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The role of habitat heterogeneity and female spacing behaviour in density regulation of *Clethrionomys gapperi*

by

Soren Bondrup-Nielsen

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled The role of habitat heterogeneity and female spacing behaviour in density regulation of *Clethrionomys gapperi* submitted by Soren Bondrup-Nielsen in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

Supervisor

External Examiner

Date 20 Jan 1984

Abstract

The social factor hypothesis states that populations in heterogeneous environments and composed of individuals that use space more or less exclusively should experience relative stability of density. Environment is defined as heterogeneous if patches of several vegetation types are available within the dispersal range of individuals. The study area met this criterion.

A live-trapping study of *Clethrionomys gapperi* was conducted near Lesser Slave Lake, Alberta to examine the conditions or premises of this hypothesis. The demographic performance of voles on different 4-ha live-trapping grids of different vegetation types was used for ranking the grids from high to low performance in this study. Two grids were dominated by deciduous trees and two were dominated by coniferous trees.

Voles on deciduous, deciduous/coniferous and coniferous grids differed in spring and late summer density, persistence, ratio of immature to total recruits, transiency and home range size. There was no difference in litter size of voles between vegetation types.

Spacing behavior of *Clethrionomys gapperi* was determined by three different methods: live-trapping on grids, removal experiments and by manipulation of density of mature individuals within enclosures. Home ranges of female *Clethrionomys gapperi* were more or less exclusive and home range size was larger in coniferous vegetation type than deciduous vegetation type.

Mature females, once settled on a home range, appeared to show only minor shifts and did not disperse even at high density. In 1982, within deciduous vegetation (grid A1) the number of mature females remained constant for 6 weeks at the density predicted from home range size and effective sampling area of the grid. I concluded that grid A1 had probably become saturated with mature females.

Removal of mature female voles from a 4-ha plot resulted in increased maturation rate of young females and acquisition by them of home ranges. Manipulation of densities of mature voles in enclosures showed that mature voles at high density prevented immature voles from maturing. At a high density of mature voles in enclosures survival of immatures was also low. The effect of mature males on females

and vice versa was not elucidated. I conclude that density of mature females was regulated by spacing behavior.

Two conditions of the social factor hypothesis were satisfied and I cannot reject the hypothesis and therefore predict stability rather than cyclicity of *Clethrionomys* [illegible] study area. The results of this study are discussed within the framework [illegible]namics and hypotheses of regulation of populations of small mammals in

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I would like to express special thanks to Bill Fuller, my supervisor. I learned much from him and will no doubt remain influenced for the rest of my life. Not only did we talk about science and voles but also about the environment and such non-zoology topics as computers and car mechanics. I thoroughly enjoyed it all.

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Introduction

Elton (1924) first documented population cycles in many species of birds and mammals, which sparked intensive research into population cycling and density regulation, and resulted in literally thousands of publications. Despite this, the advance in our understanding of population regulation has been rather modest.

Part of the blame for slow progress can be attributed to the *ad hoc* nature of the research questions asked, the naive assumptions made concerning microtine social organization and behaviour (basically that they lacked any such attributes), and methods used. The notion that all microtine rodents undergo population cycles will be difficult to bury, despite evidence that this fundamental assumption may not hold for many species or populations (Finerty 1981, Garst and Howard 1981). As recently as 1980 Tamarin (1980) stated that voles, field mice and lemmings undergo regular cycles lasting about 3-4 years and further, that the population of *Microtus breweri* on Muskeget Island "shows aberrent demography: it does not cycle" (Tamarin 1980: 128).

Hypotheses that attribute population cycles to extrinsic factors such as predation (Pearson 1966), food (Pitelka 1957, Batzli and Pitelka 1971), winter conditions (Fuller 1969, 1977a, 1977b, 1979, Fuller *et al.* 1969) have been largely rejected, although predators may have an important influence on populations (Erlinge *et al.* 1983), and Batzli (Batzli 1983, Batzli and Cole 1979, Batzli and Jung 1980, Jung and Batzli 1981) still believes in the importance of food and feels that cycles are caused by a negative feedback, with a time lag, between rodent density and plant secondary compounds.

Those who believe in intrinsic factors can be roughly divided into two schools. Christian (Christian 1980, Christian and Davis 1964) believes in phenotypic plasticity mediated through endocrine changes during periods of stress. Followers of the Chitty hypothesis (Chitty 1967, Krebs 1978) believe in behavioural plasticity mediated at the genotypic level by selection for different behavioural morphs during different phases of a cycle. The Chitty hypothesis is ardently pursued in search of a set of factors that repeats every 3-4 years. From a theoretical point of view, cycles provide a convenient model because one can manipulate populations and make predictions as to how they should respond.

The multifactor hypothesis of Lidicker (1973, 1975) is probably a reasonable approach in that nobody, I would think, would argue against the fact that several factors influence demography of populations. However, the usefulness of such a hypothesis is questionable. The multifactor hypothesis is somewhat akin to a total ecosystem model, which Stenseth (1977) believes is of little value in helping us understand the real world because of its complexity.

Early in the history of investigation of small rodent population biology, researchers paid little attention to grid placement and size, trap spacing, or vegetation type. Voles were thought to behave like mere molecules of gas, which show random motion. All animals were lumped for most analyses and one was lucky if there was even a separation of the sexes. But in studying small mammal populations it has recently been stressed that grid size is important (Bondrup-Nielsen 1983), as is vegetation type (Van Horne 1981, Batzli 1974), and that small mammals have complex and varied social organizations (Getz and Carter 1980, Jannett 1980, Lidicker 1980, Madison 1980a, Wolff 1980a). Thus, details of methods and assumptions, both explicit and implicit, are important in studies of populations.

Because of their secretive nature, small mammals are not particularly suitable for studies of behaviour and social organization. Nevertheless they do have some redeeming features - they generally occur in large numbers, they are relatively easy to capture, and adequate samples can be killed for detailed necropsy work without apparent harm to the population.

That small mammals occur at different densities in different vegetation types, and that they show annual or multiannual fluctuations in density cannot be refuted. But how much variation in amplitude of fluctuation should one expect for animals that have a life expectancy generally less than 1 year, and that do not breed for 7 to 8 months during the fall and winter (eg. northern *Clethrionomys gapperi*)? The most direct way to determine significant fluctuations in density of any small mammal would be to estimate density from several replicated trap grids, in various vegetation types, over several years, and analyse the resulting data by 2-way analysis of variance (ANOVA). However, this requires far too extensive an effort for any one researcher, and indeed, it has not been done to my knowledge. Whether or not *Clethrionomys gapperi* show 3-4 year population cycles

or show significant or insignificant fluctuations in numbers I leave to others to determine. The fact that individuals of northern populations of *Clethrionomys gapperi* do not breed during autumn and winter, that thay are iteroparous, and that young may breed in the year of their birth, makes them a good species for studying density regulation during the period when one can conveniently spend time in the field.

Regulation requires the operation of a density-dependent negative feedback mechanism which causes a process to be stable. If there is a time lag in the negative feedback mechanism, the process will oscillate around the mean and can be considered a cycle. The shorter the time lag of the negative feedback, the more the process will approach constancy.

Many researchers have recognized the importance of habitat heterogeneity, spacing behaviour and dispersal in population processes (Brown 1969, Anderson 1970, 1980, Watson and Moss 1970, Klomp 1972, Lidicker 1975, 1978, Birney et al. 197[illegible] Hansson 1977, Myllymaki 1977, Lomnicki 1978, 1980, Rosenzweig and Abramsky 1980, Stenseth 1980, Hestbeck 1982, and Erlinge *et al*. 1983). Recently, Tamarin (1983) applied the criteria of Watson and Moss (1970) to show that spacing behaviour regulates density of voles.

If spacing behaviour is operating, ie. some individuals maintain exclusive use of the majority of their home range; and if home range size is a function of some resource such as food; and if the environment is heterogeneous, i.e. contains a set of habitats of varying quality which are available to individuals; then 'excess' animals in one habitat will be forced to disperse to habitats of inferior quality resulting in density stability within, at least, high quality habitats. I will term this hypothesis the social factor hypothesis after Tamarin (1983).

For this dissertation, populations of *Clethrionomys gapperi* in central Alberta were used to determine whether both conditions of the social factor hypothesis of density regulation, namely habitat heterogeneity and spacing behaviour were satisfied.

Study area and methods

This study was carried out 25 km SE of Lesser Slave Lake, Alberta, in the Mitsue Oil Field (Chevron Std. Ltd. Fig. 1), which is in the Lower Foothills Region (19a) of the boreal forest (Rowe 1972). The area is characterized by rolling topography, is underlain by Mesozoic rock, and there is no exposed surface rock. Mixed forest (trees 20-30 m tall) of trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) characterize 43% of the area, and upland black spruce forests (*Picea mariana*, trees 10-20m tall) cover 23%. Black spruce bogs (13%, trees 0.5-3m tall), trembling aspen stands (trees 20-30 m tall; 13%) and cut over areas (8%) constitute the rest of the area (Bondrup-Nielsen 1978).

Intensive field work was carried out during the summers of 1980 to 1982. The study involved capture-mark-recapture (CMR) and snap-trapping of *Clethrionomys gapperi*; experimental manipulation of voles in enclosures and; and selective removal experiments on study plots. A colony of voles was maintained in the field as a source of experimental animals.

Censuses of voles by CMR were done on live-trapping grids. Each *C. gapperi* caught was individually identified by 'toe-clipping' (last joint of two toes removed) on first capture. On each capture voles were weighed with a Pesola spring balance and reproductive condition was noted (males: testes scrotal or abdominal; females: vagina perforate or imperforate, nipples prominent, visible, barely visible or not visible, pubic symphysis closed, parting or parted). The trapping station at which an animal was caught was recorded and animals were always released where caught. Counts are based on minimum number known to be alive in each period, that is, animals actually captured, together with those previously marked animals that were missed at the time but captured later (Chitty and Phipps 1966).

Museum Special snap traps were used to obtain *C. gapperi* for necropsy. In addition all voles found dead in live-traps were necropsied. The following data were recorded for each animal necropsied - unique number, date, habitat, line or grid, total length, tail length, sex, gross weight, skull length, morphology of second upper left molar (M^2) for age determination (Tupikova *et al*. 1968). In addition position, length and width of testes, presence/absence of sperm in smears of testis and epididymis, size of epididymis and whether tubules were visible or not, and size of seminal vesicles were

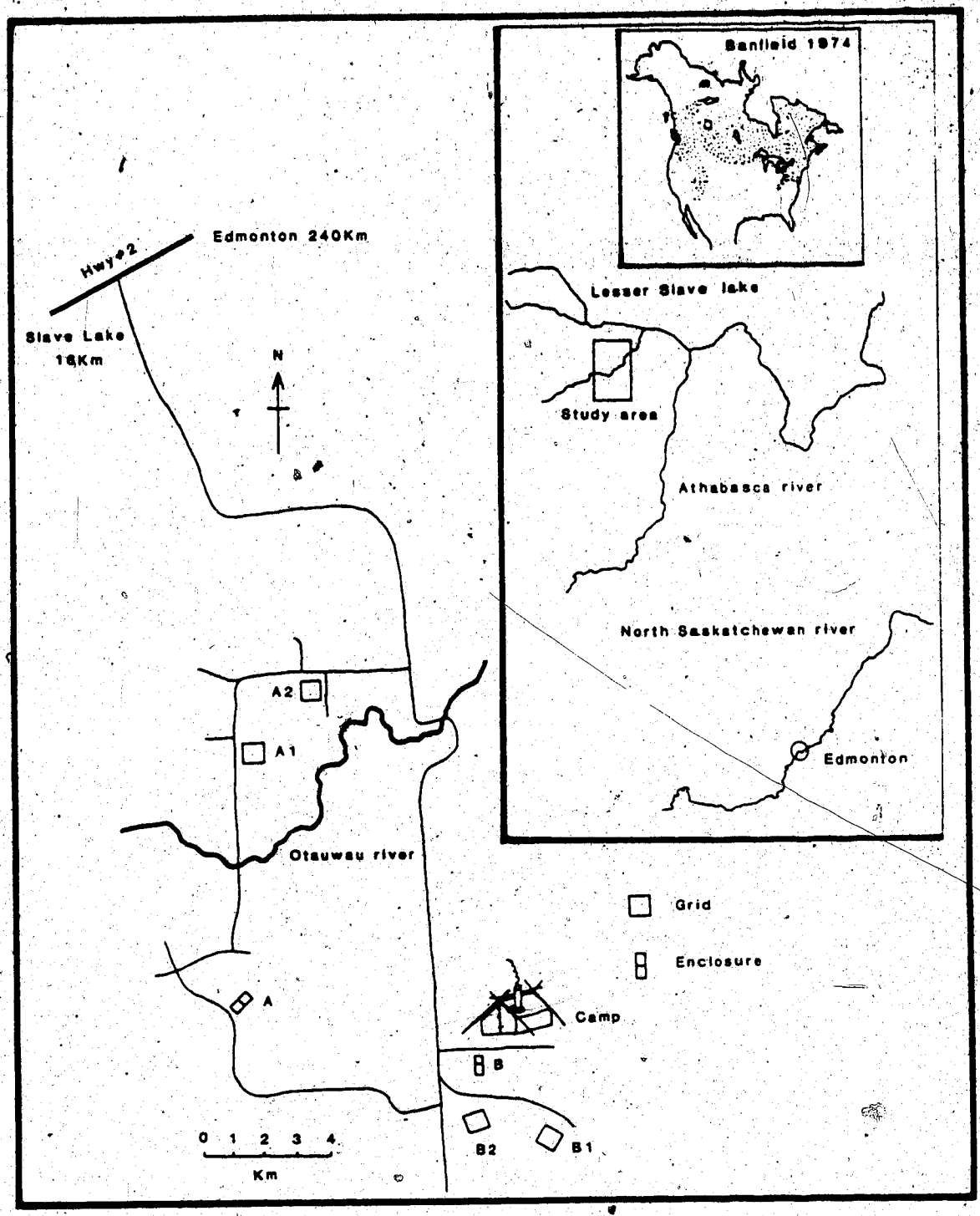

Figure 1. Distribution of *Clethrionomys gapperi* in North America and location of study area, grids and enclosures.

recorded for males. For females the following were recorded: vagina perforated or not, number and size of follicles or number of corpora lutea in ovary, state of uterus, number of embryos or placental scars, size and weight of embryos, relative amount of mammary tissue, relative size of nipples.

Voles in captivity were kept individually in opaque plastic shoe-box mouse cages (28x18x12cm) with metal tops. They were fed Purina Lab Chow and water *ad libitum*. Cages contained terylene fiber and wood shavings for bedding and were cleaned weekly. Captive voles were housed in a tent and hence exposed to approximately natural photoperiod and temperature.

The following abbreviations and definitions will be used throughout the balance of this dissertation:

OW- overwintered vole (born the previous summer, year t-1)

YG- young vole (born the current year, t). May be divided into:

Age class 1- M^2 with open anterior groove

Age class 2- M^2 with closed anterior groove

Age class 3- M^2 with roots formed

Mature- a) Live- females weighing more than or equal to 16 g or having prominent nipples or having a parted pubic symphysis, males having scrotal testes.

b) Necropsy- females having embryos, placental scars or corpora lutea, males showing positive sperm smear of testis or epidydimys. Age may be OW or YG.

Immature- voles not sexually mature. Usually age YG, but some age OW in early spring.

In expressing the results of statistical tests:

*- $P<0.05$

**- $P<0.01$

***- $P<0.001$

Demography of *Clethrionomys gapperi* in two diverse habitats

Introduction

The importance of comparative studies in zoology cannot be disputed. In the field of density regulation of microtine rodents this approach has been used extensively. Most studies have drawn comparisons among species (Krebs and Meyers 1974, Krebs 1979), but only a few studies have compared a single species among vegetation types. (Batzli 1974, Van Horne 1981, West 1982, Ostfeld and Klosterman in prep). Comparisons of demography of a species between vegetation types may suggest processes of population regulation.

The term "habitat" is used rather loosely in the ecological literature. Habitat may refer to a botanically distinct segment of a geographical area, or it may also refer to the type of areas occupied by some species of animal. Confusion may therefore arise in that the habitats of an animal may only be a subset of the botanically-defined habitats. Furthermore, there may be some habitats that animals occupy only during certain years. I will therefore term the botanically-defined units of space vegetation types, and habitat will be the subset of vegetation types occupied, in this case, by *Clethrionomys gapperi*.

We may be able to define x botanically distinct vegetation types, and determine that a species occupies x-y of them but how that species responds to vegetation types is of importance (Weins 1976). We can approach this question by determining differences in demographic parameters, including home range size, of a species on grids containing various vegetation types. Based on demography of a species these grids can then be ranked from high performance to low performance. Whether or not a particular species recognizes vegetation types is not of concern. So habitat types must be defined as functions of the animal in question. Demographic performance of a species may be the same within two different vegetation types in which case these two vegetation types are one habitat type of the species in question.

This chapter then compares demography (density, persistence, transiency, recruitment and litter size) and home range size of *Clethrionomys gapperi* among grids with different vegetation types during the breeding seasons 1980 to 1982.

Methods

Habitat quantification and analysis

On all grids the vegetation of a 20 x 20 m area centered on each of 100 trap stations was scored for 9 variables (Table 1). This resulted in 100 observations for each variable for each grid and univariate comparisons were made by use of the Kolmogorov-Smirnov test. Multivariate analysis of vegetation types was done by use of the program TAXMAP (Carmichael and Sneath 1969) to search for similarities among grids.

The TAXMAP program searches for natural clusters of OTU's (Operational Taxonomic Units) where each OTU is described by a set of attributes or variables. OTU's can hence be envisioned as ordered in a hyperspace defined by considering each attribute as a range of values along an orthogonal axis. The ranges of the attributes are determined and their relative information content is calculated. Raw data values are then normalized as factors of the range. A weighted average relative proximity is calculated between each pair of items. OTU's are then partitioned statistically into clusters whose members form a continuous, relatively dense population, which is separated from other OTU's by a completely surrounding, relatively empty space. TAXMAP accepts a variety of variable types from continuous to presence / absence. For the present purpose the original variables were modified (Table 2).

Census technique and snap trapping

Based on habitat studies of *Clethrionomys gapperi* (Iverson and Turner 1973), and snap trapping I did in the same study area for cricetid rodents in 1976 (Bondrup-Nielsen 1978), two diverse vegetation types were chosen. Vegetation type A, predominantly deciduous, generally had a high density of *C. gapperi*; vegetation type B, predominantly coniferous, generally had a low density of *C. gapperi*. Populations on three 4-ha grids

Table 1. Eight vegetation variables measured at each trap station on grids A1, A2, B1 and B2.

Tree Groups		Av. dist. between trees		Tree diameter	
Code	Group	Code	Dist	Code	Dia.
1	Mainly *Populus* spp.	1	<2 m	1	<5 cm
2	Yg. deciduous (2-4 m tall)	2	2<5 m	2	5<10 cm
3	Coniferous/*Populus*	3	5<10 m	3	10<20 cm
4	Coniferous/*Betula papyrifera*	4	>10 m	4	20<40 cm
5	Mainly Coniferous			5	>40 cm

Shrub groups		Shrub height		Shrub density	
Code	Type	Code	Height	Code	Density
1	Mainly *Viburnum edule*	0	NA	0	none to very sparse
2	Mainly *Lonicera involucrata*	1	<1m	1	Scattered
3	Mixture of *V. edule*, *L. involucrata* and *Rosa* spp.	2	1-1.5m	2	Medium
4	*Abies balsamea* (<1m) and some deciduous shrubs	3	>1.5m	3	Dense
5	None				

Herb Cover		Forest floor	
Code	Type	Code	Type
1	None	1	Leaf litter
2	Few	2	Moss
3	Fair	3	Leaf/moss
4	Medium	4	Moss/spruce needles
5	Mainly grass		
6	Mixed grass and herbs		

Table 2. Fifteen habitat codes used in TAXMAP analysis of the four grids (grid A1, A2, B1 and B2).

A. Trees

1. Mainly deciduous trees
2. Deciduous/coniferous (1/2 / 1/2)
3. Mainly coniferous
4. Tree density
5. Tree diameter

B. Shrubs

6. Deciduous shrubs
7. *Abies balsamea* <1m tall
8. No shrubs
9. Shrub density
10. Shrub height

C. Herbs

11. No herbs
12. Up to several herbs
13. Many herbs and grasses

D. Forest floor

14. Leafy forest floor
15. Mossy forest floor

(Fig. 1), two in vegetation type A (grids A1 and A2) and one in vegetation type B (grid B1) were enumerated by CMR in 1980. In 1981 a fourth 4-ha grid was added (grid B2). In 1982 only grids A1 and B1 were live-trapped, and grid B1 was enlarged to 6.24 ha. Grids A2, B1 and B2 (1981) and grids A1 and B1 (1982) were snap trapped during the last trapping session of the season.

The period May to September was divided into 11 two-week periods (Table 3). A live-trapping session (rota) was carried out on each grid during most periods. For each rota, traps were checked morning and evening over three consecutive days, beginning and ending with a morning check. Thus animals were at risk of capture 5 times per rota.

All grids consisted of a 10x10 array (Grid B1 was enlarged to a 12x13 array in 1982) with 20 m spacing. One Longworth trap, baited with sunflower seeds and Purina Lab Chow, and supplied with terylene bedding, was set within 1 m of each station. On all early and most late rotas, traps were pre-baited (doors locked open) one day before trapping started. Bedding and bait were replenished as necessary, and and traps were checked for proper functioning before each rota and after every capture.

Trappability

Trappability, T, was calculated by the method of Boonstra and Krebs (1978):

$$T = \sum_{i=1}^{N} \frac{\text{number of actual captures of individual } i}{\text{number of times } i \text{ is at risk of capture}} \cdot N^{-1}$$

where N is the number of voles caught more than two times. First and last capture are not counted in either the number of captures or the number of times at risk of capture, because an animal is necessarily caught at those times.

Table 3. Dates on which the grids were trapped in 1980, 1981 and 1982 (Ma=May, Ju=June, Jy=July, Au=August, Se=September).

	1980 GRIDS				1981 GRIDS				1982 GRIDS	
Rota	A1	A2	B1		A1	A2	B1	B2	A1	B1
1	--[1]	15-17 Ma	17-19 Ma		7-9 Ma	7-9 Ma	14-16 Ma	--	10-12 Ma	10-12 Ma
2	--	28-30 Ma	28-30 Ma		19-21 Ma	19-21 Ma	28-30 Ma	28-30 Ma	24-26 Ma	23-25 Ma
3	--	9-12 Ju	9-12 Ju		4-6 Ju	4-6 Ju	8-10 Ju	4-6 Ju	7-9 Ju	9-11 Ju
4	16-18 Ju	23-25 Ju	23-25 Ju		22,25,26Ju	18-20 Ju	22,25,26Ju	18-20 Ju	21-23 Ju	21-23 Ju
5	2,4,5 Jy	8-10 Jy	5-7 Jy		1,3 Jy	5-7 Jy	1-3 Jy	1-3 Jy	1-3 Jy	1-3 Jy
6	16-18 Jy	24-26 Jy	24-26 Jy		17-19 Jy	17-19 Jy	17-19 Jy	17-19 Jy	12-14 Jy	12-14 Jy
7	29-31 Au	4,7,8 Au	4,7,8 Au		4-6 Au	28-30 Jy	4-6 Au	28-30 Jy	26-28 Jy	26-28 Jy
8	19-21 Au	22-24 Au	22-24 Au		19-21 Au	18-20 Au	19-21 Au	--	8-10 Au	8-10 Au
9	--	--	--		--	--	3-5 Se	--	--	--
10	--	8-10 Se	8-10 Se		--	10-12 Se	--	10-12 Se	--	--
11	--	--	27-30 Se		--	--	--	--	--	--

1-Voles on grid not enumerated

Estimate of persistence

Persistence may be calculated as the proportion of voles that survive from one rota to the next. Alternatively, if we assume constant rate of loss with time, average persistence can be computed as:

$$\left[\sum_{i=1}^{n}\left[\left[\sum_{t=1}^{r} e^{\left[\ln N(t+1) - \ln N(t)\right]\cdot t^{-1}}\right]\cdot r^{-1}\right]\right]\cdot n^{-1}$$

where r = number of rotas during which an animal could have been alive, n = number of animals involved, N(t)= number of animals alive in rota t, and N(t+1)= number of animals alive in rota t+1, where t=interval length.

Estimate of transiency

Voles caught during only one rota (usually caught only once) were defined as transients, although some of them may have died. The proportion of transients is computed as

$$\left[\sum_{i=1}^{r} ai\cdot bi^{-1}\right]\cdot r^{-1}$$

where ai = number of new voles during rota i, bi = number of these new voles not caught in a later rota, and r = number of rotas.

Estimate of recruitment

Total recruits are all animals caught for the first time beginning with rota 2. For the comparison of immature to total recruits the initial period is the rota in which immature animals are first caught. Because only 11 days elapsed between the end of one rota and the start of the next, most immature recruits were probably born on the grid, whereas mature recruits most likely immigrated onto the grid.

Estimate of home range size

Various methods exist for estimating home range size from data acquired by live-trapping at certain discrete points on a grid (Hayne 1949, Stickel 1954, Harvey and Barbour 1965, Jennrich and Turner 1969, Mazurkiewicz 1971, Wierzboraska 1972, Metzgar and Sheldon 1974, Ford and Krumme 1979). Each method has its drawbacks, some more severe than others. For instance, the polygon methods reviewed by Stickel (1954) are sensitive to number of observations, and may include areas the animal never uses. The method of Metzgar and Sheldon (1974) assumes that the number of capture points for an animal reaches an asymptote which may not be the case. In this study three indices of home range size were used 1) number of trap stations at which an animal was caught, 2) mean 'area use radius' and 3) mean 'activity radius'. Only animals caught at least five times and having less than 20% of all captures in traps on the perimeter of the grid were used in analysis. Mean 'area use radius' and 'activity radius' were calculated by use of the same formulas except that the former index was based on a single observation (weight=1) of the trap stations at which an animal was caught; the latter index included all captures (weight=number of captures at that trap station).

The radius is computed as

$$r = \left[\sum_{i=1}^{n} ri \right] \cdot n^{-1}$$

where n is the sample size, and the ith distance (Pythagorean) to the center of gravity is

$$ri = \left[(xi-\bar{x})^2 + (yi-\bar{y})^2\right]^{1/2}$$

where $(\bar{x}, \bar{y})$, the center of gravity is computed as

$$\bar{x} = \left[\sum xi\right] \cdot n^{-1} \qquad \bar{y} = \left[\sum yi\right] \cdot n^{-1}$$

Results

Vegetation Types

Vegetation of the A grids was mainly deciduous with grid A1 being more deciduous than grid A2 (Fig. 2). The density of trees was not different between the two grids (Table 4), but grid A1 had a fairly even distribution of moderate diameter trees whereas grid A2 had a high proportion of large diameter trees (Fig. 2).

Vegetation of the B grids was mainly coniferous with grid B1 being more coniferous than grid B2 (Fig. 2). Both of the B grids had mainly small diameter trees compared to the two deciduous grids (Fig. 2). The frequency distribution of tree diameter differed among all the grids (Table 4). The density of trees was greatest on grid B1 (Fig. 2).

Grid A1 had a very uniform distribution of low bush cranberry (*Viburnum edule*), bracted honeysuckle (*Lonicera involucrata*) and rose (*Rosa* sp) up to 1.5 m tall (Fig. 2). The predominant shrubs on grid A2 were low bush cranberry and bracted honeysuckle with some rose, and density and height of shrubs were lower than on grid A1 (Fig. 2, Table 4). Scattered small balsam fir (*Abies balsamea*) and a few deciduous shrubs dominated 75% of grid B1 with the rest of the grid being devoid of shrubs. Grid B2 had mainly low bush cranberry but they were low and scattered (Fig. 2).

The herb layer on grid A1 was mainly dense and grassy and on grid A2 was less dense and a mixture of grass and herbs (Fig. 2). The B grids generally had few herbs, and grass was not a component (Fig. 2). The forest floor on the A grids was mainly leaf litter and on the B grids was mainly moss (Fig. 2). Debris (fallen trees and dead branches) on the forest floor was prominent on the two deciduous grids but was a minor component on the coniferous grids.

A TAXMAP classification of the four grids produced four single member clusters (Fig. 3). The two A grids were closer to each other than they were to either of the B grids.

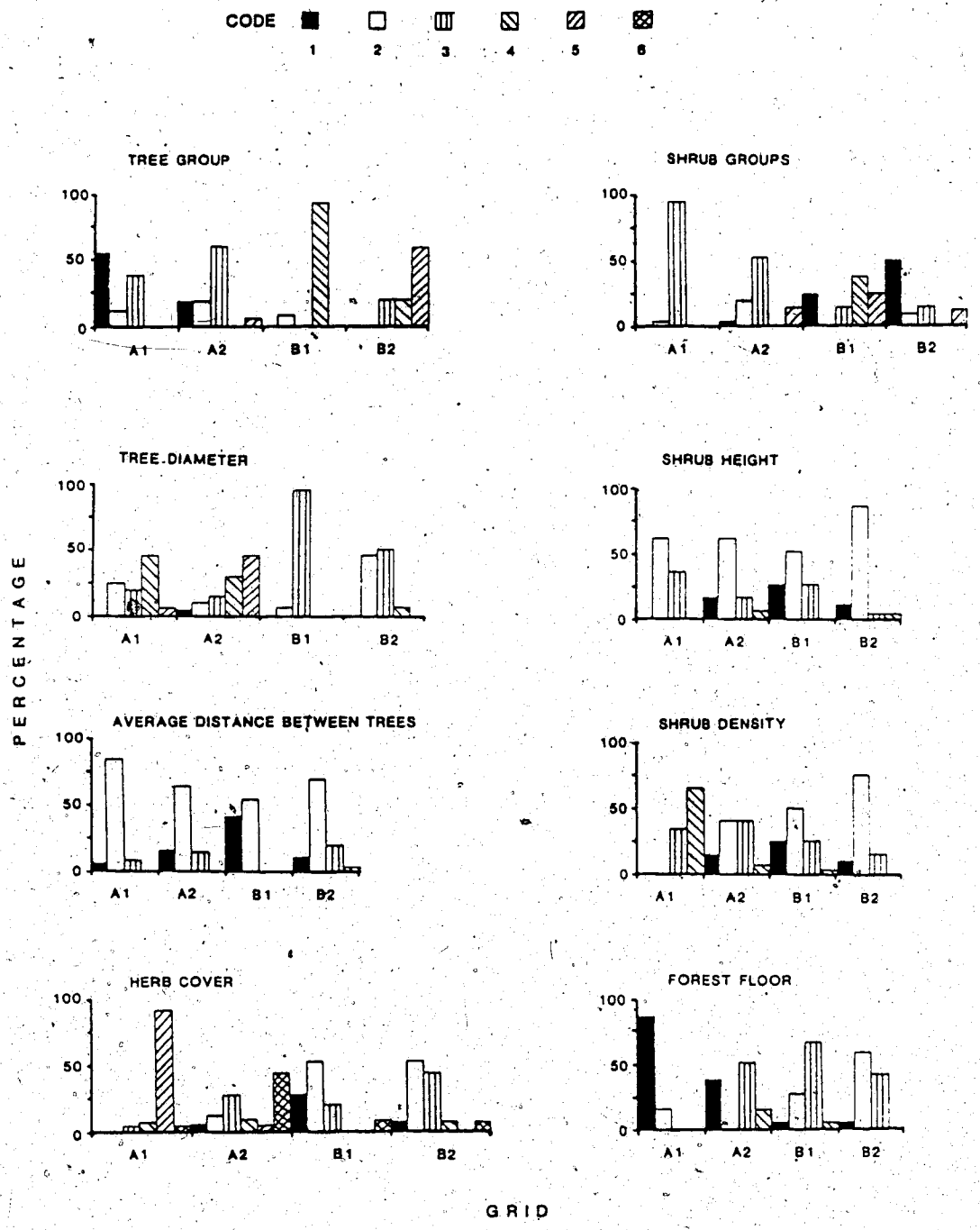

Figure 2. Histograms of vegetation variables on four grids (grids A1, A2, B1 and B2, see Table 1 for explanation of codes).

Table 4. Kolmogorov-Smirnov test (D) for goodness of fit of 4 vegetation variables compared between all grid pairs.

	Grid Pairs Compared					
	A1 A2	B1 B2	A1 B1	A1 B2	A2 B1	A2 B2
Tree density	0.10 N=100 NS	0.32 N=100 **	0.26 N=100 **	0.06 N=100 NS	0.36 N=100 **	0.14 N=100 *
Tree diameter	0.20 N=100 **	0.38 N=100 **	0.72 N=100 **	0.64 N=100 **	0.52 N=100 **	0.44 N=100 **
Shrub height	0.12 N=100 NS	0.27 N=76 **	0.09 N=100 NS	0.18 N=100 *	0.03 N=84 NS	0.30 N=84 **
Shrub density	0.57 N=100 **	0.21 N=76 **	0.15 N=100 *	0.36 N=100 **	0.64 N=84 **	0.65 N=84 **

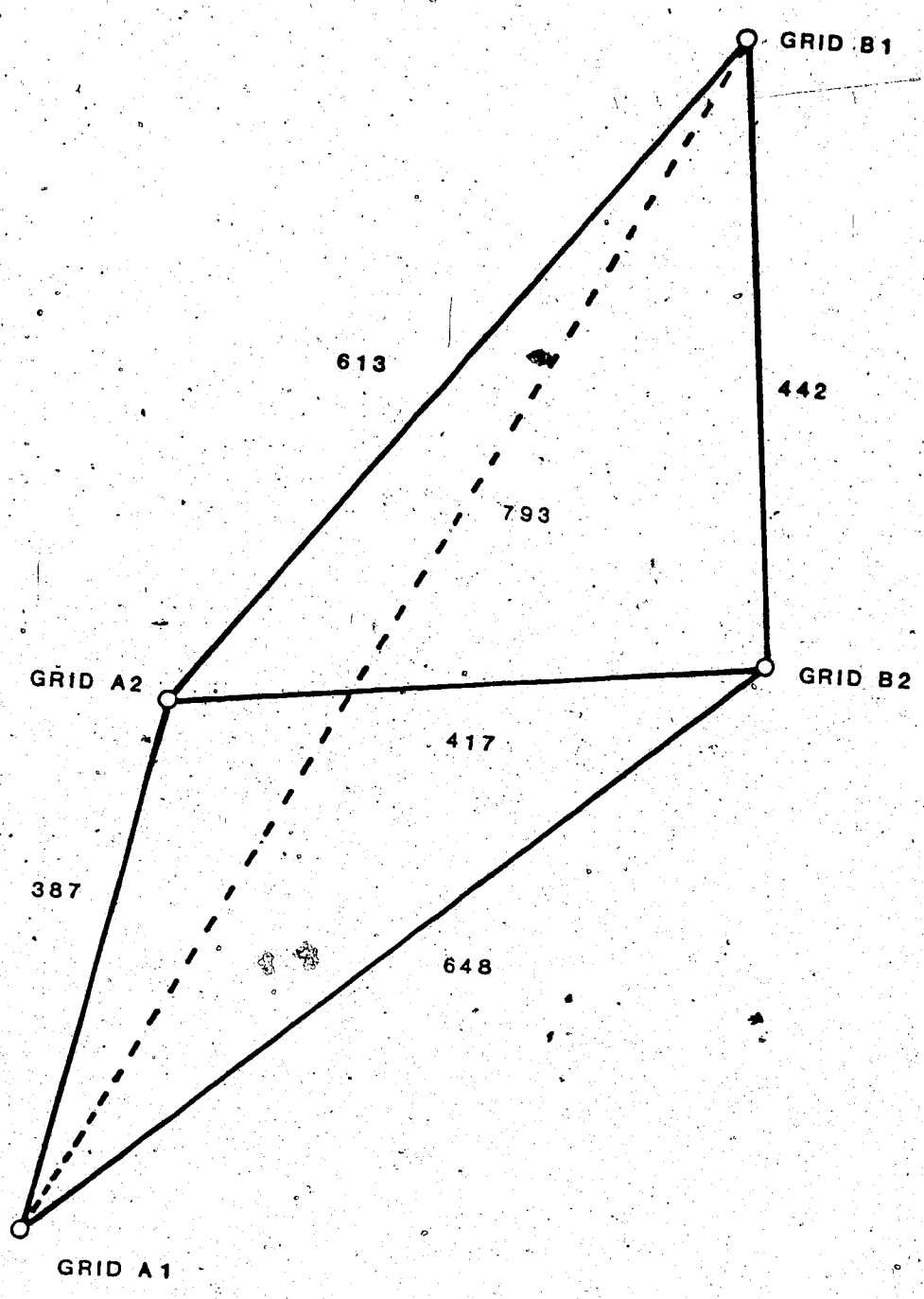

Figure 3. Taxometric distance between grids A1, A2, B1 and B2 generated by the program TAXMAP.

Trappability

Trappability was generally high. Females tended to have higher trappability than males and trappability was higher on the A grids than on grid B1 (Table 5).

Minimum Number Alive

The live-trapping census results were based on approximately 37,000 trap-nights and a total of 861 different *C. gapperi* caught.

Data from two periods, rotas 1 and 8, were used to test the hypothesis that there was a higher density of *C. gapperi* on the A grids than on the B grids. Because I could not calculate mean densities for the two grid types for each rota, the null hypothesis tested was that the ratio of MNA did not differ from a ratio of 1:1 between the two habitat types.

MNA was always higher in deciduous than in coniferous vegetation type (Table 6). However, only in 1982 did the ratio of voles in rota 1 differ significantly from 1:1 (31 voles / 4 ha on grid A1 and 7.7 voles / 4 ha on grid B1, Table 6). In 1981 grid B2 was not trapped until rota 2, when the MNA ratio between it and both grids A1 and A2 differed significantly from 1:1, and there was no difference in MNA ratio between it and grid B1 (Table 6). During rota 8 (rota 7 for comparisons with grid B2) there were significant departures from a 1:1 ratio of voles between the A grids and the B grids; however, there was no difference within the A or B grids (Table 6).

After a slight decrease in numbers during the early rotas, especially in 1980 and 1981, increase in numbers was generally exponential, with similar rates of increase on grids A1, A2 and B1 (Fig. 4). However, MNA on the B grids remained low and relatively constant during most of the summer in 1981 and did not start to increase until late in the summer (rota 7 on). In 1980 the MNA on all grids decreased in mid summer, mainly because of poor persistence of young (Fig. 5). However, densities did increase later in the year. In 1982, MNA on grid B1 did not increase after rota 6, mainly as a result of a low appearance rate of young (Fig. 5), whereas exponential growth continued on grid A1. Grid B1 generally had a higher proportion of overwintered voles, though a much lower absolute number, than the A grids (Fig. 5). In 1982, when MNA was very high on grid A1 the population consisted of a higher proportion of overwintered animals than in other

Table 5. Trappability of male and female voles on grids A1, A2 and B1, 1980 to 1982, (sample size in parenthesis).

	A1			A2			B1		
	male	female	all	male	female	all	male	female	all
1980	0.96 (12)	0.94 (10)	0.95 (22)	0.71 (19)	0.96 (20)	0.86 (39)	0.75 (4)	0.82 (10)	0.81 (14)
1981	0.89 (18)	0.71 (12)	0.81 (30)	0.82 (14)	0.93 (16)	0.86 (30)	--	0.73 (3)	0.73 (3)
1982	0.89 (37)	0.92 (27)	0.90 (64)				0.80 (13)	0.95 (17)	0.87 (30)

Table 6. Ratio of Minimum Number Alive between grids in spring (rota 1) and late summer (rota 8) tested for departure from 1:1 by Chi-square.

1980

SPRING \ LATE SUMMER	A1	A2	B1	B2
A1	35:52 NS	14:52 ***	--	
A2	--[1]	4:35 ***	--	
B1	--	8:4 NS	--	
B2	--	--	--	

1981

SPRING \ LATE SUMMER	A1	A2	B1	B2[3]
A1	66:87 NS	12:87 ***	4:87 ***	
A2	10:12 NS	12:66 ***	4:66 ***	
B1	10:5 NS	12:5 NS	4:12 NS	
B2[2]	10:1 ***	12:1 ***	5:1 NS	

1982

SPRING \ LATE SUMMER	A1	A2	B1	B2
A1	[illegible]	--	25:128 ***	--
A2	--		--	--
B1	31:7.7 **	--		--
B2	--	--		

1- voles on grid not separated
2- rota 2
3- rota 7

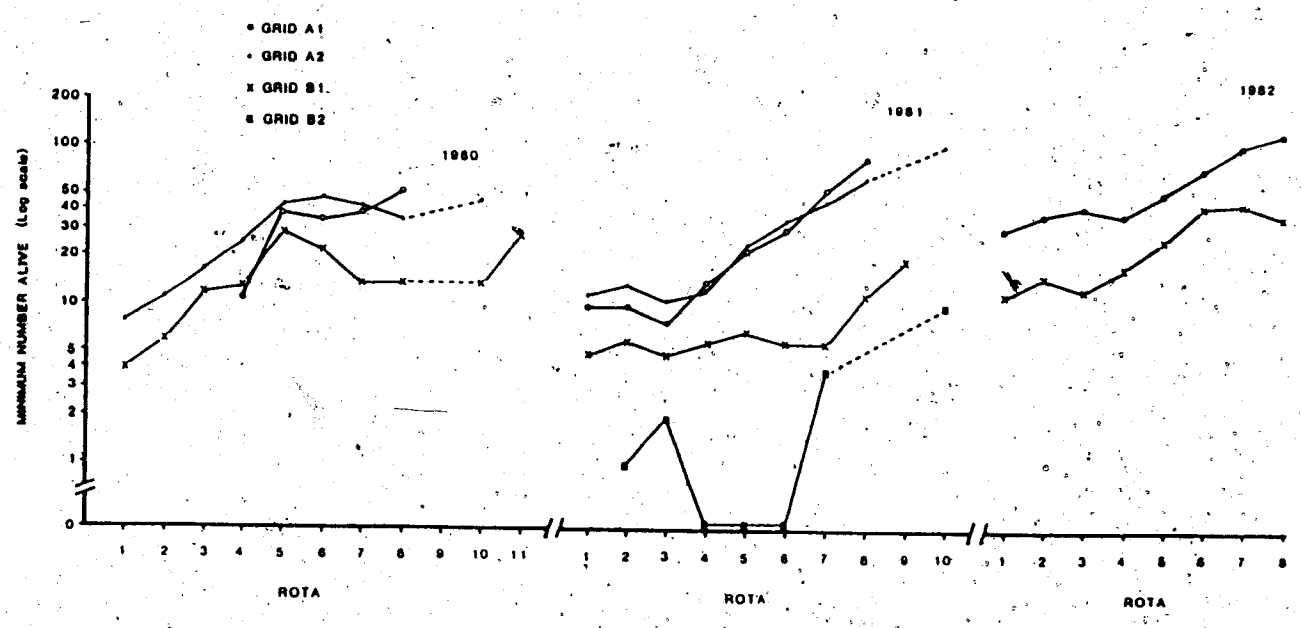

Figure 4. Minimum number of *Clethrionomys gapperi* known to be alive on live-trapping grids in 1980, 1981 and 1982.

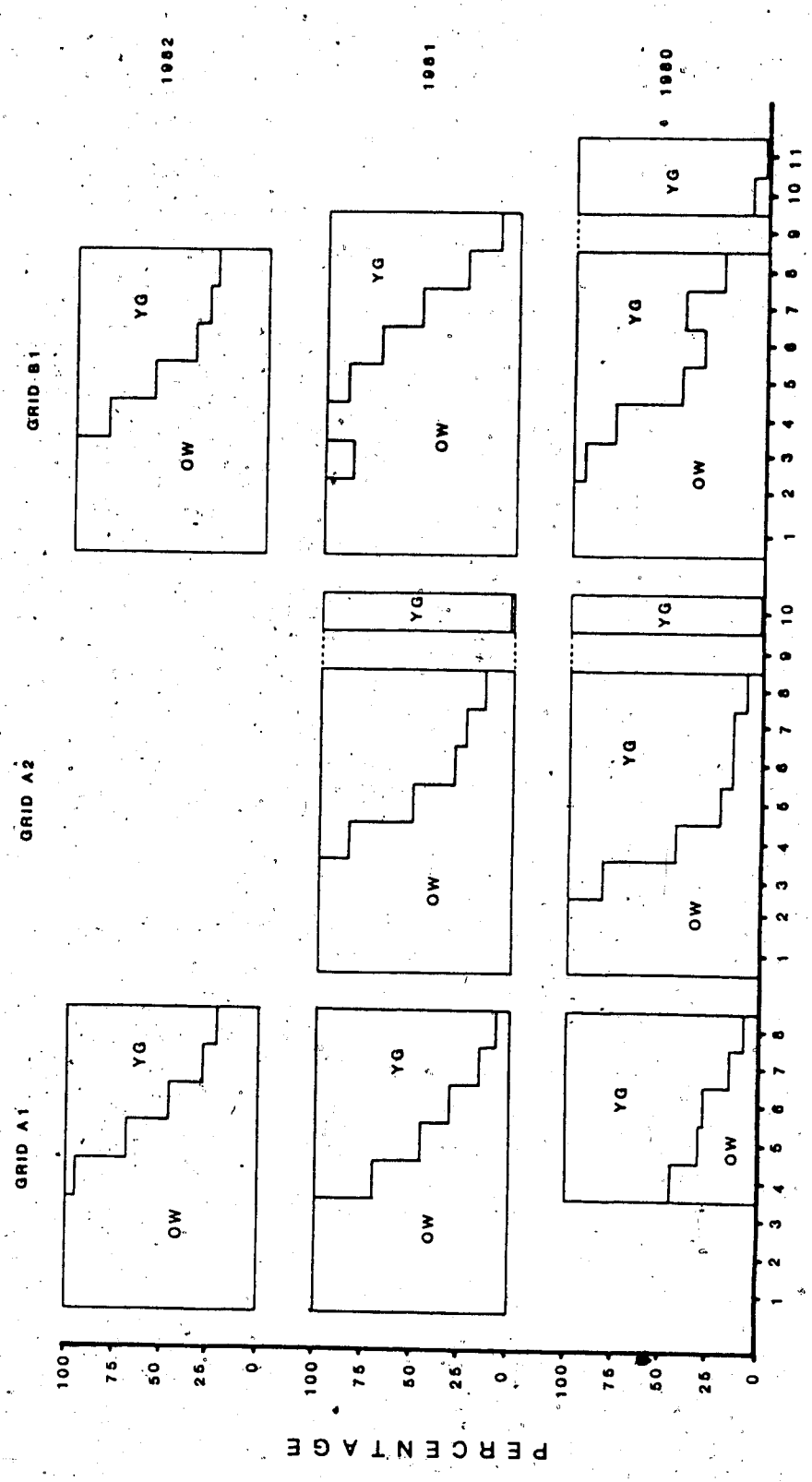

Figure 5. Percentage of overwintered and young of the year *Clethrionomys gapperi* on live-trapping grids in 1980, 1981 and 1982.

years (Fig. 5). By September (Rotas 10 and 11) the population consisted almost entirely of young of the year, at least in 1980 and 1981 when trapping continued through Rota 11.

MNA of overwintered animals was similar between 1980 and 1981 but was much higher in 1982. Late summer MNA was low in 1980 compared to 1981 and 1982 and was highest in 1982. We may therefore consider 1980 a low density year, 1982 a high density year and 1981 intermediate.

Persistence

Mean persistence by grid, age class, sex, and year is presented in Table 7. Persistence was lower in 1980 than in 1981 and 1982 (Table 8) on all grids but the difference was only significant on grid A2. Persistence was significantly different between grids A1 and B1 but not between grids A1 and A2 or between A2 and B1 (Table 8). Overwintered females persisted significantly better than did overwintered males but there was no difference among the sexes of the young of the year (Table 9). Overwintered animals persisted significantly longer than did young of the year (Table 9). Overwintered animals persisted equally well on grids A1 and B1; however, there was a significant difference in persistence of the young of the year with higher persistence on grid A1 (Table 10). Persistence of overwintered females was significantly lower in 1981 on grid B1 than during the other years, but on grid A1 there was no difference among years (Table 11).

Transiency

Wide variations occurred in the percentage of transients among years, grids, age class and sexes (Table 12). Overall there was no significant difference in transiency among years, but there were significantly more transients among young of the year than among overwintered animals, and significantly more transients among males than among females (Table 12). Among the grids there was a trend from fewest transients on grid A1 to most on B1, and the differences were significant. Transiency among overwintered females on grid A1 and B1 was very low and not significantly different. Only transience among young males differed significantly between grids.

Table 7. Mean persistence ±S.D. of Clethrionomys gapperi by grid, age class, sex and year

			1980			1981			1982		
Grid	Age	Sex	Persistence	r[1]	#voles	Persistence	r	#voles	Persistence	r	#voles
A1	OW	M	0.58±0.39	4	5	0.86±0.07	7	11	0.92±0.02	7	28
		F	0.86±0.10	4	7	0.96±0.05	7	5	0.94±0.02	7	23
	YG	M	0.79±0.13	4	24	0.50±0.35	4	27	0.48±0.32	4	52
		F	0.50±0.35	4	24	0.93±0.04	3	26	0.79±0.14	3	40
A2	OW	M	0.74±0.05	7	14	0.89±0.05	7	14	--[2]		
		F	0.50±0.35	7	10	0.84±0.05	7	6	--		
	YG	M	0.60±0.30	6	43	0.77±0.13	6	37	--		
		F	0.49±0.34	7	27	0.85±0.08	5	29	--		
B1	OW	M	0.52±0.26	7	11	0.80±0.09	7	5	0.78±0.09	7	19
		F	0.95±0.04	7	6	0.76±0.12	7	4	0.95±0.06	7	8
	YG	M	0.19±0.21	6	21	0.33±0.47	2	3	0.37±0.26	4	24
		F	0.40±0.33	8	20	0.53±0.42	6	6	0.59±0.40	4	21

1-Number of rotas animals could have been alive
2-Voles on grid not enumerated

Table 8. Comparison of mean persistence +S.D. (arcsine transformed data) between grids and years (superscripts refer to means among which comparisons were made).

	1980	1981	1982	Grid mean
Year Mean	48.55±25.54[1]	63.39±18.52[1]	63.85±21.01[1]	
Grid A1	55.55±23.77[2]	68.77±19.45[2]	67.94±17.57[2]	64.82±20.57[5]
Grid A2	47.02±23.06[3]	67.30± 7.85[3]	--[6]	56.77±20.11[5]
Grid B1	45.94±28.88[4]	53.82±22.81[4]	59.95±23.58[4]	52.72±25.83[5]

1- F2,178=9.96 ***
2- F2,60= 2.36 NS
3- F1,50=17.42 ***
4- F2,60= 1.85 NS
5- F2,178=4.61 *
6- Voles on grid not enumerated.

Table 9. Comparison of mean persistence ±S.D. (arcsine transformed data) between sex and age class.

Age	Male	Female	Mean
OW	61.88±14.76[1]	69.54±17.84[1]	65.71±16.74[3]
YG	43.91±26.04[2]	48.95±26.38[2]	46.53±26.16[3]

1- $F_{1,104}=5.80$, *
2- $F_{1,60}=0.69$, NS
3- $F_{1,179}=36.10$, ***

Table 10. Comparison of mean persistence ±S.D. (arcsine transformed data) between grids A1 and B1 and age class.

Age	Grid A1	Grid B1		
OW	71.44±14.94	65.07±16.06	F1,76=3.24	NS
YG	54.00±24.07	34.83±27.02	F1,49=6.9	*

Table 11. Comparison of mean persistence ±S.D. (arcsine transformed data) of overwintered females betweeh years for grids A1 and B1.

	1980	1981	1982	
A1	71.13±13.05	82.37±9.55	76.33±1.80	F2,15= 2.35 NS
B1	79.02 ± 7.74	61.24±8.33	80.13±9.[illegible]	F2,18=10.55 **

Table 12. Percent transient voles (N) by grid, age, sex and year (superscripts refer to means among which comparisons were made).

			Percent transient			TOTAL					
			1980	1981	1982	Indiv.	Grid	OW	YG	Male	Female
GRID A1											
		Male	20.0 (5)	27.3 (11)	10.7 (28)	15.9 (44)					
	OW										
		Female	0.0 (7)	0.0 (5)	8.7 (23)	5.7 (35)					
		Male	37.5 (24)	31.6 (38)	40.4 (52)	36.8[6] (114)	25.4[5] (283)				
	YG										
		Female	16.7 (24)	11.5 (26)	~~35.0~~ (40)	23.3 (90)					
GRID A2											
		Male	30.8 (13)	21.4 (14)	--[1]	25.9 (27)					
	OW										
		Female	30.0 (10)	16.7 (6)	--	25.0 (16)					
		Male	29.6 (44)	36.8 (38)	--	32.9[6] (82)	32.6 (181)				
	YG										
		Female	40.7 (27)	34.5 (29)	--	37.5 (56)					
GRID B1											
		Male	36.4 (11)	12.4 (5)	36.8 (19)	37.1 (35)					
	OW										
		Female	0.0 (6)	25.0 (4)	0.0 (8)	5.6 (18)					
		Male	71.4 (21)	33.3 (3)	62.5 (24)	64.6[6] (48)	39.2[5] (148)				
	YG										
		Female	30.0 (20)	33.3 (6)	23.8 (21)	27.7 (47)					
ALL GRIDS			33.0[2] (212)	28.1[2] (185)	31.2[2] (215)			19.4[3] (175)	35.5[3] (437)	36.3[4] (350)	23.7[4] (262)

1- voles on grid not enumerated
2- G=[illegible]3, NS
3- G=9.51, ***
4- G=11.37, ***
5- G=8.54, **
6- G=13.90, ***

Recruitment

There were no differences in recruitment among grids; however, recruitment was significantly lower on all grids combined in 1982 than in both 1980 and 1981 (Table 13). The ratio of immature to total recruits was significantly lower in 1981 than in 1980 and 1982 and was different between grids when all years were lumped (Table 14). In 1982, the ratio of immature to total recruits was significantly higher on grid A1 than on grid B1 (Table 14). This type of analysis, is of course, plagued by edge effect, i.e. a disproportionate number of mature recruits may be caught in the perimeter traps. Disregarding all recruits caught in the perimeter traps in 1982 (the year for which sample size was high enough to do this and still be left with enough recruits for analysis) 94.8% (N=58) of all recruits on grid A1 were immature whereas only 46.4% (N=28) were immature on grid B1, and this difference is highly significant (G=25.96, ***).

Home range

Average 'activity radius' was smaller than average 'area use radius' but the difference was not significant (Table 15). Male home ranges were approximately twice the size of female home ranges and the difference was significant (Table 16). Female home range size was significantly smaller on the A grids than on the grid B1 (Table 16), but only grid A1 differed significantly from grid B1, and then only by the 'activity radius' measure, among male[redacted]982 ($F_{1,20}=7.11$, *). There was no difference in mean home range size for either sex between years whether measured by 'activity radius' or 'area use radius' (Table 17).

Litter Size

Mean litter size was calculated from the number of embryos in pregnant females and the number of scars in the most recent set of scars. There was no statistically significant difference in mean litter size between voles in deciduous and coniferous vegetation types compared by years ($F=0.65$, NS, Table 18).

Table 13. Total recruitment expressed as percentage of Minimum Number Alive.

	Grid			
	A1	A2	B1	All
1980	45.1 (113)	43.0 (223)	49.1 (110)	45.1 [2] (446)
1981	51.2 (211)	43.5 (193)	34.9 (43)	46.3 [2] (447)
1982	32.5 (486)	--[1]	32.4 (225)	32.5 [2] (711)
All	39.1 (810)	43.3 (416)	37.6 (378)	

1- Voles on grid not enumerated.
2- G=29.14, ***

Table 14. Immature recruits expressed as percentage of total recruits.

	Grid			
	A1	A2	B1	All
1980	61.9 (21)	65.0 (80)	62.2 (37)	63.8[2] (138)
1981	43.3 (60)	57.1 (42)	28.6 (7)	47.7[2] (109)
1982	86.9[4] (99)	--[1]	50.9[4] (55)	74.0[2] (154)
All	69.4[3] (180)	62.3[3] (122)	53.5[3] (99)	

1- voles on grid not censused
2- G=19.00, ***
3- G=7.00, *
4- G=23.19, ***

Table 15. Mean ±S.D. (N) activity and area use radii as indices of home range size of mature Clethrionomys gapperi by grid and year.

		1980	1981	1982	Mean
Activity Radius					
Grid A1	M[1]	1.71±0.38 (10)	2.06±0.96 (7)	1.60±0.79 (13)	1.74±0.72
	F[2]	0.85±0.15 (11)	1.04±0.40 (9)	0.88±0.28 (11)	0.91±0.31
Grid A2	M	1.81±0.96 (7)	2.30±0.57 (6)	--[3]	2.03±0.82
	F	0.94±0.25 (6)	0.84±0.42 (4)	--	0.90±0.31
Grid B1	M	1.65±0.74 (4)	2.52±0.41 (3)	2.40±0.53 (9)	2.23±0.64
	F	1.11±0.44 (5)	0.98±0.44 (3)	1.25±0.45 (9)	1.16±0.43
Mean	M	1.73±0.66	2.23±0.73	1.93±0.79	1.94±0.74
	F	0.93±0.27	0.97±0.39	1.04±0.40	0.98±0.35
Area Use Radius					
Grid A1	M	1.91±0.39 (10)	2.34±0.89 (7)	1.84±0.71 (13)	1.98±0.68
	F	0.95±0.15 (11)	1.11±0.50 (9)	0.97±0.31 (11)	1.00±0.33
Grid A2	M	2.08±0.89 (7)	2.39±0.71 (6)	--	2.22±0.80
	F	0.93±0.24 (6)	0.96±0.33 (4)	--	0.94±0.26
Grid B1	M	1.92±0.64 (4)	2.64±0.39 (3)	2.38±0.54 (9)	2.31±0.56
	F	1.29±0.39 (5)	1.11±0.51 (3)	1.48±0.71 (9)	1.35±0.59
Mean	M	1.96±0.60	2.41±0.72	2.06±0.69	
	F	1.02±0.27	1.07±0.44	1.20±0.58	

1- Male
2- Female
3- Voles on grid not enumerated

Table 16. Comparison of mean ±S.D. activity and area use radius, in units of trap spacing (20 m), for mature male and female Clethrionomys gapperi between grids.

Grid	Male	Female	
	Activity Radius		
All	1.94+0.74	0.98+0.35	F1,115=78.49 ***
A1	1.74+0.73	0.91+0.29	F1,59 =34.49 ***
A2	2.03+0.82	0.90+0.31	F1,21 =17.31 ***
B1	2.23+0.64	1.16+0.43	F1,31 =32.71 ***
	F2,56=2.55 NS	F2,55=3.32 *	
	Area Use Radius		
A1	1.98+0.68	1.00+0.33	
A2	2.22+0.80	0.94+0.26	
B1	2.31+0.56	1.35+0.59	
	F2,56=1.42 NS	F2,55=4.83 *	

Table 17. Comparison of mean ±S.D. activity and area use radius in units of trap spacing (20 m), for mature male and female Clethrionomys gapperi between years.

	Activity		Area Used	
	Male	Female	Male	Female
1980	1.73+0.66	0.93+0.27	1.96+0.60	1.02+0.27
1981	2.23+0.73	0.97+0.39	2.41+0.72	1.07+0.44
1982	1.93+0.79	1.04+0.40	2.06+0.69	1.20+0.58
	$F_{2,56}=2.21$ NS	$F_{2,55}=0.5$ NS	$F_{2,56}=2.19$ NS	$F_{2,55}=0.87$ NS

Table 18. Mean litter size based on embryo and new placental scar count by vegetation type and year.

Vegetation Type	Year	Mean	S.D	N
Deciduous	1980	5.66	1.10	37
	1981	6.13	0.83	15
	1982	5.59	0.98	29
Coniferous	1980	5.71	1.11	7
	1981	5.71	1.11	7
	1982	5.75	0.85	20
		$F_{5,110}=0.65$, NS		

Discussion

The vegetation of the four grids differed in several of the variables measured. The most important difference was in tree cover. Both A grids were mainly deciduous and the B grids were mainly coniferous. Since the canopy cover influences the understory, it is no surprise that the coniferous-type grids had few herbs and a forest floor mainly of moss and conifer needles, whereas the deciduous-type grids had many herbs and a forest floor mainly of dead leaves. The TAXMAP classification of the four grids did not place the A and B grids within clusters but produced four, single-member clusters. Grids A1 and A2 were more similar to each other than they were to grid B1. Grid B2 was definitely a coniferous-type grid that I subjectively rated similar to grid B1; however, TAXMAP placed grid B2 closer to grid A2. Data from grid B2 will be largely ignored in this discussion because it was only trapped during one summer, the number of voles on it was very low. The two A grids and two B grids were not meant to be replicates so the fact that all grids were different from each other is of no consequence.

In this study minimum number alive (MNA) was used for direct enumeration. When trappability is greater than about 50%, MNA is considered to be quite close to the actual population density (Hilborn *et al.* 1976). Trappability was generally very high, easily meeting the criterion for confidence in MNA. Direct enumeration by MNA, however, has recently been criticized by Jolly and Dickson (1983), and Nichols and Pollock (1983). They reason that estimators of population size based on the Jolly-Seber capture-recapture model are less biased than direct enumeration. Jolly and Dickson (1983) argue that unequal catchability among individuals in an open population may result in a greater negative bias in the MNA estimate than proposed by Hilborn *et al.* (1976). In this study, I do not treat MNA as an estimate of actual population size on the grids, but rather as an indicator correlated with actual density and density change. Throughout, MNA data from the different grids are used to compare demographic parameters between grids and should, despite the shortcommings, be adequate for that purpose. Furthermore, it is my feeling, albeit intuitive and not quantified, that the mature segment of the vole populations on the grids is fully enumerated, whereas the immature animals may cause the greatest negative bias. During trap-out of enclosures (see Chapter 4) the snap-traps never caught mature animals, but they did catch immatures that had not been.

captured during earlier live-trapping. Boonstra and Krebs (1978) suggested that mature *Microtus townsendii* are fully enumerated by MNA whereas immatures are not. Other authors have argued similarly for other species (Hall 1974, Joule and Cameron 1974).

I do not wish to make too much of the density data as estimated by MNA on the grids. MNA on the A grids were very similar and were higher than on the B grids, especially in late summer. However, changes in MNA were not necessarily correlated between the A and B grids as evidenced in 1981 and 1982. That there can be differences in densities among vegetation types is well known for small mammals (Miller and Getz 1972, 1973, Van Horne 1981, Iverson and Turner 1973, West 1982, Sullivan 1979, 1980, Petticrew and Sadleir 1974, Sadleir 1974).

Since there are differences in MNA between grids it is necessary to show that other demographic differences between grids are not a result of those density differences but of vegetation differences. There are numerous studies comparing demography between different phases of the "population cycle" (for a review see Krebs and Myers 1974), however, different densities between grids and between years in this study can not necessarily be equated with different phases of the "population cycle". After all, there is no evidence that populations of *Clethrionomys gapperi* in the Mitsue study area cycle. It is more appropriate to compare other demographic parameters on any one grid between years with differences in MNA to determine whether differences in those parameters are independent of density.

I have used the term persistence rather than survival which is the term commonly used to express how long animals are caught on a live-trapping grid (Krebs and Myers 1974). When an animal is not caught on a grid anymore we do not know whether it died or left the grid and consequently the term persistence is more appropriate.

At first glance mean persistence appears to be correlated with density. In 1980, the low density year, persistence was low and in the other two years, with comparatively high density, persistence was high. However, density was higher in 1982 than in 1981 yet persistence was the same. On grid A1 mean persistence did not differ between years despite density differences. Persistence of overwintered females did not differ between grids A1 and B1 but persistence of overwintered males and young of the year did. It can therefore be concluded that the observed differences in persistence among

the grids were a result of differences in grids *per se*.

Transiency differed among grids with the lowest proportion of transients on grid A1. However, despite differences in density between years there was no difference in transiency. Differences in transiency, therefore, appear to be a result of different grids and not different density. Van Horne (1981), comparing demography of *Peromyscus maniculatus* between different seral stages of coastal coniferous forest, found no difference in proportion of transients between vegetation types despite differences in other demographic parameters.

Recruitment appeared to be negatively correlated with density. However, recruitment was similar among grids except maybe in 1981. In 1982 significantly more recruits on grid B1 may have been immigrants. Overall recruitment may be a function of density but the ratio of immature to mature recruits seemed to be function of vegetation type when density was high. Boonstra (1978) found that adult female *Microtus townsendii* inhibit recruitment, that is, where there is a high proportion of adult females recruitment is low.

Home range size for many species of small rodents decreases in size with increased density (Getz 1961, Sanderson 1966, Van Vleck 1969, Maza *et al*. 1973, Gaines and Johnson 1982). However, in this study home range size was smaller on the high density A grids compared to the low density B grids and home range size was not significantly different between years despite significant differences in density among years. Therefore, home range size, as well, appears to respond to vegetation type and not density. Van Horne (1981) found no difference in home range size of *Peromyscus maniculatus* between vegetation types. Van Horne had expected differences in home range size; however, her results were consistent with those of Metzgar (1971), who found that with increased density there was an increase in overlap between adjacent home ranges. I found that with increased density on a particular grid, the number of captures of adjacent mature female voles at the same trap station increased. This may indicate that overlap increased.

Although the energy demand during pregnancy for a vole is minimal (Migula 1969, Kaczmarski 1966), one might expect differences in litter size between vegetation types as found by Krohne (1980) for *Microtus californicus*, but such was not the case for

Clethrionomys gapperi.

It appears that the differences in demography and home range size among the grids were generally not a result of differences in density but rather a result of the vegetation type found on the grids. These differences have been summarized in Table 19. Based on density, persistence, transiency, recruitment and home range size of *Clethrionomys gapperi* the two major vegetation types represented on the A and B grids can be considered distinct habitats of populations of *Clethrionomys gapperi* in the Mitsue study area. The vegetation type on grid A2 was intermediate between the vegetation types on grids A 1 and B 1 and the voles appeared to respond to it in that fashion. However, MNA was lowest of all on grid B2 yet TAXMAP placed grid B2 closer to grid A2 than to B 1.

What is it about the grids that make some more favourable to voles than others? Miller and Getz (1972, 1973) found that at the southern edge of the range of *Clethrionomys gapperi*, in southern Connecticut, voles were limited by moisture availability. High densities of voles were only found in coniferous swamps. However, further north in Vermont, density was not correlated with moisture but rather with amount of debris, that is, fallen trees, dead branches and rocks. Debris was of secondary importance to *Clethrionomys gapperi* in southern Connecticut. Density of voles in both Connecticut and Vermont was not correlated with herbaceous cover. Iverson and Turner (1973) found that density of *Clethrionomys gapperi* in Manitoba was correlated with shrub diversity. In this study shrub diversity was high on the A grids and low on the B grids but what the diversity of shrubs has to do with voles neither Iverson and Turner (1973) nor I know. The A grids also had much debris thus supporting Miller and Getz (1972, 1973). Miller and Getz (1972, 1973) argued that in the south voles are limited by water because of high ambient temperatures and an inefficient kidney, whereas in the north water is not limiting and cover is important because of high predator pressure. Water would not be limiting in the Mitsue study area because there was often standing water on the grids, but as far as predator pressure on the study area, I know nothing. During the study I only caught 4-5 Shorttail Weasels (*Mustela erminea*). However, populations of *Clethrionomys gapperi* in the Mitsue study area appear to respond to the vegetation types as a continuum from deciduous (high Darwinian fitness) to coniferous

Table 19. Differences in demographic parameters and home range size between grids A1, A2 and B1.

Parameter	Grid A1	Grid A2	Grid B1
DENSITY	HIGH	HIGH	LOW
PERSISTENCE	HIGH	MEDIUM	LOW
overwintered	HIGH		HIGH
young of year	HIGH		LOW
overwintered female	SAME BETWEEN YEARS		DIFFERENT BETWEEN YEARS
TRANSIENCY	LOW	MEDIUM	HIGH
RECRUITMENT (Imm/Total) at high density	HIGH		LOW
HOME RANGE SIZE	--------SMALL---------		LARGE
LITTER SIZE	----------SAME----------		

(low Darwinian fitness). But let me reiterate - although I call the habitat types deciduous and coniferous, this distinction is not necessarily the factor the voles respond to.

Spacing behaviour of *Clethrionomys gapperi*: I The natural situation

Introduction

Spacing behaviour I define as a form of social behaviour that has the effect of distributing organisms in space in a non-random manner through some form of mutual repulsion. If there is a lower limit to the amount of space an organism requires for maintenance and reproduction, that is, at a certain density all suitable space is occupied and no more organisms can squeeze in and obtain space, then spacing behaviour acts to limit density.

Spacing behaviour has been invoked as a density regulating mechanism in *Clethrionomys glareolus* (Bujalska 1970, 1973), and Mihok (1979) showed that female *Clethrionomys gapperi* have exclusive home ranges, as revealed by captures in multiple-capture traps on live-trapping grids. Thus spacing behaviour may be operating in this species. Although exclusivity is best arrived at by the use of bio-telemetry (see for instance Madison 1980b), bio-telemetry is not always feasible, and data from live-trapping studies can be collected and analysed in such a fashion as to indirectly [illegible] questions about spacing behaviour, and whether spacing operates in density re[illegible]

In this chapter I try to answer, from live-trapping results, the following questions about northern populations of *Clethrionomys gapperi*:

1) Are home ranges of *Clethrionomys gapperi* exclusive?

2) Do home range locations shift with time?

3) Does home range size change with density?

4) Do mature *Clethrionomys gapperi* disperse?

5) With density increase, does a live trapping grid become saturated with mature female *Clethrionomys gapperi* ?

Methods

The data for this chapter come from censuses of *Clethrionomys gapperi* on three grids (A1, A2 and B1) in 1980, 1981 and 1982 (see **Demography of *Clethrionomys gapperi* in two diverse habitats**).

All estimates of home range size were based only on animals caught at least 5 times and for which 80% of the capture points occurred inside the perimeter of traps stations on live-trapping grids. In order to determine whether or not home range size changed with density the range length technique (Abramsky and Tracy 1980) which is based on the maximum distance between two capture points for each animal was used as an index of home range size.

To determine whether or not mature voles that had been established on an area would disperse, the following assumptions were made: 1) voles caught during rotas one and two were considered to be the original group of animals on the grid and were therefore not considered in the analysis, 2) all other animals caught were divided into two age classes: A) voles weighing 20 g or more were considered immigrants that had matured elsewhere and had been reproductively active before they were caught for the first time on the grid, and B) voles weighing less than 20 g were considered either immigrants that had not matured elsewhere, or recruits born on the grid. Voles weighing 20 g or more at first capture are therefore considered possible dispersers that had already been established on a home range.

Home range size estimated by the exclusive boundary strip method (Stickel 1954) was used to determine the number of mature females on breeding home ranges to be expected on the grid. The number of actual females on breeding home ranges was determined by summing all mature females in rota r as well as females immature in rota r that were present, mature and on the same site in rota r+1.

Results

If animals have exclusive home ranges (territories) then one would expect that two or more different individuals of the same sex would seldom be caught at the same trap site during a particular rota. Two or more mature females were seldom caught at the same trap site during any rota, especially in the low density year, 1980 (Table 20).

Table 20. Comparison of the percentage of trap stations at which two mature males or two mature females were caught during any rota, during a high (1982) and a low (1980) density year.

		Mature Male	Mature Female	G	Prob.
Coniferous Habitat	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		
Prob.		*	NS		
Deciduous Habitat	1980	10.8 [1] (148)	4.6 [3] (110)	3.03	NS
	1982	27.6 [2] (340)	11.2 [4] (214)	15.29	***
G		12.44	3.75		
Prob.		***	*		

1- G=1.64, NS
2- G=6.01, *
3- G=0.12, NS
4- G=0.06, NS

Different mature males were caught at the same trap-site during any rota more often than females but the difference was only significant in deciduous habitat in the high density year, 1982 (Table 20). Percentage of capture of different individuals of either sex at the same trap-site during a particular rota increased significantly with density, except for females in coniferous vegetation type (Table 20). Only for mature males and only in the high density year, 1982, were different individuals caught more often at the same trap-site in deciduous than in coniferous habitat (Table 20).

This type of analysis of space use does not paint the true picture, however, as captures of mature males often revealed extensive overlap with each other, whereas when different mature females were caught at the same trap station, that trap station was peripheral to both.

The more trap stations found within the home range of an animal the more captures are necessary for the animal to reveal its home range. *Clethrionomys gapperi* males have significantly larger home ranges than females but male home range size did not differ between grids whereas female home range size was significantly larger in coniferous vegetation than in deciduous vegetation (see **Demography of *Clethrionomys gapperi* in two diverse habitats**). For the following analysis therefore, males on all grids were lumped but females from deciduous and coniferous vegetation types were treated seperately. There was a positive linear relationship between the length of time that a mature animal was present over the breeding season and the number of different trap stations at which it was caught for both males ($Y=1.34+1.38X$, $R^2=0.61$, Appendix IIa) and females, in both deciduous (grids A1 and A2, $Y=3.11+0.49X$, $R^2=0.27$, Appendix IIb) and coniferous (grid B1, $Y=0.64+1.13X$ $R^2=0.70$, Appendix IIc) vegetation types (Table 21). The difference in slope of the regression between males and females on grids A1 and A2 was significant ($t=4.07$, $df=94$, ***). Over running four week periods (3 rotas) a positive linear relationship existed in three out of five cases for males but did not exist for females in deciduous vegetation type (Table 21). There were not enough data to do a similar analysis for females in coniferous vegetation type (Table 21). Two of 13 females and five of 10 males that were caught on six consecutive rotas showed significant changes of "activity center" (see **Methods, Demography of *Clethrionomys gapperi* in two diverse habitats** for definition) between the first set of three rotas and the second

Table 21. Regression of number of different trap stations a vole was caught at against the number of rotas the vole was alive for (calculated for all rotas and running sets of 3 rotas).

Rotas	Slope	R^2	F	P
		Male (Grids A1, A2 and B1)		
2-8	1.38	0.61	84.73	0.000
2-4	1.70	0.46	22.70	0.000
3-5	1.07	0.23	9.69	0.004
4-6	0.40	0.02	0.57	0.456
5-7	1.16	0.11	2.15	0.160
6-8	2.20	0.31	6.68	0.021
		Female (Grids A1 and A2)		
2-8	0.49	0.27	14.71	0.000
2-4	0.35	0.06	1.68	0.206
3-5	0.48	0.06	1.20	0.287
4-6	1.27	0.25	4.56	0.051
5-7	0.58	0.06	0.55	0.480
6-8	-0.50	0.03	0.22	0.651
		Female (Grid B1)		
2-9	1.13	0.70	34.76	0.000

set of three rotas but the difference between males and females was not significant (G(adj.)=0.75, NS).

Home range size as measured by range length was not a function of density of mature females in deciduous habitat (Y=26.8+0.0004X, R^2= 0.002, Appendix IIIa) or in coniferous habitat (Y=48.4-0.006X R^2=0.12, Appendix IIIb).

Animals immigrating onto a grid may either settle on the grid first and then start to enter traps or they may enter traps as they move onto and across the grid. The former appears to be the case, especially for females, as only a low proportion of animals (28.5% for males and 12.2% for females) showed a shift in location of more than two trap stations (40 m) between the site of first capture and subsequent captures (Table 22). Therefore, if new animals show up randomly on the grid one would expect the frequency of first capture by trap band to be similar to the ratio of number of traps in each band of traps. In a 10x10 array of trap stations there are five successive trap bands with a ratio of traps from outer to inner band of 0.36, 0.28, 0.20, 0.12 and 0.04. In the 13x12 array of trap stations of grid B1 in 1982 the ratio of traps is 0.29, 0.24, 0.19, 0.14, 0.09 and 0.04.

The frequency of first capture by trap band of new animals by age class, sex and grid is presented in Table 23. Female voles, greater than or equal to 20 g, were caught disproportionately in the outer band of traps (Table 23). Only on grid A2 did voles of both sexes less than 20 g depart significantly from the expected frequency (Table 23). When the frequencies of first capture of new males and females less than 20 g are summed for grids the frequencies depart significantly from expected (Table 23). More voles than expected are captured in the outer band of traps, which is generally recognized as edge effect (see Appendix I). The summation of frequency of first capture of new females greater than or equal to 20 g for all grids is significantly different from expected whether the expected is calculated from the number of traps in each trap band, or on the combined frequency of captures per band of males and females weighing less than 20 g (Table 23). A similar treatment of males weighing greater than or equal to 20 g was not significant (Table 23).

If spacing behavior of mature female voles operates in density regulation then one would expect the number of mature females to reach a plateau even while the total

Table 22. Percentage of voles that shifted location between first capture and subsequent captures by more than 2 trap stations.

	A1		A2		B1		Average	
	M	F	M	F	M	F	M	F
1980	32.3	15.6	28.3	8.3	22.7	15.2	27.8	13.0
1981	33.3	14.7	32.4	13.3	33.3	14.3	33.0	14.1
1982	14.8	10.3	--[1]	--	34.8	8.7	24.8	9.5
Average	26.8	13.5	30.4	10.8	30.3	12.7	28.5	12.2

1-Voles on grid not enumerated.

Table 23. Trap band in which Clethrionomys gapperi weighing 20 g or more or less than 20 g were first caught.

Grid	Sex		Weight	Perimeter 1	2	3	4	5	6	D	P
A1	F		≥20g	21	5	3	1	0	-[1]	0.34	**
			<20g	41	24	13	7	4	-	0.10	NS
	M		≥20g	5	0	0	0	0	-	0.64	NS
			<20g	53	33	22	21	3	-	0.04	NS
A2	F		≥20g	13	4	1	2	0	-	0.29	*
			<20g	37	10	8	7	0	-	0.22	**
	M		≥20g	8	4	2	0	0	-	0.21	NS
			<20g	53	26	12	5	3	-	0.18	**
B1	F		≥20g	8	0	0	1	0	-	0.53	**
			<20g	16	11	11	4	5	-	0.07	NS
		1982	≥20g	5	3	0	0	0	0	0.32	NS
			<20g	8	4	1	1	2	1	0.24	NS
	M		≥20g	3	2	1	1	1	-	0.09	NS
			<20g	17	11	8	4	3	-	0.03	NS
		1982	≥20g	2	2	2	0	0	0	0.22	NS
			<20g	12	4	3	2	3	1	0.22	NS
All			<20g	217	121	74	43	20	-	0.10	**
All	F		≥20g	42	9	4	4	0	-	0.35	**
										0.29	**[2]
All	M		≥20g	16	6	3	1	1	-	0.23	NS
										0.13	NS[2]

1-Perimeter does not exist.
2-All observations <20g used as standard.

number of females was increasing. In 1980 there was no indication that density of mature females levelled off whereas density of all females continued to increase (Fig. 6). In 1981 there was an indication that density of mature females was starting to level off at about 22 individuals on grid A1 and 19 on grid A2 (Fig. 7). The clearest expression of the prediction occurred on grid A1 in 1982 (Fig. 8), 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. 8). The density of mature females on grid B1 in 1982 did not show a substantial increase until rota 5, the period when the density of mature females stabilized in deciduous habitat (grid A1). In 1981 the density of mature females on grid B1 was low and stable until rota 7 after which it appeared to increase slowly as did the total density, while the rate of increase of mature females on grid A1 was decreasing and A2 was declining (Fig 7).

After rota 8 no young females of the year appeared to mature sexually during the three years of the study. So apparently only in 1982 and only in deciduous habitat did the density of mature females reach saturation of approximately 26 animals on the 4 ha grid.

A second estimate of saturation density can be obtained by estimating home range size and determining the number of home ranges on a 4 ha grid. Home range size of mature females as calculated by the exclusive boundary strip method was 0.26 ha (Table 24). The number of female home ranges in 4 ha should therefore be between 15 and 16, rather than 26: but the number of mature females stabilized at about 26. From Appendix I, when the ratio of grid size to home range size is 16 the animals on the grid are overestimated by a factor of 1.6. 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 home range size for mature females was 0.33 ha (Table 24) one would have expected approximately 21 mature females when that grid was 4 ha in size, and approximately 28 mature females when it was 6.24 ha in size. In 1982 the maximum density of mature females on grid B1 was 22 which was well below the predicted saturation level carrying capacity.

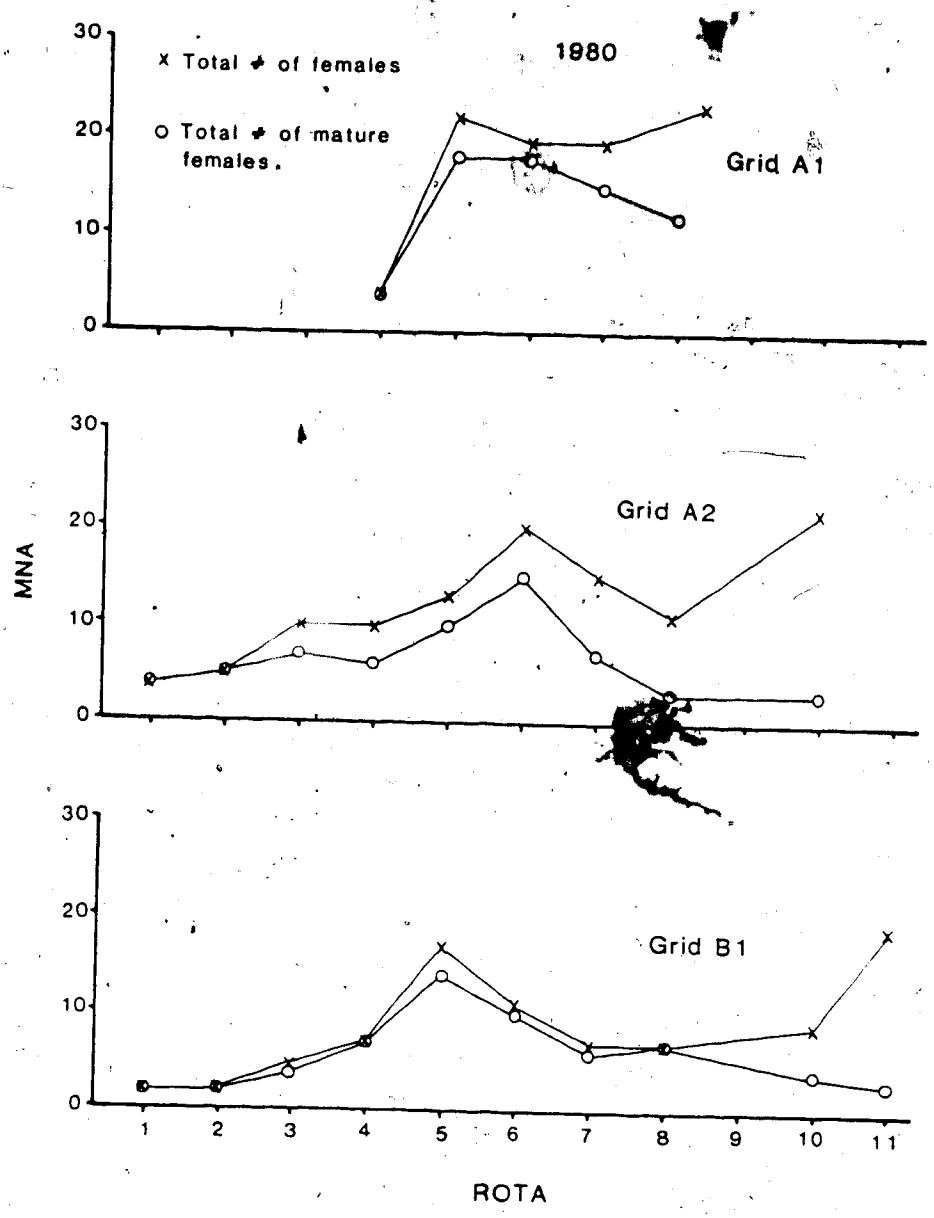

Figure 6. Density change of total number of female and mature female *Clethrionomys gapperi* on three grids in 1980.

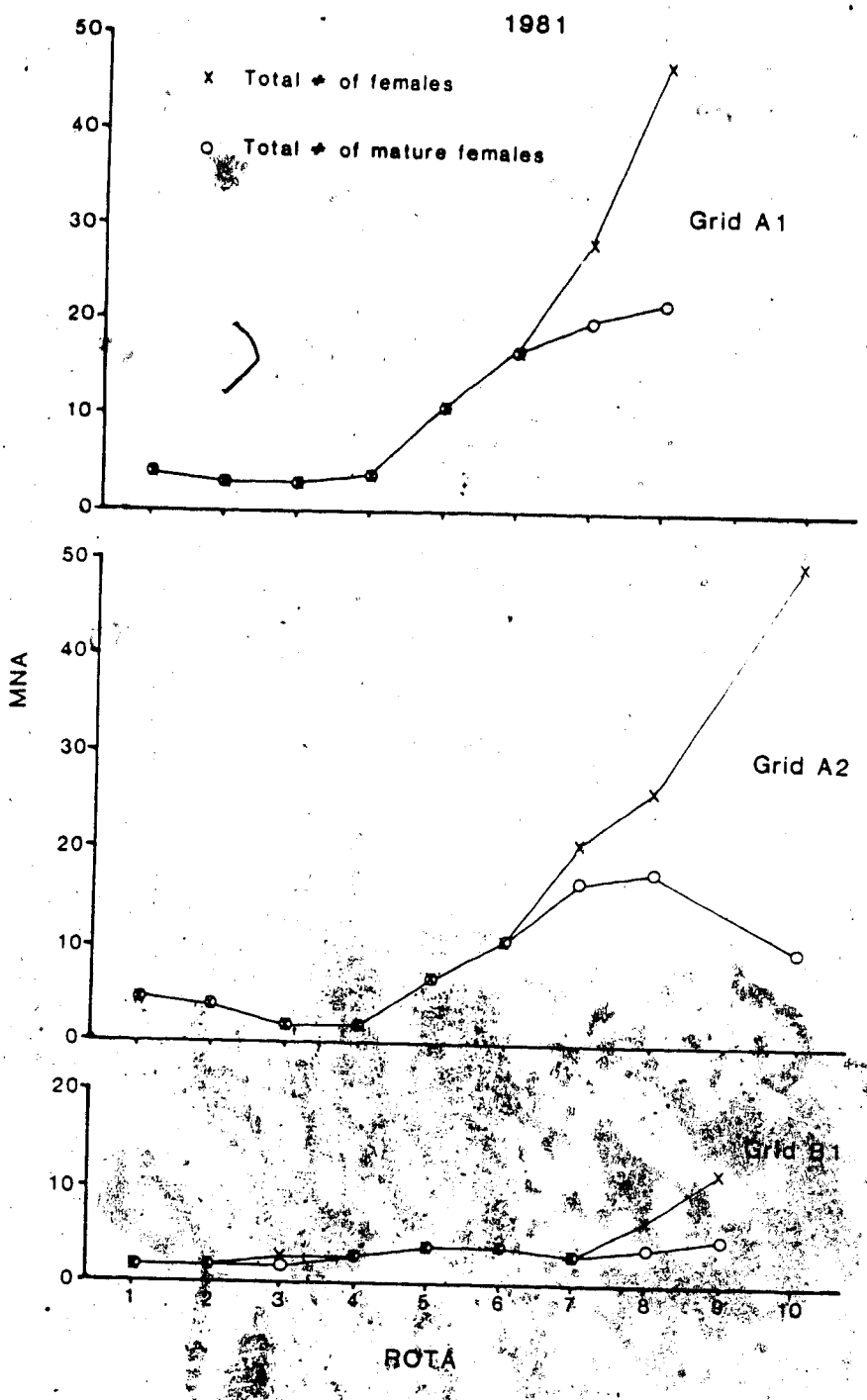

Figure 7. Density change of total number of female and mature female *Clethrionomys gapperi* on three grids in 1981.

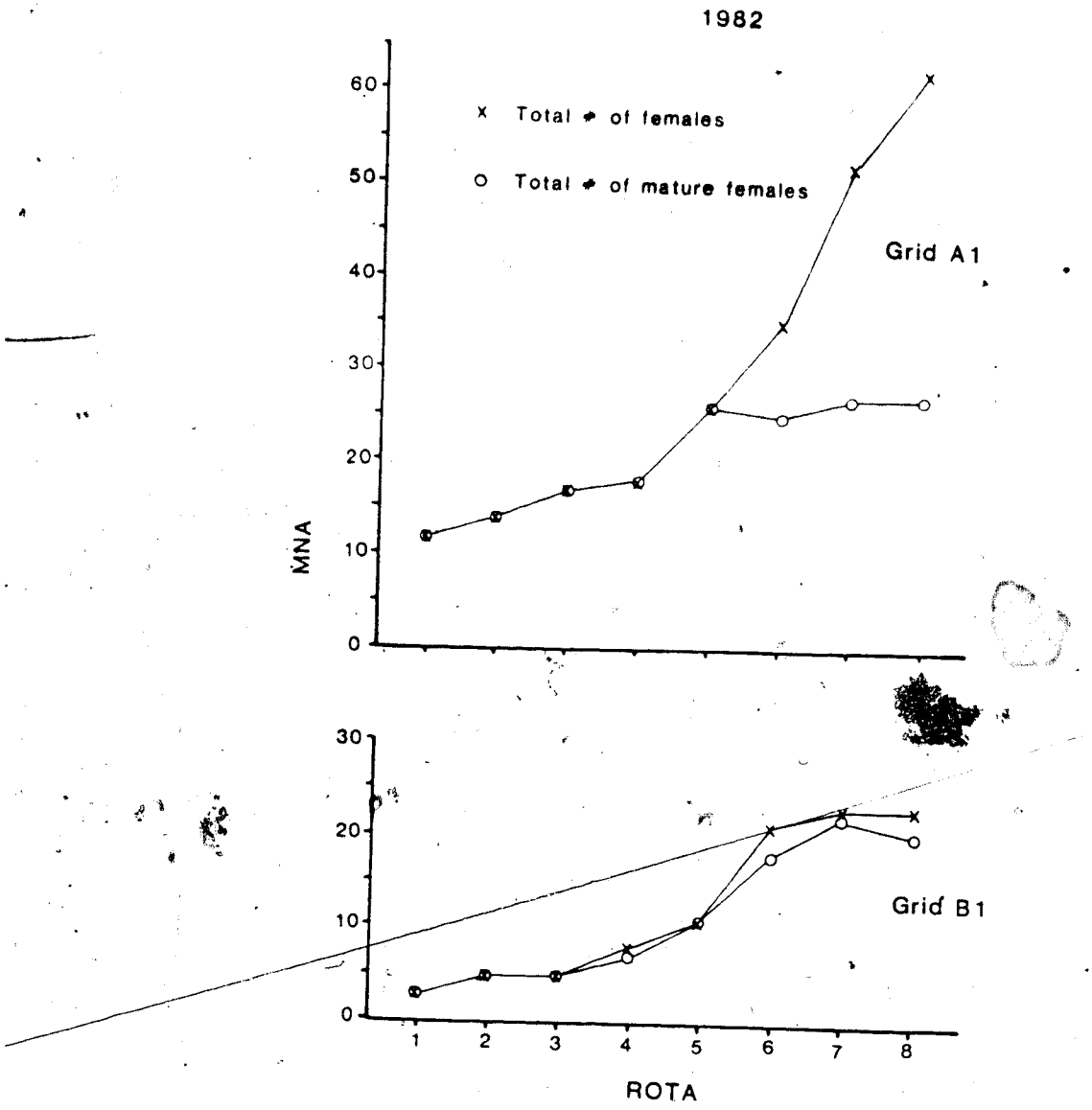

Figure 8. Density change of total number of female and mature female *Clethrionomys gapperi* on three grids in 1982.

Table 24. Estimate of female Clethrionomys gapperi home range size based on the exclusive boundary strip method.

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

Discussion

There have been many studies of small mammals by means of live-traps placed in a grid pattern, but such studies are fraught with problems when one wants to understand use of space by the animals on the plot. For instance, what is the most appropriate study plot size (Bondrup-Nielsen 1983)? What is the optimum trap spacing that will allow the animals to express their movements (Nikitina 1965)? How many captures are required for reliable estimates of home range size (Stickel 1954, Mazurkiewicz 1971, Tanaka 1972, Myllymaki 1977)? That there are numerous methods for calculating home range size has already been alluded to in the **Methods** section (see **Demography of *Clethrionomys gapperi* in two diverse habitats**).

Obviously, data from live-trapping grids on use of space by animals can only be used to hint at what is going on. Experimentation and use of bio-telemetry is necessary to elucidate more accurately how space is used by different age classes and sexes of animals.

As stated in the introduction this analysis concerns mainly female voles for it is in this sex that spacing behaviour may act in density regulation (Kalela 1957, Koshkina 1965, Bujalska 1970, 1973, Mihok 1979). Mihok (1979), using multiple capture traps, recorded only 6% multiple captures of two mature females and recorded only 15 cases (%?) of two mature females caught at the same trap site in any one rota. As well, Mihok (1976, 1979) found that overwintered females were dominant over all other age and sex classes. From this evidence Mihok suggested that female *Clethrionomys gapperi* maintain exclusive home ranges; however, this is not apparent to me. In this study the percentage of captures of two or more mature females at the same trap site during any rota was low especially in coniferous vegetation type and did not increase with density within vegetation type. From this I would infer that there was probably some overlap of mature female home ranges. That there was less overlap in coniferous vegetation is probably a result of the even dispersion of the few mature females. Bujalska (1970, 1971, 1973) working with *Clethrionomys glareolus* on a 4 ha. island in Poland found that overlap of mature female home ranges increased with density of mature females; however, the density of mature females on the island levelled off each year of her study at about 60 individuals which is far more than the maximum number of mature females in

my study.

The home range size of female voles in this study did not appear to change with density as has been found to be the case with some other small mammals (Forsyth and Smith 1973, Maza *et al*. 1973, O'Farrell *et al*. 1975). However, Gaines and Johnson (1982) found that range length was not an accurate index of home range size. Mares *et al*. (1982), in a detailed study of spacing of *Tamias striatus* in northwestern Pennsylvania, found that home range size was not a function of density but of food. This is what one would expect since the optimization of reproductive success involves maximizing benefits and minimizing costs associated with increased territory or home range size (Maynard-Smith 1974). This is supported by findings of Smith (1968) that red squirrel, (*Tamiasciurus*) territory size is a function of food quantity. Myllymaki (1977) found no evidence that home range size of *Microtus agrestis* was a function of density and suggested, based on weak evidence, that home range size was a function of food. Home range size as estimated in this study by mean area radius and mean activity radius did not differ significantly between years but did differ between vegetation types.

In some species of rodents mature females change or shift home range after weaning litters (Tast 1966, Brooks and Banks 1971, Myllymaki 1975, 1977, Jannett 1980). This is thought to be a strategy to increase fitness in temporary environments (Tast 1966, Lidicker 1975), and Stenseth (1978) has shown by modelling that r-strategists compared to alpha-strategists should be more likely to select a new nest when another litter is imminent (whether Stenseth equates nest with home range is unclear). It can be argued that forests are relatively stable environments and it is therefore not surprising that only 2 of 13 mature females changed activity center between the first three rotas and the subsequent three rotas for which they were alive. Also, the analysis on number of traps used with time indicates that female *Clethrionomys gapperi* show only minor shifts over time. However, I know nothing about nest placement within the home range and females may indeed change nest with each litter.

For several *Microtus spp.* adults are believed to disperse, although when this evidence comes from removal grids I question the results because edge effect is generally not considered (Myers and Krebs 1971, Hilborn and Krebs 1976, Krebs *et al*. 1976, Tamarin 1977, Fairbairn 1978). However, mature female *Clethrionomys gapperi* in this

study did not appear to disperse as revealed by non-random settlement of mature females on live trapping grids. The majority of mature female recruits that had most likely reproduced elsewhere first were caught in the outer band of traps. These were likely females peripheral to the grid that by chance got caught. It therefore appears that once a mature female is settled on a home range she is not likely to show a significant shift over a short period nor to disperse.

All this evidence suggests one conclusion: that spacing behaviour of female *Clethrionomys gapperi* may act in density regulation. Only in 1982 and only on grid A1 did the number of mature females stabilize for a 6 week period. It so happened that this density corresponded to the number one would have expected based on home range size, grid size and an allowance for edge effect. Mihok (1979) did not find evidence that female spacing behaviour acted in density regulation but the density on his plot was low and may have been below saturation, in which case one would not expect to see regulation.

It appears then that under circumstances of relatively high density, regulation of density of mature females, through spacing behaviour, is operating in the same way as described for *Clethrionomys glareolus* (Bujalska 1970). I must reiterate, however, that this finding is based on data from live-trapping and must be viewed with caution. To confirm that spacing behaviour of females operated in density regulation needs to be tested experimentally, and the following two chapters deal with such experiments.

Spacing behaviour of *Clethrionomys gapperi*: II Effect of removal of mature animals

Introduction

That there can be far more potential breeders in a population than actually breed was first documented dramatically by the experiments of Stewart and Aldrich (1951) and Hensley and Cope (1951). These investigators enumerated 50 species of birds in a 16 ha plot and then shot as many birds as possible. At the end of a three week period they had removed three times as many birds as they originally counted. This phenomenon now appears general for a variety of organisms (Wilson 1975:276). Does this kind of evidence imply that spacing behaviour is acting in preventing potential breeders from breeding?

Watson and Moss (1970) drew up a set of conditions that they felt had to be satisfied in order to show that territorial behaviour limits breeding populations. Klomp (1972) reviewed those conditions and found them restrictively narrow. He reformulated the conditions as follows: 1) if potential breeders are excluded by breeders already in an area and 2) if the proportion of potential breeders becoming surplus tends to rise with an increase of potential breeders, then the density of the population is limited by territorial behaviour (Klomp 1972).

Most birds are obviously territorial and many removal studies done have tested whether territorial behaviour can limit the density of breeding populations (see Klomp 1972). Krebs (1966) and Smyth (1968) were some of the first investigators to carry out removal studies of small mammals, not for the purpose of studying spacing behaviour but rather to create dispersal sinks. However, they had problems maintaining voles at low density because of immigration which hints at the possibility that spacing behaviour might have been operating.

Some early studies of the effect of removals of *Clethrionomys* spp. involved males (Elliott 1969, Watts 1970) and were generally inconclusive. Bujalska (1973) carried out removals of females, the more appropriate sex since female *Clethrionomys*

spp. use space more or less exclusively.

Small rodents are secretive and consequently are not good candidates for behavioural observations in the field. It is therefore not possible to observe whether female *Clethrionomys gapperi* defend home ranges (territories) and whether potential breeders are prevented from settling by adult females already present on an area. A removal experiment was therefore carried out to test the hypothesis that spacing behaviour of mature females limits the density of mature females in northern populations of *Clethrionomys gapperi*.

Methods

Three woodlots near Edmonton, Alberta, each approximately 4 ha in size were chosen to serve as male removal, female removal and control plots. All three were surrounded by open fields, and all were similar in vegetation type to grid A1 in the Mitsue study area (see **Demography of *Clethrionomys gapperi* in two diverse habitats**). In 1981 voles on the male and female removal areas were enumerated between 21 and 25 July. In 1982 census of voles on the female removal and the control areas took place between 18 and 20 July. Approximately 120 Longworth live-traps, set out in a grid pattern were used on each area and animals caught were processed as described under **Study area and methods**. At the time of live-trapping (initial census) approximately half the mature individuals of the appropriate sex were removed by selecting every second qualifying animal caught. Animals on the control area were not enumerated during the initial census in 1981 but were in 1982.

Approximately two weeks after removals, between 9 and 18 August in 1981, and between 2 and 5 August in 1982, voles on the removal and control areas were snap trapped and necropsied as described under **Study area and methods**.

Results

In 1981, 40 *C. gapperi* were counted on the male removal area of which 16 were mature males and of those 8 were removed; on the female removal area 30 *C. gapperi* were present and of those, 12 were mature females of which 8 were removed (Table 25).

On the male removal area in 1981, persistence of marked animals was 40% and there were two fewer animals caught in snap traps than were enumerated 2 weeks previously (Table 25). Of 19 males caught only 2 were mature, and of 19 females caught, 10 were mature, a drop of 2 from 12 mature females present 2 weeks before.

On the female removal area in 1981, persistence of marked animals was 55% (Table 25). Of 34 females 22 were mature, which was an increase of 550% over the 4 that were left after removal. Six females, four mature and two immature, were left on the female removal area after initial enumeration. Of these, four survived the two week period - three of the mature females and one of the immatures which was now mature. The rest of the females (ie. 30) were new individuals that had either moved onto the area or were too young at the time of the initial census to be caught. Of the 30, 6 were in age class 3 and were mature. Of the remaining 24 only 12 were mature (2 in age class 1 and 10 in age class 2) and 7 of them were pregnant for the first time (Table 26).

Only one new mature male showed up on each of the male and female removal plots after the initial census. As well, on both plots density of mature males decreased from the number released during the initial census. However, on the female removal plot the density of females went up from the original number censused, although on the male removal area density of females decreased slightly (Table 26).

The ratio of mature to immature females on the female removal plot were significantly higher than on the control plot for age classes 1 and 2 (Table 26, $X^2 = 11.30$, ** and $X^2 = 6.27$, * respectively). The ratio of mature to immature males in age classes 1 and 2 was not significantly different between control and female or male removal plots (Table 26).

In 1982, 55 *C. gapperi* were enumerated on the female removal area (the same area as the year before) of which 26 were mature females and of those 12 were removed; on the control area (the same area as the year before) 92 *C. gapperi* were live-trapped and all were released except 2 that died in traps (Table 27). Persistence of

Table 25. Results of removal of mature Clethrionomys gapperi in 1981.

			Live-trap census		Snap-trap census		
			Caught	Released	Recaptured	New	Total
Male Removal	Mature	F	13	12[4]	6	4	10
	Immature	F	7	6[2]	0	9	9
	Mature	M	14	6	1	1	2
	Immature	M	6	6	5	12	17
	Total		40	30	12	26	38
Female Removal	Mature	F	12	4	3+1[1]	18	22
	Immature	F	2	2	0	12	12
	Mature	M	12	11[2]	7	1	8
	Immature	M	4	3[2]	0	14	14
	Total		30	20	11	45	56
Control	Mature	F					16
	Immature	F					19
	Mature	M					8
	Immature	M					33
	Total						76

1- animal was immature at time of live-census
2- fewer released due to trap-death

Table 26. Age distribution of females and males from female removal and control areas in 1981 approximately two weeks after removal of a proportion of mature individuals.

		Age class				Total
		1	2	3	OW	
		Females				
Control	Mature	0	3	11	2	16
	Immature	15	4	0	0	19
Female Removal	Mature	2	13	6	1	22
	Immature	7	5	0	0	12
Male Removal	Mature	0	6	1	3	10
	Immature	6	3	0	0	9
		Male				
Control	Mature	0	0	1	7	8
	Immature	8	25	0	0	33
Female Removal	Mature	0	3	2	3	8
	Immature	4	10	0	0	14
Male Removal	Mature	0	0	0	2	2
	Immature	3	14	0	0	17

Table 27. Result of removal of mature female Clethrionomys gapperi in 1982.

		Live-census		Snap-trap-census		
		Caught	Released	Recaptured	New	Total
Female Removal	Mature F	26	14	13	5	18
	Immature F	6	6	5	16	21
	Mature M	15	15	11	2	13
	Immature M	8	8	4	29	33
	Total	55	43	33	52	85
Control	Mature F	34	33[2]	19	13	32
	Immature F	12	12	5	17	22
	Mature M	13	13	7	2	9
	Immature M	33	32[2]	16	22	38
	Total	92	90	47	54	101

1- animal was immature at time of live-census
2- fewer released due to trap-death

marked animals on the control area in 1982 was 52% and on the female removal area was 77% (Table 27). Between the initial census and the snap-trap census the density on the female removal area doubled because of an increase of immatures, but on the control area density increased by 11% (Table 27). On the female removal area 14 mature females were left after removal. Only 18 mature females were snap trapped (13 marked, 93% persistence) which is only 4 more females than were left and 8 fewer mature females than were initially present. Of the five mature females that were new, three were pregnant for the first time and two had new placental scars.

In 1982 few females became mature in the 2-week period between initial and final trapping. The ratio of mature to immature females in age class 2 on the removal area was not significantly different from that of the control (Table 28). On the female removal area there were four females in age class 2 that were classified as immature with opaque rather than transparent uteri whereas on the control plot there were no females classified as such. I found that an opaque uterus may indicate commencement of maturity.

Discussion

The interpretation of the experiments involving removal of mature voles is far from straightforward. A census of the voles on the control plot was not made during the initial census period in 1981 but was made in 1982. However, I do not believe that this difference was of any consequence. During the first live census of a population of voles some individuals may not be caught, that is, trappability is low. However, when voles on an area are snap-trapped, the captured individuals are removed and consequently the presence of dominant individuals, thought to be a factor in preventing subordinate individuals from entering traps (see for instance Kikkawa 1964) is no longer a factor. Furthermore, the snap traps were in operation for four days and on the final day only recently weaned individuals were caught.

The results from the male removal plot can be interpreted in at least two ways. Altogether 40 voles were enumerated during the initial census, 30 were released and 38 were snap-trapped. Does this indicate a population at a stable density? The number of mature females decreased slightly but was this a significant drop in density or could the

Table 28. Age distribution of females and males from female and male removal and control areas in 1982 approximately two weeks after removal of a proportion of mature individuals.

		Age class				Total
		1	2	3	OW	
				Female		
Control	Mature	0	5	16	11	33
	Immature	8	14	0	0	22
Female Removal	Mature	0	4	11	3	18
	Immature	5	16	0	0	21
				Male		
Control	Mature	0	3	0	6	9
	Immature	10	27	1	0	38
Female Removal	Mature	0	1	2	10	13
	Immature	16	17	0	0	30

density of mature females be said to be stable as well? The ratio of mature to immature females on the male removal plot was not significantly different from than on the control.

So if we accept the argument that the population was stable then the removal of mature males had no effect on overall density or on the females. That removal of mature males had no effect on the immature males may be a consequence of timing. That is, by late July early August the photoperiod may be such that immature males can no longer mature. On all plots, in both years, the density of mature males dropped slightly between the initial and last census and no immature males appeared to mature in the interim.

There is another possible interpretation of the results of the male removal experiment. The density on the female removal plot nearly doubled between the original enumeration and the period of snap-trapping. Why did density on the male removal plot not increase as well? Both plots were similar in vegetation type and were only separated by approximately 300 meters, although the male removal plot was quite irregular in shape with two long narrow extentions. So if we argue that the overall density and density of mature females should have increased, did it fail to do so because of the removal and lack of replacement of mature males? Elliott (1969), in a study of dynamics of *Clethrionomys gapperi* populations, found that mature females tended to leave areas from which mature males had been removed. Watts (1970), however, in a study of the effects of removal of mature male *Clethrionomys gapperi* found that immature animals were caught in live traps at an earlier age on the removal grid than on control areas. This caused an apparent increase in the density of immature voles although the number of immature voles on the male removal plot did not increase following removal of mature males.

On the female removal plot I do not think there can be any argument about the results. A removal of mature females was followed by a significant increase in the ratio of mature to immature females in age classes 1 and 2 compared to the control area in 1981. Bujalska (1973) obtained similar results in a similar study on *Clethrionomys glareolus*. Six mature females in age class 3 were caught for the first time during the second census. Did those individuals move onto the plot after the removals or were they missed during the initial census? Elliott (1969) found that a low proportion of

mature females dispersed and I found similar evidence (see **Spacing behaviour of *Clethrionomys gapperi*: I The natural situation**). If the six females were missed during the initial census, then the density of mature females during the initial census was minimally 18. 10 of these were released. During the second census 22 mature females were caught so the density of mature females was relatively stable over the experimental period. This assessment of the results does not alter the interpretation of the experiment but lends support for the first interpretation of the results of the male removal experiment. That is, the density of mature females was more or less stable over the experimental period on both removal plots.

The results of the female removal experiment in 1982 do not support the hypothesis that spacing behaviour acts in density regulation. On the control area the density of mature females decreased by 6% between the start and finish of the experiment. Therefore for all practical purposes the density of mature females was stable. On the female removal plot the density of mature females did not increase to the original level but was 31% lower than the initial number. Why did the population not respond in the same fashion as it did the year before or was 1981 an aberrant year? I believe that 1982 was the aberrant year and that there are at least two explanations for the observed response. The duration of the experiment was shorter by 5 days in 1982 than in 1981. Consequently the voles in 1982 may not have had a long enough period to respond. There was some evidence for this interpretation in that there were four immature females on the female removal plot with opaque uteri whereas there were no females on the control plot in that condition.

The results of the male removal experiment in 1981 and the female removal experiment in 1982 are unclear and open to interpretation. However, the female removal experiment in 1981 does support the hypothesis that spacing behaviour of mature females acts to regulate the density of mature females in populations of *Clethrionomys gapperi*.

Spacing behaviour of *Clethrionomys gapperi*: III Experimental manipulation of mature voles in enclosures

Introduction

One way of testing the hypothesis that spacing behaviour operates in density regulation is by carrying out removal experiments (Klomp 1972). An alternative method, if direct observations of animals cannot be made, is experimental manipulation of numbers of mature voles in enclosures.

Early experiments with voles in field enclosures (Krebs *et al.* 1969) revealed the importance of dispersal as a demographic characteristic of populations of small mammals. If dispersal was frustrated population density could increase dramatically (Boonstra and Krebs 1977). Consequently, experiments with voles in enclosures have generally addressed questions of dispersal (Krebs 1969, Myers and Krebs 1971, Beacham 1980), such questions as the effect of castrated males on populations (Gibbs and Jewell 1979) and habitat use (Wecker 1963, Hoffmeyer 1973, Grant 1975) have also been addressed. Saitoh (1981) used large enclosures in natural habitat of *Clethrionomys rufocanus* to determine the role of density in maturation of females.

Experiments with voles in enclosures must contend with the problem of animals escaping (see for instance Gibbs and Jewell 1979). This is especially a problem in long term studies and with enclosures in forests. Nevertheless a study in enclosures was undertaken to test the hypothesis that mature *Clethrionomys gapperi* at saturation prevent immature from maturing.

Methods

Four enclosures were constructed, two in deciduous vegetation type (Enclosures A1 and A2) and two in coniferous vegetation type (Enclosures B1 and B2). Pairs of enclosures had one side in common. The borders of the enclosures were cleared of all small trees, shrubs, herbs and debris to a width of 2 to 3 meters. Pieces of galvanized roofing tin 61 cm high by 91 cm wide sunk approximately 20 cm into the ground along the center of the swaths constituted the enclosure fence. Individual sheets were bolted together. Enclosures A1 and A2 were each 1 ha (100 x 100 m) in size, whereas enclosures B1 and B2 were each 0.56 ha (75 x 75 m) in size. Construction of the A enclosures was completed in early June 1980 and the two B enclosures were completed in early May 1981.

The enclosures were not totally 'leakproof' and voles could and presumably did escape, probably by jumping over or digging under the fence or by following subterranean tunnels. In 1981, the height of the fence was extended from approximately 40 cm to 60 or 70 cm by stapling strips of plastic to stakes hammered into the ground outside and flush with the fence, at 2 to 3 meter intervals. The bottom edge of the plastic was taped to the top of the tin. Trees up to one meter from the fence were wrapped with 30 cm wide plastic strips to prevent voles from climbing up and jumping over the fence if this was indeed a method by which they could escape. This made the B enclosures virtually 'leakproof'. To further increase the difficulty of escape, clay and/or sand was spread along the inner side of the fence and packed down in 1982. In spite of all precautions, however, the two A enclosures never became totally 'leakproof'.

A grid pattern of trap-stations was laid out in each of the two A enclosures (5x5=25) and two B enclosures (4x4=16). Each spring animals were trapped and removed from the enclosures by live-trapping followed by a period of snap-trapping. Similar live-trapping followed by snap-trapping was used to terminate each experiment in the enclosures. During each experiment the fences were checked daily to remove dead branches or trees that occasionally fell over the fence, and to repair any torn plastic.

Voles to be used in enclosure experiments were captured in the wild and kept in captivity (see **Study area and methods**). Litters born in captivity were weaned at 18 to 21 days of age. If the young of a litter were to be used in an enclosure experiment litter

mates were kept together in the same cage until initiation of the experiment, to retard maturation (Batzli *et al*. 1977). As far as possible only young of very recently weaned litters were used in enclosure experiments.

In 1980 the experiment in enclosures A1 and A2 was long term. On 11 June 1980 two mature males and two mature females were released in enclosure A1 and four mature males and four mature females were released in enclosure A2. On 14 June 1980 two immature males and two immature females were introduced into enclosure A1 and four immature males and four immature females were introduced into enclosure A2. Censuses of the two enclosures were then made during rotas 4 to 8 (17 June to 21 August). The two enclosures were cleared of all voles by snap-trapping during rota 11 (27 to 29 September).

Only short-term experiments (13 to 24 days in length) were conducted in 1981 and 1982. For each experiment a high density of mature adults was released in one enclosure and a low density of mature adults was released in the adjacent enclosure. For most experiments in 1981, young were introduced just prior to weaning, with their mother, in a nest box. In 1982 varying numbers of recently weaned voles, depending on availability, were released in the enclosures. If young were not released with their mother, care was taken not to release sister-sister or brother-brother pairs in any enclosure. Nor were young released in the same enclosure occupied by their mother. All animals released in the enclosures were individually identified by toe-clipping. The details of number, age and sex of animals used in different experiments appear in Appendix IV.

Results

In 1980 the density of voles in enclosure A1 fluctuated between 5 and 9 animals up to rota 8 and by rota 11, when the enclosure was trapped-out, there were 13 animals (Fig. 9). In enclosure A2 the density dropped and stabilized at approximately 9 animals up to rota 8, and by rota 11 there were still 9 animals. The density of mature females fluctuated around the number introduced into each enclosure up to rota 8 (1 to 3, average 2.2 in enclosure A1 and 3 to 6, average 4.3 in enclosure A2, Fig. 10). When all voles were trapped-out during rota 11 there was only one female vole in each enclosure that had been mature. The density of mature females in enclosure A2 was almost twice that in enclosure A1, however, the number of immatures that showed up in the population was not markedly different between the two enclosures. By rota 11 the density of voles was in fact higher in enclosure A1 than in enclosure A2 despite enclosure A1 being the one with the lower density of mature females during the summer.

Four enclosure experiments were conducted in 1981, one in the A enclosures and three in the B enclosures. The experiment in the A enclosures lasted 24 days. None of the young introduced, 13 in enclosure A1 and 15 in enclosure A2 were recaptured (Appendix IVa). Three new animals entered enclosure A1 and five new animals entered enclosure A2. There were three mature animals of each sex in enclosure A2 and in enclosure A1 there were four mature females and three mature males.

The first experiment in the B enclosures lasted 14 days (Appendix IVb). All mature adults released survived the duration of the experiment except for two mature females in enclosure B1 (Appendix IVb). Only one immature female was recaptured in the low density enclosure (B1) whereas none were recaptured in the high density enclosure (B2). Four males, immature when released, were recaptured, two in each enclosure and they all were mature (Appendix IVb). One immature female and four immature males, all new, were captured in the high density enclosure.

The second experiment in the B enclosures lasted 17 days (Appendix IVb). Here only enclosure B1 was used because of a lack of animals. All animals released were recaptured except for one mature female and one mature male. There was one new mature female. Three males released as immature were mature on recapture and one female released as immature had opaque uteri on recapture.

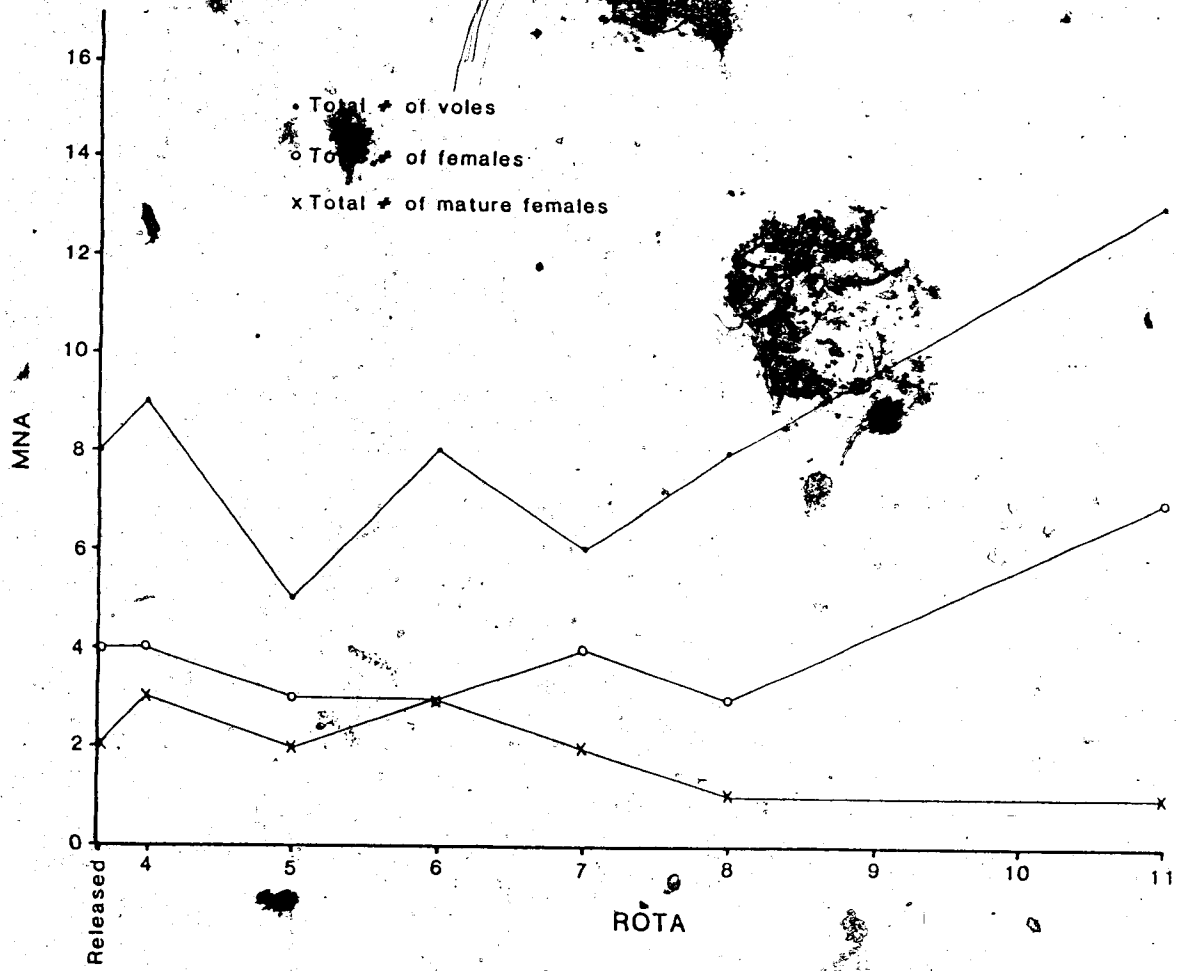

Figure 9. Density change of *Clethrionomys gapperi* after initial introduction in enclosure A1 in 1980.

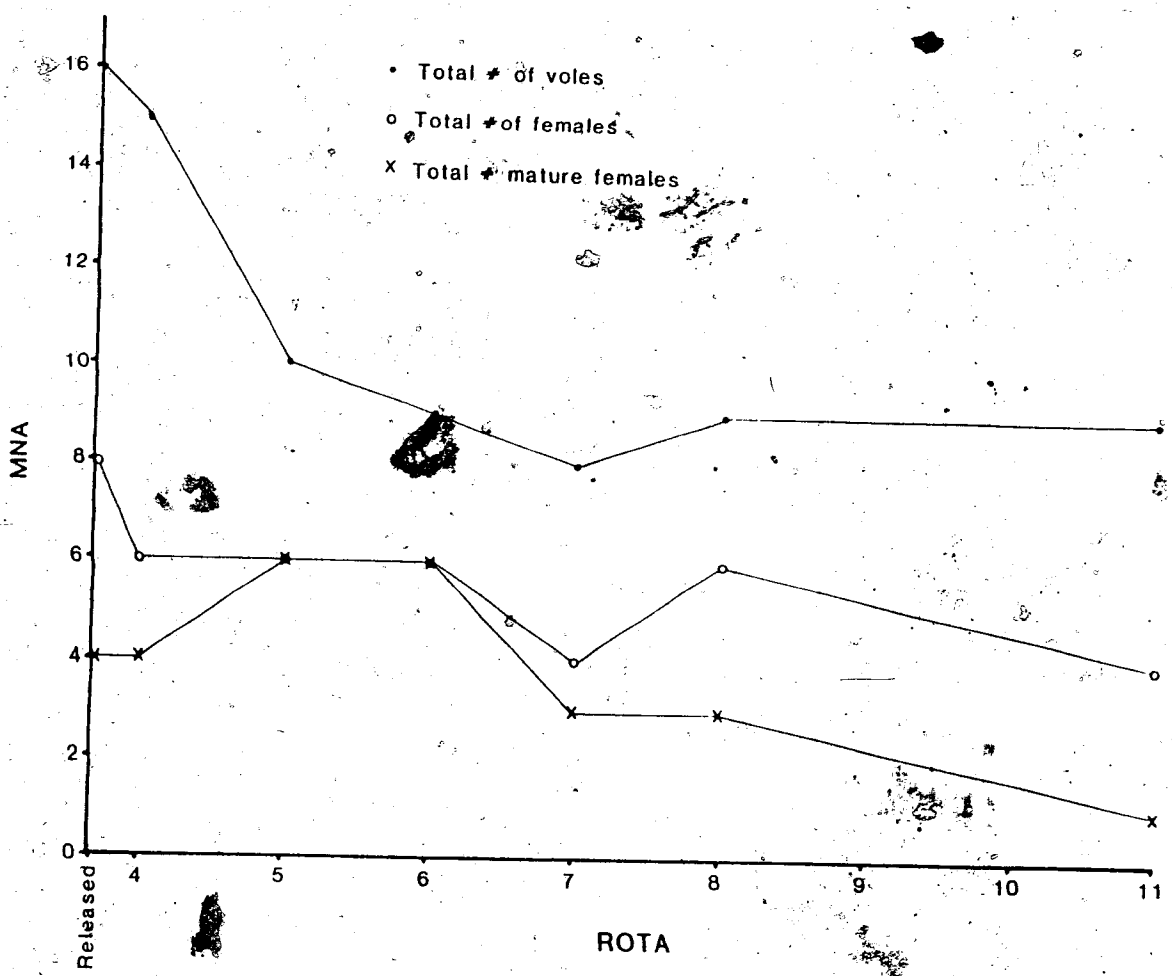

Figure 10. Density change of *Clethrionomys gapperi* after initial introduction in enclosure A2 in 1980.

The third experiment in the B enclosures was 21 days in length (Appendix IVb). Persistence was good. Of the mature adults released, only two males in enclosure B1 and one male in enclosure B2 were not recaptured. Of eight immature voles released in enclosure B1, two females and three males (immature) were recaptured and of eight immature voles released in enclosure B2, two males and two females (immature) were recaptured. Three new mature females and one mature male entered enclosure B2. New immature voles entered both enclosures, one female and one male in enclosure B1 and one female and three males in enclosure B2.

In 1982, six enclosure experiments were conducted, three in each of the A and B enclosures. Only adults were involved in the first experiment which lasted 13 days in the A enclosures and 14 days in the B enclosures (Appendix IVc, 29). This experiment was run mainly to test whether or not the enclosures were 'leakproof'. Some animals escaped from enclosure A1 (determined by trapping outside the enclosure) and some may have been killed by a Great Grey Owl (*Strix nebulosa*) that was seen inside the enclosure. Of ten mature females released in enclosure A1 only two were recaptured 13 days later and two new mature females had entered the enclosure. Of six mature males released only one was recaptured and there was one new individual (Appendix IVd).

No marked animals were captured outside the B enclosures. Of four animals released in enclosure B2 none was recaptured and of ten animals released in enclosure B1 only five were recaptured (Appendix IVc).

The second experiment using the A enclosures lasted 23 days (Appendix IVc). Fourteen new animals entered enclosure A1 and seven entered enclosure A2. Both mature voles released in enclosure A2 were recaptured but only three of five mature females and four of five mature males were recaptured in enclosure A1. In the high density enclosure (A1) only two of seven immature females were recaptured and both were pregnant. In the low density enclosure (A2) six of seven immature females were recaptured and five of them were pregnant. Only one of the immature males was recaptured in each enclosure and only the one in enclosure A2 had matured. At the end of the experiment there were 10 mature females in enclosure A1 and seven mature females in enclosure A2.

The third experiment in the A enclosures lasted 13 days (Appendix IVc). Six new animals entered both enclosures. Persistence of mature voles in the low density enclosure (A2) was 100% whereas in the high density enclosure (A1) three of six mature females survived and two of six mature males survived. Three immature females released in enclosure A1 all survived but only one was mature when recaptured. One of two immature females released in enclosure A2 survived and it had matured. In total there were four mature females caught in enclosure A1 and five in enclosure A2.

For the B enclosures, the second experiment lasted 21 days (Appendix IVd). In the high density enclosure (B1) two of three mature females were recaptured and none of the five immature females was caught. In the low density enclosure (B2), however, three of five immature females were recaptured and they had all matured. One of four and three of five immature males were recaptured in enclosure B1 and B2 respectively and they had all become mature. At the time of recapture there were two mature females in enclosure B1 and three mature females in enclosure B2.

Experiment number three in the B enclosures lasted 23 days (Appendix IVd). None of three mature females survived in enclosure B1 but one new mature female had entered this enclosure. Of six immature females released in enclosure B1 one survived and matured; all five immature males released survived but all failed to mature. A new mature female had entered enclosure B2 and two of five immature females released survived and matured. In enclosure B2 only one of five immature males survived and it was still immature at recapture. At the end of the experiment there were two mature females in enclosure B1 and three in enclosure B2.

In analysing the experimental results from the enclosure studies one may compare densities between pairs of enclosures or density change within enclosures over the experimental period. The number of mature females and males released in the the high and low density enclosure for the short-term experiments were significantly different, but at the termination of the experiments there was no statistical difference between pairs of A and B enclosures (Tables 29 and 30). Density of mature females did not change over the experimental period in the high density enclosures but increased significantly in both the A and B low density enclosures (Table 29). Survival and maturation of immature females were higher in the low density enclosures in both deciduous and coniferous

Table 29. Comparison of mature females released and recaptured in the enclosure experiments by Kruskal-Wallis test.

High Density		Low Density	
Released	Captured	Released	Captured
A enclosures			
5	4	2	3
5	10	1	7
6	4	1	5
5.3±0.58[1]	6.0±3.46[2]	1.3±0.58[1]	5.0±2.00[2]
H=0.45 NS		H=3.97 *	
B enclosures			
3	3		
3	1	1	1
3	3	1	4
3	2	0	3
3	2	0	3
3.0±0.00[3]	2.2±0.84[4]	0.5±0.58[3]	2.8±1.26[4]
H=3.75 NS		H=4.40 *	

1-H=4.09, *
2-H=0.05, NS
3-H=7.35, *
4-H=0.82, NS

Table 30. Comparison of mature males released and recaptured in the enclosure experiments by Kruskal-Wallis test.

High Density		Low Density	
Released	Captured	Released	Recaptured
A enclosures			
5	2	3	3
5	10	1	2
6	3	1	2
5.3±0.58[1]	5.0±4.36[2]	1.7±1.15[1]	2.3±0.58[2]
H=0.44 NS		H=0.83 NS	
B enclosures			
3	5	1	3
3	5	1	1
3	1	2	6
3	2	2	2
2	1		
2.8±0.45[3]	2.8±2.05[4]	1.5±0.58[3]	3.0±2.16[4]
H=0.19 NS		H=1.47 NS	

1-H=4.09, *
2-H=0.89, NS
3-H=5.55, *
4-H=0.14, NS

vegetation type than in the high density enclosures (Table 31). Maturation of immature males was highest in the low density enclosures but survival was highest in the high density enclosures in the A and B enclosures (Table 31).

Discussion

Clethrionomys gapperi have large home ranges and it would have been ideal if the enclosures could have been 3 to 4 ha in size so that more animals could have been used in the experiments. Nevertheless the experiments did reveal some interesting results.

In 1980 voles could readily escape from and into the enclosures and the experiment was long term so 'leakage' was a problem. The results from 1980 are therefore questionable. Based on home range size of mature females on the two A grids, I expected approximately 4 to 5 mature females in each of the 1 ha enclosures. This was approximately the density about which the numbers of mature females fluctuated in enclosure A2 but the density of mature females in enclosure A1 was only half the expected over the summer.

The rate of escape from and entry into the enclosures was low in 1981 and 1982, and short-term experiments were run, hence 'leakage' was of little consequence. The results show quite convincingly that the density of mature voles affects maturation of immatures and that spacing behaviour appears to be operating, at least among females. For the females the results were consistent in all short-term experiments. The density of mature females equalized between pairs of enclosures, with numbers of mature females in the high density enclosures not changing and numbers in the low density enclosures increasing significantly. Immature females survived better, and a higher percentage matured, in the low density enclosure than in the high density enclosure. The results were not as consistent for males. For instance the density of mature males within enclosures did not change significantly over the experimental period, however, the density did equalize between pairs of enclosures. At first sight this may appear incongruous, but not when the high variance is considered. Survival and maturation of immature males was not as I predicted. Survival was high at high density but maturation was high at low density.

Table 31. Percentage of immature voles (N) released in enclosures that survived and matured.

		Female		Male	
		Survived	Matured	Survived	Matured
A Enclosures	High	30.3 (16.5)[1]	60.0 (5)	20.5 (19.5)[1]	0.0 (4)
	Low	42.4 (16.5)[1]	85.7 (7)	5.1 (19.5)[1]	100.0 (1)
B Enclosures	High	21.6 (18.5)[1]	25.0 (4)	59.5 (18.5)[1]	[illegible]
	Low	44.4 (18)	62.5 (8)	44.4 (18)	62.5 (8)

1- sex ratio of 1:1 assumed when sex of young released with mother was unknown, therefore some sample sizes are non-whole numbers.

One question of importance is which comes first, maturation or settlement on a home range? This I can not get at directly from the experimental design. However, for both males and females, maturation rate was higher at low density compared to high density of mature individuals. However, I cannot separate the effect of density and available space. Bramble and Rowlands (1936) found that 50% of young of the year female *Clethrionomys glareolus* undergo a number of sterile oestrus cycles. This may serve as a clue to the mother that her daughters are approaching maturity and she may become aggressive towards them which causes them to disperse in search for vacant home ranges. However, this can only be a part of the picture as maturation rate was slow in the high density enclosures.

Saitoh (1981) carried out enclosure studies of *Clethrionomys rufocanus* in Japan. He introduced high densities of voles in two adjacent enclosures in suboptimal habitat in the fall. The following spring, numbers were manipulated so that there were equal densities of voles in both enclosures, but in one enclosure the density of mature females was 26, 16 of which were overwintered. In the other enclosure there were 19 spring-born females that were in the process of maturing. Although his experiment was long term his results were similar to mine in that density of mature females equalized in the two enclosures, mature females occupied space more or less exclusively, and immature females did not mature in the presence of a high density of mature females.

The density of mature males may have an effect on the density of mature females. Elliott (1969) found that following removal of mature males the mature females also tended to leave. One interpretation of the removal experiments I conducted indicated a similar trend (see **Spacing behaviour of *Clethrionomys gapperi*: II Effect of removal of adults**). However, due to the time-consuming nature of the experiments, experiments to determine the effect of mature males on females and mature females on males were not conducted. The experimental results do indicate that at a high density of mature voles, immature voles are prevented from maturing.

Concluding Discussion

In his monumental work, The Origin of Species, Darwin (1859) pointed out that all species produce more young than are needed for replacement. Darwin used this observation to construct, in part, his theory of evolution through natural selection. To a population ecologist, this observation begs the question - why do populations not increase without limit?

Two groups of factors affect population size, those that cause an increase (natality and immigration) and those that cause a decrease (mortality and emigration). A balance between the actions of the increase and decrease sets of factors produces population stability. Factors operating on the dynamics of populations may be divided into density-dependent and density-independent categories. Density-independent factors can certainly affect population size but will not, by definition regulate, it. Only density-dependent factors which act through negative feedback, can regulate population size because the intensity of their effect varies with the interaction of population size and factor(s) in the environment.

What is the most appropriate measure of density? In a seasonal breeder, the annual maximum density normally occurs just after the end of the breeding season, and the annual minimum density usually occurs just after the onset of the next breeding season. Another possible index is the density of mature individuals, which contribute through reproduction to population increase, ie. one side of the equation that must be balanced for population stability. The majority (97%) of mammalian species are polygynous (Kleiman 1977) and consequently the density of mature females is the critical parameter. If there is a limit to the number of females breeding, then there is necessarily a limit to the number of young produced.

Much theory and some empirical evidence suggests that a population exhibiting spacing behaviour (i.e. requires exclusive use of at least the majority of its home range, and lives in a heterogeneous environment) should experience stable density, especially within habitats of high quality. Stability of density over a large area encompassing several habitat types may not be apparent each year. This hypothesis of density stability I have termed the social factor hypothesis after Tamarin (1983).

Spacing behaviour has probably evolved to ensure that an individual has enough resources for its exclusive use (Wilson 1975:266). The amount of space occupied by an animal depends in part on the amount of food available (Wilson 1975:266, Mares *et al.* 1982). During the non-breeding season an animal only needs resources for its own maintenance but during the breeding season there must be enough resources for successful reproduction and rearing of young. Since an inverse relationship usually exists between the size of space needed and the availability of resources in a particular area, a consequence of spacing behaviour then, is that a finite area will only support a certain number of mature individuals. Spacing behaviour is dependent on the density of resources but is independent of the density of individuals.

I have already alluded to the set of criteria necessary for showing that spacing behaviour operates (Watson and Moss 1970, Klomp 1972). Brown (1969) developed a graphical model for birds to show how spacing behaviour (territoriality) sets a limit on the number of territorial individuals in an area. Once the limit is reached in high quality habitat, excess animals are forced to establish in lower quality habitat. He further hypothesized a category called "floaters", which were birds that were chronologically old enough to mature but were prevented from doing so because of a lack of territory. Klomp (1972) showed that the density of some species of birds is limited by spacing behaviour. Skeel (1983) recently presented indirect evidence that spacing behaviour limits the breeding density of Whimbrels (*Numenius phaeopus*) at Churchill, Manitoba.

If an animal must have exclusive use of a home range in order to breed then, when there is room for no more mature animals, any excess must remain subdominant and refrain from breeding or disperse in search of another, unoccupied, suitable site. In his study of the California vole (*Microtus californicus*) Lidicker (1962, 1975) identified two types of dispersal movements. He defined pre-saturation dispersal as dispersal of individuals in search of unoccupied sites (not necessarily of high quality) with successful establishment. Saturation dispersal, on the other hand, is dispersal of doomed individuals at high density that cannot find unoccupied sites. Lidicker (1975) defined a dispersal sink as an area that can accommodate dispersers. Such an area may only operate as a sink until saturation is reached or it may operate continuously as a sink by draining away dispersers. A dispersal sink need not necessarily be a result of the action

of predators. A sink may just as well be an area where survival or birth rate is extremely low for whatever reason. Lidicker (1975) further defined "frustrated dispersal" as total prevention of dispersal such as may occur in enclosures or on small islands. The presence of a dispersal sink therefore ensures that frustrated dispersal will not come about and the density of the individuals exhibiting spacing behaviour in a population will have an upper limit.

In dealing with dispersal, investigators generally assume, or look for, advantages to the dispersing individual (Howard 1949, 1960, Murray 1967, Lidicker 1975). It is difficult to see how dispersers gain any evolutionary advantage, especially in the case of saturation dispersal. However, when offspring disperse, the advantage to established individuals, through reduced competition, can be great. Anderson (1980) argued this point and it makes much intuitive sense. A logical consequence of spacing behaviour of established mature individuals is dispersal, through repulsion, of immatures about to mature.

Heterogeneous environments are mosaics of different habitat patches where patches of several different habitats lie within the dispersal range of an individual of a particular species. A homogeneous area would be a habitat patch many times the dispersal range of a particular individual so that animals in the core of this area could not disperse outside the patch because of sheer distance.

Hansson (1977) and Anderson (1980) recognized the importance of heterogeneity of the environment to small mammals and their contribution lies mainly in giving names to the various types of habitats. Hansson (1977) recognized four types of habitat that he called donor, reception, induced donor and transition. Anderson (1980) recognized survival, colonization, traversable and barrier habitats. The names of these habitat types are self explanatory. Traversable and transition habitats are equivalent and barrier habitat (Anderson 1980) was not considered important by Hansson (1977).

Lomnicki (1978, 1980) showed theoretically that, given spatial and temporal heterogeneity of the natural environment, and unequal resource partitioning among individuals, populations will be regulated by emigration. However, Uchmanski (1983) has recently shown that stable equilibrium points may exist for systems with and without emigration. Stenseth (1980) modelled populations in heterogeneous and homogeneous

environments and came to the conclusion that population stability is a consequence of spatial heterogeneity.

How do the data from this study relate to the social factor hypothesis of population regulation thus far expounded? Parameters that indirectly measure Darwinian fitness of *Clethrionomys gapperi* clearly differed among vegetation types in the Mitsue study area. However, this in itself does not mean that the environment was heterogeneous to the voles. Mean patch size of different habitat types is important. In the Mitsue study area 12 vegetation types have been described (Bondrup-Nielsen 1978). Based on unpublished data the mean diameter and standard deviation of 10 common vegetation types are presented in Table 32. The mean diameter of the 10 vegetation types was less than 450 m, except for the cut-over areas, and all standard deviations were very high. Although I do not know how far *Clethrionomys gapperi* will travel in the Mitsue study area, I do know that some mature males moved throughout the 4-ha study grids and I recorded a few cases of immature voles moving up to 200 m across the grids. No doubt the voles can move distances much greater than 200 meters, and I therefore conclude that much of the habitat mosaic in the Mitsue study area was heterogeneous with respect to *Clethrionomys gapperi*.

The social factor hypothesis of population regulation investigated requires that when an area (regardless of quality) becomes saturated with mature animals (established on home ranges), excess animals on the verge of maturing are forced to leave. Saturation and dispersal are then consequences of spacing behaviour. From this study it is apparent that at least mature females do space themselves out; female home range size appears to be inflexible within habitat type; and, at saturation, mature females on home ranges prevent immature females from establishing and maturing.

Factors other than spacing behaviour appear to have affected populations of *Clethrionomys gapperi* in the Mitsue study area. Two instances can be cited. First, in 1980, density on all grids decreased in mid-summer (Fig. 4) and only showed a recovery after approximately four weeks. Density of mature females never approached saturation. The cause of the decrease may well have been the action of a density-independent factor. The weather during the density decrease was wet and cold and could have reduced survival of young. Second, in 1982 total density on grid B1

Table 32. Mean diameter, standard deviation and sample size (unpubl. data) of vegetation types found in the Mitsue study area after Bondrup-Nielsen (1978).

Vegetation Type	Mean (m)	S.D.	N
Stag	283.2	267.2	89
Spruce flat	147.2	115.2	92
Spruce slope	182.4	148.8	117
/Some evergreen trees	233.6	219.2	35
Hardwood			
\Few evergreen trees	441.6	364.8	33
/More hardwood trees	208.0	97.6	16
Mixed young			
\More evergreen trees	203.2	233.0	80
/More hardwood trees	268.8	187.8	40
Mixed old			
\More evergreen trees	336.0	287.2	124
Cut-over	521.6	476.0	28

levelled off between rats 7 and 8 (Fig. 4), when the density of mature females was below saturation. Again, I believe some density-independent factor came into play although I am pressed to think of what it might have been.

A requirement of the hypothesis for density stability is that saturation never be reached in at least one habitat. The B grids appear to have been such habitats, at least for the duration of the study. It is possible that grid A1 was not in the best habitat for *Clethrionomys gapperi*, but if it had been, maybe saturation of mature females would have been reached even in 1980.

The two conditions of the social factor hypothesis appear to be satisfied and the hypothesis cannot be rejected. I would therefore predict that density of *Clethrionomys gapperi* in this area will be stable.

With only three years of density data it is impossible to determine whether or not the above prediction is true or false. Clearly, we cannot look at density data from just a few years or from just one grid but must consider many years of density data and take the whole area into consideration. It was only in 1982 that the density of mature females on grid A1 was high enough to reveal regulation through spacing behaviour. This is unlike the study of Bujalska (1970, 1973), in which the density of mature female *Clethrionomys glareolus* reached approximately 60 individuals on a 4-ha island each year. Density regulation of *Clethrionomys gapperi* has been studied extensively at Heart Lake, N.W.T. (Fuller 1969, 1977a, 1977b, 1979, Fuller *et al*. 1969). Home range of mature female *Clethrionomys gapperi* at Heart Lake was approximately 0.3 ha (Fuller pers. comm.). A density high was recorded in 1974, when, in early August, there were approximately 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 (Appendix I). This means that the true number of mature females was 5.2, or 2.31/ha. With a mature female home range size of 0.3 ha one would expect approximately 7.5 mature females on the 2.25 ha grid, and, allowing for edge effect, about 18 should have been caught. There was another peak in the population of *Clethrionomys 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. I propose therefore, that at Heart Lake mature females *Clethrionomys gapperi* only came close to saturation in 1974 and 1976. Regulation through spacing would therefore not be apparent and consequently it is no surprise that there was no relationship between maturation rate of females and density (Fuller 1979).

[redacted]ina and Korotkov (1975) in a study of *Clethrionomys rutilus* found that in [redacted] density was stable and maturation rate of females was inversely [redacted]e density of overwintered females. In suboptimal habitat density fluctuated and there was no relationship between maturation rate of females and density of overwintered females. Density below saturation does not mean that a population cannot show multiannual fluctuations, it is just difficult to conceive of a population crash of the kind involved in typical cycles (Krebs and Myers 1974), ie. that a large, aggressive, poor-breeding genotype had been selected.

Clethrionomys glareolus undergoes cycles in northern Sweden whereas in southern Sweden populations are stable (Wiger 1979, Hansson 1979, Jensen 1982). Recently Erlinge *et al.* (1983) determined, for a number of small rodents including *Clethrionomys glareolus*, that predators were responsible for keeping density down by removing most of the yearly production of biomass. That study took place in southern Sweden in a heterogeneous area. Predators were more successful at removing prey in some habitats than in others. Erlinge *et al.* (1983) argued that facultative predators were mainly responsible for removing excess voles, which they did by switching to a particular species of prey when that prey reached high density. I would argue that it was not the predators *per se* that were important in regulating the populations studied but rather the dispersal sink created by them. The presence of the dispersal sink, in turn, maintained a stable density of the various species of mice and voles.

Abramsky and Tracy (1979) studied *Microtus ochrogaster* on watered and fertilized plots in Colorado. The population studied did not cycle but attained a similar density each year. The authors argued that the population studied was stable because of emigration. The area surrounding the study plot supported few voles and clearly can be interpreted as a dispersal sink.

Snowshoe hares (*Lepus americanus*) cycle in Alaska and Alberta (Wolff 1980b, Keith 1974), whereas in Colorado and Utah they maintain stable densities (Dolbeer and

Clark 1975). Stable densities in the south are thought to be a result of heterogeneous habitat and the presence of several facultative predators (Dolbeer and Clark 1975). This is similar to the situation described for voles and mice in southern Sweden by Erlinge *et al.* (1983). Again it can be argued that it is the presence of a dispersal sink that is of importance rather than the predators *per se*. In Alaska (Wolff 1980b) although vegetation was patchy (heterogeneous) in the study area, there may have been no dispersal sink. There are few species that prey on hares in Alaska and those few tend to be obligate. Obligate predators show a time lag response to an increase in prey numbers so that the density of prey (hares) reaches very high numbers and then crashes (Wolff 1980b). Although the few [redacted] that survive a crash do so in so-called refuge habitat (Wolff 1980b), I think it [redacted]ued, that because of [redacted]nature of the predators there is no dispersal sink during the increase phase of popu[redacted]h when a dispersal sink should theoretically function to stabilize density. It is noteworthy that snowshoe hares cycle in the absence of lynx on Anticosti island (Keith 1963).

From the foregoing discussion it appears that, for a number of species, spacing behaviour and the presence of a dispersal sink may result in relatively stable density, at least within habitats of high quality. However, it has been argued that spacing behaviour (Krebs 1978) and the presence of a dispersal sink (Tamarin 1977) are necessary for cycling. Where does the discrepancy lie? Animals may be spaced out but if home range size decreases (Gaines and Johnson 1982) and overlap increases (Metzgar 1971) with increased density, extreme overcrowding may develop. However, if home range size is dependent on the amount of some resource such as food rather than on population density, and if adjacent home ranges only overlap minimally, then extreme crowding will not develop.

Tamarin (1977) bases his argument that a dispersal sink is necessary for cycling to develop, on a comparison of the demography of an insular population of *Microtus breweri* on Muskeget island and a mainland population of *Microtus pennsylvanicus* in Massachusetts. Tamarin detected differences in dispersal tendencies of these two species. He considered dispersal in the stable population of *Microtus breweri* to be of the saturation type and dispersal in the cyclic mainland *Microtus pennsylvanicus* to be of the pre-saturation type. On the basis of different dispersal types he concluded that the

mainland vole had a dispersal sink while the insular vole did not. The fact that there were no predators on the island was cited as evidence by Tamarin that there could be no dispersal sink there. However, I have already pointed out that a dispersal sink need not be maintained by predators.

Tamarin is a proponent of the Chitty hypothesis (Chitty 1967, Krebs 1978) and argues that a dispersal sink is necessary for cycling, which means that only pre-saturation dispersal occurs, which in turn results in strong selection for the large, aggressive, poor-breeder genotype hypothesized by Chitty (1967) to be characteristic of population peaks. Although there is evidence that differences in reproductive attributes between cyclic and stable *Clethrionomys glareolus* are genetic (Gustafsson *et al.* 1983), there is as yet little evidence that there is a change in genotype of voles during the cycle. The best evidence that selection occurs during a cycle comes from changes in allozymic frequencies (Semeonoff and Robertson 1968, Canham 1969, Tamarin and Krebs 1969, Gaines and Krebs 1971, Kohn and Tamarin 1978, Gaines *et al.* 1978, Mihok *et al.* 1983), but doubt as to the significance of these results has been expressed (McGovern and Tracy 1981). McGovern and Tracy (1981) found differences in transferrin and leucine aminopeptidase within individuals of the same order of magnitude as those reported between individuals during different phases of a cycle. Mihok and Ewing (1983) have recently questioned the results of McGovern and Tracy (1981) and suggest their variable results were due to poor technique. However, one must still question general work on alloenzymes related to population cycles because if McGovern and Tracy (1981) can be accused of using poor technique why not other workers?

I would like to advance the hypothesis that strict spacing behaviour and the presence of dispersal sinks, are necessary for population stability and that populations with relaxed spacing behaviour (home ranges show increase overlap and compression with increase density) that do not have dispersal sinks available to them tend to cycle (show multiyear fluctuations). A flow chart of the hypothesized events is presented in Figure 11.

If young female *Clethrionomys gapperi* are weaned before about August first they will mature, otherwise the photoperiod is such that the young are physiologically incapable of maturing. The young will probably stay on their mother's home range where they are

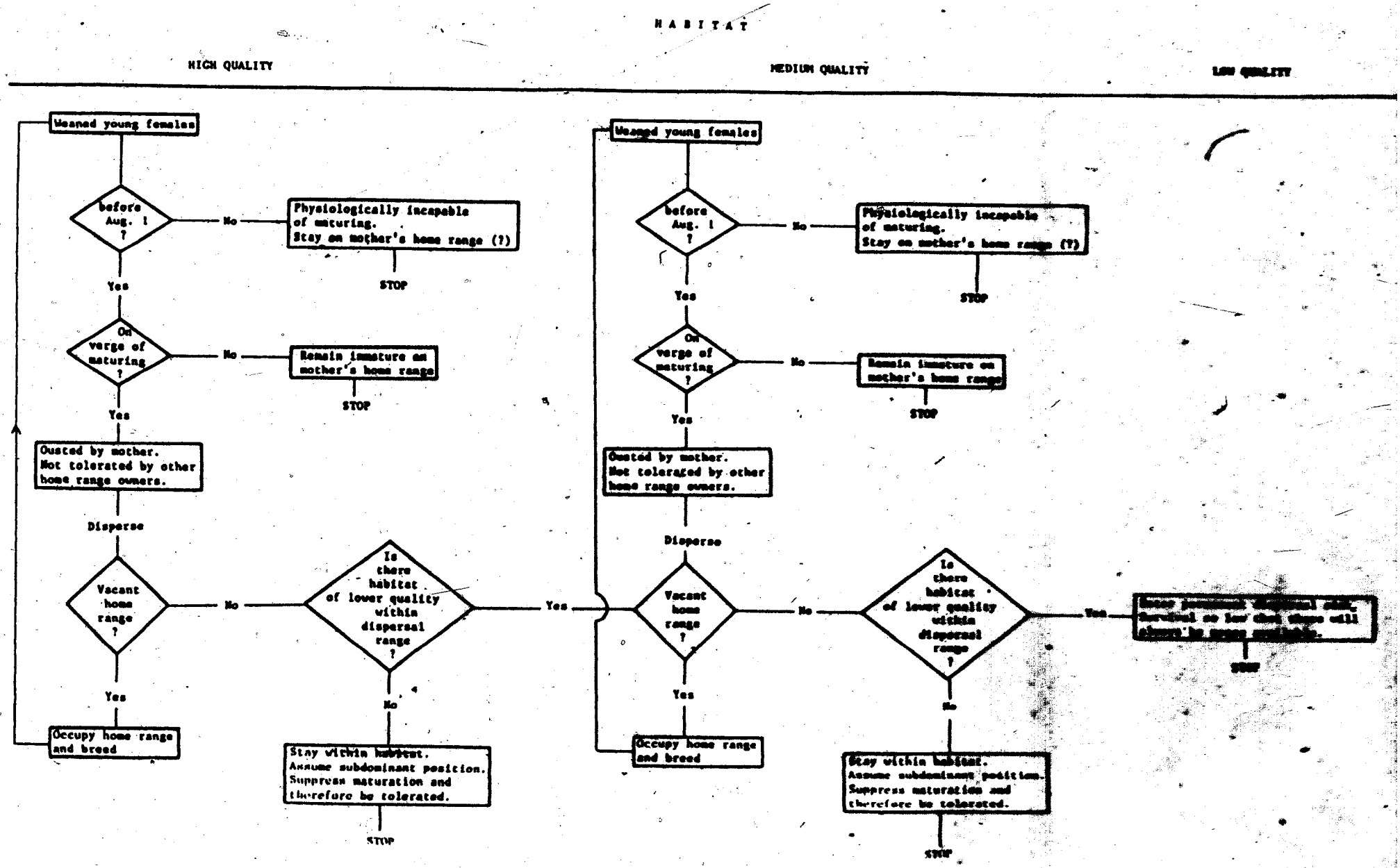

Figure 11. Flowchart of hypothesis of density regulation based on habitat heterogeneity and spacing behaviour.

more likely to survive than if they dispersed. The total density increases dramatically due to the sudden high survival of the young as occurred on grid A1 in 1982. If the date is before August first, young females may have an infertile estrus (Bramble and Rowlands 1938), which the mother probably detects. This may serve as a trigger to the mother to drive out those of her daughters that are about to mature. A young maturing female within high quality habitat will probably settle and breed if there is a vacant home range. Otherwise she will probably continue to disperse until she finds a vacant home range in medium quality habitat. A vole may be capable of dispersal only within a certain area and if it does not find a vacant home range it may assume a subdominant position and not mature (Koshkina and Korotkov 1975) and therefore be tolerated. If a female finds a vacant home range in medium quality habitat it will breed and rear young. If dispersing young females from both high and medium quality habitat cannot find vacant home ranges in medium quality habitats, but can enter a dispersal sink, (low quality habitat) they will probably do so because they may encounter low aggression there. They may be able to breed in the dispersal sink but their survival is so poor that there will always be vacant home ranges available.

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Appendix I. Density estimation as a function of live-trapping grid and home range size.

ABSTRACT

Edge effect is an inherent problem when using live-trapping grids to census animals in populations. The relationship between grid size and home range size, shape and dispersion pattern was investigated by a mathematical model and computer simulation. A simple relationship between overestimate of population density and grid size to home range size was found. To minimize the effect of home range size, shape and dispersion pattern on census results, grid sizes at least 16 times larger than the average home range size should be used.

INTRODUCTION

Live-trapping grids are often used when censusing small mammals (Smith *et al.* 1975). It is usually assumed that all animals on the grid are captured and marked, and numbers are expressed as minimum number known alive (MNA, Chitty and Phipps 1966). However, census grids usually cover only a fraction of the area occupied by the population except when censusing animals on small islands or animals restricted to isolated habitat patches where the whole population can be enumerated. For most live-trapping grids therefore, some animals have only parts of their home ranges overlap the grid which results in "edge effect". That is, animals censused on the grid occupy a larger area than the grid which results in proportionately more animals being caught in the outer perimeter of traps (see Barbehenn 1974 and Smith *et al.* 1975 for reviews). Similar "edge effect" is also of concern when snap-trapping on grids. Several methods have been developed to correct for "edge effect" (Grodzinski *et al.* 1966, Aulak 1967, Pelikan 1968, Hansson 1969, Faust *et al.* 1971, Gentry *et al.* 1971, Kaufman *et al.* 1971, Smith *et al.* 1971, Smith *et al.* 1972, Stenseth *et al.* 1974, Swift and Steinhorst 1976, Stenseth and Hansson 1979). But there has been little work done to quantify the effect of grid size and "edge effect" on census information.

The circumference of a square grid is directly proportional to the length of a side, whereas its area is proportional to the length of a side raised to the second power. It therefore follows that for a population of animals with a given mean home range size and a dispersion pattern that is not affected by the grid, the larger the census grid used the less the "edge effect". This leads to the following questions: 1) What is the relationship between grid size, home range size and actual population density? 2) Is this relationship affected by shape and dispersion pattern of home ranges? These questions are examined by a mathematical model and computer simulation.

MATHEMATICAL MODEL

A mathematical model was developed to determine the function relating the ratio of grid size to home range size in estimating animal density.

Model

Assume contiguous square home ranges of area 1.

Let Y equal the length of one side of a square trapping grid in units of home range size (Fig. 1).

Let F equal fractional part of Y (eg. for Y=4.4, F=0.4)

Let I equal integer part of Y (eg. for Y=4.4, I=4)

Let a home range be counted if it overlaps the grid.

In order to determine the expected number of home ranges which would be counted on the grid, we find how many home ranges, on average, would be counted in a single row, and how many in a single column of home ranges and multiply.

To find the average number of home ranges counted on the grid in a column we move the entire grid one unit up the columns and average how many home ranges are counted (Fig. 1).

Through a distance 0 to (1-F) we count (I+1) home ranges.

Through a distance (1-F) to 1 we count (I+2) home ranges.

Therefore on the average we count

$$\underline{(1-F)(I+1) + (F)(I+2)}$$

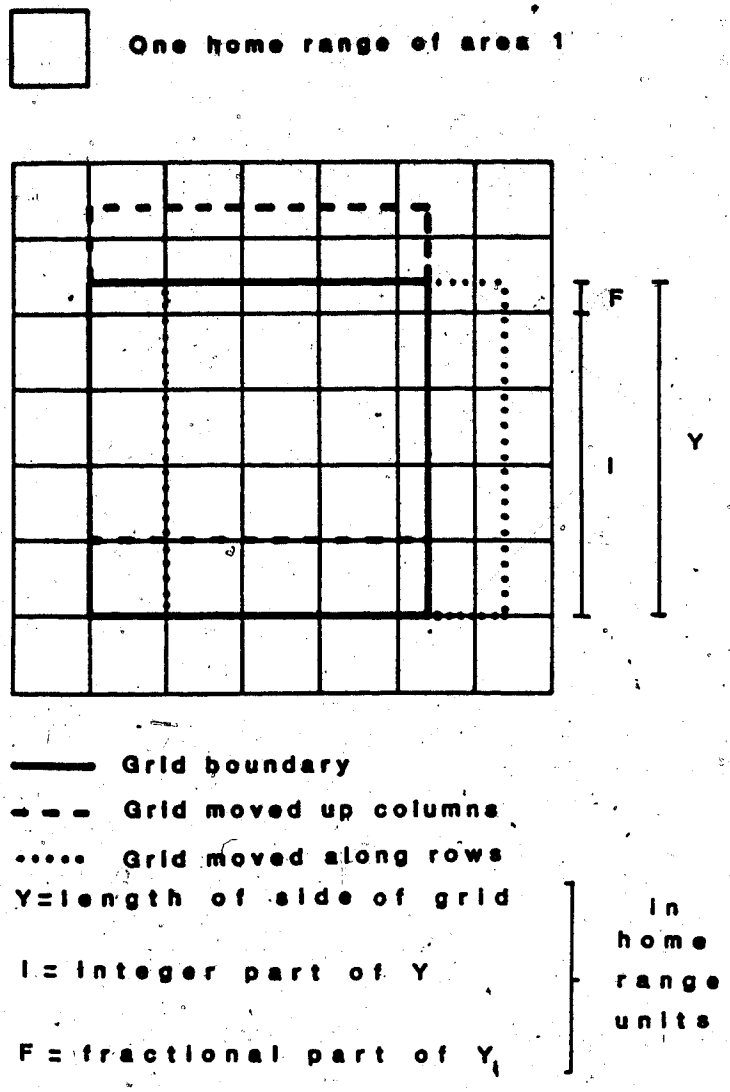

Figure 1. Mathematical model.

$$(1-F)+(F)$$

$$= 1+1-FI-F+FI+2F$$

$$= 1+F+1$$

$$= Y+1$$

home ranges.

If we move the grid one unit along the rows of home ranges then by the same argument we count $Y+1$ home ranges.

Therefore, overall we count $(Y+1)^2$ home ranges on the grid where in reality there are only Y^2 home ranges since the area of each home range is 1.

Therefore

$$\frac{\text{\# counted}}{\text{actual \#}}$$

$$\frac{(Y+1)^2}{Y^2}$$

Let $A=Y^2$=area of grid relative to area of home range, that is, the ratio of grid size to home range size. Therefore

$$\frac{\text{\# counted}}{\text{actual \#}}$$

$$\frac{(\sqrt{A}+1)^2}{A}$$

This function is graphed in Figure 2. It is asymptotic to Y= 1 (overestimate) and X=0 (grid size / home range size). Therefore, when using a live trapping grid to estimate the density of a population of animals, we will always overestimate the actual density and the smaller the size of the grid used in relation to the home range size, the greater the overestimate. But with grid sizes approximately 10 times larger than the home range size, the estimate of actual density is not much affected. However, animals do not have square home ranges so how realistic is this function? The effect of home range shape and dispersion on the function was determined by simulation.

COMPUTER SIMULATION

A computer program was written in BASIC for the Sinclair ZX8.1 mini-computer to simulate a population of animals and census them. To determine the effect of home range shape on the estimate of density as a function of the ratio of grid size to home range size, five different home range shapes (square, size= 1 unit; 2 rectangular, one of size=2 units and one of size=3 units; L-shaped, size=3 units; and hexagonal, size=4 units) were used that were contiguous and non-overlapping. For different grid sizes, 10 censuses were replicated five times to give five estimates of mean density for each home range shape. Each run consisted of placing a grid randomly on the configuration of home ranges and counting how many home ranges were totally or partially enclosed by the grid. Two random numbers determined the location of one corner of the grid, and a randomly chosen angle (1-45°) determined the rotation of the grid about one corner. Points spaced 0.5 units apart around the perimeter of a home range (eg. 8 points for a square of area 1, or 16 points for an L-shape of area 3) were tested against the four linear equations that described the grid boundaries. A home range was included in the census if any of the test points on its perimeter fell on the grid boundary, or within the grid. Because home ranges were contiguous, adjacent home ranges shared the points along their common boundary. The amount by which a census overestimated the number of home ranges sampled by the grid was calculated as the mean number of home ranges counted over five replicates (CM) divided by the ratio of grid size (GS) to home range size (HS) or

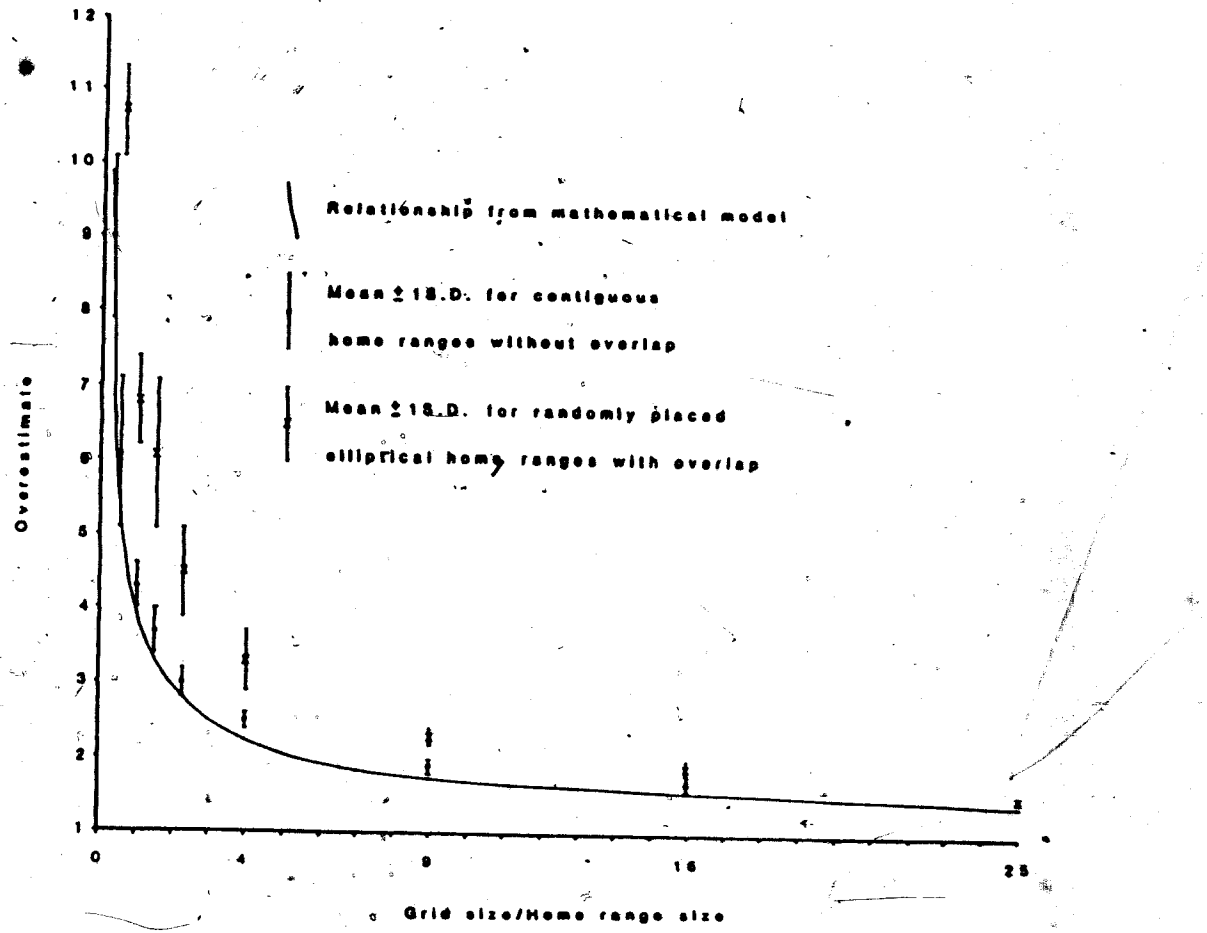

Figure 2. Relationship between grid size to home range size and overestimate of density determined by mathematical model and computer simulation for contiguous home ranges without overlap and randomly placed elliptical home ranges with overlap.

$CM(GS/HS)^{-1}$

The computer simulation results (Fig. 2) are very similar to predictions arising from the mathematical model. They are particularly convergent in cases where the grid size is larger than home range size. The two rectangular and the L-shaped home ranges resulted in slightly higher overestimates of density than did the square and hexagonal shaped home ranges. With increase ratio of grid size to home range size, standard deviation of the mean overestimate decreases. Clearly, as the ratio of grid size to home range size increases the overestimate of density becomes less sensitive to home range shape.

Although these home range shapes are what one might obtain by mapping the stations at which animals are caught in a live trapping study on orthogonal grids, how realistic are contiguous non-overlapping home ranges? Dispersion of home ranges is often irregular with some areas inside a grid having a higher density of home ranges than others and some areas are probably never used (Jannett 1978, Mihok 1979, Pers. obs.). Male *Clethrionomys gapperi* (Mihok 1979, Pers. obs.) and male *Microtus pennsylvanicus* (Madison 1980) have overlapping home ranges whereas female home ranges overlap only minimally, and a home range of a male overlaps those of several females.

To investigate the effect of randomly-placed, overlapping, uniform home ranges on the overestimate of density as a function of the ratio of grid size to home range size the following computer simulation was run. Ellipses, which have been used to estimate the size of home ranges (Mazurkiewicz 1969), of the form $X^2+2Y^2=1$ (area=1.57 units) were randomly placed and randomly rotated about their centers within a large area which was sampled 10 times with five replications as before, by random placement of different grid sizes. Elliptical home ranges were included in the census if any one of 14 points spaced evenly around their perimeters were found on or within the grid boundary. Adjacent ellipses, if sharing the same major axis, would overlap by approximately 25% and if sharing the same minor axis would only just touch. Approximately 18% of the ellipses shared the same center but probable rotational differences would result in less than 100% overlap.

Densities of 0.82, 0.41 and 0.21 home ranges per unit area were chosen. The overestimates for the smaller ratios of grid size to home range size are about 1.5 to 2 times higher than the results based on the mathematical model (Fig. 2). At a value of 16 for the ratio of grid size to home range size the overestimate for overlapping elliptical and non-overlapping square home ranges are very similar, and at a value of 25 they are virtually the same. Therefore, the main conclusions drawn from simulating contiguous square home ranges also hold for randomly placed overlapping elliptical home ranges.

DISCUSSION

Results from the mathematical model and computer simulations show that when the size of the live-trapping grid used in censuses is less than about 4 times the average home range size, marked overestimates of population size will occur. At ratios less than about 16 of grid size to home range size the variation in overestimate caused by home range shape and dispersion is considerable.

Home range size may differ markedly between species and between sexes of small mammals and may even differ between populations of the same species in different localities (eg. *Peromyscus maniculatus*, Stickel 1968). This means, that a grid of a particular size may be appropriate for census of only one species, or even one sex of a single species.

Results of live trapping studies are often used to discuss differences or similarities in demography between different species, or the same species between different areas (eg. Krebs and Meyers 1974), and to discuss aspects of demographic strategies based on sex ratios (Hansson 1978, Jannett 1981). How realistic are such comparisons if, in one study, the density was overestimated by a factor of five but in another study was only overestimated by a factor of two? As a point of illustration, Blair (1942) recorded 27 adult male deer mice *Peromyscus maniculatus* with a mean home range size of 2.31 acres (0.93 ha) and 14 adult females with a mean home range size of 1.39 acres (0.56 ha) on an 18.18 acre (7.4 ha) live trapping grid. This gives a ratio of grid size to home range size of 7.9 for males and 13.1 for females. This means that males are overestimated by

1.85 and females are overestimated by 1.6 based on the function derived from the mathematical model. If a 1 ha live-trapping grid had been used to census this population males would have been overestimated by approximately 4 and females by approximately 3. Assuming that the same number of animals had been caught, a significantly different sex ratio of 27 males to 14 females ($X^2=4.12$, d.f.=1, $P<0.05$) would have been reduced to an actual density of 6.8 males and 4.7 females, which is not significantly different from 1:1.

For comparative analyses, therefore, if the ratio of grid size to home range size of the sexes and/or species involved is less than about 16, one should correct for "edge effect" due to the variation caused by differences in home range shape and dispersion pattern.

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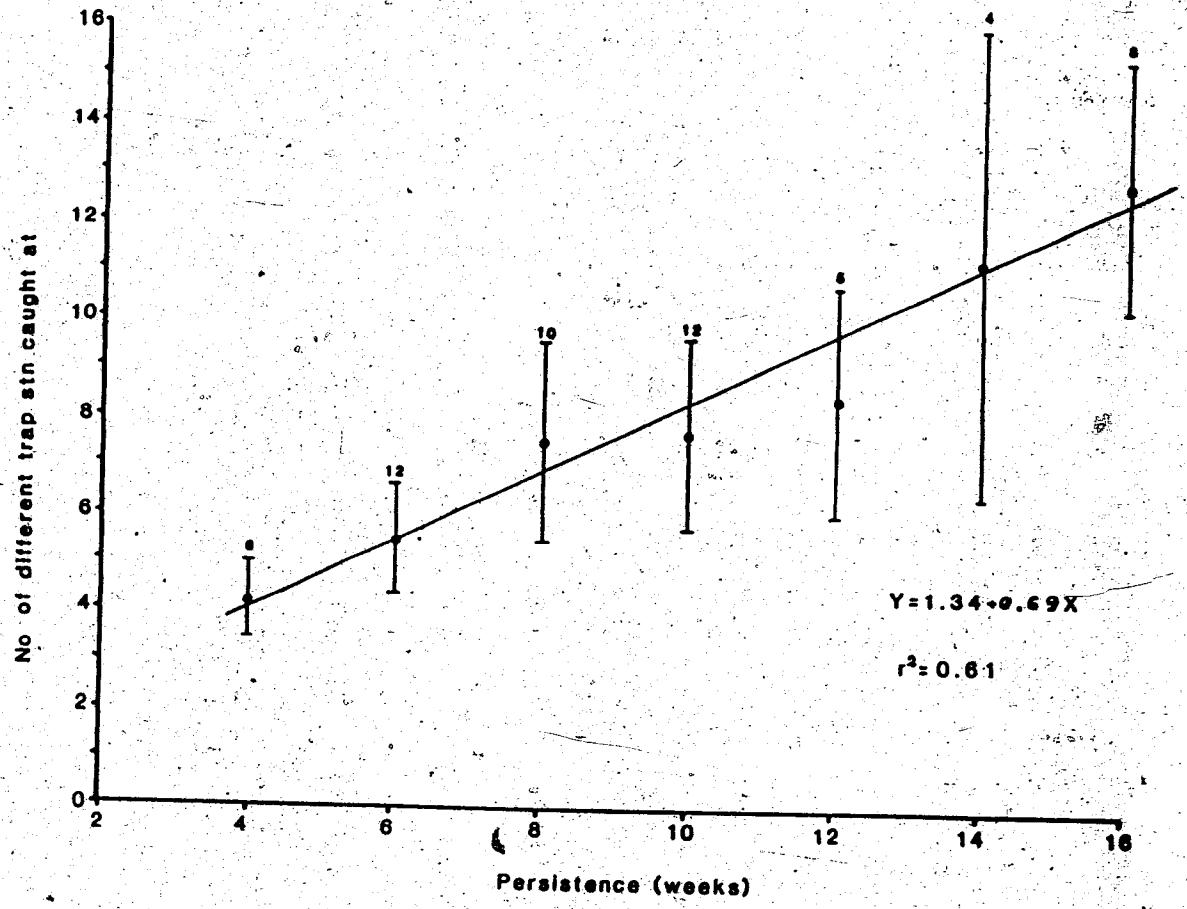
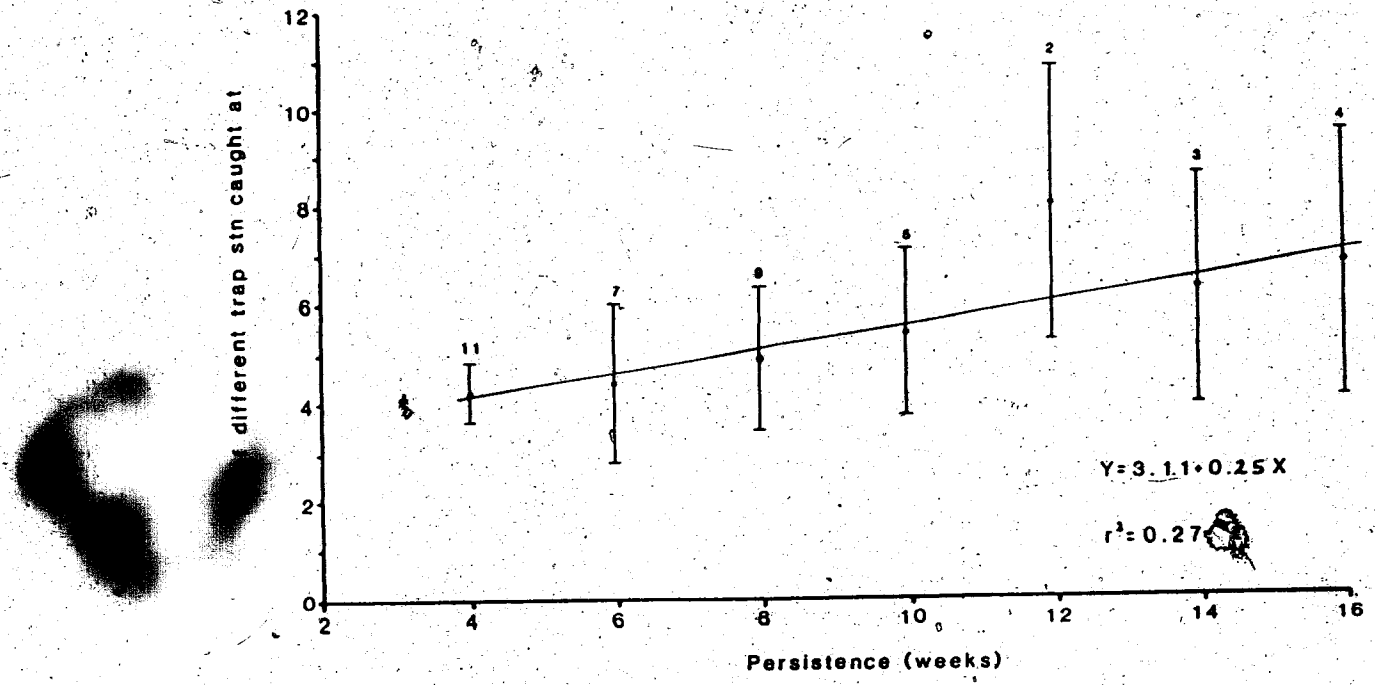
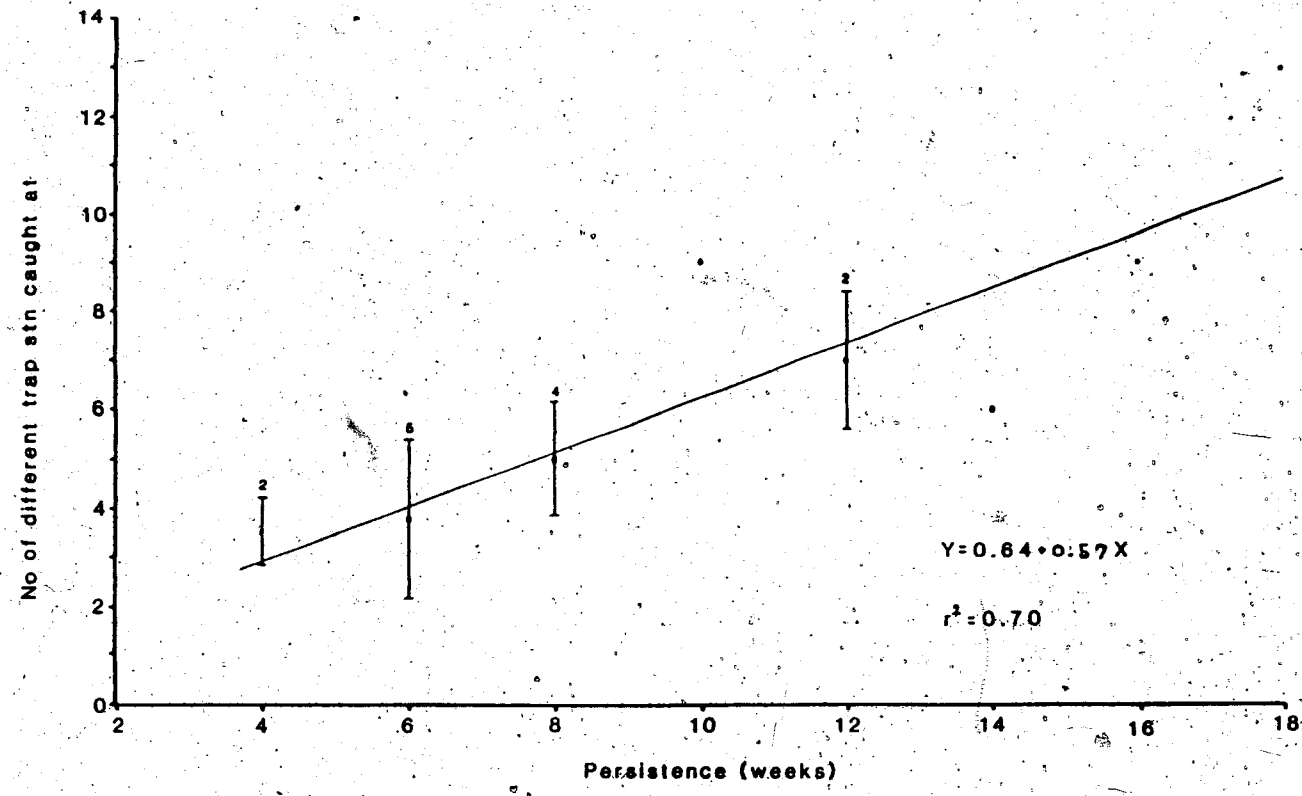
Appendix II. Regressions of number of different trap stations an animal is caught at against persistence.



Appendix IIa. Regression of the number of different trap stations an animal was caught at for mature males caught at least five times and with 80% or more of captures occurring inside the perimeter of traps against persistence.

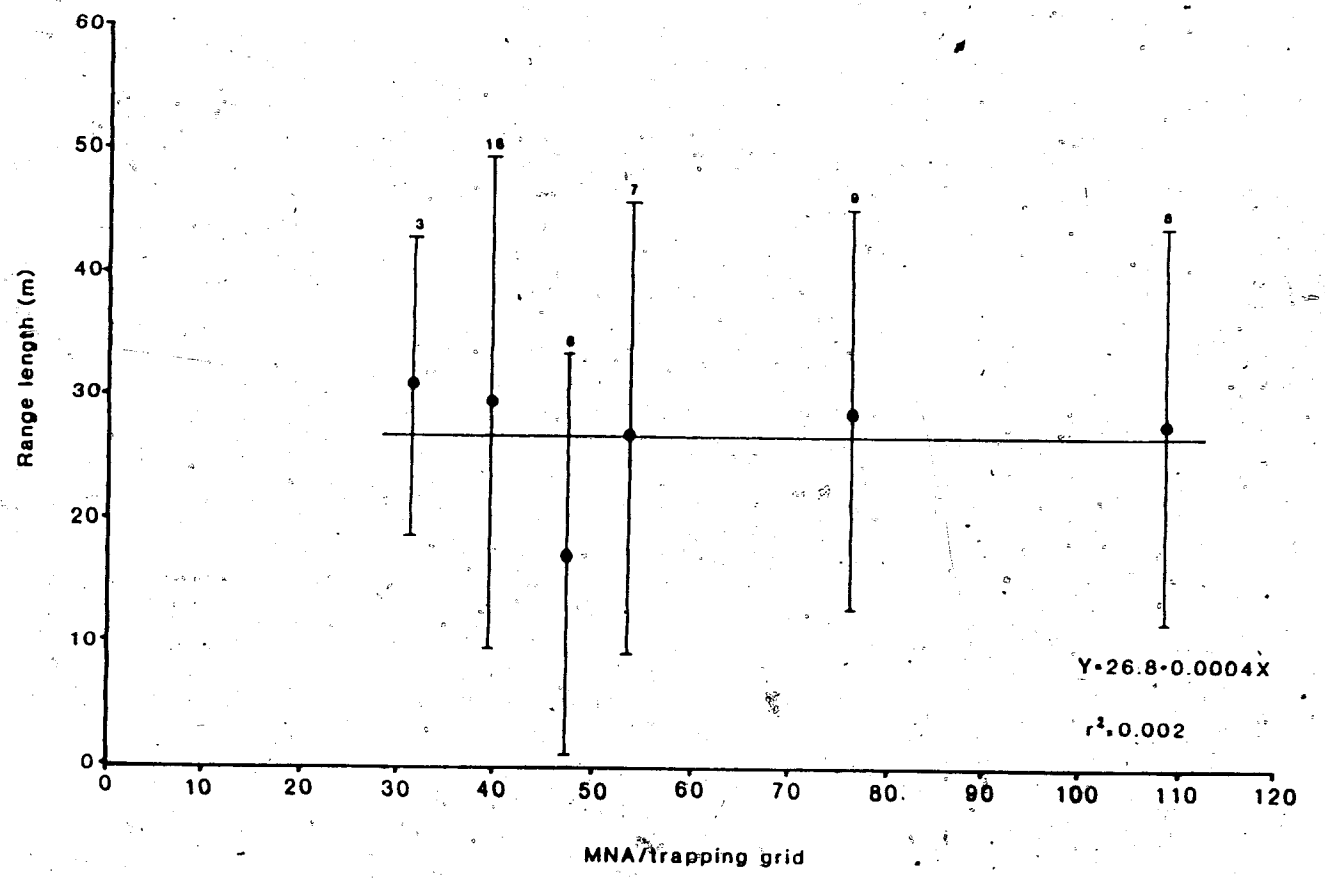


Appendix IIb. Regression of the number of different trap stations an animal was caught at for mature females on grids A1 and A2 caught at least five times and with 80% or more of captures occurring inside the perimeter of traps against persistence.

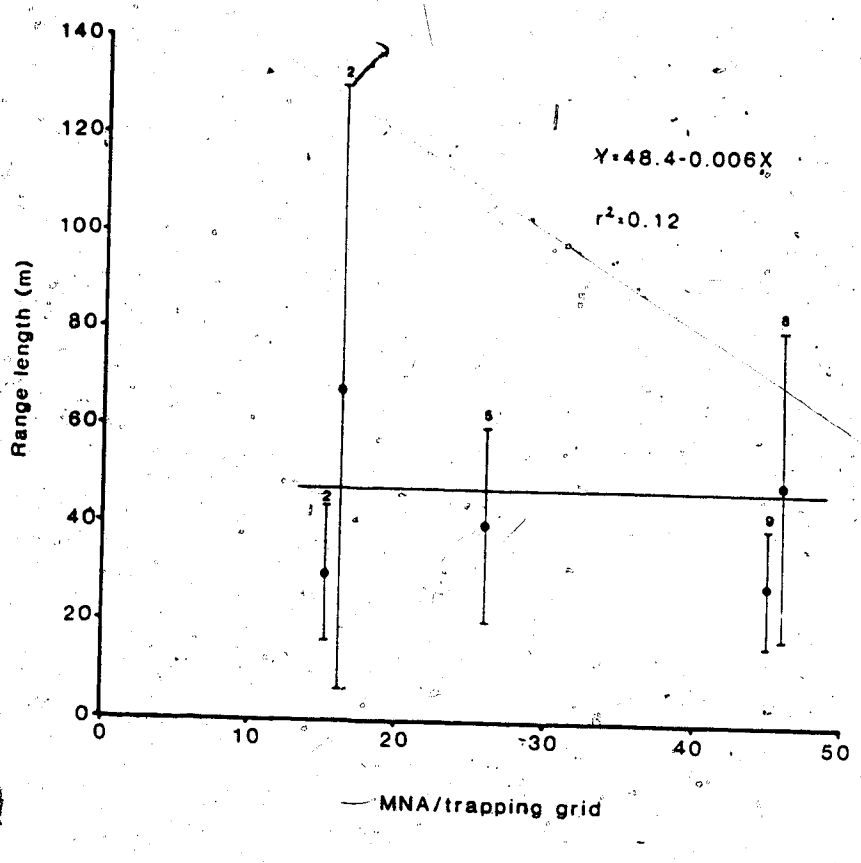


Appendix IIc. Regression of the number of different trap stations an animal was caught at for mature females on grid B1 caught at least five times and with 80% or more of captures occurring inside the perimeter of traps against persistence.

Appendix III. Regressions of range length against density.



Appendix IIIa. Regression of range length (m) of mature females on grid A1 in 1982 caught at least five times and with 80% or more of captures occurring inside the perimeter of traps against density.



Appendix IIIb. Regression of range length (m) of mature females on grid B1 in 1982 caught at least five times and with 80% or more of captures occurring inside the perimeter of traps against density.

Appendix IV. Data from experiments with different densities of *Clethrionomys gapperi* in enclosures.

Appendix IVa1 Result of experiment in the A enclosures in 1981.

Experiment 1

			Released	Captured Marked	Captured Unmarked	Total
Date			23-6	16, 19-7		
Duration (days)				24		
Enclosure A1	Condition	Sex				
	Mature	Female	3+2[4]	3	1	4
		Male	5	1	2	3
	Immature	Female	7+6[5]	0	0	0
		Male		0	0	0
	Total		23	4	3	7
Enclosure A2	Mature	Female	2[4]	1	2	3
		Male	2	1	2	3
	Immature	Female	6+9[5]	0	1	1
		Male		0	0	0
	Total		19	2	5	7

1-mature animals released
2-immature animals released
3-immature animals released have become mature
4-mother released with young in nest box
5-young released with mother
6-uterus opaque

Appendix IVb1. Result of experiment in the B enclosures in 1981

Experiment 1.

			Released	Captured Marked	Captured Unmarked	Captured Total
Date			17-6[1] 21-6[2]	30-6, 4-7		
Duration (days)				14		
Enclosure B1	Condition	Sex				
	Mature	Female	1	1	0	1
		Male	1	1	0	1
	Immature	Female	4	1	0	1
		Male	4	2[3]	0	2
	Total		10	5	0	5
Enclosure B2	Mature	Female	3	1	0	1
		Male	3	3	0	3
	Immature	Female	3	0	1	1
		Male	5	2[3]	4	6
	Total		14	6	5	11

1-mature animals released
2-immature animals released
3-immature animals released have become mature
4-mother released with young in nest box
5-young released with mother
6-uterus opaque

Appendix IVb2. Result of experiment in the B enclosures in 1981.

		Experiment 2			
		Released	Captured		
			Marked	Unmarked	Total
Date		19-7	4, 8-8		
Duration (days)			17		
Condition	Sex				
Enclosure B1					
Mature	Female	2+1[4]	2	1	3
	Male	3	2	0	2
Immature	Female	2	1+1[6]	0	2
	Male	3	3	0	3
Total		11	9	1	10
Enclosure B2					
Mature	Female				
	Male				
Immature	Female				
	Male				
Total					

1-mature animals released
2-immature animals released
3-immature animals released have become mature
4-mother released with young in nest box
5-young released with mother
6-uterus opaque

Appendix IVb3. Result of experiment in the 8 enclosures in 1981.

Experiment 3

		Released	Captured Marked	Captured Unmarked	Captured Total
Date		14-8	3.5-9		
Duration (days)			21		
Enclosure B1					
Condition	Sex				
Mature	Female	2+1[4]	3	0	3
	Male	3	1	0	1
Immature	Female	9[5]	3	1	4
	Male		3	1	4
Total		23	10	2	12
Enclosure B2					
Mature	Female	1[4]	1	3	4
	Male	1	0	1	1
Immature	Female	8[5]	2	1	3
	Male		2	3	5
Total		10	5	8	13

1-mature animals released
2-immature animals released
3-immature animals released have become mature
4-mother released with young in nest box
5-young released with mother
6-uterus opaque

Appendix IVc1. Result of experiment in the A enclosures in 1982.

Experiment 1:

			Released	Captured Marked	Captured Unmarked	Captured Total
Date			13-5	25-5		
Duration (days)				13		
Condition	Sex					
Enclosure A1 Mature		Female	10	2	2	4
		Male	6	1	1	2
Immature		Female				
		Male				
Total			16	3	3	6
Enclosure A2 Mature		Female				
		Male				
Immature		Female				
		Male				
Total						

1-mature animals released
2-immature animals released
3-immature animals released have become mature
4-mother released with young in nest box
5-young released with mother
6-uterus opaque

Appendix IVc2. Result of experiment in the A enclosures in 1982.

		Experiment 2.			
		Released	Captured Marked	Unmarked	Total
Date		1-7	23.26-7		
Duration (days)			23		
Condition	Sex				
Enclosure A1					
Mature	Female	5	3	5	8
	Male	5	4	6	10
Immature	Female	7	2[3]	1	3
	Male	9	1	2	3
Total		26	10	14	24
Enclosure A2					
Mature	Female	1	1	1	2
	Male	1	1	1	2
Immature	Female	7	1+5[3]	1	7
	Male	8	1[3]	4	5
Total		17	9	7	16

1-mature animals released
2-immature animals released
3-immature animals released have become mature
4-mother released with young in nest box
5-young released with mother
6-uterus opaque

Appendix IVc3. Result of experiment in the A enclosures in 1982.

Experiment 3.

			Released	Captured Marked	Captured Unmarked	Captured Total
Date			26-7 27-7	7.9-8		
Duration (days)				13		
Enclosure A1	Condition	Sex				
	Mature	Female	6	3	0	3
		Male	6	2	1	3
	Immature	Female	3	2+1[3]	2	5
		Male	4	3	3	6
	Total		19	11	6	17
Enclosure A2	Mature	Female	1	1	3	4
		Male	1	1	1	2
	Immature	Female	2	1[3]	0	1
		Male	4	0	2	2
	Total		8	3	6	9

1-mature animals released
2-immature animals released
3-immature animals released have become mature
4-mother released with young in nest box
5-young released with mother
6-uterus opaque

Appendix IVd1 Result of experiment in the B enclosures in 1982.

Experiment 1.

			Released	Captured Marked	Captured Unmarked	Captured Total
Date			12-5	25-5		
Duration (days)				14		
Enclosure B1	Condition	Sex				
	Mature	Female	5	3	0	3
		Male	5	2	0	2
	Immature	Female				
		Male				
	Total		10	4	0	5
Enclosure B2	Mature	Female	2	0	0	0
		Male	2	0	0	0
	Immature	Female				
		Male				
	Total		4	0	0	0

1-mature animals released
2-immature animals released
3-immature animals released have become mature
4-mother released with young in nest box
5-young released with mother
6-uterus opaque

Appendix IVd2. Result of experiment in the B enclosures in 1982.

		Experiment 2.			
		Released	Captured		
			Marked	Unmarked	Total
Date		21-6[1] 22-6[2]	11, 14-7		
Duration (days)			21		
Enclosure B1					
Condition	Sex				
Mature	Female	3	2	0	2
	Male	3	0	1	1
Immature	Female	5	0	0	0
	Male	4	1[3]	0	1
Total		15	3	1	4
Enclosure B2					
Mature	Female	0	0	0	0
	Male	2	2	1	3
Immature	Female	5	3[3]	1	4
	Male	5	3[3]	0	3
Total		12	8	2	10

1-mature animals released
2-immature animals released
3-immature animals released have become mature
4-mother released with young in nest box
5-young released with mother
6-uterus opaque

Appendix IVd3. Result of experiment in the 8 enclosures in 1982.

Experiment 3.

			Released	Captured Marked	Captured Unmarked	Captured Total
Date			14-7	5.7-8		
Duration (days)				23		
Enclosure B1	Condition	Sex				
	Mature	Female	3	0	1	1
		Male	2	1	0	1
	Immature	Female	6	1[3]	0	1
		Male	5	5	0	5
	Total		16	7	1	8
Enclosure B2	Mature	Female	0	0	1	1
		Male	2	2	0	2
	Immature	Female	5	2[3]	0	2
		Male	5	1	0	1
	Total		12	5	1	6

1-mature animals released
2-immature animals released
3-immature animals released have become mature
4-mother released with young in nest box
5-young released with mother
G-uterus opaque