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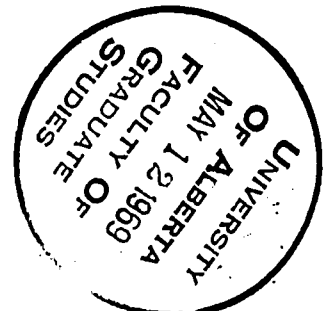
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THE UNIVERSITY OF ALBERTA

DYNAMICS AND REGULATION OF A *CLETHRIONOMYS*
POPULATION IN CENTRAL ALBERTA

by



PETER WAYNE ELLIOTT

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY


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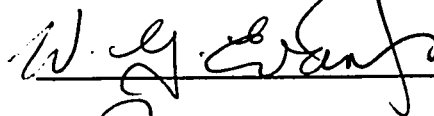
FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled *Dynamics and regulation of a Clethrionomys population in central Alberta* submitted by Peter Wayne Elliott in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

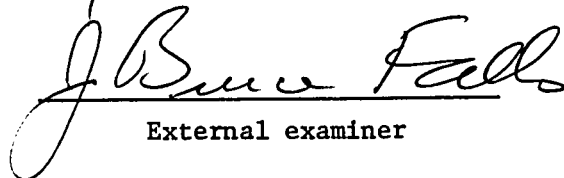


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ABSTRACT

A population of *Clethrionomys gapperi* was sampled intensively over four breeding seasons with the objective of examining how intraspecific interaction and meteorological conditions might change or affect levels of density. The effects of interaction were studied experimentally on some woodlots through removal or addition of voles.

Densities reached the same levels in 1965 and 1966, went down slightly in 1967, and dropped sharply in early 1968. Voles did not breed under the snow; the onset of breeding was correlated with the time of thaw. All overwintered voles matured and the females produced young for as long as they remained on the area. Summer males seldom matured but females from the first litters of the season usually had at least one litter within the season. Litter size and number of litters per resident female changed little with area or year. Winter losses were low except in 1967-68. With the snow gone, losses were higher but rates of loss were still lower than for most microtine populations.

Adults tended to be distributed uniformly and extended their ranges into areas vacated by neighbours. Dispersing voles usually settled on areas having densities lower than those they left. Removal of adults in spring did not markedly affect rates of reproduction or loss other than by influencing the residency of the remaining adults.

Results suggested that interaction between mature voles was responsible for the patterns of dispersion and dispersal, and for determining the numbers of adults on an area. The drop in numbers in 1968 was correlated with unusual conditions of temperature and precipitation. These findings were compared with those of other studies.

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INTRODUCTION

Review of problem

Two basic questions in population ecology are:

1. What are the forces that cause a species to show different mean levels of density in different parts of its geographical range?
2. What, if any, are the forces that hold the density of a given population near this average level?

It is useful to refer to the first set of forces or factors as *limiting* and the second set as *regulatory*. Short-term or seasonal changes often make the average level hard to determine. To offset this, such long-term averages are often based on data gathered at a particular time of the year or stage of the life cycle.

Regulation then would be any process that tended to bring the population's density back to the long-term average. Such a definition implies processes based on feedback; that is, based on increased interaction between animals or increased effects on the habitat or other species present with increased density of the given population. It also implies that regulation would not be involved if a population showed a sharp deviation away from the average level. Regulatory mechanisms undoubtedly exist but they are likely to avoid detection for several reasons. There will always be a lag in time between the increase or decrease in density and the reaction via the feedback from the change. These processes will be masked, particularly at low densities, by the random mortality caused by such things as accidents or occasional cases of disease. Also, some mechanisms may act as a result of feedback from certain sex or age groups in the population rather than from the whole.

Some populations of microtines fluctuate somewhat periodically (Ashby, 1967; Koshkina, 1966; Shelford, 1943). A regulatory mechanism acting after a considerable lag in time may be a reasonable explanation of such "cycles". Alternatively, the reaction of the population to feedback may change in a periodic way following changes in the behavioural or physiological make-up of the individuals. If the possibility of lapses or changes in the action of a regulatory mechanism is assumed, the given definition may be useful even for populations that show cyclic or irruptive changes in density.

With these definitions in mind I examine some of the factors that have been proposed as important in the dynamics of populations of rodents. The literature on rodent ecology is extensive and I limit discussion to studies that seem most important or relevant, stressing those involving microtines.

Quantitative or qualitative shortage of food has sometimes been implicated in population declines (Pitelka, 1957; Schultz, 1964). Adding food allowed some rodent populations to increase (Bendell, 1959) but had little effect on others (Krebs and DeLong, 1965). When populations show cessation of breeding at high densities or sharp differences in mortality between sex or age groups, food is probably not the proximate factor involved (see Chitty, 1952; Kalela, 1957; Zejda, 1967 and earlier). More commonly, food has been implicated in combination with some other factor. For example, Smyth (1966) felt that a great abundance of food plus some unknown, probably intrinsic, factor allowed winter breeding in a population of *C. glareolus* in some years. Other examples suggesting a combined effect are mentioned below.

The role of weather in microtine fluctuations is little understood. Changes in weather may synchronize the periodic fluctuations shown by

some microtines (Chitty, 1960; Krebs, 1964) or affect reproduction by altering the length of the breeding season. The effect of low temperatures during periods of little cover by snow may provide the simplest explanation for the demographic changes observed in a lemming population (Fuller, 1967; Krebs, 1964). Other papers suggesting that snow might be important to northern microtines are those of Beer (1961), Coulianos and Johnels (1962), Frank (1964), Fuller (1969), Pruitt (1957), Quimby (1944), and a number of Russian works such as those of Formozov (1946) and Gruzd'ev (1967). Rare species of microtines sometimes fluctuate synchronously with commoner ones (Koshkina, 1966) and climatic stress seems the best explanation of this observation at the moment. An hypothesis involving genetically-determined changes in behaviour offers an alternative explanation (Chitty, 1967). Severe weather apparently triggered the decline of a *Microtus* population that was already under stress from food shortage and crowding (Frank, 1957). The combined effects of food and climate seemed to explain regulation in an *Oryzomys* population better than effects of density (Negus *et al.*, 1961). The possible effects of weather on accessibility of food have been little studied for rodents.

High parasite loads may predispose animals to mortality from other agents; disease is sometimes associated with declines (DeLong, 1967; Krebs, 1966; Murray, 1965). However, parasitism and disease are seldom mentioned as major limiting or regulatory factors. Predation probably reduces mainly those fractions of populations which are surplus (Errington, 1967); in particular, predators may dampen microtine fluctuations (Pitelka, 1957). A few studies indicate that predators can occasionally cause drastic reductions in rodent populations (Maher, 1967; McCabe and Blanchard, 1950; Schnell, 1964). Pearson (1966) suggested that predation is an essential part of microtine cycles, but Krebs (1966) raised some doubts

about this conclusion, using data from the same population.

Many studies suggest that interspecific interaction can limit the distribution of rodents; examples involving *C. gapperi* are discussed by Cameron (1965) and Clough (1964). A few studies suggest that such interaction may limit the density of one of the species involved (Caldwell, 1964; DeLong, 1966; Martin, 1956).

The importance of intraspecific interactions in regulating numbers has been greatly disputed. Snyder (1961) felt that intraspecific competition is usually the stimulus that brings about the physiological changes which in turn often lead to limitation of numbers. He suggested, however, that social interaction need not act directly, while Christian and Davis (1964, 1966) felt that it may lead to lowered rates of reproduction and survival. The lowered survival would be a result of deficient lactation or increased intrauterine loss, both caused by endocrine exhaustion. There are varying degrees of support for density-controlled population changes caused by endocrine disturbance (Krebs, 1964; Negus *et al*, 1961; Tanaka, 1964; etc.). Some have suggested that the main effect of increased crowding is to delay maturation (Kalela, 1957; Koshkina, 1965). Others proposed that it would result in increased dispersal (Lidicker, 1962) or selection of genotypes more resistant to crowding but less resistant to environmental variables (Chitty and Phipps, 1966). The latter hypothesis deserves attention since it employs both individual variation and environmental effects in explaining certain types of fluctuations.

Any one of these factors might be regulatory. The effect of interspecific competition would likely depend on the density of the competing species as well as the species being considered. Weather could regulate in the defined manner but would more likely act to lower the density to some minimum level. The level would probably depend on

the capacity of the given habitat to support animals during that part of the year when conditions of temperature and precipitation were most severe, regardless of what densities were reached at other times. Note, though, that this capacity might again be determined by intraspecific interaction.

I began this study with the objective of examining two hypotheses used to explain fluctuations in density of rodent populations. The two might be stated generally in this way:

1. The abundance of a rodent population may be regulated intrinsically through the effects of intraspecific behaviour.
2. The density of a rodent population may be suppressed, or perhaps regulated, by the effects of severe environmental conditions at critical periods of the year.

The testing of either hypothesis, even in a preliminary way, requires analyses of demographic changes in the population. The first can be examined indirectly by studying rates of maturation, mortality, and dispersal in control areas and in areas where density has been changed artificially. Assuming that severe weather would be most likely to affect numbers at the beginning and end of the period of cover by snow (Fuller, 1967), the second hypothesis may be examined by relating conditions at these times to spring and summer densities. The effects of the snow and temperature regime on spring breeding may also bear examination.

The study animal

Why use *Clethrionomys gapperi* (Vigors) to study this problem?

Most of the work on dynamics of small rodent populations in North

America has been done on species of *Microtus* and *Peromyscus*. *C. gapperi*

is a widespread species, morphologically similar to *Microtus*, and has been little studied. Related forms have been studied in Europe and Asia (Kalela, 1957; Koshkina, 1967 and earlier; Newson, 1963; Tanaka, 1964 and earlier; etc.) so that comparisons within the genus are possible. Since some hypotheses on limitation and regulation of populations seem to have been dictated by the species studied, an examination of a related species should be revealing.

A brief sketch of the vole's life history can be drawn from the results and bibliographies of theses by Butsch (1954), Gunderson (1962), and Tanner (1950). The boreal redbacked vole inhabits a variety of forest habitats and is reputed to prefer moist situations. The diet includes a variety of green and other plant material and a small amount of animal food. Most estimates of density indicate that these voles seldom reach 15 to 20/acre. The populations studied by Fuller (1969) occasionally reached densities of 35/acre. One study gives a figure of almost 60/acre (Aumann, 1965) and Butsch (1954) mentions fall densities of up to 80/acre. Estimated sizes of home ranges are variable and probably reflect the use of different habitats by the voles and different methods of calculation by the investigators. Females are multiparous and apparently have a post-partum estrus. They are known to breed from March to October but there seem to be no records of winter breeding in the wild. The gestation period is 17 to 19 days according to Svihla (1929, quoted by various authors) and the litter size is 1 to 8 (mean varies from area to area). Beer *et al* (1957) suggest that intrauterine loss is low. In one population, both litter size and percentage of adult females breeding seemed to be inversely related to density (Patrick, 1962). Young are weaned at about three

weeks of age. Sexual maturation is said to come in the third month of life and first parturition in the fourth but this is based on rather few observations. There is little quantitative evidence on mortality but most authors agree that females live longer than males, and that no voles survive to two years in the wild.

THE STUDY AREA

Fieldwork was done on some 120 acres of mixed grassland-woodland on the northeastern shore of Ministik Lake, 23 air miles southeast of Edmonton, Alberta. Ministik Lake has served as a waterfowl refuge for about 30 years and public access has been limited.

The climate and vegetation of this area are typical of the "aspen parkland" ecotone (see Bird, 1961; Moss, 1955). The climate is of the cool temperate type with a long cool summer. Data on 1965-68 weather are presented later. Topography is flat to gently rolling. Some of the woodlots have ridges within them but none is steep enough to prevent growth of trees or other plants. Much of the Ministik area is covered by extensive deciduous or mixed woods but the part I used is broken up into woodlots separated by grassland, marshes, or temporary ponds (Fig. 1).

The plants in the woodlots divide readily into tree, shrub, and ground or low-growing species. Aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), white birch (*Betula papyrifera*), and willows (*Salix* spp.) form the tree canopy, along with a few clumps or single trees of white spruce (*Picea glauca*). On a few smaller woodlots these trees are smaller and more shrublike but the tree and shrub strata are usually quite distinct. The main shrubs are saskatoon (*Amelanchier alnifolia*), beaked hazelnut (*Corylus cornuta*), cranberry (*Viburnum edule*),

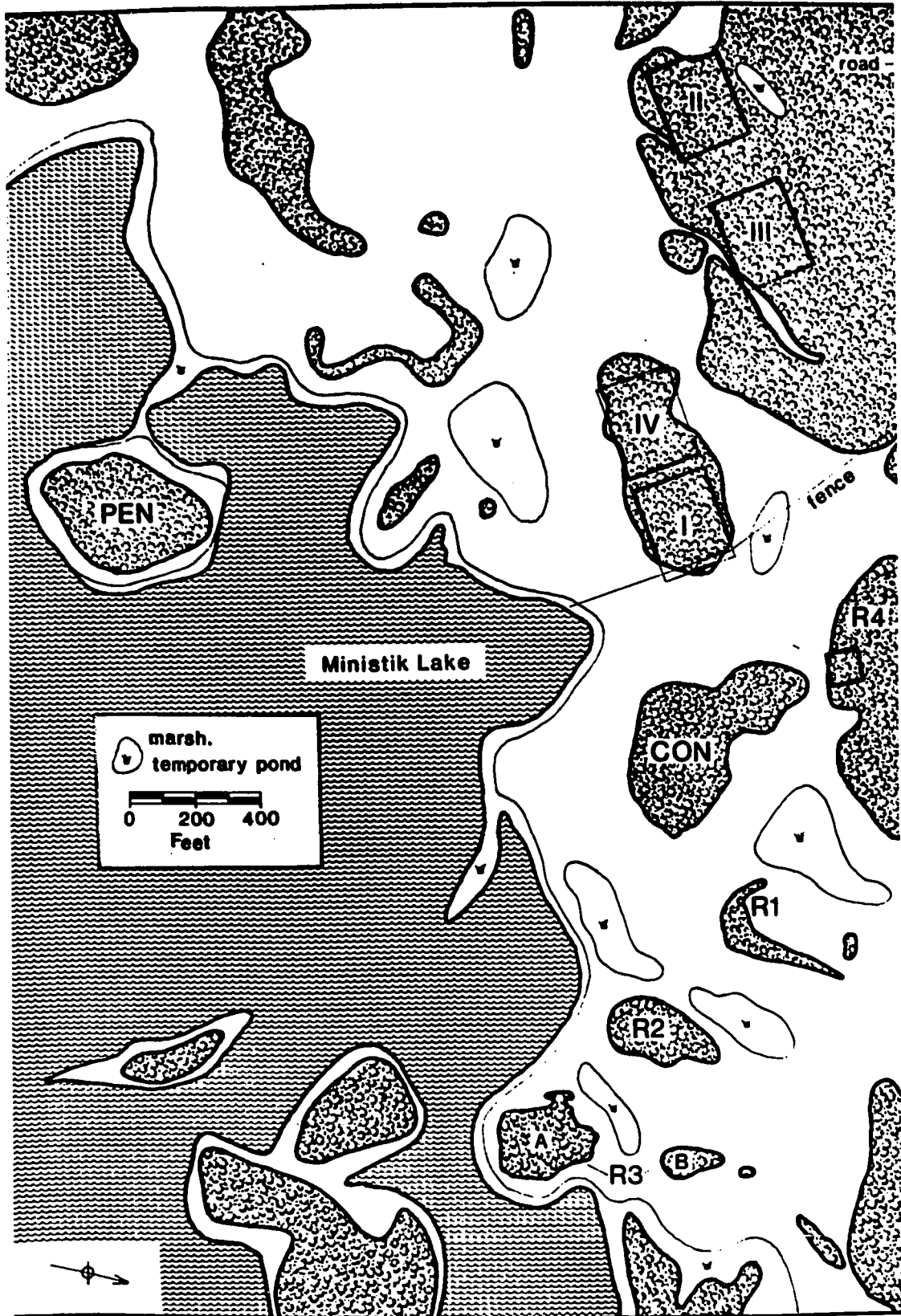
rose (*Rosa woodsii*), red-osier dogwood (*Cornus stolonifera*), and raspberry (*Rubus strigosus*). In clearings and under younger trees strawberry (*Fragaria* sp.), wintergreen (*Pyrola* sp.), and a number of less common species are found. Within older stands herbs and other low-growing species are scarce. In woodlots the humus and litter layers are composed almost entirely of deciduous leaves except directly under the few spruce trees. The percentage of dead aspens and balsam poplars is high in older stands and many fallen trees are found on the ground, along with tangles of branches and twigs.

During my study the area west of the fence shown in Fig. 1 was used for grazing of cattle from about early May to September each year. Cattle often grazed and browsed on the plots within this area and the effects of trampling were obvious, especially on the more open parts of the woodlots. The peninsular area (PEN) was usually barred to cattle by a strip of marsh but, at times of low water, cattle did get into this woodlot and cause some damage. The grassland to the east of the fence was mowed for hay each year, usually in August. This had no visible effect on vegetation in the woodlots but has probably prevented expansion of the woods onto the grassland.

Clethrionomys shared the woodlots with deermice (*Peromyscus maniculatus*) and an occasional jumping mouse (*Zapus hudsonius*). Meadow voles (*Microtus pennsylvanicus*) occurred on grassland areas but apparently did not enter the woods. Potential predators on the rodent populations were weasels (*Mustela erminea* and *M. rixosa*), coyotes (*Canis latrans*), a few skunks (*Mephitis mephitis*), horned owls (*Bubo virginianus*), redtailed hawks (*Buteo jamaicensis*), and individuals of a few other species of hawks or owls.

Figure 1

Map of northeastern edge of Ministik Lake (Lat. $53^{\circ}22'$; Long. $112^{\circ}59'$), showing lake-edge, woodlots, and plots. Plots are identified by letter/number combinations which are used throughout the text. Unshaded sections represent grassland (or marshy areas, as indicated).



METHODS

To examine the hypotheses I obtained demographic data on control and experimental areas. The principal technique was intensive live-trapping. I discuss details of live-trapping and other general procedures; experimental methods are mentioned later.

I established permanent trapsites on the plots (Fig. 1) using a square grid, the interval between trapsites being 2 rods (33 ft). Some plots were rectangular (I, II, III, IV, small plot on woodlot R4) and the others used woodlot edges as their boundaries (CON, R1, etc.). In 1965, plots I through IV contained 40 trapsites in 8 by 5 grids; after 1965, 54 sites were used (9 by 6 grids). At the start of the study, traps were placed at the trapsite or within about a yard of it. Trap locations, once established, were retained throughout the study with few exceptions -- occasionally I shifted a trap to a more sheltered location to prevent its being sprung or damaged by cattle. On each plot, trapping was carried out for two or more (usually three) consecutive nights about every three weeks. I sometimes varied this procedure during experiments, as discussed later.

Table I presents information on the plots shown in Fig. 1. For most purposes, plots I and IV were considered together as a unit, as were II and III. With one exception, the acreages given are those of the woodlots. Plots II-III and R4 were the only ones surrounded by a large area of untrapped wood. The area given for II and III includes the 9 by 6 (or 8 by 5) grids, the area between II and III, and a border strip one rod (16.5 ft) in width around the other three sides of the two plots. Plots R1, R2, and R3 were sometimes used in combination. Plot R3 was composed of two woodlots: A (34 trapsites)

Table I.

Study plots: size, number of trapsites, and utilization

Plot	Size (acres)		Number of trapsites		Principal use in:		
					1965	1966	1967
I-IV	3.75		108 (80-85 in 1965)		control	male removal	control *
II-III	3.15 **		108 (80 in 1965)		control	male removal	control
R1	0.76	3.34	20	82-85	removal *	removal	
R2	1.18		25		addition	addition	lowered spring density *
R3	1.40		37-40			removal *	
R4	3.46 (whole woodlot)		9-10 (part of woodlot only)			removal	
CON	3.52		95-105			control	control
PEN	2.58		90			establish high density	lowered spring density *

* also used for experiment on efficiency
(see next section)

** smaller in 1965 (2.25, later 2.38 acres)

and B (3 to 6 trapsites).

When a *Clethrionomys* or *Peromyscus* was captured the following information was recorded:

- date and location
- identification mark (unmarked animals were given individual marks by toeclipping)
- sex and weight
- reproductive condition
 - males: testes scrotal or abdominal; size of penis sheath (rated as juvenile, subadult, or adult)
 - females: vagina perforate or imperforate; visibly pregnant; teats undeveloped, showing slightly, or prominent
- unusual behaviour, use of burrows on release, etc.

Six females had litters while confined in livetraps. When this happened, I examined the female and litter, returned them to the trap, and left the trap locked open. All but one litter were removed by the females; the members of the litter that died were weak when I first found them.

I supplemented data from livetrapping by collecting mice on areas away from the plots. These were autopsied, as were animals that died in livetraps or were removed from plots during experiments. Information taken from dead animals included location, circumstances of death, weight, body measurements, and reproductive condition (as done for live animals). Other data were taken as follows:

- males - size of testes and seminal vesicles; epididymal tubules visible to unaided eye or not
- females - stage of development of uterus and ovary; number of uterine scars, embryos; weight of embryos

Skulls, femurs, and parasites were saved from dead mice.

For the specialist, this paragraph gives more detail on equipment and trapping methods. In 1965, the only livetraps

available were small and medium Sherman traps. I gradually replaced these with Longworth traps (described in Chitty and Kempson, 1949) and Longworths alone were used after 1965. Terylene wadding and sunflower seeds were always present in livetraps. I sometimes baited the treadles of live and snaptraps with peanut butter but traps containing only seeds seemed to be just as effective for voles. Livetraps were set out with no prebaiting. After each capture traps were scraped clean of faeces and dirt, and moisture was removed from the terylene by hard shaking. Specimens were collected with Museum Special snaptraps, sometimes supplemented by Victor mousetraps. Weights were taken on an Ohaus shot scale which had its pan replaced by a suspended tin with a plastic cover.

Some terms used below are defined. *Overwintered* refers to animals that have lived through one winter while *summer* voles are those born during the breeding season of the year being considered. Summer animals are often divided (somewhat arbitrarily) into three weight categories: *adult* (over 18 g), *subadult* (12.0-17.9), and *juvenile* (less than 12). The *trappable* fraction of the population excludes those animals too young to come into contact with traps. Animals caught and released only once during a season's work are considered *transients*; *residents* are those caught at least twice (often many times) on a given plot. Voles released on a plot other than that where they were caught I refer to as *aliens*. Finally, *vole* means *Clethrionomys* unless some other genus is specifically mentioned.

DISCUSSION OF LIVETRAPPING TECHNIQUE

In a mark-recapture study, numbers are usually estimated using modifications of the Lincoln Index (Jolly, 1965; Leslie, 1952; etc.). The calculations depend on the assumption of random capture; that is, they assume that marked and unmarked animals are equally susceptible to capture or observation. For some populations of small mammals, at least, this assumption does not hold (Chitty and Phipps, 1966; Kikkawa, 1964; Krebs, 1966; Tanton, 1965). The alternatives are to use a trapping index or a technique which will give total numbers directly. Trapping indices, such as number of animals taken per 100 trapnights, give only relative numbers at best, and may be affected by weather, trap spacing, cover, and other factors. Clearly, direct counts of animals are preferable, if they can be obtained.

The main disadvantage to using direct counts from livetrapping is that certain individuals in the population may not get caught, particularly if the ratio of traps available to animals present is not much more than one to one. Two questions, then, are considered before results from livetrapping are discussed:

1. Were there enough traps so that each individual had unused ones in its vicinity?
2. Was the entire trappable population being caught?

During most of my periods of trapping there were far more traps set than animals caught. However, in 1965, I sometimes used only half the normal complement of traps on plots I through IV. The II-III area had the highest density of animals (voles and deermice). I examined my 1965 records to see if there were any nights when more than 50%

of the traps on II-III were occupied. There were only three such nights and the highest rate of occupation was 65% (13 of 20 traps used, two nights involved). There were a few other instances involving occupation over 50%. In 1965, I occasionally used 17 traps on plot R1, and nine animals were caught on two separate nights. Sometimes I caught three animals when using only three traps on the B area (part of R3). I added traps when this happened and, in one instance, took a fourth animal. Apparently there was never any prolonged shortage of traps on any area.

In 1966, D. Chitty pointed out that not all of my Longworth traps had their triggers set to the most sensitive position (pers. comm.). I had been adjusting the sensitivity by bending the door release rather than using the method proposed by the makers (Chitty and Kempson, 1949). I had noticed that some traps were being entered and not sprung. Juvenile deermice were probably responsible since I often found two in the trap together, and twice, three. It was possible that I was failing to catch some of the smaller trappable voles in 1965 and part of 1966. From my records, I obtained the numbers of captured voles weighing less than 10 g, and the number of multiple captures (two voles in a trap at once). These figures are compared with the total captures of voles for the year:

	Total captures	Percent captures less than 10 g	Percent multiple captures
1965	420	0.7%	1.4%
1966	1260	0.3	1.3
1967	740	1.8	0.4

The percentages suggest that 1967 trapping of young voles was more efficient. Even in 1967, however, only 13 voles under 10 g were taken

and the apparent differences are not significant. I could not detect any yearly differences of this type in the heavier young. To offset any bias I use only adult and subadult voles for most comparisons between years.

I would apply this correction in any case since the capture of voles recently out of the nest could vary considerably by chance. Consider some litters born and reaching trappable age at about the same date on various plots. An area trapped just prior to the emergence from the nests would yield no small voles; the area trapped next might show several. By the time the former area was trapped again many of this group could have dispersed or died. Those remaining would now, for the most part, be in the subadult category.

Records from trapping on plot R1 in 1965 and plot A in 1966 give some tentative answers to the second question posed above. These records suggest that livetrapping for more than one night would catch all overwintered and adult voles and most, if not all, of the younger voles. This was tested more rigorously in May, 1967.

The PEN area (surrounded by water at this time) and the combined R woodlots were used. The procedure was to trap in the normal way for several nights, then to remove all livetrapped animals and supply the trapsites with snaptraps for several nights. Those studying populations of small rodents generally agree that snaptraps are much more efficient than livetraps. Seven overwintered voles were marked and later removed from PEN; eight of twelve marked voles were removed from R. Snaptrapping gave no voles on PEN and three unmarked females on R. The comparison between island and mainland suggests that the three were immigrants. This argument is strengthened by the June capture on R of an unmarked adult male and a female marked earlier on the II-III area.

Similar tests were made in the fall of 1967 using PEN and the I-IV woodlot. On PEN, four of six marked voles were removed and no more were taken by snaptraps. On I-IV, five voles were removed and snaptrapping yielded one unmarked male. On I-IV, and also in the May experiments, the first night of trapping did not catch all residents. As a rule, all were caught once traps had been out for two nights.

These last experiments were meant to test efficiency during the time of highest seasonal density. Unfortunately, the density had dropped considerably since the previous period of trapping. It is still possible that livetrapping might have missed some individuals when the numbers of summer voles were at their highest. But, the results from PEN and the high availability of traps indicate that most of the subadult voles were being caught by the intensive livetrapping.

I did not attempt to test efficiency on II-III where the plots were continuous with a large untrapped area, as removal here might have caused immigration. It is unlikely that temporary removal of residents from a woodlot would increase the amount of immigration across the intervening grassland.

Few workers doing livetrapping studies have tested the efficiency of their procedures. Such tests should probably be part of any live-trapping study. To strengthen this suggestion, I might mention that adult deermice on my plots were not always captured during these tests. Van Vleck (1968) tested a livetrapping procedure involving a population of *Microtus pennsylvanicus*, using a method similar to mine. He found that livetrapping had taken only half of the animals present. Fortunately, no such variation was uncovered at Ministik Lake. Some voles were undoubtedly "trap-prone" but none seemed to be "trap-shy".

To summarize, my records suggest that there was no shortage of traps during the study. There may have been some bias in captures of juvenile voles. Longworth traps were very efficient in catching adult voles provided traps were run for more than one night. Apparently most, if not all, resident subadult voles could be taken by two or three consecutive nights of livetrapping.

RESULTS FROM CONTROL AREAS

Numbers

Information on the density of the population is presented first to provide a base for discussion of rates of reproduction and loss. The first few paragraphs discuss the changes in density of voles with time and area. Then, data from given areas and years are partitioned by generation, sex, and weight (age).

Each estimate of total numbers combines two figures: the number of voles present *during* the census, plus any voles marked in a *previous* census and recovered in a *later* census. The latter figure was very often zero, suggesting that marked animals were easily recaptured if they were still on the area. The numbers given, while they should be very close to the absolute numbers present, are minimum estimates. For most areas the number of trapped juveniles was small, and I have combined juveniles and subadults for simplicity. In 1966, the I-IV and II-III areas were used experimentally (adult males were removed), but I have included these tabulations here for the sake of continuity. Densities were calculated by dividing the numbers of voles by the acreages given in Table I.

Figures 2 to 4 show changes in density for three areas over three or four summers. For a given area, the densities at given times were similar from 1965 through 1967. This was particularly evident on the I-IV and II-III areas. Densities on the CON area were within the same range as those of the other plots. However, on CON, the 1967 figures were only one-half to two-thirds as large as those of 1966. Densities over the entire study area showed a sharp drop in 1968. Prior to this, spring densities ranged from 1 to 6/acre; maximum densities from 5 to 15/acre.

In the section on trapping efficiency I argued that variations in numbers of juveniles caught might be related to the dates of trapping. A similar argument might be proposed for the height of the "peak" in numbers for any area in a given year. It is probable that a higher peak would have been obtained if another census had been made on II-III in late August, 1966, or late August-early September, 1967. The same might apply to I-IV for August and September of 1965. With the latter exception, trapping intervals were short enough to prevent the overlooking of any major change in numbers.

A breakdown of vole numbers might be done by separating the data into eight categories -- two sexes, two generations, and three weight categories for the summer generation. For most purposes I can combine the summer juveniles and subadults and use six categories. The only separation that presented difficulty was that of the generations.

From my autopsy records I was able to define the generation for 25 marked males and 18 marked females, using time of marking, trapping history, and weight records. I then examined data on body measurements and compared the overwintered and summer voles hoping to find a

Figure 2

Densities of voles on the CON plot. Thick lines connect estimates of density based on two or more nights of trapping. Fine lines show densities of overwintered voles. Solid circles show maximum densities *during* the trapping period; open circles the densities present at *end* of trapping period. The drop from solid to open circle indicates the loss from trap mortality or deliberate removal.

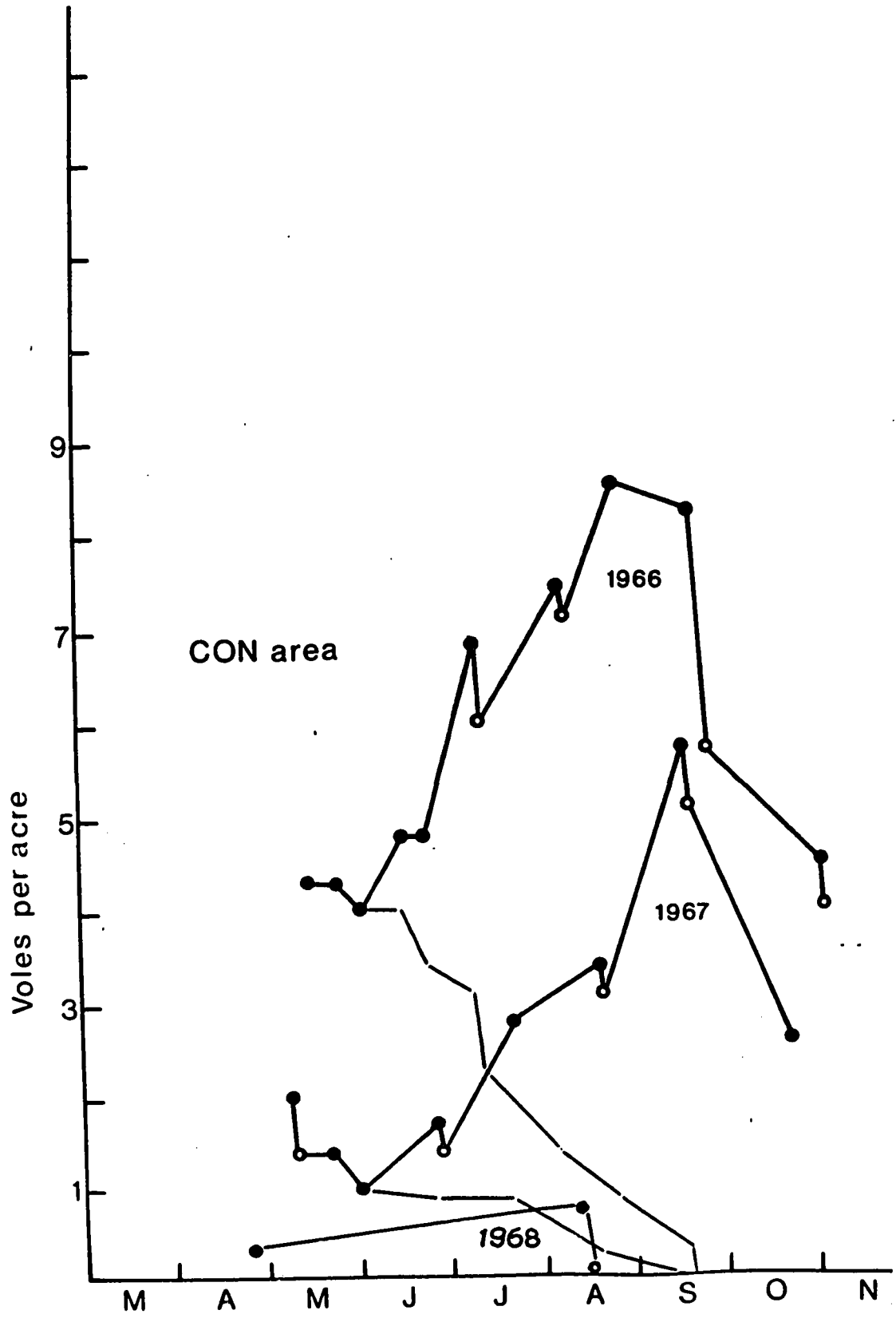


Figure 3

Densities of voles on the II-III area, shown in same fashion
as Figure 2.

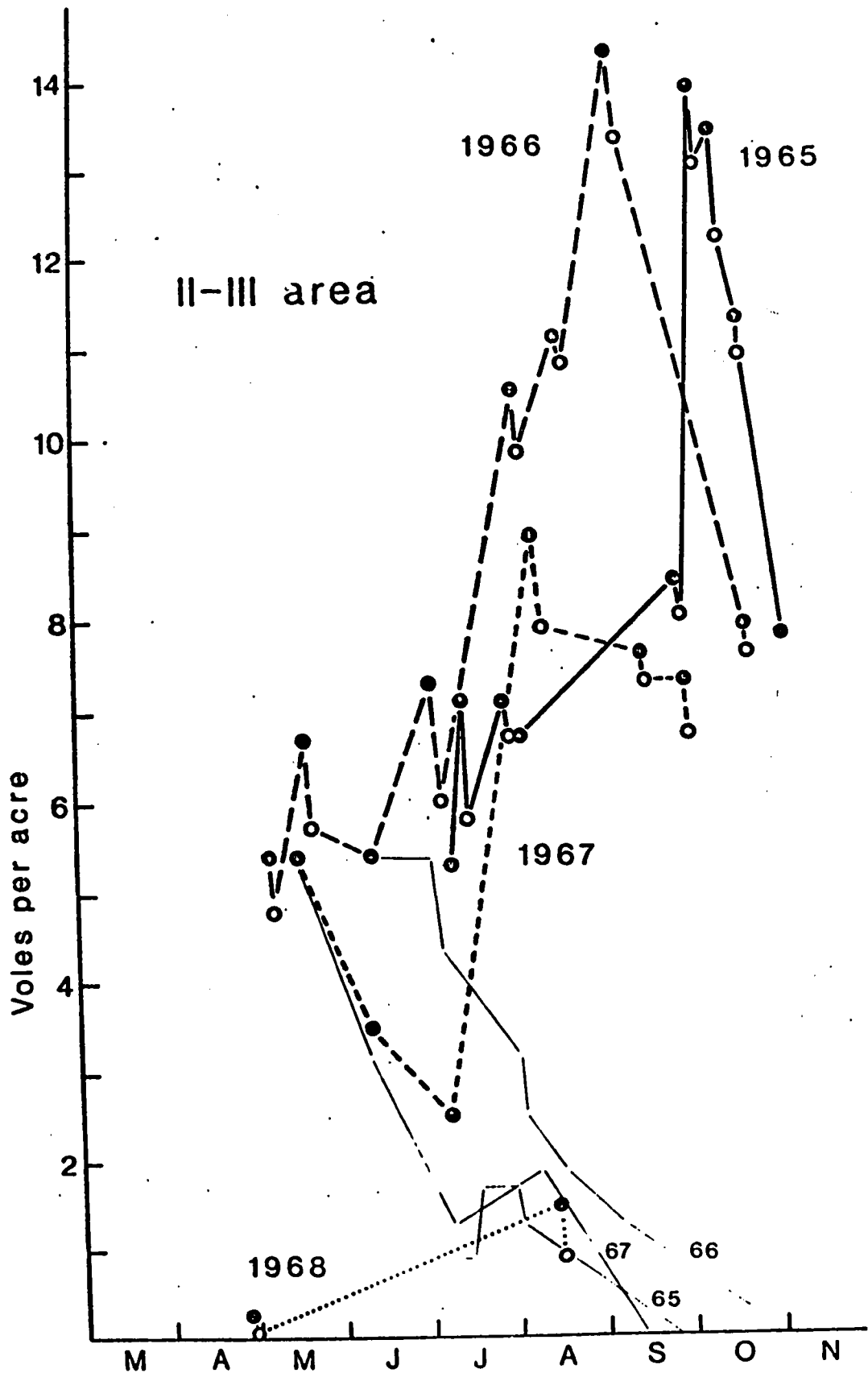
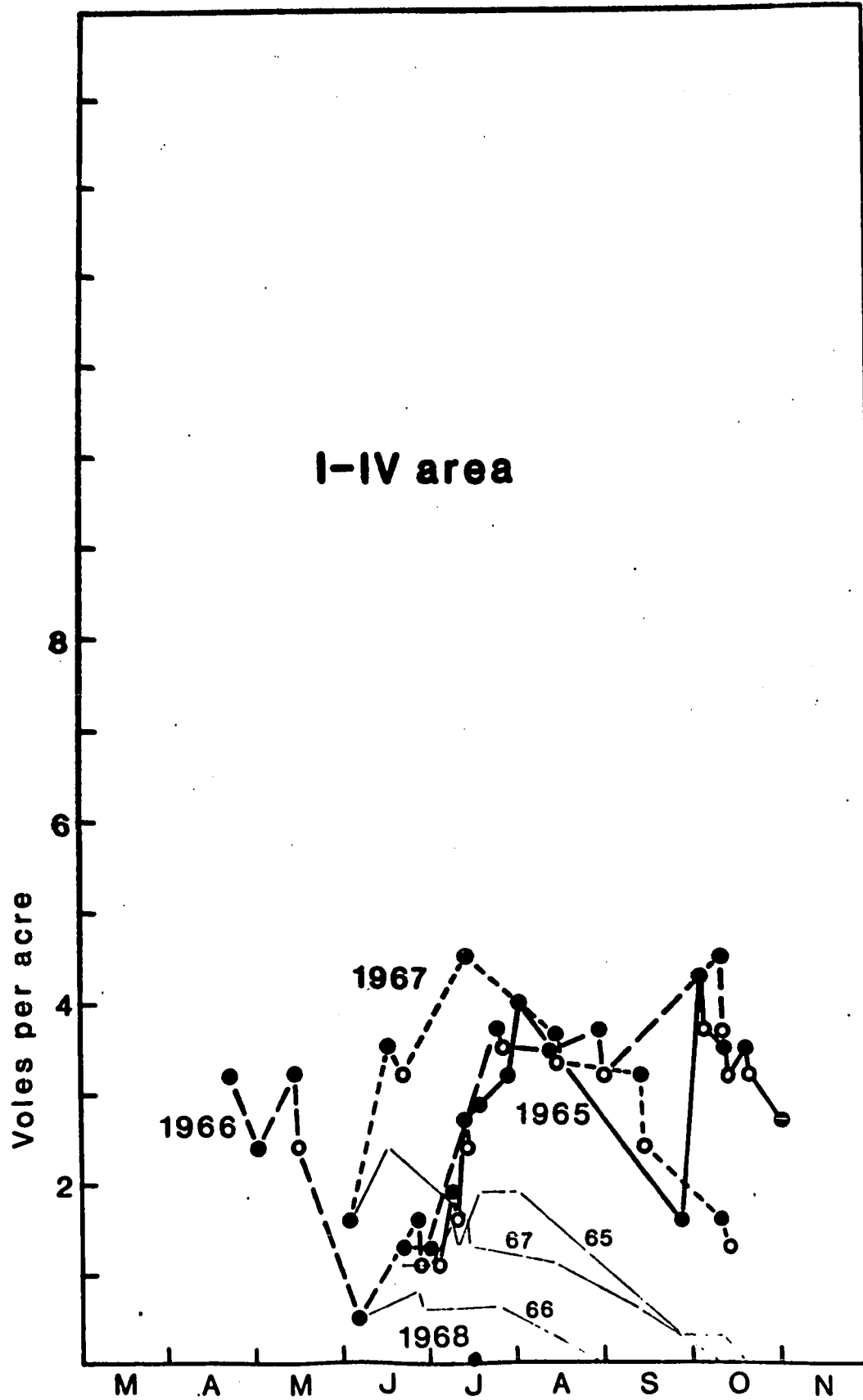


Figure 4

Densities of voles on the I-IV area, shown in same fashion as Figure 2.



character that would conclusively separate generations. Weights, total lengths, and weights of the lower jaws showed too much overlap to be useful. I then examined rooting of the molars and this gave a clearcut separation of the generations.

Examining the molar roots was quite simple (see Smyth, 1966). The cleaned dentary bones were softened in hot water and the ventral portion of one was split away so as to reveal the incisor. The remaining portion of the dentary was split sagittally so that the first molar could be lifted out. Overwintered voles showed a deep cleft between the two roots of the tooth when the tooth was viewed laterally. The ventral base of the tooth in summer voles was flat or showed a slight indentation (specimens from late summer). The difference was clear enough that measurement of the root lengths or pulp cavities was not necessary.

Using the molar roots, I classified all of the autopsied voles whose generation was uncertain. By comparing the dates of capture, weights, and other information from this group with that of voles that were released alive I classified all but a few animals.

The generation-sex-age breakdowns are presented in Table II. Where two or more censuses were made over a period of three to four weeks, only one is listed in the table unless some important change took place between the censuses. The information summarized in this table is used in several other sections.

The population consisted of overwintered voles up to the end of May or first half of June. These disappeared gradually, males disappearing somewhat earlier than females. Overwintered animals seldom remained on an area past September and never survived a second winter. Notice that, in the column for overwintered females, most areas show at least one

Table IIA. Structure of population on CON plot.

Figures represent total numbers of voles known to be present; those in parentheses the number lost through death in traps or deliberate removal. Abbreviations stand for *juveniles*, *subadults*, *adults*, *males*, and *females*.

Trapping period beginning:	Overwintered		Summer			
			JU and SA		AD	
	M	F	M	F	M	F
<u>1966</u>						
May 13	7	8				
Jun 15	4	10	1	1		1
Jul 8	4	7(3)	5	5		3
Aug 5	2	3	9(1)	8		4
Aug 24	1	2	12	10		5
Sep 18		1(1)	13(2)	13(4)		2(2)
Oct 30			8	8(2)		
<u>1967</u>						
May 8	3(1)	4(1)				
May 30	1	3				
Jun 25	1	2	1(1)	2		
Jul 19	1	2	3	4		
Aug 17	1		4(1)	5		2
Sep 15			6	13(2)		1
Oct 17			4	5		
<u>1968</u>						
Apr 27	1					
Aug 13 *		1(1)				

* partial census

Table IIB. Structure of population on II-III area.

Trapping period beginning:	Overwintered		Summer			
	M	F	JU and SA		AD	
			M	F	M	F
<u>1965</u>						
Jun 24	1	3	4	1		
Jul 11	1	2	5(2)	1	2	6(1)
Jul 25	1	3	4(1)	1	2	6
Sep 25			7(1)	10(1)		3
Oct 10			12(1)	17(2)		3
<u>1966</u>						
May 5	10(2)	7				
Jun 9	9	8				
Jul 3	10(3)	7	2(1)	3		1
Jul 30	5(1)	5(1)	9	6		8
Aug 15	4	2	20	3		6(1)
Sep 4	3	1	26(3)	11		4
Oct 17		1	14(1)	9		1
<u>1967</u>						
May 15	10	7				
Jun 7	6	4		1		
Jul 6	2	2	1	2		1
Aug 7	3	3	18(3)	1		3
Sep 12			13(1)	8		3
Sep 27			12(1)	8(1)		3
<u>1968</u>						
Apr 27	1(1)					
Aug 13 *			1(1)	1(1)		

* partial census

Table IIC. Structure of population on I-IV area.

Trapping period beginning:	Overwintered		Summer			
	M	F	JU and SA		AD	
			M	F	M	F
<u>1965</u>						
Jun 22	1	3	1			
Jul 7	2	4(1)	1			
Jul 25	2	5	1	1	2	1
Sep 25	1		3	2		
Oct 2	1		7	8(2)		
Oct 17			8	4(1)		1
<u>1966</u>						
May 12	6(3)	6				
Jun 25	1(1)	2	1	1		1(1)
Jul 23		2	2	6		4(1)
Aug 28			8	3		3(2)
Oct 9			9(3)	7(2)		1
<u>1967</u>						
May 30	2	4				
Jul 12	2	4(1)	10	1		
Aug 13	2	2	7(1)			2
Sep 12	2		4(3)	5		1
Oct 9			3	2(1)		
<u>1968</u>						
Jun 16	0	0				

increase in numbers after April. This suggests more immigration by females than by males since such increases seldom occurred with overwintered males except on the 1966 experimental plots. The number of summer voles usually reached a maximum in September. Few reached adult weight and most that did were females. On the control plots, summer males reached adult weight only in 1965. Using figures from August, the percentages of adult females in the summer generation ranged from 14 to 33%. This ignores some small samples from August, 1965, which were based on only one night of trapping.

I examine 1966 breakdowns for I-IV and II-III later. On the II-III area more adult summer females were present in 1965 than in 1967. On the CON area 1967 densities were lower in several categories compared to 1966 -- overwintered voles, adult summer females, and total number of summer voles. Notice also that the summer voles began appearing earlier in 1966, and that the overwintered voles did not disappear as quickly in 1967.

The II-III area presents a special problem -- a type of "edge effect". All areas but this were bounded by habitat in which voles did not live (grasslands were trapped intermittently and no *Clethrionomys* were taken). On II-III, the estimates of density were probably affected by the capture of voles whose home ranges were only partly within the areas. Notice though, that the plots were bounded to some extent by grassland and marsh (Fig. 1). I tried various corrections, such as not counting animals caught only in the outermost rows, and estimated that, if the II-III area had been bounded by grassland, the densities obtained there would have been roughly similar to those measured on the CON area. Applying the corrections always eliminated more males than females, suggesting that males ranged more widely or were caught more easily

near the boundaries of their ranges.

Some sex ratios for summer voles are given in Table III. The monthly samples are combined figures from Table II. Combining the samples gives male/female ratios of 1.35:1 for I-IV, 1.09:1 for II-III, and 0.68:1 for CON. The fluctuation around 1.00:1 may be related to shifts in the balance between wider movements (II-III figures are generally >1.00) and higher mortality of males (CON figures are generally <1.00). However, the data for I-IV do not fit this pattern and are hard to explain. Combining all the samples in Table III gives a ratio of 1.04:1. If the calculations are based on the numbers of voles *marked* (or removed at first capture) rather than those present, ratios become 1.33:1 for I-IV, 1.15:1 for II-III, and 1.05:1 for CON. The increase probably reflects the higher turnover rate exhibited by males (see section on mortality).

To summarize, densities on control areas were relatively stable for three years and dropped sharply in the fourth. The overwintered generation disappeared gradually over the breeding season each year, and only a few of the summer voles reached adult size. By October, the density on any area was usually not much higher than the spring density for the area.

Reproduction

In a livetrapping study most measures of reproductive performance are indirect. Such data are often good for comparative analyses only. If livetrapping is efficient and intensive, however, some absolute estimates of reproductive rates should be possible.

Table III. Sex ratios for summer voles.

Figures represent number of males per female (number of females in sample shown in parentheses). A few voles from late June are included with the July samples.

Area	Year	July	August	September	October
I-IV	1965	2.1 (8)			1.50 (20)
	1966	0.25 (12)	1.17 (12)		1.1 (8)
	1967	4.0 (3)	3.5 (2)	0.7 (6)	1.5 (2)
II-III	1965	1.14 (37)			0.68 (66)
	1966	0.61 (18)	2.2 (9)	1.73 (15)	1.40 (10)
	1967	0.3 (4)	4.5 (4)	1.14 (22)	
CON	1966	0.80 (10)	0.78 (22)	0.87 (15)	1.0 (8)
	1967	0.8 (4)	0.6 (7)	0.43 (14)	0.8 (5)

Sexual maturity in live male rodents is often assessed by the position of the testes. It was difficult to determine this objectively for *Clethrionomys*, especially on the summer males, and I sometimes resorted to an intermediate category between the "scrotal" and "abdominal" categories. Autopsies indicated that males with scrotal testes were fully mature since they invariably had large seminal vesicles and epididymal tubules that were visible to the unaided eye. Males with abdominal testes were clearly immature on the same bases. "Intermediate" cases were few and autopsies suggested that these males were probably not fertile.

Without exception, overwintered males became sexually mature by May. Observations on live males and those autopsied are consistent on this point. For analyses of summer males I used data from all animals 12 g and over. Each male was registered as either scrotal or not scrotal for each trapping period in which he was captured. Results are shown in the first half of Table IV. In October, percentages of males with scrotal testes were always zero. The other percentages are variable. On control areas there seemed to be more mature summer males in 1965 than 1966 and 1967. This is shown best by July: 62% for 1965 (I-IV and II-III), 31% for 1967 (CON, I-IV, II-III), and 17% for 1966 (CON). Chi-square testing of 2x2 contingency tables show the 1965 ratio was significantly different from the others ($\chi^2=5.0$ for 1965 vs. 1967, 4.1 for 1965 vs. 1966; $0.050 > p > 0.025$), but this is the only such difference, and one which I cannot explain. Some of these data are discussed later.

The analyses of reproductive success in females are more important in an examination of dynamics. The number born into a population is a product of the number of females bearing young, the number of litters

produced per female, and the number of young born per pregnancy. The first two must be estimated from external reproductive characters and from changes in weight associated with pregnancy; the last is calculated from data on dead and captive animals. The length of the breeding season might also influence the number of litters born to females or the number of summer females bearing young.

My information on litter size comes from five litters born in livetraps, five born in captivity, and six females snaptrapped a few days before parturition. One litter of eight born in captivity to a summer vole contained two young joined through the abdomen in "Siamese" fashion. They were not able to nurse and lost weight while the others gained. Eventually they were found partly eaten. I arbitrarily rated this litter at six young. The average litter size for summer voles was 6.4 (N=10, range 5-7), for overwintered voles 6.7 (N=6, range 6-8). The combined mean was 6.5 and this figure is used for calculations involving litter size.

Twelve other autopsied females were visibly pregnant but not near term. For this group, 7.25 was the average number of embryos (range 4-9). Half were summer females (mean number of embryos 7.7), the rest winter (mean 6.8). One might speculate that intrauterine loss in late pregnancy occurs in summer voles and is negligible in winter ones. The samples are far too small to be sure, however, and the data for two winter voles are somewhat unusual. These two involved marked voles that were carrying their third litters when killed. One had four embryos, the other four large and two much smaller ones. It may be that third litters from winter voles are smaller because of resorption during pregnancy. Eliminating these two gives 7.8 as a mean embryo

count. In this population, intrauterine loss in visible stages of pregnancy was apparently quite small, averaging about one embryo up to the time of parturition.

The onset of breeding occurred at different times in 1966 and 1967. I cannot pinpoint the time of maturation for males from live examination, but I can compare the two seasons using the times of perforation and first parturition for overwintered females in the control areas.

These data are pertinent for the comparison (each date represents the best estimate available from fieldnotes):

	1966	1967	Difference
Timing of thaw			
Depth of snow: 2 in.	April 1	April 22	21 days
Depth of snow: 1 in.	April 10	April 24	14
Depth of snow: "trace"	April 11	April 25	14
Time of first perforation:	April 22 or earlier	May 7 and later	15+
Time of first parturition			
Estimated average:	May 31	June 17	18
Actual litters:	May 31	June 12, June 3	

The 1966-1967 difference is quite consistent. The litter of June 3, 1967, was born to a female that had been in captivity during May; this was the earliest litter of 1967. The difference was also observable in the time of maturation of summer females, as one would expect if the only ones reaching were those from the first litters born to overwintered females. In 1966 the first captures of adult summer females were made on June 20, 25, and 30. The bulk of the captures came on July 23 and 30, and August 5. In 1967, one was captured on July 6 but the majority did not appear until August 7, 13, and 17. According to reproductive events

Table IV. Maturation of *summer* voles
(juveniles excluded).

Sample sizes in parentheses. A few voles from late June are included in the July samples.

	July	August	September
1. Percentage of males with scrotal testes			
Control areas, 1965	62% (29)	43% (7)	17% (6)
Control areas, 1967	31 (13)	26 (23)	0 (20)
CON, 1966	17 (6)	24 (17)	9 (11)
Removal experiment, 1966*	41 (12)	7 (28)	5 (22)
Removal experiment, 1967**	100 (2)	43 (7)	0 (5)
2. Percentage of females with perforate vagina			
Control areas, 1965	87 (15)	33 (3)	0 (11)
Control areas, 1967	77 (9)	10 (10)	0 (17)
CON, 1966	70 (10)	21 (19)	0 (12)
Removal experiment, 1966*	30 (27)	25 (20)	8 (13)
Removal experiment, 1967**	50 (2)	25 (4)	0 (5)

* adult males removed near start of breeding season

** adult males and females removed near start of breeding season

Both experiments are described in section on experimental results.

that can be dated, then, breeding in the spring of 1967 was two to three weeks later than in 1966.

All overwintered females resident on an area for more than one period of trapping had litters. A number of overwintered voles were transients, or were resident only during one period of trapping. These females were all sexually mature as judged by external characteristics, but, unless they dispersed and settled on some other area after I trapped them, they did not contribute young to the population. The ratios of numbers in the resident and non-resident groups are discussed later.

Summer females apparently became sexually mature only if they were born early in the breeding season. The timing of reproductive events suggested that only females from the first litters born to overwintered voles would become pregnant. In 1966, for example, overwintered females had their first litters at the end of May or beginning of June. Results from livetrapping and captive litters suggest that summer females could become mature at about five weeks, and, with a gestation period of 17 days, their first litters could have been born by the fourth week of July. Females from the second litters born to overwintered females would not have had their first young until the fourth week of August, and there were no records of any such litters. Some of the females born from second litters apparently became perforate or reached 18 g in weight but showed no signs of bearing young.

The second half of Table IV contains figures on percentages of summer females that were perforate in various months. The percentages for July, 1966, are the only ones showing a large difference (compare CON with the area having fewer males). However, with the sample sizes given, even this apparent difference is not significant (corrected $\chi^2 =$

3.3, $p > 0.05$). For other months the percentages are fairly constant over different areas and years.

In Table V, I show the percentages of summer adult females for various areas and years, as well as the percentages producing litters. Some of the samples are small and combined means are probably most useful. Thus, the mean percentage of adults in all the samples of Table V is 60% (range 38-100, $N=78$). If summer females from September and October are included the mean becomes 37% (24-62%, $N=140$). The percentage of resident summer females bearing litters is 92% prior to September, and 89% when September and October are included (range 67-100% in both cases). I stress *resident* here since transient adults were omitted from the calculations. The drop from 60 to 37% reflects the addition of subadults to the population in late summer. Practically no subadults became adult during this time, and a few unmarked adults caught in September and October must certainly have been immigrants. The 92 and 89% figures suggest that no litter-bearing females were added in September and October, and that any summer adult that was resident on an area prior to September would bear young the same year. For most areas and years this percentage was 100%. Over the breeding season the percentage of mature summer females varied from roughly 20 to 60%, but this did not seem to lead to a corresponding variation in total numbers.

It may be more important to examine the actual numbers of summer females that matured. For example, on the combined CON, I-IV, and II-III areas the percentage of the subadult-adult group that had litters prior to September was 43% in 1966 (16 of 37). In 1967 the figure was 50% (7 of 14). Since the percentages were similar the number of summer adults was apparently not a function of the time that breeding began.

Table V
 Percentages of summer females reaching
 adult weight and bearing young.

Juveniles are excluded, as are females caught after August.
 Parentheses show numbers that died in traps prior to bearing any
 litters -- these are excluded from calculations in right-hand column.

AREA	YEAR	NUMBER OF FEMALES	ADULTS			
			No.	Percent	Tr.	Resident adults with litters
CON	1966	13	5	38%		80%
CON	1967	8	3	38		100
I-IV	1965	7	3(1)	43	1	100
I-IV	1966	10	8(1)	80		100
I-IV	1967	2	2	100		100
II-III	1965	13	8(1)	62	2	100
II-III	1966	14	9(1)	64	2	83
II-III	1967	4	3	75	1	100
R	1967	7	3	43		67

Tr. -- transient

A much more obvious correlation is with the number of successful first litters from the overwintered females. In 1966, 17 first litters produced 16 summer adults on the three areas; in 1967, 8 litters produced 7 adults. One further point is that the number of summer females that matured before September but did *not* have any litters was 4 in 1966 and 1 in 1967. This might mean that the presence of more adult females (overwintered and summer) in 1966 in some way prevented some of the summer females from bearing young. In any case, the productivity of the summer females seemed to be related to the number of overwintered females that were resident on the areas.

How many litters did these resident females have? To determine this I scanned the individual records for every resident and used all available information on weight, condition of the teats, perforacy, etc., to estimate the number of litters born. To cut down subjectivity I repeated this analysis several times over a year without referring to earlier results. I eliminated any females that died in livetraps so as to avoid a downward bias in the average number of litters. This made some samples very small since I also eliminated transients and females that disappeared prior to having any litters. The latter figures represented a variable and often substantial fraction of the females marked and these ratios will be discussed later. Combining the data gave more useful averages. For example, overwintered residents had 2.5 litters on the average in 1965 (based on 6 females); summer adults, 1.4 (N=7). In 1967, overwintered females on the three control areas had 2.3 litters (N=7); summer adults, 1.2 (N=9). All areas gave comparable figures, even those where experiments had been done. Obviously, most overwintered females had 2 or 3 litters while summer

females had 1 or 2. One female on the CON area apparently had 4 litters in 1966 but her record of captures suggests that the first was lost. The consistency of the figures allowed me to combine samples from several areas and years, and the resulting means were 2.3 for overwintered females (N=31) and 1.2 for summer females (N=34). Females that lived permanently on an area produced high and consistent numbers of litters. Since these residents are productive and relatively long-lived (see next section) the variable loss of females prior to the birth of first litters emerges as a possible source of regulation.

In summary, all survivors from the winter became sexually mature about two weeks after the snow disappeared. Resident overwintered females had 2.3 litters on the average while mature summer females had 1.2. Reproductive rates for resident females were similar for all years and areas (including experimental areas). The average litter size was 6.5. Females from the first litters of overwintered females usually bore young within the summer and the number of summer females that did so seemed to be related to the number of successful first litters produced by overwintered females.

Mortality

This section deals mainly with the disappearance of marked voles from given areas. Disappearance might result from death, dispersal, or avoidance of traps. My experiments indicate that the latter did not occur in the population on my area. Here I am concerned with area-specific disappearance; that is, if a vole moves from area X to Y it

has disappeared so far as area X is concerned. For most of this section I use the statistic "percent loss per week", which allows me to compare rates of disappearance for various areas and times of the year.

The numbers of marked voles that survived each of the three winters studied are as follows:

1965-1966	(Areas I-IV, II-III, R1, R2)	
	7 of 18 males	(39%)
	5 of 15 females	(33%)
1966-1967	(I-IV, II-III, CON, PEN, R2)	
	12 of 30 males	(40%)
	10 of 26 females	(38%)
1967-1968	(I-IV, II-III, CON, PEN, R)	
	0 of 23 males	
	0 of 18 females	

Given these data, and assuming a constant rate of loss, the figures for percent loss/week (sexes combined) are: 2.5%/week for 1965-66, 2.1% for 1966-67, and 3.7% for 1967-68. The losses for the first two winters are not significantly different (based on separate chi-square tests on 2x2 contingency tables using figures for males, females, and sexes combined). I combine these two sets for comparison with the 1967-68 data. Based on the first two winters I would have expected the spring census in 1968 to give 16 animals on the plots mentioned. Comparing the numbers recaptured or lost with the data from the first two winters gives a highly significant difference (corrected $\chi^2=19.3$, $p<0.001$).

Why should mortality have been higher in the nonbreeding period of 1967-68? The most obvious correlation is with conditions of temperature and precipitation. Before outlining this correlation I

should describe the effect of snow on subnivean temperatures. I emphasize minimum temperatures since these should best reflect the environmental stress to which the voles are exposed. Snow and temperature readings taken on the CON area showed that a layer of snow 5 inches or more deep held the minimum subnivean temperature at 0°F. or higher, even when the minimum air temperature was as low as -30°. With similar air temperatures the minimum temperature under 10 inches of snow was 10° or more; under 15, the minimum was stable at about 18-24°. During one period, 2 inches of low-density snow held the minimum subnivean temperatures to -2° while the minimum air temperature went down to -20°. The insulating power of snow becomes somewhat less as the snow packs and its density increases. The decrease was not great within the woodlots, presumably because packing and sculpturing by wind were reduced. The minima mentioned can be demonstrated throughout the period of cover by snow.

Four year's data on minimum temperatures and cover by snow are given in Fig. 5. For these comparisons I divided each month into four "weeks" of 7 or 8 days and calculated mean temperatures and amounts of precipitation, using data from the International Airport at Nisku, Alberta. Maximum temperatures taken at Ministik Lake were always within 1 or 2°F. of those from Nisku and minimum temperatures were within 3° of Nisku readings in 90% of the comparisons made. Cumulative depths of snow in the woodlots were also similar to the Nisku figures. Notice that the graphs illustrate the variable times of the spring thaw, discussed in the section on reproduction.

Various comparisons can be made from these graphs; some representative ones are:

1. Weeks with mean minimum <20°F. and mean depth of snow <4 inches.	64-65	65-66	66-67	67-68
	2	3	5	11
2. As 1., but 20° and 2 inches	1	2	1	7
3. Total rain (in inches) during weeks with mean minimum <32°.	0.2	0.7	0.1	3.0

Compared to the other winters, 1967-68 experienced a thinner and less stable cover of snow, and the greatest amounts of rain during weeks with freezing temperatures. I do not have rates of survival for the non-breeding period of 1964-1965 but they must have been as high as those of the next two years unless the 1964 density was much higher than those studied. I do not know the proximate cause for the disappearance of voles over the 1967-1968 winter but the above suggests that the loss might have been related to unusual meteorological conditions. By my definition, this loss was not brought about by a regulatory process. But, such losses could be important even if they take place only once in a decade or more.

Consider next the disappearance of these survivors once they entered the breeding season. I calculated rates of loss from one period of trapping to the next for all areas and years. Figures for each interval were assigned to the appropriate month and combined means were calculated to produce the rates shown in Table VI.

The rates of loss are roughly similar for most months and areas (including experimental areas). Three other points emerge from the comparisons:

1. Rates of loss are at least twice as high during this period compared with the overwintering period.

Figure 5.

Temperature and precipitation conditions near Ministik Lake,
November through April, 1964-68

Lines connect mean minimum temperatures for quarter-months.
For each quarter-month, a solid circle shows *mean depth of snow* in
inches or an open circle shows *total rainfall* in inches.

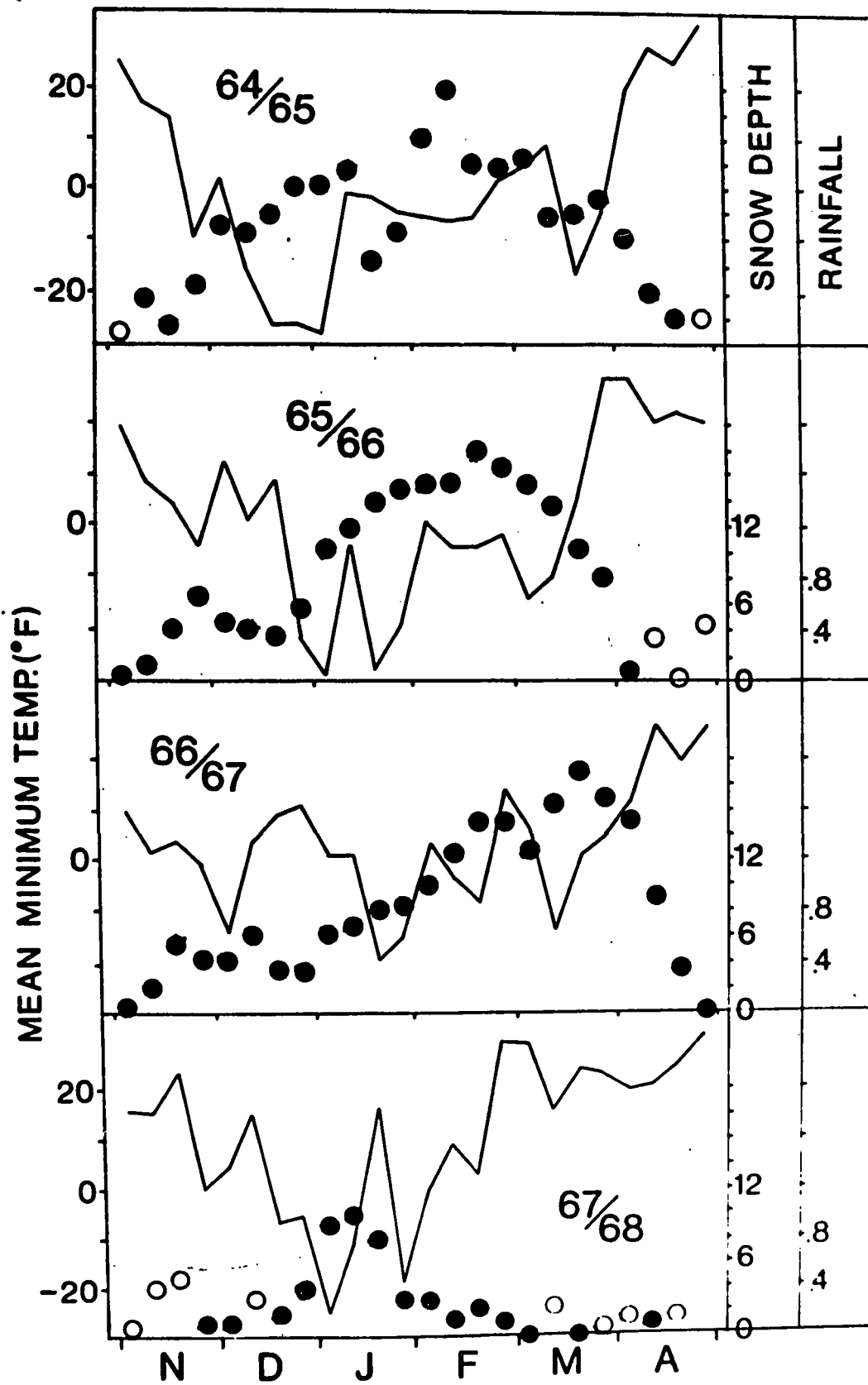


Table VI.

Disappearance of marked overwintered voles from plots. Figures represent percent loss per week (numbers present at beginning of time interval shown in parentheses).

		MAY	JUNE	JULY
CON -- 1966	Males	7 (7)	13 (24)	12 (4)
	Females	0 (5)	6 (15)	6 (4)
CON -- 1967	Males	0 (1)	0 (1)	0 (2)
	Females	14 (5)	18 (4)	14 (4)
I-IV -- 1966	Males	16 (11)	0 (1)	
	Females	22 (10)	0 (1)	0 (2)
I-IV -- 1967	Males		12 (7)	0 (2)
	Females		0 (8)	8 (3)
II-III -- 1966	Males	7 (24)	7 (10)	5 (5)
	Females	10 (24)	9 (8)	9 (7)
II-III -- 1967	Males	17 (10)	20 (7)	0 (2)
	Females	16 (7)	14 (4)	0 (2)
All above combined	Males	10.6	11.8	4.9
	Females	13.7	7.2	7.6

2. Total samples suggest that the disappearance per unit time is approximately equal for males and females
3. Monthly samples show that females are lost from the population more quickly in May than in June or July.

I compared the May rates for unmarked voles and those recovered from the group marked the previous autumn, using 1966 and 1967 data from I-IV and II-III plus 1967 data from CON. The weighted means are:

Marked males -- 13%/week (N=20)	Marked females -- 9% (11)
Unmarked males -- 9% (26)	Unmarked females -- 18% (25)

The mean for the whole overwintered group being approximately 10%, the loss of unmarked females in May is higher than expected. Many unmarked females were transient and presumably all of the unmarked females had moved in from untrapped areas prior to my first census in the spring. The tentative conclusion is that the increased rate of loss for overwintered females in May was due to dispersal rather than death. Since there were unmarked males present at this time, and since the rate of loss for this group was actually lower than for marked males, one might suspect that some dispersal of overwintered males took place prior to the first census.

Another way of examining these data is to compare the number of transients and residents in the marked and unmarked groups present in spring. Using data from the first census on each area the fractions of transients are nil for marked females (0 of 12) and 22% for unmarked females (4 of 18). For males, the corresponding figures are 12% for marked (2/17) and 31% for unmarked (5/16). Most of the transients were caught in late April or May. Again, the indication is that some overwintered females (and males) were dispersing at or near the beginning of the breeding season. However, these figures are not quite significant at the

5% level (2x2 table, corrected $\chi^2=0.9$ for males, 1.4 for females; $p>0.20$). Notice that, if some of the marked voles on a study plot were dispersing after the thaw, the survival through the period of cover by snow would be even higher than the loss rates of 2.5 and 2.1%/week suggest.

There is some evidence for a density-related loss of overwintered voles. I calculated coefficients for the regression of numbers of overwintered voles on time in days. The coefficients can be compared with the initial densities as determined by the first census of the spring. The analysis is shown in Table VII. The suggestion is that overwintered voles disappeared more quickly from areas with high initial densities. This analysis could be developed further but there is no way to compensate for trap deaths, and this limits the usefulness of the method.

None of the overwintered voles survived a second winter. Some survived until September of the second summer (Fig. 2). One male and one female survived until October.

The next step in analyzing losses is to consider the summer generation. The first question is how many summer voles are lost before they reach trappable age or size? An indirect measure of this can be obtained by comparing the estimated number of young born on an area to the number of summer voles actually captured on that area. The first statistic was obtained by multiplying the estimated number of litters born by 6.5 (see section on reproduction). I use only subadult and adult voles in the second statistic to offset any year-to-year variations in the efficiency of livetrapping juvenile voles. This figure is then expressed as a percentage of the first, which is given in parentheses. Results are shown in Table VIII.

Table VII.

Comparison of density at first spring census with coefficients of regression (loss of overwintered voles per day).

AREA -- YEAR	INITIAL DENSITY	LOSS/DAY (-b)
I-IV -- 1967	1.6 voles/acre	0.053
R -- 1967*	1.8	0.035
CON -- 1967	2.0	0.046
I-IV -- 1966*	3.2	0.101
CON -- 1966	4.3	0.130
II-III -- 1966*	5.4	0.114
II-III -- 1967	5.4	0.138

* -- spring density lowered experimentally

Table VIII

Estimates of survival from birth to subadult size. Bracketed figures are estimates of numbers of young born.

AREA	I-IV	II-III	CON
1965	41% (78)	68 (98)	
1966	31 (84)*	40 (156)*	25 (162)*
1967	28 (72)	51 (65)	42 (52)
AREA	R	PEN	
1967	35% (78)*	20 (20)*	

* experiment on spring removal

Notice first that the II-III percentages are higher in all years. I suspect that this is the "edge effect" related to the lack of natural boundaries. Some of the captured voles were probably born to females living outside the boundaries. I cannot explain the higher figures for 1965. Census periods were not as regular in 1965, and the II-III plots were smaller. The estimates, therefore, may not have been as accurate, and the II-III estimate may have been influenced by the smaller size of plot in relation to the size of home ranges for adult females. The 1966 and 1967 figures are more useful. The number of comparisons possible is limited because three variables are involved - the area, the year, and the influence of removal. However, the CON area showed a significantly higher survival in 1967 over 1966 ($\chi^2 = 5.5$, $p < 0.02$). This would seem to be a density-related change since the 1967 density was lower. The same result might have been expected for the I-IV area but densities were always low on that area and the comparison is complicated by the removal experiment. Spring densities for the II-III area were similar in the two years and the figures on survival are not significantly different ($p < 0.10$); the experiment must again be considered a complicating factor. Although a statistical comparison is not possible, removal of some adults in spring did not seem to raise the rate of survival for the R and PEN areas in 1967. Finally, combining all the data gives a weighted mean of 38%. If I assume that the subadults were about five weeks old, on the average, when first caught, the loss per week is approximately 12%. This figure is equivalent to the figures for the overwintered groups and the marked summer voles (see below). A few of the subadults were undoubtedly older than five weeks when caught and correcting for this would lower the 12% figure.

The next question is - how well did marked summer voles survive? I calculated rates of loss per week, using recapture data from all areas and years. The rates obtained were assigned to the appropriate month. The complete data are too voluminous and repetitive to present but weighted means are shown in Table IX.

When months are combined the figures are all close to the mean of approximately 11% loss per week. The mean are very similar to those calculated for the overwintered voles present during the same period. This suggests that the general level of mortality depends more on the season of the year than on the age of the animals. Separating the data into monthly samples modifies this suggestion, but only slightly. The rate of loss for summer males declines gradually as the summer progresses. Evidence given later indicates that the higher losses in July and August are the result of high rates of dispersal. Females do not show the same trend.

I can combine the small samples of animals marked as juveniles on the areas used for the above calculations. The mean rate of loss per week for this exclusively-juvenile group is 20% for males and 17% for females (samples of 25 and 33). Recall that my estimate of loss for the period from birth to first capture was 12%/week or lower. This suggests that the highest mortality suffered by a cohort of voles is in the period just after they leave the nest and start to wander on their own.

What agents are responsible for the loss of voles? Dispersal may lead to loss of animals from a given area. The majority of dispersing voles would probably be killed although I cannot give evidence from Ministik Lake to support this assumption. I suspect that

Table IX

Disappearance of marked *summer* voles from plots. Figures represent percent loss per week (samples sizes in parentheses). Juveniles are not included.

1. All months combined:

	Males		Females	
1965 - control areas (I-IV, II-III)	9%	(67)	12%	(78)
1966 - control areas (CON)	12%	(35)	6	(38)
- areas where males removed in spring (I-IV, II-III)	13	(64)	12	(53)
1967 - control areas (CON I-IV, II-III)	14	(50)	8	(40)
- areas where adults removed in spring (R, PEN)	12	(13)	15	(15)
All above combined	11.8		10.5	

2. All areas combined:

July	21	(9)	10	(19)
August	15	(67)	6	(42)
September	12	(55)	6	(43)
October	9	(98)	12	(109)

most of the losses I have mentioned are due to predation, principally from weasels. During one winter, disappearance may have been related to weather conditions. Examination of live voles and gross autopsies of dead ones indicated that mortality from disease and parasitism was negligible. Individual body weights did not deviate greatly from mean body weights for the same time interval. Autopsied voles invariably showed some reserves of fat, but I did not quantify these observations. Such findings suggest that quantitative shortage of food was not a problem for the voles at least for March through October. The few data from November through February are not sufficient to allow generalizations about the condition of voles near or during the period of cover by snow.

The results from this section allow some generalizations about death and dispersal in the population. Losses per unit time were much lower in the non-breeding than in the breeding season. Once into the breeding season, overwintered voles were lost from the population at a rate of about 10%/week. Some of the losses in April and May were apparently due to dispersal. No voles were known to live beyond 16 months. Losses per week for summer voles were fairly consistent, ranging from 6 to 20%, depending on the area and the stage of the life history being considered. Where comparisons were possible, there was some evidence that rate of disappearance was an inverse function of density.

Spacing and movement

In this section I describe movements within and between woodlots of the study area. The dispersion (spacing) of the voles should provide some insight into the use of the various habitats and the nature of the interactions between voles. Results given earlier suggest that dispersal may be important in the dynamics of this population. Before dealing with dispersal, I discuss the sizes of areas used by voles.

There are many ways of using results from livetrapping to quantify the home ranges of animals. For this discussion, all movements, apart from some arbitrarily rated as long and one-way, are assumed to be within the home range. The latter travels are treated as immigration or emigration and are discussed later. I use the greatest length of range (GLR) as my quantifying statistic. This is the greatest dimension of the area used by a vole, the area being defined by joining the plotted points of capture with a minimum number of straight lines. This is more useful than an areal statistic since it provides data for voles with only one recapture, and for any areas covered by a line of traps rather than a grid (as CON, 1966, until mid-June). The absolute sizes of the GLR measurements mean little but their variations with year and area are worth examining.

I have summarized the GLR figures in Table X. For the overwintered males there is a trend toward smaller GLR with increasing density. For example, the overwintered males show a near-linear relationship if the 1966 and 1967 data for the CON or II-III areas are compared. Data from the I-IV woodlot do not show the same trend but this may be because the GLR measurements are more variable for a given number of recaptures on

an area of low density. The tendency is visible but not so marked for summer males; the trend is not obvious in the overwintered females and younger summer females. Most areas provided data for only two or three adult summer females. I combined the data from five such areas and compared the resulting GLR data with those from the II-III area which always had the greatest number of voles and, in 1966, produced the highest density of the study. Here the trend toward smaller GLR with higher density did seem to be present.

The mean size of home ranges for overwintered voles that had been recaptured many times is approximately 0.79 acres for males (N=11) and 0.16 for females (N=25). These are based on voles for which a curve of cumulative home range against number of recaptures levelled out at a certain acreage (usually after some ten recaptures). If the home ranges were circular these areas would give GLR measurements of 13 rods for males and 6 for females. These lengths are quite comparable with those just discussed. The areas used by summer females and males fell mostly in the range 0.1 to 0.2 acres, when based on animals with several recaptures. Most summer voles were not recaptured often enough to produce a levelling of the graph of cumulative area. However, the data from these curves and the GLR measurements show clearly that overwintered males ranged over areas which were several times larger than those used by any other group.

If I use all points of capture and map the home ranges of the overwintered voles, the ranges of the males overlap considerably, those of the females much less so. There is no evidence suggesting use of particular areas by pairs of voles. Nor is there any sign of territoriality on the part of males; ranges of females are more discrete but

Table X.

Greatest lengths of ranges (GLR) used by voles. Figures are means (in rods) based on numbers of voles shown in parentheses. Samples of one are omitted. In each category the plots with highest densities are toward the bottom -- sample sizes give an approximation of density in most cases.

No. of recaptures:		2	4	6	8
OVERWINTERED MALES					
CON	1967	13 (3)			
I-IV	1967	10 (4)	21 (3)	21 (3)	22 (3)
I-IV	1966	11 (6)	13 (5)	14 (4)	
CON	1966	8 (6)	11 (5)	15 (4)	15 (4)
II-III	1967	8 (9)	12 (3)		
II-III	1966	6(11)	8 (7)	11 (5)	14 (4)
OVERWINTERED FEMALES					
I-IV	1967	6 (3)	6 (3)	6 (3)	
II-III	1967	4 (4)	8 (4)	8 (3)	8 (2)
I-IV	1966	3 (5)	4 (4)	5 (3)	
CON	1967	5 (5)	9 (4)	10 (3)	
CON	1966	4 (9)	6 (8)	6 (7)	8 (5)
II-III	1966	7(10)	7 (8)	6 (5)	7 (4)

continued...

Table X, continued...

No. of recaptures:	1	2	3	4
SUMMER MALES				
CON 1967	5 (6)	11 (3)	16 (2)	
I-IV 1966	6 (9)	9 (6)	10 (5)	
I-IV 1967	4 (7)	2 (2)	2 (2)	
CON 1966	4(12)	5 (8)	7 (6)	
II-III 1967	3(13)	6 (8)	6 (6)	5 (5)
II-III 1966	3(16)	5 (7)	5 (4)	
SUMMER FEMALES (juveniles and subadults)				
I-IV 1967	0 (2)			
I-IV 1966	3 (4)	6 (3)	7 (3)	9 (2)
II-III 1967	4 (8)	6 (7)	6 (4)	
CON 1967	5 (9)	7 (5)	7 (5)	9 (3)
II-III 1966	3 (9)	6 (3)		
CON 1966	3(15)	5(11)	6(10)	7 (6)
SUMMER FEMALES (adults)				
Five combined, less next	4(19)	6(16)	7(14)	6(10)
II-III 1966	3 (7)	5 (5)	6 (5)	6 (3)

whether these areas are defended is unknown. The question arises -- what sort of dispersion do the voles have at any one time? I cannot obtain an instantaneous distribution; the next best approach is to examine the locations of voles over a given night. This can only be done for nights when all the members of the sex or age group being considered were trapped. From records of the individual voles, I extracted as many such nights as I could, and analyzed the positions using the nearest-neighbour method of Clark and Evans (1954). In some cases I did the same for positions over a period of more than one night. This is a less reliable method since it gives positions which are even less "instantaneous", and requires that measurements be made from some "centre of activity" based on the various points of capture over the nights in question. Some of the results are shown in Table XI.

The R values are indices of dispersion -- a value greater than 1.0 indicates a trend toward a uniform distribution. The asterisks show examples of distributions that were significantly non-random (tested using Clark and Evans' "c" calculation). Most of the tested distributions showed a tendency toward uniformity. The R values for males were seldom high enough to be significant with these small samples. I suspect that males did space themselves out but that this uniformity was obscured by the wide-ranging behaviour of the males which often took them considerable distances in one night. Values of R for combined samples of overwintered males and females were close to 1.0, suggesting that superimposing patterns of males and females produced a near-random dispersion. For example, R was 1.02 for a sample of 13 (CON; June 20, 1966; 9 females, 4 males). Home ranges of females were much more discrete and this is reflected in the R values. Notice that all samples involving summer

Table XI

Dispersion of adult voles (nearest-neighbour method of Clark and Evans, 1954). * Denotes significant (** highly significant) departure from randomness. Parentheses indicate number of summer adults; (t) means that sample contains some transients.

Area	Year	No. of voles	Date (s)	R value
OVERWINTERED MALES				
CON	1966	4	June 22	0.94
		4	July 10	0.55
CON	1967	3	May 8	1.27
II-III	1966	10	May 7-9	0.97
		11	May 18-20	1.03
II-III	1967	11 (t)	May 15-19	1.23
		7	May 15-19	1.43*
		6 (t)	June 8-9	0.70
FEMALES (mostly overwintered)				
CON	1966	10 (1)	June 20	1.45 **
CON	1967	4	May 10	1.35
		4	May 8-10	1.60 *
I-IV	1966	4	May 1	1.81 **
		4	May 12	1.69 **
		5 (t)	May 12	1.33
I-IV	1967	4	June 16-21	1.60 *
		5 (t)	June 12-13	1.35

continued...

Table XI, continued...

II-III	1966	5	May 9	0.96
		8	May 18-20	1.51
		6	June 9-11	1.14
		7 (t)	June 9-11	0.95
		11 (7) (t)	July 31	1.66 **
		7 (1)	June 30 - July 3	1.61 **
		13 (8) (t)	July 30 - August 1	1.51 **
		II-III	1967	5 (t)
		3	June 7-13	1.11
		4 (t)	June 7-13	1.62 *

females gave highly significant values. These females spaced themselves quite uniformly in relation both to each other and the overwintered females still present. This held for samples containing summer transients. Voles did tend to avoid certain areas on some plots and this avoidance (presumably based on habitat preferences) would favour the formation of an aggregated distribution ($R < 1.0$). Since most values were over 1.0 in spite of this, I conclude that adult voles usually assumed a near-uniform dispersion in May, June, and July.

There is other evidence for a behavioural effect on dispersion. I illustrate by summarizing the position and numbers of adults on the CON plot in 1966 and 1967. Recall that a central line of traps was used here up to mid-June, 1966. The summary below condenses the available data on status and fate of the adults for the census periods indicated:

	ADULT MALES	ADULT FEMALES
<u>1966:</u>		
2nd half May	6 residents, 1 transient	6 residents
1st half June	2 of 6 gone, 3rd emigrates to nearby woodlot in 1st week of June	no change
3rd week June	still 3 residents, 4th male taken *	1 gone, 3 more taken *
	* probably outside area sampled by line of traps but could have moved in from other woodlots	
Early July	4 present, 1 emigrates to R1 woodlot	4 of original group left (1 dies in trap); 1 of new group gone (another dies), 1 remains
Mid-July	1 disappears	2 of original group left, both show slightly larger

		ranges; 1 of new group left; 3 summer adults now spaced among these
August	2 still present	3 still present, also 4 summer adults
<u>1967</u>		
Early May	3 residents	4 residents with discrete ranges (1 dies in trap)
Mid-May	2 disappear; remaining male expands range, uses entire woodlot from this time on	2 disappear; 2 unmarked females taken near edge
End of May		1 of new females disappears, other expands range to include area formerly occupied by 2 that dropped out in mid-May
June, July		2 remaining females continue to expand ranges; summer females present but not taken as adults until August

The sequences of events show that adult voles will expand their ranges in response to the loss of a neighbour. Notice that the expansion by females was more obvious in 1967 when summer females did not mature until late July. In 1966, one male was transient and five disappeared; of the five, two emigrated. These two records of dispersal suggest that some of the other disappearances may have been caused by emigration rather than death. In 1967, when fewer males were present, only two disappeared. In both years, three females disappeared but two more were lost through trap mortality in 1966, only one in 1967. Other females could have emigrated prior to mid-June in 1966 but I do not have the

relevant data for examination. Other data relating shifts of home range to removal of adult males are presented in the experimental section. The next topic requiring discussion is dispersal.

I documented 31 cases of dispersal by marked voles (not counting aliens, examples discussed later). The proportion of males: females (24/7) is significantly higher than the proportion of males:females marked on the control areas over three years (260 males, 229 females, 2x2 table, $\chi^2 = 6.9$, $p < 0.01$). In moving, 20 of the voles crossed grassland areas. The mean straight-line distance moved was 40 rods (660 ft); two of the movements were over 100 rods. The 11 that dispersed but stayed in the same woodlot moved 22 rods on the average. Six voles (all males) dispersed in the fall of 1965 or spring of 1966 and were recovered as adults in 1966. The six did not exhibit any density-related trend in their movements. The remaining 25 (18 males) can be examined further.

The 25 "summer" movements were made by overwintered and subadult summer voles. Eleven overwintered males were involved; 4 moved to areas with densities similar to those where they were first captured, 7 went to areas having lower densities (4 of these were apparently reacting to removal of males from plots II and IV). Of 4 overwintered females, 2 moved to areas having approximately the same density, the other 2 went to areas of lower density. Two of these females moved out of areas temporarily lacking adult males into areas where males were present, but this may have been coincidence. Of 7 subadult males, 1 moved from an area of high to an area of low density of overwintered plus maturing summer males, 4 moved to areas of comparable density, and 2 apparently moved to areas having more males. Four of the seven

were immature when first caught but showed signs of descending testes and enlarged genitalia when captured at their new locations. Three subadult females dispersed after perforation had occurred; 2 moved to plots that had densities similar to those of their original locations and 1 moved to an area with fewer females. Of the former two, one went from area A to R2 at a time when A was without adult males, the other moved within the CON area to a section having fewer overwintered adults. This is fairly consistent with earlier results which suggested that summer females, when mature, would space themselves out with respect to other adults. For the other groups the general impression was of shifts from high to low-density areas, with some exceptions.

The commonness of dispersal suggests another question - is the amount of dispersal from an area related to the density of that area? It is not possible to give a definite answer since voles were undoubtedly dispersing outside the areas trapped, and since the disappearance of any one vole could be attributed to either dispersal or death unless the animal was recaptured on some other area. Also, the disappearance of voles from the II-III area might have resulted from the "edge effect" mentioned earlier. However, I compared the numbers of residents and non-residents present in May (non-residents being transients and other voles taken only during one census). On the CON area there were 11 residents and 1 non-resident in 1966, 5-8 residents and no non-residents in 1967. On I-IV the ratios were 10/6 for 1966 and 6/0 for 1967. These data suggest more dispersal at times of higher density. However, on II-III there were 16-20 residents and 5 non-residents in 1966, 11 residents and 10 non-residents in 1967. These results are not consistent with those from the woodlots even though 4 of the 10 non-residents

of 1967 were taken only on the perimeter rows. The inconsistency may be related to the greater accessibility of this area to dispersing voles.

I tabulated data for summer voles in the same way and found that the ratios varied little by year or by area. However, the fraction of non-residents was always highest in July. The numbers of non-residents per resident summer male were 2.2 for July, 0.8 for August, and 0.4 for September (samples of 10, 42, and 41). For summer females the corresponding figures were 0.8, 0.1, and 0.4 (samples of 26, 43, and 42). Notice that the ratios in July and August are higher for males. These data seem to reinforce those given earlier on known cases of dispersal by summer subadults, which involve mainly males from July and early August. Most of the examples of dispersal involved voles that were sexually mature or nearly so. If I divide the samples just discussed by separating all non-residents that showed signs of maturity from those that did not, the immature groups show higher non-resident/resident ratios than the mature or nearly-mature groups. The ratios, then, do not entirely agree with the dispersal results. Perhaps this is to be expected since there are probably variations in the frequency of occurrence of dispersal and death.

To sum up, analyzing the movements of voles reveals trends which may be important in the dynamics of the population. Records of captures indicate that voles space themselves somewhat uniformly during the breeding season and range over smaller areas when the density is higher. Indices of dispersion suggest that overwintered females were spaced out in a near-uniform manner and that maturing females of the summer generation conformed to the pattern already established. Overwintered males

ranged more widely but still showed some tendency toward uniform dispersion. Instances of dispersal came mostly from males, and usually involved overwintered or maturing summer voles moving to areas with somewhat lower densities. Dispersal seemed to be density-related but this is open to question, primarily because of the difficulty of separating losses due to dispersal and death.

RESULTS FROM EXPERIMENTATION

Removal of adult males

I removed resident males from plots IV and II in May, 1966, to test the influence of adult males on survival, dispersion, and maturation of other voles. Males captured only in the outermost rows of traps on II were not removed.

The number of overwintered males on plot IV may have been as high as 5 in early May. A resident and a transient present in April were not retaken in May. In mid-May 3 males were removed; 2 of these had moved on to IV from I in early May. During May and June I recorded 2 residents and 1 transient on the control plot (I). A case of dispersal came to light in mid-May when I removed a male from IV and found that he was an alien that had been released on plot R2 a few days earlier. He was released on R2 again; one day later he was back on I. He moved from I on to IV in several steps and was removed again in June.

Data from the same censuses revealed a drop in numbers of overwintered females on I-IV. In mid-May 6 marked females were present (2 transients) and a 7th had disappeared since being marked in early May. In early June only 1 of the 4 residents was recovered; 1 other had been weak at last capture and may have died after release. The other 2 residents had disappeared, perhaps because of the lack of males.

On II there were an estimated 6 males in early May (1 transient). Two were removed and another disappeared until September, having presumably moved into untrapped habitat. Another of the 6 was removed later in May, along with 2 newcomers (1 from plot III). A 3rd newcomer

was marked but not removed, being trapped only in the perimeter rows. Another unmarked male moved on to II in mid-June and was removed at the beginning of July. On plot III, the intended control, there were 8 residents in May. At the beginning of July the number remaining was 6, 2 of which shifted to II and were removed. A 3rd moved back and forth between II and III several times. Up to the end of June, then, the number of adult males remained at about 7-10 on the pair of plots, despite the removal of 8. This was a higher density than that of 1967, or CON, 1966.

In May and June the number of overwintered females on II-III was 7-9. One shifted from II to III in mid-May and after May the number of females was higher on III than on II. By the end of June there were 5 on plot III, 1 on plot II, and 1 that apparently ranged over the strip between the two plots. Again, there is some suggestion that females chose the plot with more adult males but recall that there were always some males on II.

On both areas the removal failed to produce a clear-cut lowering in the density of males for comparison with other areas or the same areas in other years. The removal apparently caused an influx of males from the controls and from the surrounding woods in the case of plot II. It follows that there were some periods when the numbers of males on the pairs of plots were lower than for other areas. However, I could detect no differences in numbers of summer voles; in reproductive rates or numbers of subadult females reaching adult weight; in percentage of summer males with scrotal testes; or in rates of disappearance when I compare 1966 data for I-IV or II-III with that of 1967 or CON, 1966. As mentioned, the ratios of perforate to non-perforate summer females

were lower on the removal areas. Perhaps maturing summer females also vacated areas with fewer adult males. The sex ratios for II-III favoured summer males over females in August but this was true for 1967 as well as 1966. August was apparently a time of increased movement by subadult males and the ratios were affected on the plots that did not have natural boundaries.

These experiments showed that adult males will move into areas vacated by other adults. This supports the conclusion that interaction was the principal factor determining dispersion of males. The removal apparently caused some adult females to leave. The density of adult males might then be a factor determining productivity if females tend to settle on areas that have the most males.

Lowering of spring density

By the end of the breeding season of 1966 it was clear that the density of the population was not varying over wide limits. To allow better analysis of the effects of varying density, I artificially lowered the spring density on the R and PEN areas in 1967.

In mid-May I removed 3 of 7 overwintered males and 5 of 8 females from the woodlots of R. One of the 4 remaining males was recaptured in early June, and removed (another had been transient). Two unmarked overwintered males were removed during June. One woodlot, R2, was probably without adult males after the beginning of June. In early June I reintroduced a male removed from R2 in May, but this male moved to woodlot A by the end of June and was removed.

At the end of May the 3 females were still present and a marked female from plot III had moved on to woodlot A (part of R3). Two females were resident on R2 in early July; one shifted to A, the other

was removed for a time, replaced, moved to woodlot R1, and died in a livetrapp. Two females on A were more sedentary, one remaining until October (the longest residence by an overwintered vole in 1967). Again it appeared that mature females were leaving the area that was devoid of adult males. There were no transient females on the R woodlots in 1967, perhaps because the density was lower. The average number of litters produced by the 3 residents (2.3) was similar to that of other areas. Three summer females reached adult weight and bore litters. One of these came as a subadult from the CON area to R1 (which was empty of adult voles). Notice that on R the ratio of summer adult females to first litters produced by overwintered females (3) was 1:1 (similar to control areas).

Using the small samples from R, I found no differences in rates of disappearance as compared to other areas. There were usually more males than females among the summer voles present but the sex ratios were not significantly different from those of other areas. The percentage of summer males with scrotal testes was slightly higher than on other areas but, again, the difference is not significant when compared to 1967 data from control areas. A relevant point is that two subadult summer males were found dead in late June; on dissection, both proved to be sexually mature. Another summer male, taken in August, was over 18 g, one of the few to reach this weight. I did not compare GLR and other measures of dispersion because of the small size of the R woodlots.

The voles on PEN in 1967 were survivors of a group introduced in 1966 (experiment described below). In mid-May, 2 of the 4 males present died in traps and I removed 2 of 3 females. The remaining female

survived till late July and had an estimated two litters. Trapping records indicated one other litter, born to an alien summer female released on the island in early July. One of the resident males disappeared by mid-June and the other died at that time. This left the area with no adult males until I released an alien male in mid-July; this male must have sired the second litter from the overwintered female and the litter from the alien summer female (unless the latter was pregnant when introduced). Several other alien summer voles were released on PEN but few survived.

On the island there were no differences in rates of disappearance or reproduction in 1967 but the samples were very small. None of the summer voles born on the area reached 18 g or showed signs of maturity; one of the alien subadult females matured and reached 18 g after introduction. I calculated GLR measurements for the seven overwintered voles. For males the mean was approximately 6 rods when 2 or 3 males were present. The alien male present from July to September had a maximum GLR of about 15 rods. The lone overwintered female that survived until July increased her range so as to give a maximum GLR of 15 rods. Apart from these increases in range, the removal seemed to have little effect. It may be significant that there were no overwintered transients on PEN (and only one on R) in 1967.

Addition of alien voles to established groups

In 1966, I added voles to the existing population on R2 and to an introduced population on PEN. This was done to test the effect of aliens on the productivity and survival of the residents and to create a population with a higher density for comparison with control areas.

The R2 woodlot was used for some preliminary additions in 1965 and I describe this first. Any meaningful analysis of this material must distinguish aliens and residents, time of the year and density at that time, etc., so it is very difficult to graph or otherwise quantify this information.

In October of 1965 I removed 9 voles from R2, marked 4 others, and added 16 aliens (juveniles and subadults, half males). One of the alien males returned to the woodlot from which he had been removed (R1); no other aliens were found alive. One resident female survived until 1966.

The R2 woodlot held 8 voles (4 males) in early May, 1966. Even if a few summer voles escaped capture in 1965, most of the 7 must have immigrated to R2 in April or earlier. During May I added 13 aliens (11 males). One male and one female alien remained on the plot for a few weeks, the rest disappeared. Six records of dispersal resulted, showing clearly that the majority of the alien males had emigrated. One alien female returned to her original point of capture (woodlot B) and later shifted back to R2. An adult summer female that was resident on A moved to R2 in mid-August when numbers on R2 were much reduced.

What happened to the original eight residents when aliens were added? One point is that 3 of the 4 females were transient, and the 4th was only present in May. The alien female that returned from B remained until July and bore an estimated two litters. Apparently these were the only litters born on R2 in 1966, unless the female that came from A in August was pregnant. Assuming 13 young born, the survival to trappable age was nearly 40% which is similar to that recorded from control areas. There were no transients in the original group of

males and 3 of the 4 stayed at least until June. It is possible, then, that the addition of aliens caused some adult females to leave.

Several summer voles became mature on R2. Since practically no summer males reached adult weight on control areas, it is interesting that two appeared on R2 (1 in July, 1 in August). However, both were transient as was a mature female of subadult weight in July. One other summer female of adult weight was present in July and August but apparently did not bear any litters.

The 1967 spring census on R2 should be mentioned. Note first that in November, 1966, I found only one live vole on the area. In May of 1967 there were 4 males and 2 females, all unmarked. It is unlikely that many juveniles escaped trapping in the fall of 1966. Even if a few were missed, most of the six present in the spring must have immigrated to R2. Woodlots A, B, and R1 also showed very low densities in the fall of 1966, and in spring of 1967 there were 7 unmarked voles on the three areas. All these descriptive data suggest that interaction between voles affected their dispersion, and that mature or maturing voles favoured areas of low density for settlement.

The other addition was to the PEN area, which had no voles prior to the experiment. From June to August I released 59 aliens at various points on PEN, and 26 were recaptured. Of the 26, only 16 remained on the area for more than two weeks. The group of 16 contained 6 of 18 adult males released, 5 of 15 adults females, 3 of 14 subadult females, and 2 of 12 subadult males. Twelve adult males and 5 adult females made up the first group released, 2 of each sex remained for over a month, the longest periods of residency during the experiment. Few voles from the releases of subadults in July and August survived.

The number of residents in any month was never more than eight. The results indicate that adults survived the release better than younger voles, and that the group released on the unpopulated island first survived best.

The number of litters born on the area was 2, possibly 3. This gives a ratio of litters per resident female lower than those of other areas but this merely reflects the faster rate of disappearance of the alien females. One juvenile male was marked on the plot in August. This suggests a low survival to trappable age but only one litter was born early enough to have produced this juvenile.

In mid-September there were 8 voles on PEN. All had been present for 3 weeks or more. In May of 1967 there were 7 voles present and only 1 was marked. It is not likely that any immigration occurred (recall that the island was devoid of voles originally) so that 6 unmarked voles were probably present in 1966. Some juveniles could have been missed in mid-September. Also, two mature females were present in mid-September and might have had litters near that time. This would have raised the number of litters born in August and September to three. Given these two possibilities, it is not difficult to explain the presence of the six in 1967. It may be that the constant addition of aliens resulted in some unseasonal reproductive activity.

Continuous removal through breeding season

The principal experiment involving continuous removal was done on the R1 woodlot from late April to October, 1966. The woodlot was trapped

13 times at roughly equal intervals. I felt that removal on R1 might provide good data on the extent of dispersal across grassland because of the position and elongated shape of the woodlot.

The average density of overwintered voles on control areas was approximately 4/acre. On R1, the expected number would be 3 (2 were present in the spring of 1967). Overwintered voles made up 25% of the number marked on control areas. From this, one would expect to mark some 12 voles or less on R1 during a season. Compare these estimates with the results from continual removal.

In 1966, 31 voles were removed (this omits 2 overwintered males that were aliens from R2). Of the 31, 17 were overwintered (11 males). I estimated that the original April population was 2-6, probably 3. The chronology of captures for the 17 was:

April : 2 males (1 in from plot I)
 early May: 3 males, 3 females (1 present 1965, 1 in from plot A)
 late May: 2 males, 3 females
 June: 2 males
 July: 2 males (1 previously resident on CON)

The number of overwintered voles present long enough to be trapped was 5 or 6 times higher than expected. Most of them were unmarked and at least 11, more likely 15, came in from other woodlots. Most of the immigration occurred in May.

The catch of 14 summer voles is revealing. It consisted of 1 adult male, 3 adult females, 5 subadult males, 4 subadult females, and 1 juvenile female. In addition to the 4 adults, 2 each of the subadult males and females were sexually mature. Adults normally comprised about 9% of the summer generation (based on 3 year's data from control areas).

On R1, the adults made up about 30% of those caught, and the fraction of mature subadults was higher than normal. Nearly 60% of the summer voles taken were mature. The 4 mature subadults were taken in July; immature subadults were taken from June through September. The adult females were taken in July (2) and September, the adult male in August. The July females were in early and mid-pregnancy, the September one had born young and was perforate.

These results suggest strongly that some overwintered voles were inclined to disperse in April and May, and settle on areas with fewer residents. Maturing summer voles from the first litters of overwintered females showed the same trend in July.

Some 1966 data from woodlot A reinforce these conclusions. Most of the overwintered voles were removed from A in May. From June on, 8 summer voles were marked or removed: 1 adult male (July), 2 adult females (July), 2 *mature* subadult males (July), 2 immature subadult males (June, August), and 1 subadult female (July). The subadult male marked in June was taken from R1 in early July and, on dissection, proved to be mature. These data lead to exactly the same conclusion as those from R1. One would not expect the total number of immigrants on A to be as high as on R1, since A had a smaller ratio of perimeter to area, and was situated on the lake edge. Also, the removal on A was not always total.

I did one more experiment of this type on the R4 area in 1966. A 3x3 grid of traps was located on the edge of this woodlot just opposite the end of the CON woodlot. Trapped voles were removed from May through August. A total of 26 was removed:

May: Overwintered - 1 male, 3 females

June: Overwintered - 4 males, 1 female (1 male was from
the CON area)

: Summer - 1 adult female, 2 subadults

July: Overwintered - 1 male, 1 female

: Summer - 1 adult male, 1 adult female, 3 subadults

August: Summer - 1 adult male, 1 adult female, 4 subadults,
1 juvenile

This woodlot was virtually the same size as CON. From the 4/acre density mentioned earlier, the expected number of overwintered voles would have been 14 (17 were marked on the CON area in 1966). On R4, 11 overwintered animals were removed, one being an immigrant from CON. This suggests that the removal on the small grid of 0.22 acres was gradually drawing voles from over the whole woodlot, and perhaps from CON which was only a few feet away. Judging from the results of removing males on other areas, some of the resident overwintered voles might have remained sufficiently sedentary to avoid coming in contact with the small grid.

As one would predict from the removal done on R1 and A, this area produced more adult summer voles than expected. Here, the fraction was 33% (5 of 15) with two of the adults being males. By comparison, only two summer adults were marked on the CON area in 1966 (4% of the summer voles taken there). These results confirm those of R1 and A, and also strengthen the conclusion that overwintered voles would shift their home ranges in response to a vacancy in some other part of their woodlot. Some of the summer voles that moved in were likely "surplus" wanderers. The same might apply to some of the overwintered voles but the influx

of marked voles that resulted from removal of males on IV and II suggests that they were neighbouring residents.

Summary of experimental results

Overwintered males moved into areas made vacant by removal of other males. Mature females tended to move away from such areas while they were lacking males. On plots where the spring density was lowered there were fewer overwintered transients and more mature adult and subadult voles than would be predicted from the controls. Woodlots containing very few animals in fall had increased numbers of unmarked overwintered voles in spring, mostly due to immigration. Most aliens added to established populations or vacant areas died or dispersed, and the additions may have caused some mature resident females to disappear. Removal and addition experiments did not noticeably affect reproductive or disappearance rates of the voles that remained on the experimental areas. All experiments indicated that interaction between voles was important in determining how many mature animals would be present on an area.

DISCUSSION

In this section I first compare my results with those from other studies. Since there have been few intensive studies of *C. gapperi* I refer to literature on other species of *Clethrionomys* and related microtines. Following this, the usefulness of the two original hypotheses is examined, and some speculations and suggestions for further work are given.

I emphasize that many studies on small rodents are of relatively little use for studying limiting or regulatory processes since the methods of trapping give only rough indices to density. For some purposes these will suffice but such indices are also questionable in that they may not be sampling the trappable population randomly. If they are not, the data may give misleading rates of mortality, reproduction, etc. Lately, three approaches are being used to overcome this difficulty in field studies. Some workers are attempting to modify the results from extensive trapping to give more accurate data on population structure (Brant, 1962; Chelkowska and Ryszkowski, 1967; Packard, 1968; Webb, 1965; etc.). Webb has shown that a widely used trapping procedure, the North American Census of Small Mammals, did not reflect the relative or absolute density of individual species; among the rodents he studied the main example was *C. gapperi*. Other workers are testing the applicability of mark-recapture formulae, and are either applying them if their samples prove to be random (Ashby, 1967; DeLong, 1967) or rejecting them and attempting total counts (Chitty and Phipps, 1966; Krebs, 1966; this study).

The literature suggests that most populations of *C. gapperi* do not reach high densities and do not fluctuate widely. This generalization may not hold near the northern limit of the species (Fuller, 1969). Other species of *Clethrionomys* do show wide extremes of density and some appear to fluctuate in a cyclic manner (Ashby, 1967; Brown 1954; Kalela,

1957; Koshkina, 1966 and 1967; Newson, 1963). The population of *C. glareolus* studied by Ashby was cyclic but never exceeded a density of 30/acre, even on favoured habitats. Other microtine populations seem to fluctuate widely, and sometimes periodically; for example, see Aumann, 1965; Chitty and Chitty, 1962; Krebs, 1964 and 1966; Pitelka, 1957; Shelford, 1943; etc. Some possible reasons for the stability of southern populations of *C. gapperi* are mentioned below.

The reproductive rates for the Ministik plots were surprisingly stable especially where they were based on data from females that remained on a given area for long periods. Whether any of the three parameters involved (litter size, number of litters per female, and percent of females breeding) would vary with a great increase in density is still an open question. Since virtually all resident adult females bred, the last parameter would seem not to be involved in regulation of this population. However, if we visualize the percent of females breeding as being the fraction that *remains* on a given area to breed, then the last parameter is very much involved. Some of my data suggest that the percentage of reproductively active summer females would decrease at higher densities. Such a decrease has been demonstrated in populations of *C. rufocanus* (Kalela, 1957; Koshkina, 1957). Koshkina has found similar decreases in *C. rutilus* (1965, 1967). There was no evidence for density-related variation in the rate of pregnancy or litter size. Some *Clethrionomys* populations do show a decrease in mean litter size with increased density (Koshkina, 1967; Tanaka, 1964). It is not clear what governs the autumn cessation of breeding in this population. Overwintered females, once resident, seem to produce litters for as long as they live. Earlier breeding might have allowed the population to reach much higher levels if it had provided time for

the females born in the *second* litters from overwintered voles to mature and bear young. However, the presence of numbers of mature females might have suppressed maturation or pregnancy in this group even if the members had had an earlier date of birth. At latitudes lower than that of Edmonton *C. gapperi* apparently has longer breeding seasons (Butsch, 1954; Gunderson, 1962). I cannot visualize the Ministik population increasing much beyond the levels mentioned unless winter breeding was to occur, and this has never been documented for *C. gapperi* in the field.

The rates of survival were quite stable (depending on the season) and were generally higher than those quoted in other studies (for example, note the variable survival of subadult and juvenile *Microtus californicus* in Krebs, 1966). The survival rates for marked *C. glareolus* on one of Newson's areas (1963) were comparable to mine but his second area had lower survival. As in other studies, losses were highest around the time young voles were leaving the nest (Hoffman, 1958; Newson, 1963; Krebs, 1966; etc.) but my results were different from most in that estimated survival from birth to subadult size was almost as high as the survival of overwintered and older summer voles. This means that survival of young at birth and in the nest must have been as high as that of the older voles since survival of juveniles was not as high. By contrast, Getz (1960) calculated that almost 90% of the young produced in a population of *M. pennsylvanicus* were lost in the first month. I can suggest two reasons for the difference. Most extrinsic losses in microtine populations are probably due to predation, and *Clethrionomys* populations seem to be less vulnerable to predators than the other well-known microtines (Ognev, 1950; unpublished data on predation from University of Wisconsin Wildlife Research Station, Rochester, Alberta; my observations at Ministik Lake; cf. Pearson, 1966). Also, the summer generations of *C. gapperi* do not seem to suffer any sharp increases in

mortality from intraspecific strife or related causes as do some microtines (Chitty and Phipps, 1966; Krebs, 1966). Further, Chitty and Phipps noticed that, while *M. agrestis* showed sudden losses (especially in spring), *C. glareolus* did not.

I do not know whether the increase in rate of loss with the onset of breeding is related to increased vulnerability through loss of the protective cover of snow or to the process of maturation itself. Presumably the exposure factor is more important since the immature summer voles show rates equivalent to the mature animals, but the loss of younger voles might have been related to the presence of mature animals. One explanation for the higher loss over the winter of 1967-68 might be that the interval between thaw and first census was several weeks longer, on the average, than for the other years and that the voles were undergoing the summer rates of loss during this time. Even allowing some 8 weeks at the higher rate, however, would not lower the survival to nil - some 10 to 15% should still have been left. Most of the plots were checked within 8 weeks of the thaw. Results from removal experiments suggest that the few unmarked voles caught in 1968 may have wandered in from untrapped areas. My observations indicate that the *Microtus* population living in the grassland between the woodlots also suffered a sharp loss over the winter of 1967-68. In contrast to the two microtines, the *Peromyscus* population showed a slight decline in 1968. Examination of weather records for a number of years prior to the study suggests that the precipitation-temperature conditions of 1967-68 were unusual. Apparently the 1967-68 loss should be regarded as a catastrophic one. In 3 of 4 years meteorological conditions did not seem to have any great effect on spring numbers.

Apart from figures on home range, very little has been published

on the dispersion of *Clethrionomys*. The nearest-neighbour method has seldom been used for small mammals (one example - Hansen and Remmenga, 1961), and might be useful in other cases where the population has been trapped intensively. Disadvantages must be mentioned. Voles occasionally, though not often, move long distances in one night (see Blackith, 1958). Also, a trap, once occupied, is not available to the remaining voles so that the nearest-neighbour distance can never be zero. A third point is that the density of the group being considered must be known exactly before the index of dispersion can be calculated.

Butsch (1954) felt that the adult female *C. gapperi* in his population were distributed uniformly but his trapping was not very intensive. He also mentioned that adult females sometimes appeared suddenly on his plots, and that young adults probably disappeared mainly through emigration. My results agree with these, suggesting that some degree of territoriality or avoidance may be typical of mature females in this species, and that large-scale dispersal may be typical of populations of *C. gapperi*. My records suggest some variation in the individual's tendency to emigrate as suggested by French *et al* (1968), Howard (1960), and Lidicker (1962), but the interspersed nature of grassland and woodlots makes statistical treatment difficult. Dispersal should tend to equalize the density on various parts of an occupied area. However, my woodlots seemed to have characteristic levels of density, perhaps determined by habitat preferences or the effects of varying cover on the number of encounters between voles in the spring. This leads away from discussion of regulation toward the question of what determines the absolute density of animals on an area, a rather different problem (Chitty, 1960).

Removal experiments suggested that adult males were also spaced somewhat uniformly. The experiments, while they did not uncover any

changes in rates of reproduction or loss with lowered spring density, did provide some evidence for a relationship between density and dispersal, as did checking the spring reoccupation of areas that had low densities in the preceding fall. Almost complete loss of aliens added to established groups and increased settlement of overwintered or mature summer voles on areas where density had been lowered underline the importance of intraspecific interaction in dispersion. Possibly some of the mature voles that settled on the near-vacant areas I established would not have been able to settle without this interference.

The microtines whose densities fluctuate and reach high levels seem to be those that occasionally bear litters outside the normal breeding season. For example, there are no field records of breeding outside the March-October period for *C. gapperi* while *C. glareolus* is known to breed in winter (Ashby, 1967; Newson, 1963; Smyth, 1966; Zejda, 1962) and apparently reaches higher densities than *C. gapperi*. The onset of reproduction in *C. gapperi* may be inhibited by the blocking of light by snow (Evernden, 1966; this study). These forest voles may never be stimulated to breed in winter while species in open habitats may receive enough light to elicit breeding in some winters through blowing and weathering of their more exposed cover of snow. *Microtus pennsylvanicus* apparently bred during the winter of 1965-66 in the Edmonton area, and reached plague numbers in the spring of 1966. An early thaw might be expected to produce a summer population of high density due to increased production of litters by summer voles but, for *C. gapperi* at these latitudes, the reproductive advantage would likely be cancelled by increased mortality such as I observed over 1967-68.

I had hoped that my results would allow comment on the interesting hypotheses on intrinsic regulation proposed by Chitty (1967) and

Christian and Davis (1964) but a test of these requires data from increasing and declining populations, preferably taken at the same time from the same general area. The boreal redbacked vole is probably more useful for studying population phenomena at low densities, and the factors determining densities on different areas. The behaviour of adult females should be examined to see if females are intolerant of each other all the time they are mature, or just at parturition or around the nests. More work on emigration and immigration by *C. gapperi* would be worthwhile.

This study has demonstrated that dispersal can be important in determining numbers on a given plot, and over a larger area (assuming most voles that disperse die without settling). Even without curtailment of breeding numbers in spring it is not likely that densities would have increased much beyond those found. Reproduction by summer females would likely have been inhibited as in Kalela's (1957) population. The drop to near extinction in 1968 showed that extrinsic forces can be of prime importance at times, and that knowledge of the history of a population should be obtained, where possible, before any general conclusions on its mode of limitation or regulation are made. My hypothesis implicating intraspecific interaction in regulation seems to be a useful one for this population but further study would be needed to prove it adequately.

SUMMARY

1. A population of *Clethrionomys gapperi* was studied for three years on an area of aspen parkland in central Alberta. The objectives were to gather detailed information on population parameters by intensive livetrapping, and to examine the effects of meteorological conditions and intraspecific interaction on population density.
2. Experiments involving temporary removal indicated that livetrapping for more than one night would catch most, if not all, of the voles on an area.
3. Numbers on control woodlots were similar in 1965 and 1966, dropped slightly in 1967, and were down sharply in the spring of 1968. Densities were never higher than 15/acre.
4. Onset of breeding was related to the time of thaw, and there was no evidence for any breeding during the period of cover by snow. All overwintered voles matured; the females produced young for as long as they remained on the area. Summer males seldom matured but females from the first litters of the season usually had at least one litter within the season. The mean number of litters per resident was 2.3 for overwintered females, 1.2 for summer adults. Mean litter size was 6.5 young.
5. The survival of marked voles through the non-breeding season was about 40% up to 1967-68 when it dropped to nil, probably because of adverse weather in early spring. During the breeding season, overwintered voles were lost at a rate of about 10%/week; summer subadults and adults at about 11%/week. For summer juveniles the rate was roughly 18%/week. An estimated 4 of 10 young survived from birth to subadult size. No voles lived beyond 16 months even

though survival in the non-breeding period was much higher than in the breeding season.

6. Adult voles showed a tendency toward uniform dispersion and extended their ranges into areas vacated by neighbours. Males ranged over much larger areas than females. Data from marked voles suggested that dispersal of overwintered voles in April and May, and older summer voles in July, was common. Dispersing voles usually settled on areas having lower densities.
7. Removal experiments suggested that interaction between mature voles was responsible for the observed patterns of dispersion and dispersal. Removal of adults in spring did not markedly affect rates of reproduction or loss other than by influencing the residency of the remaining adults.

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