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Bank vole biology: Recent advances in the population biology of a model species				

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## DISPERSAL IN THE BANK VOLE

**ABSTRACT:** The objective of this chapter is to review progress made in the studies of dispersal in the genus *Clethrionomys*, and particularly in *C. glareolus*. This is presented in a comparative context to *Microtus* voles. From reviewed data the following is evident: (1) Habitats of *Clethrionomys* voles range from relatively homogeneous in the north-eastern landscapes dominated by forest to mosaic ones in the central and western Europe. (2) Dispersal was studied on different spatial scales; for each spatial scale specific techniques were used. New methods employing mtDNA markers proved especially useful for studies in very small and large spatial scales. (3) Natal dispersal, studied usually in small enclosed population, was found to be male-biased as in *Microtus* voles; a possible effect of population confinement on the obtained results is discussed. (4) Breeding dispersal of adult voles, after recent reexamination of evidence, seems to be less common and less adaptive than previously reported. (5) As future directions of vole dispersal studies spatial-temporal dynamics and landscape ecology are indicated.

**KEY-WORDS:** breeding dispersal, *Clethrionomys*, landscape ecology, natal dispersal, new techniques

### 1. INTRODUCTION

The aim of this chapter is to review progress made in the studies of dispersal in bank voles during last decade or so. During this time several books covering many theoretical

aspects of dispersal in small mammals appeared (Stenseth and Lidicker 1992, Stenseth and Ims 1993, Lidicker 1995, Barrett and Peles 1999). Here an effort is made to address issues specific to the genus *Clethrionomys*, with special reference to *C. glareolus*. In this review we use definition of dispersal proposed by Stenseth and Lidicker (1992), as one-way movements of individuals away from their home sites. We examine dispersal from the perspective of habitat and spatial scale, as well as individual age- and sex-specific characteristics.

We also present *Clethrionomys* in a comparative context to those other microtine rodents for which new empirical evidence on dispersal has accumulated, especially *Microtus*. Since it is common in the literature for dispersal of *Clethrionomys* and *Microtus* voles to be treated as fully comparable, the pros and cons of such an approach will be considered.

One of the main advances made is related to the use of new techniques. In particular, the application of molecular techniques has proved to be helpful in many aspects of dispersal studies. They have opened new possibilities for estimating indirectly the rate and distance of dispersal and their effect on genetic structure and population dynamics. Molecular genetic techniques have also helped to

verify characteristics of dispersers (Ishibashi *et al.* 1998). Through the new techniques the range of spatial scales employed in dispersal studies has been extended, covering a few dozen meters on one end and many kilometers on the other. Still there are plenty of opportunities for more innovative use of various methods, both conventional and new, in the study of *Clethrionomys* dispersal.

## 2. DISPERSAL STUDIES: HABITATS, SPATIAL SCALE AND METHODS

### 2.1. HABITATS OF THE BANK VOLE

Dispersal patterns and associated effects on population dynamics may be affected by features of the habitat (Wiens *et al.* 1993, Andren 1994). Usually habitats of forest dwellers such as bank voles are viewed as less heterogeneous than those of other microtine rodents. *Microtus* landscapes are considered more fragmented, composed of patches of different quality, such as grasslands, mires and forest clearings, spatially isolated and surrounded by transient areas. *Clethrionomys* habitats, on the other hand, are considered more continuous or consisting of patches of similar quality that are contiguous (e.g. Bondrup-Nielsen 1985, Bondrup-Nielsen and Karlsson 1985). Thus, dispersal in the patchy habitats of *Microtus* might be more restricted or risky than that in homogenous habitats of *Clethrionomys*. Moreover, flow of individuals in fragmented landscapes may be more of "source-sink type" (Lidicker 1975, Pulliam 1988), while in continuous large forested areas "balanced dispersal" (*sensu* Diffendorfer 1998) may prevail.

However, such a view on *Clethrionomys* habitats is, perhaps, biased by the northern perspective of Canadian and Fennoscandian studies carried out in forest dominated landscapes. Although modern forestry creates vast clearcuts in northern boreal forests, the re-forestation areas become suitable habitats for *Clethrionomys* even in early successional stages. In western and central Europe, due to advanced forest fragmentation, contemporary habitats for bank voles are composed of small forest patches surrounded by agroecosystems, uninhabitable for these voles (Fig. 1). Besides structural aspects such as patch size and isolation, the quality of forest patches and, consequently, their suitability to bank voles varies greatly. The edges are under

strong influence of surrounding open (matrix) habitats and richness and persistence of a herb layer (a factor important for the bank vole – Pucek 1983) may vary dramatically, both seasonally and spatially (Gliwicz 1989). Therefore, the spatial arrangement and variation in a quality of habitats for the bank vole in western and central Europe may be much the same as in the model by Hansson (1977), developed for *Microtus*.

Various types of *Clethrionomys* landscape: less and more fragmented (Fig. 1), may affect dispersal processes, and require different methodological approaches as well as different spatial scales of dispersal studies.

### 2.2. SPATIAL SCALE AND METHODS

In recent years dispersal in *Clethrionomys* was studied at three spatial scales. Small-scale dispersal studies were carried out on plots of about 1 ha in size (rarely several hectares), usually enclosed by vole-proof fence or isolated by natural barriers such as water (Ylönen *et al.* 1988, Ims 1987, 1989, Kawata 1989, Bujalska and Grüm 1994, Saitoh 1995, Ishibashi *et al.* 1998). In these studies dispersal was usually defined as a shift of home range within the studied plot; (though in few cases emigration outside the confined area was also included in the analysis – Ims 1987, Kawata 1989). The shifts within the plots imitate natural dispersal within homogeneous habitat of a local patch, without risks associated with crossing of non-habitable areas and choices between habitats of different quality.

The limitations to studies of dispersal on small enclosed plots vary between *Clethrionomys* and *Microtus*. In case of *Microtus*, patchy landscapes perceived in a coarse grained manner by voles (Wiens 1976) can be created even on quite small plots, by mowing strips of grass and thereby creating hostile matrix areas between habitat patches (Ims *et al.* 1993, Diffendorfer *et al.* 1995, Barrett *et al.* 1995). Female *Microtus* home ranges are typically small and may overlap extensively (Andreassen *et al.* 1998; Wolff *et al.* 1997). Therefore small patches of *Microtus* habitat may even harbour independent demographic units (Aars *et al.* 1999). On the other hand, in case of forest-dwellers such as the bank vole, where females require large, mutually exclusive home ranges (i.e. territories), experimental designs imitating coarse grained spatial heterogeneity require much larger areas.

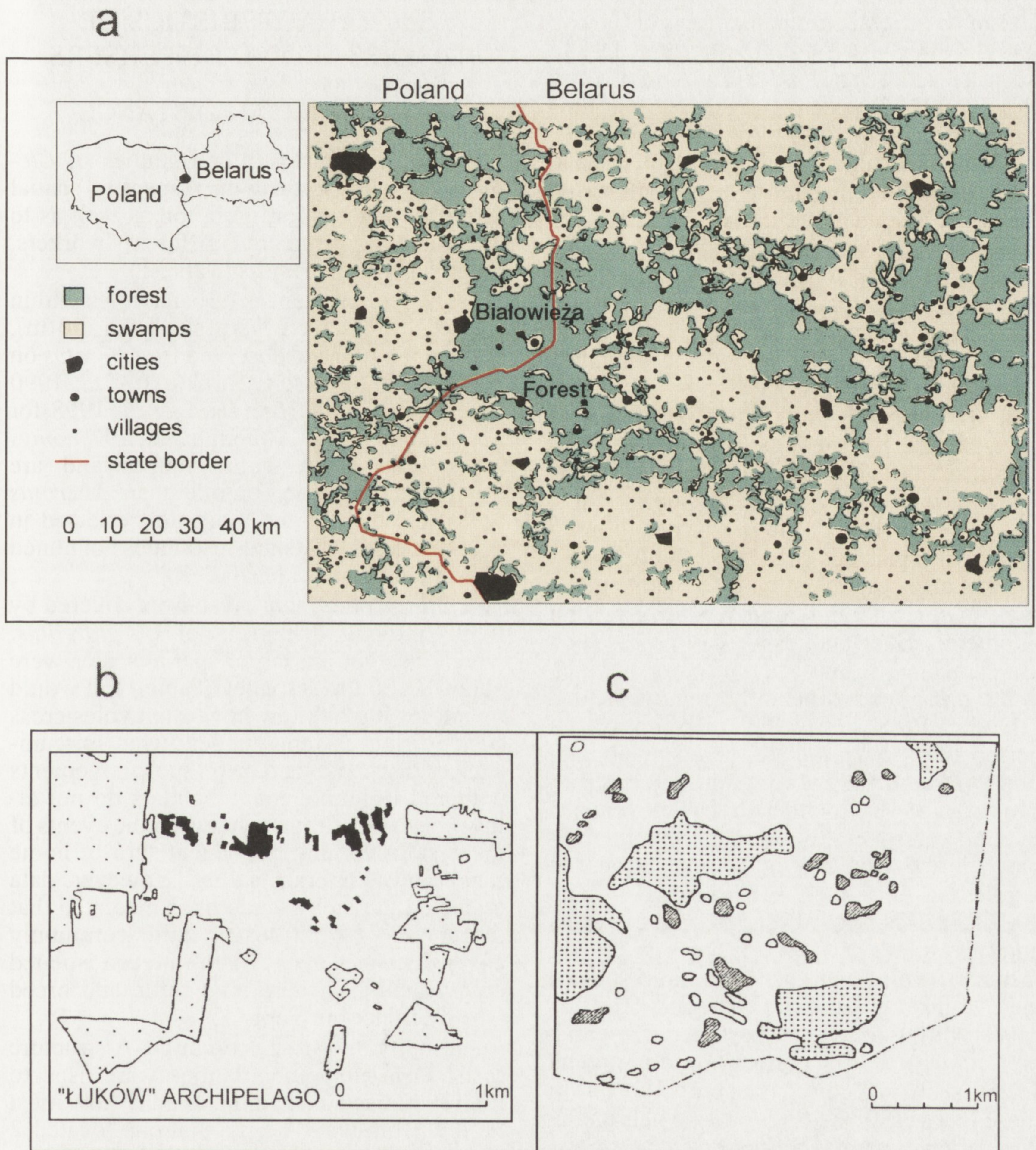


Fig. 1. Naturally continuous (a) and culturally fragmented (b, c) forest habitats of the bank vole (*Clethrionomys glareolus*). Continuity of habitats may affect quality of dispersers, dispersal distances, risks associated with dispersal, and flow of individuals which would be more balanced in continuous habitats and more of source-sink type in fragmented space.

a – Białowieża Forest as a part of extensive, continuous forests of Eastern Poland and Belarus (with permission of the authors: B. Jędrzejewska and W. Jędrzejewski); b – an example of recent forest fragmentation in agricultural landscape of eastern Poland; this archipelago of 22 forest islands (black) is composed of fragments with size range 0.04–15.4 ha (after Cieślak and Dombrowski 1993 – with permission); c – fragmented forests of north-eastern Poland as habitats for forest rodents: dotted – donor habitats; hatched – patches seasonally inhabited by breeding rodents; white – transient habitats, only temporally used by dispersers as short-term shelters (after Gliwicz 1990c – with permission)

To determine the effect of landscape on dispersal in *Clethrionomys*, several studies were conducted in which dispersal of bank

voles was studied in habitats consisting of patches of different quality separated by hostile transient areas ranging in distance from

500 m to several kilometers (e.g. Gliwicz 1989, 1990a, b, 1992, Demidov 1991, Szacki and Liro 1991, van Apeldoorn *et al.* 1992, Rajska-Jurgiel 1992, Kozakiewicz *et al.* 1993). At this spatial scale, individuals could disperse from their natal site while remaining in the same patch, and they were treated by the authors as patch residents. Only those voles that moved between patches, crossing transient areas and settling in a new habitat patch were regarded "true" dispersers. The characteristics of dispersers derived from such studies are somewhat different from those revealed on small spatial scale (see below); also potential effects of inter-patch dispersal on population dynamics are different than those of intra-patch dispersal (see Krebs 1992 for discussion).

The dispersal of the bank vole in relatively homogeneous space of continuous forest was also studied on an equivalent spatial scale of several hundred meters up to several kilometers. Such studies were often based on assessment of colonisation of plots in which voles were experimentally removed (e.g. Gliwicz 1988) or in which immigration occurred into unmanipulated resident populations (Mazurkiewicz and Rajska-Jurgiel 1998). In other studies movements of bank voles were followed along long trapping lines, with use of various kinds of marked bait (Andrzejewski and Babińska-Werka 1986, Andrzejewski and Owadowska 1994). In one case, movements of voles marked with radioisotopes were followed (Bolshakov and Bozhenov 1988). Finally, the most recent research on *C. glareolus* was performed on a regional spatial scale in a continuous boreal forest. In these Norwegian studies spatial synchrony in population dynamics was assessed over a distance of 250 km (Steen *et al.* 1996). Combined with studies applying mtDNA markers which allowed estimation of spatial genetic structure and to indirectly assess the gene flow (Stacy *et al.* 1997, Aars *et al.* 1998), the studies gave important evidence on the distance and rate of dispersal.

Summing up, the studies on dispersal of the bank vole have been conducted at a wide range of spatial scales, in landscapes with different types of spatial heterogeneity, and use of a variety of methods. However, experimental work employing habitat manipulations at the habitat mosaic scale, applied many times in studies of *Microtus* dispersal, has yet to be done on *Clethrionomys*.

### 3. CHARACTERISTICS OF DISPERSAL AND DISPERSERS

#### 3.1. DISPERSAL DISTANCE

The differences among studies of *Clethrionomys* dispersal with respect to spatial scale and habitat configuration as well as to the methods used by different workers, greatly affect the results (Table 1).

Dispersal distances of bank voles within enclosed areas were very short (ca. 50 m), and similar to those observed for *Microtus* on comparable plots (e.g. Sandell *et al.* 1990 for *M. agrestis*, Bjørnstad *et al.* 1998 for *M. oeconomus*). Although *Clethrionomys* voles hold larger home ranges and are thought to be more mobile than *Microtus* voles, these differences are not reflected in the dispersal distance estimates obtained from such small scale studies.

On the other hand, distances covered by freely moving dispersers of *C. glareolus*, when observed on larger spatial scales were about 10–20 times longer (Table 1). It would be interesting to know how often voles cross such distances and under what circumstances. The existing data on such movements gathered in homogenous habitats do not allow one to discriminate between the events of dispersal involving permanent shift of home range and temporary sallies. However, data collected in patchy landscapes indicated that dispersers of both sexes, quite commonly cover distances over 500 m to reach isolated empty habitats where they settle and breed (see references in Table 1).

Finally, the studies on mtDNA structure in *Clethrionomys* populations were used to infer that dispersal leading to gene flow must be quite limited. The populations located 2 km apart in a continuous linear habitat were equally different from each other as from more distant ones, indicating lack of exchange of female bank voles across such distance (Aars *et al.* 1998). In the same region the dispersal distance of females in two-dimensional habitat was inferred to be somewhat longer (Stacy *et al.* 1997). It was proposed that territorial defence of resident females may restrict female dispersal more in a one-dimensional (linear) than in a two-dimensional spatial setting. Anyhow, the very restricted mtDNA gene flow evident from both studies is surprising, when one knows that voles can cover distances of several hundred meters during one or few days (Table 1, see also Steen 1994 for evidence

Table 1. Dispersal distances of *Clethrionomys* voles, estimated in studies within different spatial scale

Spatial scale		Distance (m)	Type of the study and source
Small-scale dispersal		Mean shift of h.r. center	
<i>C. glareolus</i>	F	27–49	Small island; lower values in high density; M a z u r k i e w i c z, R a j s k a (1975).
	M	28–63	
<i>C. glareolus</i>	F	30–50	Small enclosure; Y l ö n e n <i>et al.</i> (1988).
<i>C. rufocanus</i>	F	48	Small island (some voles emigrated farther by swimming); I m s (1989).
	M	99	
<i>C. rufocanus</i>	F	35	Small enclosure; S a i t o h (1995).
	M	65	
Landscape-scale dispersal		Estimated movement* (m)	
<i>C. glareolus</i>		200–300	In continuous forest area; voles self-marked with characteristic bait; A n d r z e j e w s k i, B a b i ń s k a - W e r k a (1986).
<i>C. glareolus</i>		up to 300	In heterogeneous space; marked voles trapped in different patches; R a j s k a - J u r g i e l (1992).
<i>C. glareolus</i>		250–460	Radioisotope marking, lowest value for overwintered, highest for immature voles; B o l s h a k o v, B o z h e n o v (1988).
<i>C. glareolus</i>		> 500	In heterogenous space; min. distance between „source” and „recipient” patches; G l i w i c z (1989).
<i>C. glareolus</i>		up to 1000	In continuous forest; voles discriminating between friends and strangers by olfactory cues; O w a d o w s k a (1999).
<i>C. glareolus</i>		> 1000	In heterogeneous suburban landscape, voles self-marked with colour bait; S z a c k i, L i r o (1991).
Regional-scale dispersal		Indirect assessment (km)	
<i>C. glareolus</i>	F	< 2 km	In continuous linear forest habitat; assessed by difference in mtDNA found on sites 2 km apart; A a r s <i>et al.</i> (1998).
<i>C. glareolus</i>	F	up to 8.5 km	In continuous boreal forest; assessed as above; S t a c y <i>et al.</i> (1997).

\*In majority of cases studied in medium spatial scale, dispersal movements could not be distinguished from occasional sallies of residents.

from *Microtus*). However, mtDNA markers reflect only female dispersal whereas males may be more mobile than females. Thus it would be important to conduct new studies where nuclear genetic markers are used. It is

also possible that dispersal distances (and gene flow) are more restricted in continuous forest habitats than in fragmented habitats where dispersal of a “stepping stone” type is more likely.

### 3.2. MALE AND FEMALE NATAL DISPERSAL

Among mammals, natal dispersal is generally male-biased. According to a majority of evolutionary ecologists, natal dispersal in males evolved as a mechanism for inbreeding avoidance in species with philopatric females (Greenwood 1980, Pusey 1987, Clutton-Brock 1989, Pusey and Wolf 1996; see also discussion in Saitoh 1995, but see Sandell *et al.* 1991). Female philopatry is believed to be common in voles and maintained due to higher fitness of females when breeding on overlapping or adjacent home ranges with kin (Boonstra *et al.* 1987; Kawata 1990, Mappes *et al.* 1995).

In *Microtus* populations male biased dispersal evidently exists (see review in Cockburn 1988). Boonstra *et al.* (1987) found in four species of New World *Microtus* that twice as many males as females left natal sites before maturation. Among European species, similar bias was reported for *M. agrestis* of which 58% of males and only 23% of females dispersed from natal area (Sandell *et al.* 1990).

It is not certain, however, whether dispersal in the genus *Clethrionomys* is biased in the same way. The major difference between *Clethrionomys* and *Microtus* voles, which may generate differences in dispersal between those rodents is territoriality of female *Clethrionomys*. In most *Microtus* species young females mature and breed on home ranges overlapping those of their mother and older sisters (Boyce and Boyce 1988, Lambin and Krebs 1991a, b, Lambin 1994, Salvioni and Lidicker 1995, Bjørnstad *et al.* 1998, Pusenius *et al.* 1998). In contrast, in all *Clethrionomys* species young females must acquire exclusive home ranges before they become mature (Bujalska 1970, 1985). Thus, young female bank voles are likely to disperse from the natal sites in search of vacant areas. Therefore, it could be expected that dispersal in *Clethrionomys* is more sexually balanced than in *Microtus* (Bondrup-Nielsen and Karlsson 1985; Brandt 1992, Gliwicz 1992). However, data do not support these expectations. On the contrary, there is a growing body of evidence, mostly from research conducted in small enclosed populations that natal dispersal in *Clethrionomys* is also male biased. For *C. glareolus* this was reported over 20 year ago from an island population in Poland, where

80% of young males and only 49% of young females moved from the immediate neighbourhood of their natal sites, especially in years of low density. Males moved also farther than females (Mazurkiewicz and Rajska 1975). Similar data were gathered by Ylönen *et al.* (1988) in a small fenced population of the bank vole.

Experimental studies regarding sex-biased dispersal in *Clethrionomys* were conducted in *C. rufocanus*, both in Scandinavia and in Japan. In a population on a small island Ims (1988) found that at the time of sexual maturity all males left their natal sites while only one third of females did so. The same sex bias was found in young animals that apparently emigrated from the island. Moreover, Ims (1987, 1989) found that female dispersers exhibited more asocial behaviors than residents and he proposed that dispersal in females may be a masculine behavior, caused by overexposure of females to testosterone *in utero* (as dispersing females were born in male-biased litters). In another enclosure study of *C. rufocanus*, Saitoh (1995) found that at the time of maturation 50% of males and only 22% of females dispersed (moved farther than 2 home range diameters from their natal site); dispersing males settled on average about 30 m farther than females. A recent study of genetic structure of an enclosed population of *C. rufocanus* fully confirmed the prevailing dispersal behavior in young males, and philopatry in young females (Ishibashi *et al.* 1998).

To what extent were these results affected by confinement of the study populations and by the small spatial scale of the research? They need to be confirmed by detailed studies in larger, open habitats before we reject the possibility that what was really observed in enclosed small populations was rather a response of individuals to frustrated dispersal than the natural course of dispersal events. Theoretical speculations and empirical evidence from other territorial species allow one to argue as much for as against fitness benefits of natal dispersal *versus* philopatry in territorial females (Table 2).

On the other hand, we do not know how frequent is longer-distance natal dispersal in *Clethrionomys* voles, particularly females, outside the natal patch. From the fact that they are common seasonal inhabitants of small patches of fragmented forest, it can be deduced that such behavior is common especially in a fragmented setting.

Table 2. FOR and AGAINST natal dispersal in female *Clethrionomys* and other species with territorial females: speculations and empirical evidence

FOR	AGAINST
<p>Ready-to-mature young <i>Clethrionomys</i> females when unable to find vacant territory in a local population next to their natal site should emigrate rather than remain on a maternal home range as immature individuals. Natal dispersal may increase their individual fitness and inclusive fitness of kin females (Kawata 1987, Gliwicz 1993).</p>	<p>In the case of high spatial covariance between local and regional densities (Steen <i>et al.</i> 1996; Ims, Andreasen 1999) local crowding may be perceived as a signal of low probability of finding vacant space elsewhere, and will suppress rather than stimulate natal dispersal of females.</p>
<p>Fitness benefits of philopatry, through spatial association between breeding female kin, are less obvious in <i>Clethrionomys</i> than in <i>Microtus</i>, since the former live in exclusive breeding territories and do not share nests. This precludes many advantages potentially available to those rodent females which inhabit highly overlapping home ranges and may nest communally (see discussion by Lambin and Krebs 1991a).</p>	<p>There may still be an advantage of establishing spatially associated kin groups, because this will decrease the likelihood of intrusion of eventual infanticidal conspecifics (Wolff 1993).</p>
<p>Low relatedness coefficients among adult female neighbours were found in <i>Microtus pennsylvanicus</i> (Pugh and Tamarin 1990). This implies low philopatry/high natal dispersal in this vole species, known for female territoriality (Madison 1980).</p>	<p>Strong spatial kin structuring was found prevalent in another strongly territorial vertebrate – the red grouse, <i>Lagopus lagopus</i> (Matthiopoulos <i>et al.</i> 1998).</p>

In the study of between-patch movements in fragmented landscapes it was found that young bank voles (both males and females) born early in the breeding season dispersed in high proportion (78%) from a natal habitat and established breeding home ranges and territories in other patches, where 100% of immigrants acquired territories and reproduced. At the same time in a nearby enclosed (island) population only 37% of young females found vacant areas and matured locally. Thus, dispersal of spring born young was evidently due to emigration from growing population and judging from reproductive success of dispersers (Gliwicz 1990a), it was adaptive (presaturation or adaptive dispersal – *sensu* Stenseth and Lidicker 1992). In the same study, young born later in the season remained in the local habitat, where young females waited for local vacancy (due to death of another territo-

rial female) before they became mature (Gliwicz 1989).

### 3.3. BREEDING DISPERSAL

Breeding dispersal is defined as a shift of home range by adult breeding individuals (Greenwood 1980). Breeding dispersal in *Clethrionomys* females as in many other adult female mammals is considered to be low. Adult females of *C. gapperii* and *C. glareolus* once established on breeding territories were only rarely observed to disperse (Bondrup-Nielsen and Karlsson 1985). However, some evidence exists to suggest that adult female bank voles may disperse. Mazurkiewicz and Rajska-Jurgiel (1998) reported that as many as 34% of unmarked immigrants to trapping plots consisted of adult females of *C. glareolus*, many of which were lactating and some pregnant.

A strong theoretical argument that has been raised against breeding dispersal in microtines is that such behavior would act against preservation of spatial association among kin females (see discussion in Lambin 1997). However, in case of *Clethrionomys* fitness benefits of spatial association between kin females are not obvious (see Table 2). On the other hand, the most attractive argument for breeding dispersal in vole females is the so-called "territory bequeathal hypothesis". This hypothesis states that mother may move to a new home range between consecutive litters, leaving previous breeding range to her daughters, as a form of parental investment. Such behavior was repeatedly reported for voles, e.g. for *M. agrestis* by Myllymäki (1977), for several New World *Microtus* species by Jannett (1980, see also Lidicker 1985 for review). There is also a report of this occurring in *C. glareolus* (Kikkawa 1964). Unfortunately, the evidence provided in support of this hypothesis was usually weak (see review in Lambin 1997). Recent studies, some of which used radiotracking techniques, did not support earlier findings and showed that the territory bequeathal was not a common cause of breeding dispersal (eg. Sandell *et al.* 1991 for *M. agrestis*, Lambin 1997 for *M. townsendii*).

Breeding dispersal may be affected to some extent by habitat quality. For bank voles inhabiting heterogenous space, the length of residency of mature females in optimal patches was significantly greater than in suboptimal patches (Gliwicz 1989). In suboptimal patches over 60% of mature females stayed no longer than 6 weeks, which is about the period necessary for gestation and weaning of one litter. In this particular study it was not possible to estimate how many of them died *in situ*, and how many dispersed in search of better habitats. It is, however, probable that intensity of breeding dispersal depends on habitat quality, and that females which once changed habitat as natal dispersers, may be more prone to do so again. Higher dispersal of adult bank voles in low quality habitats was also reported by Lukyanov and Lukyanova (1996).

Mature males are relatively mobile and might be expected to move over large areas to increase their probability of encountering receptive females, especially when female oestrus is asynchronous (Ims 1988). However, breeding dispersal of males does not seem to be common and perhaps only marginally more

frequent than that of adult females. Data on breeding dispersal of adult males have been collected by radio-tracking for several species of *Microtus*. In *M. pennsylvanicus* only 3 out of 56 adult males dispersed (McShea and Madison 1992), in *M. oeconomus* – 5 out of 23 radiotracked males (none of 22 females) (Steen 1994), and in *M. agrestis* neither males nor females dispersed (Sandell *et al.* 1991). These findings indicate that fitness benefits of adult males might be greater if males remain in residence than if they disperse. This could be due to two factors. First, access to receptive females in a local population depends on rank in a social hierarchy among local males, and immigrants in vole populations have lowest ranks in a social hierarchy (Gliwicz and Rajska-Jurgiel 1983, Kawata 1988) therefore dispersing males are less likely to gain access to attractive females. Secondly, dispersing adult males suffer higher mortality than residents (Steen 1994). In an experimental study, Kawata (1989) found that in *C. rufocanus*, mature males most often dispersed from the study plot when they failed in male-to-male competition for estrous female. The dispersing males were usually smaller than successful male residents. All these findings indicate that breeding dispersal in adult males might sometimes be non-adaptive.

#### 4. CONCLUDING REMARKS AND PERSPECTIVES

1. During the last decade, few studies have directly examined dispersal in *Clethrionomys glareolus*. Therefore, relatively few facts have emerged since the completion of earlier reviews (eg. Bondrup-Nielsen and Karlsson 1985, Stenseth and Lidicker 1992). This could be partly caused by a switch in interest of rodent ecologists, particularly those who share geographical range with *C. glareolus*. Earlier, the opinion prevailed that dispersal is a phenomenon of great importance to population dynamics, either as a factor stabilizing or – on the contrary – destabilizing it and producing multiannual cycles (see Stenseth and Lidicker 1992 for discussion). Now, microtine cycles are viewed more often as community processes (Hansson and Henttonen 1988) than population processes, and therefore the focus has been changed from dispersal to prey-predator studies. However, we predict that interest in dispersal in *Clethrionomys* will soon be re-



newed. Recently, a new twist has developed in population and community ecology where spatial-temporal dynamics is in focus (Bjørnstad *et al.* 1999). In this context dispersal is the key process, and we believe that rodent species, including *Clethrionomys*, may serve as empirical models, both in experimental and observational study settings.

2. In the late 1980's and in the 1990's the majority of good data on *Clethrionomys* dispersal were obtained from small confined populations, usually of *C. rufocanus*. This small-scale research focused mainly on behavioral aspects, spatial relations between related and unrelated individuals, and the genetic structure of local populations. At the same time, research at a larger scale in patchy landscapes and in continuous habitat was conducted. Here dispersal between patches and long-distance movements in continuous forest was recorded with less precise methods. These larger-scale studies focused on population dynamics consequences of dispersal. There are some conflicting results obtained from the two spatial scales with respect to rate of dispersal and what characterises animals leaving their natal sites. Whether this is only due to different methods or whether it reflects real biological differences between short-distance and long-distance dispersal/dispersers has to be resolved in future studies.

3. Recently, studies on gene flow in bank vole populations over regional scales in northern boreal forest revealed that dispersal of females over long time periods (many generations) is very limited and presumably has little effect on spatial demographic synchrony observed in boreal populations at a regional scale. This view may change when similar studies are conducted in the more fragmented temperate forest landscapes farther south in Europe, where bank vole populations may show less spatial synchrony and longer dispersal distances.

4. New tools applied in dispersal studies will be important in unraveling the causes and consequences of dispersal. Genetical markers are obviously one set of tools that will yield new insight. Moreover, the application of new statistical methods for estimating emigration/immigration rates from/to local populations based on catch-mark-recatch data (see Ims and Yoccoz 1997 for a review) will give better estimates of quantitative aspects of dispersal and its effects on local demography. Finally, studies on dispersing animals, for example with the aid of

radio-telemetric techniques (e.g. Steen 1994, Larsen and Boutin 1994), will give more direct information about the fates of dispersers. Such information is necessary for evaluating hypotheses on the adaptiveness of dispersal in bank voles and other small rodent species.

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