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An evaluation of the effects of space use and habitat patterns on dispersal in small mammals

Søren Bondrup-Nielsen

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This paper discusses how space use (home range size, home range dispersion and spacing behaviour) of small mammal populations and the habitat patterns within which they find themselves affect dispersal. Home range is defined as a tight cluster of an animal's life time track over a period of time: natal, breeding and non-breeding home ranges are considered. Mainly two patterns of home range dispersion are considered: female "territoriality" with much overlap among males (e.g., *Clethrionomys*) and male "territoriality" with much overlap among females (e.g, some *Microtus*). Habitat types are defined as areas on which animals perform equally well demographically. Habitat patch size is measured in terms of dispersal distance of the species. Dispersal is defined as movement in a random direction by an individual out of one home range for the purpose of establishing a new home range. Dispersal is affected by space use, and by habitat quality and configuration. If animals are territorial, then when there is no more space available in a patch, subadults if they wish to breed must necessarily disperse. If animals are not territorial, dispersal should respond in a more gradual density-dependent manner. It is argued that inbreeding depression and instability of habitat patches could cause the evolution of dispersal. However, for territorial species, dispersal may mainly be a consequence of spacing behaviour. It is cautioned against using "removal grids" for quantifying, and especially for identifying dispersers. Appropriate grid size should be used and correction for edge effect in live trapping studies should, in general, be made. In future studies of dispersal particular attention should be given to habitat configuration and quality. A new method for marking infant voles is presented, the application of which may advance our understanding of dispersal in a population dynamical context.

Søren Bondrup-Nielsen, Department of Biology, Division of Zoology, University of Oslo, P.O.Box 1050, Blindern, N-0316 Oslo 3, Norway.

1. Introduction

The importance of dispersal in demography of microtine rodents is widely recognized and it is becoming increasingly obvious that a thorough understanding of dispersal is needed if we are to understand population processes (Gadgil 1971, Krebs et al. 1973, Bekoff 1977, Gaines & McClenaghan 1980, Stenseth 1983, Vance 1984). In the litterature on small mammals, there is far more speculation than there are actual data on dispersal (for recent reviews, see Gaines & McClenaghan 1980, Stenseth 1983). The paucity of data stems mainly from the fact that dispersal is difficult to study, and consequently theoretical speculations can flourish.

Dispersal is critical in hypotheses of population density cycles (whether cycles are a result of changes in genotype frequency (Chitty hypothesis; Chitty 1967, Krebs 1978) or a result of changes in phenotype frequency (Charnov-Finerty hypothesis; Charnov & Finerty 1980)) and in hypotheses of population density stability (e.g., Lomnicki 1978, 1980). Models incorporating dispersal in discrete habitat patches of identical quality (Vance 1984) and dispersal in heterogeneous habitat (Stenseth 1980, 1983) have also been constructed: both population cycles as well as stability may result. Therefore, dispersal is not a simple parameter.

The consequences of dispersal will depend on which animals disperse and where they disperse to. For example, if so called surplus individuals in a population are forced to disperse, then according to Stenseth (1983) this would be non-adaptive dispersal and although it would serve to reduce population size, there would be no evolutionary consequences. However, if a particular genotype disperses, then this would be adaptive dispersal (Stenseth 1983) and there could be rapid alteration in gene frequency. How animals use space and the habitat configuration of the area occupied by a particular population may furthermore have important effects on dispersal.

In studying dispersal we must try to separate the evolutionary driving force from the consequences of dispersal. Any behaviour will have evolved due to a particular selective pressure; however, at the same time there will also be certain ecological consequences of that behaviour. A case in point is territoriality: Wynne-Edwards (1962) once argued that territoriality evolved by group selection as a population regulating mechanism. However, territoriality is now accepted as having evolved to ensure an adequate resource supply for the territory owner whereas the limitation to the number of territory owners is only a consequence (Wiens 1966, Wilson 1975).

In this paper I will show how space use of small mammal populations and the habitat pattern within which these populations find themselves may place certain constraints on the evolution and consequences of dispersal behaviour. Although the framework I construct will apply to microtines in general, it will mainly refer to *Clethrionomys*. Part of this review will also be a critical evaluation of the methodology used for the study of dispersal; an alternative method for studying dispersal will be presented.

2. Space use

Dispersal of animals is affected by how they use space. In this section I will therefore discuss 1) the home range (what it is, how we measure it, and how home ranges are spaced) and 2) spacing behaviour (the behaviour of home range owners toward other individuals both between and within different age and sex groups).

2.1. Home range

Myllymäki (1977) pointed out that the traditional concept of a life long home range (Burt 1943) is unrealistic for microtines.

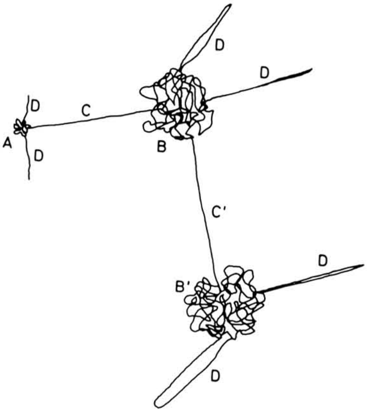

Fig. 1. A speculative model of the life time track of an individual (Baker 1978, 1982) showing natal home range, breeding home ranges, dispersal and occasional sallies. A — natal home range, B — first breeding home range, B' — second breeding home range, C — first dispersal movement, C' — second dispersal movement , D — occasional sallies.

Microtus agrestis, for example, may shift home range and wander extensively (Hansson 1977, Myllymäki 1977) thus producing a life time track (Baker 1978, 1982) that is rather scattered. I will consider the home range as a discrete area traversed by an animal during its daily activity excluding occasional sallies outside this area, such that a tight network of its tracks is evident over a period of time (Fig. 1).

The *natal home range* is the area the animal becomes familiar with while associated with the nest where it was born. A *breeding home range* is a home range on which the animal is sexually mature and breeds, while a *non-breeding home range* is a home range occupied by a subadult (an animal of reproductive age but not yet reproducing, Myllymäki 1977) or occupied by an animal during the non-reproductive season in winter. These three home range types may of course share the same home range center (HRC, Hayne 1949).

In a study of *Clethrionomys gapperi* Bondrup-Nielsen (1984) found that all trap stations within the home range (determined by the exclusive boundary strip method, Stickel 1954) of sexually mature females were visited in deciduous habitat (optimal), whereas in coniferous habitat (suboptimal) all trap stations were not visited. This suggests that females in optimal habitat use more of the space available within their home range than they do in suboptimal habitat. Sexually mature males did not visit all trap stations within their home ranges regardless of habitat.

The number of trap sites within the true home range of an animal will greatly affect the home range we deduce. If the trap site density is too low or too high, the pattern and size of home range may be very inaccurate. For example, if the density of traps within the home range of an animal is very high, animals may not be able to express their true home range size as they may continually intercept traps and get caught. Optimal trap spacing for this purpose has been dealt with by Nikitina (1965). However, no single trap spacing seems adequate for all sex and age groups of a population.

Many methods exist for estimating home range sizes (Hayne 1949, Stickel 1954, Harvey & Barbour 1965, Jenrich & Turner 1969, Mazurkiewicz 1971, Wierzboraska 1972, Metzgar & Sheldon 1974, Ford & Krumme 1979). These are all indices of home range size and the calculation of these indices, when based on live trapping result, will be affected by the edge effect (see Bondrup-Nielsen 1983 and references therein). The smaller the trapping grid in relation to true home range size the greater the proportion of animals around the edge and the smaller the estimated index of home range size. For example, Perrin (1979) estimated home range size for overwintered female *C. gapperi* on an 1.89 ha grid to be 429.2 m^2. However, in his fig. 11 he shows the distribution of home ranges and only two out of six are completely contained within the grid. The four home ranges around the edge of the grid average 280.6 m^2 while the two within the grid average 725.0 m^2. In order to increase the accuracy of home range size estimates, sufficiently large grids should therefore be employed such that there is a large sample size of home ranges contained totally within the grid boundary.

For some species home ranges are mutually exclusive (territories) while for others they overlap. In squirrels *Tamiasciurus* both mature males and females are territorial inter- and intra-sexually (Smith 1968). In *Microtus agrestis* there is little overlap among the home ranges of males while there is much overlap among the females (Myllymäki 1977). This same pattern exists for *M. xanthognatus* (Wolff 1980) and for *M. californicus* at high density (Lidicker 1980). In *Clethrionomys* species (Bondrup-Nielsen & Karlsson 1985) the reverse trend is found. Mature females have mutually exclusive home ranges while there is much overlap among mature males. This same pattern is found for *M. pennsylvanicus* (Madison 1980).

Why might this reversal in home range use exist between *Clethrionomys* and some *Microtus*? Mature female *Clethrionomys* have much larger home ranges than mature female *Microtus* (Bondrup-Nielsen & Karlsson 1985). Furthermore, many *Microtus* species tend to live in their food resource, grassy meadows, where the food resource is abundant and continually replenished. It is therefore conceivable that the evolutionary force for territoriality does not exist for females as the threshold level of food abundance for territorial defence may be exceeded (Wilcox & Ruckdeschel 1982). However, if the distribution of females is slightly clumped males may be able to defend groups of females thus explaining why males tend to be territorial. *Clethrionomys* on the other hand live in forests where their food is scattered or patchy and probably not as easily replenished as it consists to a large degree of forbs, berries and seeds (Hansson 1985). Mature females must therefore be territorial to ensure an adequate food supply for themselves and their offspring. This will cause a more even distribution of females which may not be as readily defended by males (see Davies & Houston 1978) resulting in large home ranges of males with much overlap among them to ensure optimal mating. The skomer vole *Clethrionomys glareolus skomerensis* has evolved to subsist on bracken, stands of which cover much of Skomer Island (Fullagar et al. 1963). Here the voles live in their food supply much as *Microtus*: it is therefore interesting to notice that apparently mature females have small overlapping home ranges while mature males tend towards territoriality (Gipps & Healing pers.comm.).

Home range size in small mammals has often been considered to decrease with increased density (Forsyth & Smith 1973, Maza et al. 1973, O'Farrell et al. 1975). However, this relationship, on closer inspection, appears not to be the case. Rather there appears to be an inverse relationship between food quantity and quality and home range size (Mace et al.

1983). Smith (1968) found a close correlation between the annual cone crop and territory size in the squirrel (*Tamiasciurus*). Mares et al. 1982 found that when food was added to a study plot, the mean home range size of *Tamias striatus* decreased in size. Bondrup-Nielsen & Karlsson (1985) have reviewed dispersal and space use in *Clethrionomys* and found such an inverse relationship between food quantity and home range size for this genus.

The amount of overlap among home ranges on the other hand may often increase with density (Metzgar & Hill 1971, Myllymäki 1977, Van Horne 1981). Increased overlap among mature females, however, does not appear to be the case in *Clethrionomys* (Bondrup-Nielsen & Karlsson 1985). It therefore seems that home range size is probably closely linked to food quantity and quality while home range overlap may be a function of density to varying degree for different species and populations.

How the degree of home range overlap of a particular population may affect dispersal rates will be developed in Section 4.2.

2.2. Spacing behaviour

If animals have mutually exclusive home ranges and home range size does not decrease with increase density then it follows logically that some form of spacing behaviour must be operating. Then, when all space is occupied by individuals these territorial individuals will prevent others from settling. Spacing behaviour appears to be a common phenomenon among passerine birds (Klomp 1972), and Krebs (1979) and Tamarin (1983) suggest that it is also prevalent among microtines. Bujalska (1973), Saitoh (1981) and Bondrup-Nielsen (1984) have demonstrated that spacing behaviour operates among female *C. glareolus*, *C. rufocanus* and *C. gapperi* respectively.

3. Habitat

The term habitat is used rather loosely in the ecological literature: habitat may refer to a botanically distinct segment of a geographical area or to the type of areas occupied by a particular species of animal or plant (see Carpenter 1962:125). I would like to make a distinction and treat what I will term vegetation and habitat types as two separate entities.

It is relatively easy to classify vegetation types by measuring various botanic variables. However, what this classification means to a particular population of animals we do not know. Although such a classification is necessary, so that we can recognize the different vegetation types, superimposed on this must be a classification based on functions of individuals within a population. These functions include such variables as survival, litter size, weaning success, growth rate, maturation rate, home range size etc. of the population. With such a classification, the habitat types of an animal become areas on which animals perform equally well demographically. These habitat types will then be subsets of the vegetation types defined by the botanic variables. On the basis of demographic performance and assuming all else being equal, habitat types of a population can then be ranked from high to low quality.

The size of a patch (of a particular habitat type) and configuration of patches are important as these may affect the possibility for dispersal. The size of a patch must be determined either in units of mean home range size, that is, the number of home ranges a patch will contain, or better, in units of mean dispersal area of the population. I am assuming that a population of a particular species will have a normal distribution for dispersal distance such that there exists a dispersal area outside of which dispersers will rarely reach. If patches are smaller than the mean dispersal distance of a population, patches of different habitat types are available to dispersing individuals: such an area we may think of as heterogeneous (Fig. 2I and II; terminology after Hansson 1977). If a patch is larger than the mean dispersal distance of a population then individuals in the central area of this patch cannot disperse outside the patch in search of space on which to settle and breed (Fig. 2III). For this group of individuals the area can be considered homogeneous.

Different patches may be contiguous such as depicted in Fig. 2I which is probably a fair representation of the characteristic forest habitat patch structure of *Clethrionomys* (see Bondrup-Nielsen 1984). Alternatively, habitat patches of high and medium quality may be located in a larger area of low quality habitat patch; this is probably a fair representation of the situation for many *Microtus* species (Hansson 1977).

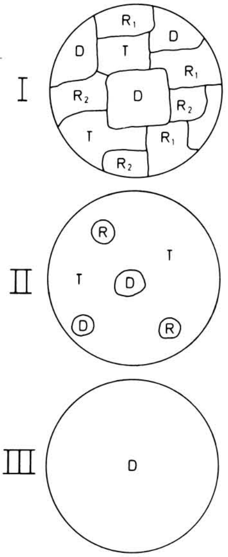

Fig. 2. Examples of habitat configuration within dispersal area for a population. I — heterogeneous area consisting of contiguous patches. II — heterogeneous area consisting of isolated patches in transition habitat. III — homogeneous area. D — donor habitat, R_1 — reception habitat (moderate quality), R_2 — reception habitat (low quality, T — transition habitat.

Hansson (1977) and Anderson (1980) have considered dispersal in heterogeneous landscapes. Hansson (1977) depicts a typical rodent habitat to consist of isolated patches of donor and reception habitat in a larger area of transition habitat (see Fig. 2II): this pattern seems typical for many *Microtus* species, but not for *Clethrionomys* species. Although no habitat type starts out being donor habitats, high quality habitat patches become donor habitat and voles then disperse through transition habitat in search of reception habitat. As density increases in reception habitat, some reception habitats may become induced donor habitats (Hansson 1977). Reception habitats then serves a dispersal sinks (Lidicker 1975) until they become induced donor habitats.

Anderson (1980) has developed what he terms the "fried egg" model of habitat quality with survival, colonization, traversable and barrier habitats. Barrier habitats are simply habitats that voles cannot physically cross such as mountain ranges or oceans. Traversable habitat occurs as a "sea" of habitat of the kind Hansson (1977) called transition habitat: these can be crossed by dispersing voles but no breeding can take place there. Survival habitat is similar to donor habitat. However, Anderson seems to imply that colonization habitat is of low quality; it serves as a sink and vole populations often experience extinction after two or three generations. It therefore seems mainly to serve as a graveyard although Anderson does state that traversable habitat "serves as a sink for emigrants from either survival or colonization habitat". I believe that Hansson's (1977) view is slightly more realistic although it seems specific for *Microtus* species.

4. How does space use and habitat structure affect dispersal?

4.1. Dispersal

Lidicker (1975) defines dispersal as movement of individual organisms or their propagules off their home range sometimes to establish themselves on another home range. The word "sometimes" infers that settlement on a new home range is a rare event. Endler (1977) on the other hand defines dispersal merely as a short non-directional movement away from a home site. But what does "short" mean? I will define dispersal as movement in a random direction by an individual out of one home range for the purpose of establishment on a new home range (Fig. 1). For *Clethrionomys*, dispersal mainly applies to young animals leaving their natal home range in search of a breeding home range. However, mature animals on breeding home ranges may also disperse and this may indeed occur regularly in some species (e.g. *M. agrestis*, Hansson 1977, Myllymäki 1977; *Arvicola terrestris*, Stoddart 1970).

Animals may leave their home range for short periods of time (Crawley 1969, Viitala 1977). These movements I will refer to as occasional sallies (Fig. 1). If these movements have evolved for the purpose of finding suitable space on which to settle, then they must also be defined as dispersal. That is, dispersal may take the form of occasional sallies. Not all occasional sallies are dispersal, however. In *C. rufocanus*, mature females will leave their home range on what are called oestrus runs for the purpose of mating (Viitala 1977).

4.2. Dispersal in relation to home range size and habitat patch size

If individuals have mutually exclusive home ranges of constant size and with a constant proportion of overlap among home ranges (Fig. 3A), then within any patch the number of home ranges will equal the actual patch size divided by the mean home range size. When the patch becomes filled with home range owners (breeding, Fig. 3B) then young born on the patch attempting to acquire breeding home ranges have two choices. Remain as non-reproductive floaters (Brown 1969) in the patch and wait for a home range owner to die and compete for that home range with other floaters, or disperse in search of available space elsewhere. This scheme applies to many passerines (Brown 1969, Klomp 1972). This may also apply to female *Clethrionomys* (Bondrup-Nielsen & Karlsson 1985). With home range characteristics as depicted in Fig. 3A resulting in a limit to the number of home range owners (Fig. 3B) it is difficult to infer any crowding of mature individuals on breeding home ranges such as implied by the Chitty theory (Chitty 1967, Krebs 1978) or the social subordination theory (Christian 1970). An area may, however, become crowded by floaters and this causes density-dependent dispersal among them. That is, the rate of dispersal may increase with increase density of floaters as seems to be the case in many microtines (Gaines & McClenaghan 1980, Stenseth 1983).

Home range size may also respond as an elastic disc (Wilson 1975) (Fig. 3C); that is, home range size decreases slightly with increase density, or there may be a slight increase in degree of overlap with increase density. There is still a limit to the number of breeding home ranges within a patch; this limit is reached gradually (Fig. 3D).

A different situation occurs if home range size decreases or overlap increases with increase density (Fig. 3e). Here the number of individuals on breeding home ranges will continue to increase (Fig. 3f). Crowding among mature individuals will result and it is conceivable that animals on breeding home ranges may eventually disperse. Sexually mature *Microtus* females may be a case in point here. Although home range size does not appear to be a function of density, degree of overlap does (Myllymäki 1977).

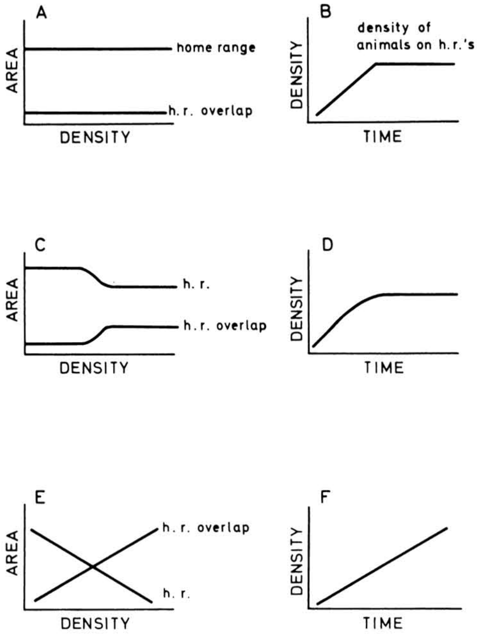

Fig. 3. Theoretical relationship between home range (h.r.) size and degree of home range overlap with density of home range owners.

So there appears to be two different strategies. If home range size is constant or nearly so, mature animals on breeding home ranges will not become crowded, but floaters, if they exist, may, and dispersal among these individuals may be density dependent. This situation may apply to *Clethrionomys*. On the other hand, if home range size decreases or overlap increases with increase density, mature animals on breeding home ranges will become crowded and dispersal among these may be density dependent. This may apply at least to some *Microtus* species.

4.3. Dispersal in relation to habitat patch configuration

Let me now consider habitat patch configuration and dispersal. I will analyze this in relation to *Clethrionomys* species. That is, I will assume that breeding home range size of females is constant and depends on habitat patch quality and there is little overlap among home ranges.

If a habitat patch is much larger than the mean dispersal area of a population then a part of the population will not be able to disperse to another habitat patch. That is, when the limit to the number of breeding home ranges is reached, young animals cannot increase their fitness by dispersing as there is no space available to them within a reachable distance. A mature animal that allows its offspring to remain on its breeding home range, as long as they remain sexually immature, will potentially have higher fitness: young should survive better on their natal home range than if they moved off and may eventually acquire their parents breeding home range or home range of adjacent individuals as they die.

If the space available is heterogeneous but the difference in quality between habitat types are only slight, then all patches may still become saturated with occupied breeding home ranges, especially if overall habitat quality is high. The effect is then the same as in the example above where available space was homogeneous. Again young cannot increase their fitness by dispersing as there is no available space within the dispersal area. It therefore follows that the importance to a disperser is whether space is available or not. Once all space for breeding home ranges is occupied, overall density should reach dramatic levels as there is a build-up of immature individuals. Such a similar build-up of immature animals may be what characterizes the peak density in cyclic populations of microtines (Bondrup-Nielsen & Ims in prep.).

An altogether different situation occurs if patches of habitat of very low quality are interspersed among suitable patches of high quality. Here low quality patches may not fill up with breeding home range owners. There is always somewhere for individuals to disperse and density remains constant at least within habitats of higher quality. One factor that may maintain low density of voles in low quality habitat patches may be generalist predators as suggested by Erlinge et al. (1983).

4.4. Dispersal in relation to instability of habitat patches

Not all patches are stable: their quality may change from high to low or vice versa. This Southwood (1977) refers to as temporal heterogeneity. Stable habitats are predictable as they have a low variance of favourability, whereas unstable habitats are unpredictable having a great variance of favourability (Southwood 1977). However, these measures are all relative and will depend on both the generation time and life expectancy of the individuals in a population. Species with short generation time will tend to track variations in the environment whereas species with long generation times will be more stable (Southwood 1977).

How does this apply to dispersal and population dynamics of microtines? In *Microtus agrestis* females often disperse between litters (Hansson 1977, Myllymäki 1977). The meadows, in which they live, tend to be unstable, often flooding in spring after snow melt or after heavy rains or drying up during draught. Furthermore, meadows may periodically be grazed by domestic animals or are mowed for hay production. All these potential changes in the quality of the meadow habitat for *Microtus* occur on a time scale shorter than the life expectancy of the individuals and it may indeed be advantageous for females to disperse between litters. *Clethrionomys*, on the other hand, live in comparatively stable habitats. Forests habitats tend to be more predictable and the changes in quality, apart from the increase in amount of food from spring to fall, occur on a time scale much longer than the life expectancy of voles. As one would predict, female *Clethrionomys* do not disperse between litters (Bondrup-Nielsen & Karlsson 1985).

5. Evolution of dispersal

Many authors have stressed the increased risk of predation during dispersal (e.g., Tamarin 1980, Stenseth 1983). However, dispersal behaviour would not have evolved if the fitness of an individuals was not higher by dispersing than by staying at "home".

In studying the evolution of dispersal we must be careful not to interpret situations where dispersal is a consequence of some other evolved behaviour with situations that could cause the evolution of dispersal. For example, in *Clethrionomys* it appears that a female needs a certain amount of space for her exclusive use in order to breed. Clearly then, once all space in a habitat patch is occupied, a subadult female wishing to breed must disperse to another patch with available space. Here dispersal is a consequence of spacing behaviour. In microtines dispersal increases with increase rate of population growth but during the peak and decline phase in population cycles, dispersal nearly stops (Stenseth 1983). This as well may be taken as evidence that dispersal behaviour is a consequence rather than an evolved trait.

The advantage of outbreeding may be one selective pressure that would select for dispersal behaviour. Bengtsson (1978) has developed a simple model for outbreeding and he shows how important dispersal may be for achieving this.

In the case of *Clethrionomys* where the home ranges of several males overlap with each female (Bondrup-Nielsen & Karlsson 1985) the probability of a female mating with a close relative may not be all that great even if a female settles close to her mother. However, the situation in *Microtus* may be quite different: In *M. agrestis* males have home ranges with little overlap among each other, but each male overlaps the home ranges of several females. Therefore, if a daughter settles close to the mother, the probability that she will mate with her father is very high. If inbreeding in *M. agrestis* is deleterious (see, e.g., Wright 1977), then it is quite conceivable that dispersal of females will have evolved to ensure outbreeding.

Another factor that may select for dispersal is the stability of habitat patches. If patches are unstable, animals that disperse between litters in search for patches of high quality will be selected for (see Section 4.4.).

6. Critique on studies of dispersal

Theoretical considerations of dispersal have generally dealt with dispersal between habitat patches (Gaines & McClenaghan 1980, Stenseth 1983). However, empirical studies of dispersal have tended to deal with dispersal within habitats (removal grids next to control grids) and then equated the results to dispersal between habitats (see, for example, Kozakiewicz 1976, Krebs et al. 1976, Tamarin 1977, Fairbairn 1978, Krebs et al. 1978). These empirical studies have generally found that a high proportion of dispersers are mature individuals. Tamarin (1977) found over 50% of the dispersers to be mature in (a typical) dispersal study on *M. pennsylvanicus* employing a removal grid next to a control grid on a isolated meadow. However, in a similar study run over 4 years, employing an enclosure, Tamarin et al. (1984) caught only 98 individuals, only 12% mature, in a forested section, assumed to be a dispersal sink.

Kozakiewicz (1976) found a high dispersal rate among mature *C. glareolus* from 86% in males to 55% in females. However, Watts (1970) found the dispersal rate among mature *C. glareolus* to be very low from 6% in males to 2% in females. Bondrup-Nielsen (1984) likewise found a low dispersal rate among mature *C. gapperi*. Kozakiewicz (1976) employed a removal grid for his study while Watts (1970) and Bondrup-Nielsen (1984) analyzed settlement onto areas from which individuals were not removed. A high dispersal rate among mature individuals may therefore under natural conditions not be all that common.

It is appropriate to stress here the importance of correcting for edge effect so that resuls between studies can be compared (see Bondrup-Nielsen 1983). For example, Beacham, (1981) in a study of dispersal in *Microtus townsendii* employing enclosures, found that when a dispersal sink was incorporated within an enclosure, the density of animals in the enclosure was approximately the same as on an unenclosed control grid. However, he did not correct for edge effect: when this is done, assuming conservatively that the density was overestimated by 1.5 (see Bondrup-Nielsen 1983) on the control grid, the density within the enclosure was almost twice that of the control grid. Clearly the dispersal sink was not as "effective" as stated by Beacham (1981).

7. Future research

The study of dispersal is difficult, especially in small rodents. There are methodological difficulties in identifying dispersers and in quantifying dispersal rates — the two most critical parameters in models of dispersal (Gaines & McClenaghan 1980, Stenseth 1983).

As seen, habitat quality, configuration, and stability are of considerable importance as they may greatly affect dispersal. In studies on dispersal, therefore, the habitat types and patch sizes of the habitat complex available to a population must be considered. Furthermore, researchers should study their populations in low quality habitat as well as in optimal habitats. Only few have done this (Batzli 1974, Van Horne 1981, Bondrup-Nielsen 1984).

I would advise abandoning the use of removal plots as a method for identifying dispersers. An alternative method would be to map the movement of marked individuals. During the summer of 1983 I have developed and tested a field technique (unpubl.) for marking infant voles. I regularly censused *C. gapperi* on a 4 ha plot. Pregnant females close to giving birth were brought into captivity, the average duration of which was 3.7 days. After parturition the young were marked by toeclipping. Mother and young were subsequently released in a nest box at the original site of capture of the mother. No female when released abandoned her original home range and percentage recapture of marked young was high decreasing from 60% in early summer to 30% in late summer. With this technique important data on dispersal distance and habitat occupancy of dispersers could be acquired and compared to habitat complex and population characteristics.

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