenkov (1979), Gliwicz (1980), Mazurkiewicz (1981), Bujalska & Janion (1981), Andrzejewski & Mazurkiewicz (1976)
C. rufocanus: Viitala (1977)

Spacing behaviour regulated density of mature females
C. gapperi: Bondrup-Nielsen (1984)
C. glareolus: Bujalska (1970)
C. rufocanus: Saitoh (1981)

Decreased maturation rate at high density
C. gapperi: Bondrup-Nielsen (1984)
C. glareolus: Gipps & Jewell (1979), Bujalska (1970, 1973), Zejda (1967)
C. rutilus: Koshkina & Korotkov (1975)
C. rufocanus: Abe (1976), Kalela (1957), Saitoh (1981)

Very low (approx. 5 %) dispersal of mature females
C. gapperi: Bondrup-Nielsen (1984)
C. glareolus: Watts (1970a)

Movement of dispersing individuals from optimal to low quality habitat
C. gapperi: Bondrup-Nielsen (1984)
C. glareolus: Mazurkiewicz & Rajska (1975)

Data on distance moved between successive trappings are obtained from live-trapping studies and are often interpreted as movement (e.g., Bergstedt 1966, Crawley 1969, Watts 1970a). These data are of course a very poor substitute for actual movement. When moving from one spot to another voles often make use of natural paths such as under fallen trees and available shelters as frequently as possible (Kalela 1957, Johnels 1964, Brown 1966, Olsweski 1968, Mironoc & Kozhevnikov 1982). In winter they sometimes construct tunnels above ground in the subnivean space (Coulianos & Johnels 1962, Karlsson unpubl.).

Typically *Clethrionomys* do not travel in runways while *Microtus* do (see, e.g., Banfield 1974).

Karlsson (1984) has shown experimentally that sexually mature *C. glareolus* in contrast to immatures at the end of the breeding season and overwintered individuals just prior to the breeding season demonstrate orientation tendencies when displaced. Robinson & Falls (1965) studied homing in *M. pennsylvanicus* and found that voles showed a strong homing tendency but did not return when displaced greater than about 425 m. Homing was significantly greater among mature than immature individuals and the ability to home appeared to be a function of previous familiarity with the general area. For example, voles confined to a large field enclosure throughout summer had a significantly reduced homing ability. Homing ability in *M. pennsylvanicus* may indicate that voles make frequent sallies off their home range which familiarizes them with rather large areas.

3.2. Home range size and dispersion

Mature *Clethrionomys* females tend to have mutually exclusive home ranges while there is much overlap among the males (Table 1). Mature males have larger home ranges than females, sometimes by as much as a factor of six times for overwintered *C. glareolus* (Mazurkiewicz 1971). This large size of male home ranges seems excessive and may be a result of the fact that the study was conducted on an island where the density of mature females was rather high (60 mature females on 4 ha; see Bujalska 1970). It seems more common that mature males have home ranges no more than twice the size of those of mature females (*C. gapperi*, Bondrup-Nielsen 1984; *C. glareolus*, Crawley 1969).

In *Microtus agrestis* (Myllymäki 1977), *M. californicus* (Lidicker 1980) and *M. xanthognathus* (Wolff 1980) there is much overlap among mature females while the mature males tend to have mutually exclusive home ranges. However, *M. pennsylvanicus* is more similar to *Clethrionomys* species in space use, as there is overlap among males but little overlap among females (Madison 1980). *M. ochrogaster* appears to be monogamous with pairs having exclusive home ranges according to Getz & Carter (1980). In *M. montanus* on the other hand, mature males and females are territorial separately and the mating system is polygamous like most other microtines (Jannett 1980). It is unclear why these different types of social organization have evolved. However, whether or not males or females are "territorial" must have to do with the economics of defensability of different types of resources within various habitat complexes (Wittenberg 1981).

Microtus tend to have smaller home ranges than *Clethrionomys* although there is much variation within each genus (Brown 1966). In *Clethrionomys* (including *C. glareolus, C. rufocanus* and *C. gapperi*) the average range size is 0.23 to 1.34 acres (i.e., 0.09 to 0.5 ha) and in *Microtus* (incuding *M. pennsylvanicus, M. montebelli, M. arvalis, M. agrestis* and *M. ochrogaster*) 0.07 to 0.46 acres (i.e., 0.03 to 0.18 ha) (Brown 1966). *Microtus* males also have home ranges that are about twice that of females; i.e., similar to *Clethrionomys* (Brown 1966).

Home range size of mature *Clethrionomys* females is relatively constant within a particular habitat type and year. However, with improved habitat quality or with the addition of food home range size tends to decrease (Table 1). By adding food to a 4 ha island Bujalska & Janion (1981) found that the mean home range size of mature female *C. glareolus* decreased from 810 m^2 to 616 m^2. Home range size of mature female *C. gapperi* (measured by the exclusive boundary strip method; Stickel 1954) was 0.26 ha in deciduous habitat (i.e., high quality habitats) and 0.33 ha in coniferous habitat (i.e., low quality habitat) (Bondrup-Nielsen 1984).

Home range size has been claimed to decrease from spring to fall (Mazurkiewicz 1971). This is not surprising when the whole population is considered: From spring to fall there is an increase in the number of immature animals which have smaller home ranges. So when considering averages home range size will appear to decrease. It has also been claimed that with increased population density, average home range size decreases (Viitala 1977, Kutenkov 1979, Mazurkiewicz 1971, Gliwicz 1980). However, again the increased proportion of immature animals in the population is a confounding factor. Average home range size of sexually mature female *C. gapperi* was found to be independent of population density (Bondrup-Nielsen 1984).

During fall and winter when most populations of *Clethrionomys* do not breed, females often have overlapping home ranges (Perrin 1979, Karlsson unpubl. data).

3.3. Spacing behaviour and sexual maturation

For *Clethrionomys* the density of mature females seems to be limited by spacing behaviour and at high density, maturation rate is low (Table 1). When a proportion of mature females were removed from an area a high proportion of young animals attained maturity in both *C. glareolus* (Bujalska 1973) and *C. gapperi* (Bondrup-Nielsen 1984). The age distribution of mature females on the experimental areas was significantly different compared to controls (controls equal other years in Bujalska's study; control plots were used by Bondrup-Nielsen) indicating that these young animals are usually prevented from maturing. That spacing behaviour limits the density of mature females was also found experimentally by use of enclosures for *C. gapperi* and *C. rufocanus* (Bondrup-Nielsen 1984, Saitoh 1981) respectively. The enclosure experiments by Saitoh (1981) and Bondrup-Nielsen (1984) also revealed decreased maturation rate of young females at high density. In the enclosure experiment by Bondrup-Nielsen (1984) spacing behaviour by mature male *C. gapperi* appeared very weak; results were not significant and trends were not consistent. Gipps & Jewell (1979) studying the effect of castrated males on population dynamics of *C. glareolus* in enclosures (outdoor enclosures 550 m^2) and Watts (1970b) studying the effect of removal of mature male *C. gapperi* found no evidence for spacing behaviour in males. Removals of 50–70 % of mature male *C. gapperi* on experimental plots did not appear to affect the spacing of mature females (Bondrup-Nielsen 1984), although, when all mature male *C. gapperi* were removed from an area, mature females left (Elliott 1969).

In *Microtus*, spacing behaviour, mainly of the females (?), also appears to be operating (Krebs 1979, Tamarin 1983).

3.4. Dispersal

There is very little data available on dispersal in *Clethrionomys*. What little there is, is presented in Table 1.

In winter, when mobility is low, the rate of dispersal is moderate (Kozakiewicz 1976, West 1977). For example, on a 6.75 ha continuous removal plot Kozakiewicz (1976) recorded an average of 11.8 individuals arriving on the plot per month between November and May. During the other 6 months of the year (breeding season) the average number of individuals arriving on the grid was 44.3. Of all animals arriving (dispersers), 79 % arrived in summer and 21 % in winter. In spring, prior to the onset of breeding, increased mobility of males causes an increase in male home range overlap. This, plus an increase in antagonistic behaviour between males, not only leads to increased dispersal before the onset of breeding, but also to access to more females (Kikkawa 1964, Crawly 1969, Perrin 1981, Karlsson unpubl. data). In females, too, an increased rate of mobility is observed with the onset of breeding leading to the establishment of mutually exclusive home ranges. Although densities in spring may be very low, competition for high quality space sometimes occurs and generates dispersal (Viitala 1977, 1980). It has been suggested, and reasonably so, that females compete for space during spring while males compete for acquisition of as many mating partners as possible (Boonstra 1977, Mihok 1981, Perrin 1981).

There are somewhat diverging observations on the rate of dispersal in sexually mature *Clethrionomys* species: Watts (1980a) found from 6% in mature male to 2% in mature female *C. glareolus* do disperse. Bondrup-Nielsen (1984) likewise found a similarly low dispersal rate among sexually mature *C. gapperi*. However, Kozakiewicz (1976) found a high dispersal rate among mature *C. glareolus*, from 86% in males to 55% in females. Kozakiewicz (1976) employed a removal (vacuum) grid for his study and did not consider edge effect while Watts (1970a) and Bondrup-Nielsen (1984) analyzed settlement onto areas from which individuals where not removed. Methodology may account for the observed differences in dispersal of mature individuals.

A high dispersal rate among *M. agrestis* (Myllymäki 1977) and *M. oeconomus* (Tast 1966) is common. Dispersal of mature females tends to take place between litters and is probably a function of the unstable habitat that these two species occupy.

There is some confusion in the literature between actual dispersal and abandonment of the brood nest as a means of weaning a litter: Jannett (1980) presents a table (see his table 1) in which he lists a number of microtines where the female abandons the brood nest as a means of weaning her litter. However, some of these examples include actual dispersal between litters (Tast 1966, Stoddart 1970, Myllymäki 1977), whereas in others the female merely changes nest site within the same home range (Kikkawa 1964, Brooks & Banks 1971 (for some females); Jannett 1980 (at low density only).

Mazurkiewicz & Rajska (1975) studying *C. glareolus* found that the majority (82 %) of the juveniles remain within their natal area when born in suboptimal habitat, whereas only about half (42 %, including 51 % of the females and 20 % of the males) stay when born in optimal habitat. Bondrup-Nielsen (1984) found a similar difference in *C. gapperi* when population density was high. Animals caught for the first time in optimal habitat were mainly immature individuals weighing less than 16 g, whereas over 50 % of the animals caught for the first time in suboptimal habitat weighed 16 to 20 grams and were sexually mature. These mature individuals were most likely immigrants from optimal habitat, this was supported by data from a study of marked infants (Bondrup-Nielsen unpubl. data).

In *C. glareolus* (Smyth 1966) and in *C. gapperi* (Bondrup-Nielsen unpubl. data) dispersal usually takes place in both sexes just prior to puberty. Mazurkiewicz & Rajska (1975) found dispersal distance, as a whole, to be inversely proportional to population density.

4. Summary

To summarize, in the genus *Clethrionomys*, mature females have mutually exclusive home ranges, and home range size does not appear to be a function of density but rather depends on food quality and quantity, and quality of habitat type. Female home range size decreases with addition of food and with increased quality of habitat. Mature females have overlapping home ranges and the home range size is about twice that of mature females. Spacing behaviour of females limits the density of mature females within habitat patches. Sexual maturation of females is low at high density and habitat structure is important in dispersal. Spacing behaviour of mature males does not appear to operate and there is no clear effect of density on maturation rate of males.

Dispersal of female *Clethrionomys* appears to be largely a consequence of spacing behaviour possibly influenced by the habitat (patch quality, size and configuration). The effect of habitat patch size, quality and configuration on dispersal should guide future research (see Bondrup-Nielsen 1985).

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