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THE UNIVERSITY OF ALBERTA

POPULATION DYNAMICS OF ISLAND POPULATIONS OF SUBARCTIC *CLETHRIONOMYS RUTILUS* AND *PEROMYSCUS MANICULATUS*

by

GORDON R. BURNS

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

SPRING, 1980

THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled

POPULATION DYNAMICS OF ISLAND POPULATIONS OF SUBARCTIC
CLETHRIONOMYS RUTILUS AND *PEROMYSCUS MANICULATUS*

submitted by GORDON R. BURNS

in partial fulfilment of the requirements for the degree of Master of Science.

W. A. Fuller
Supervisor

W. G. Evans

Fred C. Zwickel

Date 8 November 1979

ABSTRACT

Demography of populations of Clethrionomys rutilus and Peromyscus maniculatus on two islands in the Mackenzie River was studied by means of live trapping on grids and snap trapping in the summers of 1977 and 1978. Vegetation at live trap grid points was analyzed in July 1978 to correlate vegetation variables and animal captures.

Clethrionomys numbers reached a summer maximum in early July in 1977 on Island 2 and remained high thereafter. In 1978, numbers increased exponentially until late August when they were still only about 50% of the 1977 maximum. In 1977, a high but declining number of young was recruited into the trappable population, juvenile survival was lower, and a smaller proportion of both sexes reached sexual maturity than in 1978. Centers of activity of mature females were uniformly dispersed in both years, whereas they tended to be randomly dispersed in other classes. Adjusted range lengths of males were significantly larger in 1978 than in 1977. The number of voles increased more slowly to a lower summer maximum both years on Green Island. The number of recruits into the trappable population increased exponentially through the summer, and a high proportion of young matured each summer. Adjusted range lengths were significantly larger in 1978 than in 1977 except for overwintered females where the difference was not significant. Litter sizes did not differ significantly between islands or years. With the possible excep-

tion of a small sample from Green Island in 1978, prenatal mortality was negligible. Differences in body weights and lengths appeared unrelated to variations in population density. Voles on Green Island experienced more wounding than those on Island 2, largely because of much wounding among immatures on Green Island in 1977. Regulation of numbers of voles was suggested by an inverse relationship between density of adult voles and recruitment, juvenile survival and maturation and, by uniform dispersion of centers of activity at high density.

On Island 2 in 1977, Peromyscus numbers reached a summer maximum in mid-July and showed slow growth thereafter. In 1978, numbers increased exponentially through the summer to a level similar to that reached in 1977. Breeding began earlier and with a smaller breeding population in 1977 than in 1978. Deer mice on Island 2 in 1977 suffered declining juvenile survival and recruitment of young into the trappable population. No mice matured in the summer of birth. Centers of activity of mature males were uniformly dispersed while other mice tended to show random dispersion. Adjusted range lengths of mature males were significantly larger than those of mature females. In both years, numbers of mice on Green Island increased exponentially through the summer. Numbers of recruits into the trappable population increased exponentially in both summers. Densities of mice were higher on Island 2 than on Green Island in both years. Differences between islands or years in body lengths or

weights did not relate to variations in population density. Losses of up to 50% were estimated among nestlings. Wounding was more prevalent among matures than immatures and among mice on Green Island than those on Island 2. Regulation of numbers was suggested by an inverse relationship between the size of the spring breeding population and recruitment and juvenile survival, but reproductive output was invariable and no young of the year matured.

Observed spatial variability in density may be explained by moisture demands by Clethrionomys and cover needs of Peromyscus. Differences in capture rates associated with habitat types explain some of the differences in densities between islands. Lower capture rates for Green Island than for Island 2 on the same habitat type are without explanation. Spatial segregation of voles and deer mice was suggested only in 1977 on Island 2 when both population densities were high.

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INTRODUCTION

Population growth does not continue indefinitely. Berry (1968) saw an island population of Mus increase 10-fold in the breeding season when it had the potential to increase 150-fold. Annual population peaks of Clethrionomys rutilus, the northern red-backed vole, varied between years by only a factor of three (Koshkina 1965). Fuller (1969, 1977a), working with Clethrionomys gapperi, observed on average 2-fold increases in snap trap indices of population density between May and August. He also found years when density dropped by a half (1967) or increased by over 4-fold (1976) during the breeding season. Higher annual population growth rates have been associated with cyclic peaks in numbers.

The phenomenon of population cycles and the control and regulation of growth have been under study since Elton (1924) treated the subject. Such studies demonstrate varying attitudes toward fluctuations in population size. If we adopt the position of Cole (1954a) that population fluctuations are random, there may be no regulating mechanism to study. Alternatively Lidicker (1966) proposed the interaction of multiple factors to explain a decline in Mus on an island. Krebs et al. (1973) and Krebs and Myers (1974) argued that some fluctuations fit a cyclic pattern and that a single mechanism operates during each cycle.

That population size can vary between breeding seasons indicates that growth does not always reach its full potential and it is therefore important to ask how growth is limited. In this paper, I shall distinguish between control and regulation. The latter term will be reserved for situations in which a factor (or factors) seem to be acting as a result of negative feedback triggered by increasing density, whereas the former implies no negative feedback.

To explain the breeding densities of *Peromyscus*, Fairbairn (1977a) had to add controlling factors of spring weather and overwinter food supply to regulating factors of onset of female breeding and male aggression. Unfavorable weather was not seen by Fuller (1969) to affect breeding in *C. rutilus*. He did not find year to year variations in cessation of breeding and observed that later spring breeding could be compensated for by more intensive breeding. Failing to find an explanation for demographic changes in extrinsic factors, Krebs (1966) favored regulation through genetic shifts in the population reflected in quality and fitness of individuals. Also in studies on *Microtus*, Hoffman (1958) concluded that population regualtion was effected by weanling and juvenile mortality, not by any reproductive change. However, Koshkina (1965) suggested that increase in *C. rutilus* abundance stops more because of a cessation of breeding than because of increased mortality. Chitty (1967) assumed that some behavior trait of all species of animals could prevent unlimited increase in population density. Such a behavior trait persists because of its survival value. Survival rates change in response to changes in behavior.

Grant (1976) concluded that extrinsic factors are superimposed on an underlying behavioral regulation. Christian (1970) saw dispersal as the variable related to social tolerance and population density. Krebs (1970) proposed that dispersal, differential reproductive success or differential survival of young could be the mechanism through which behavioral changes operate. When survival is high, most disappearing individuals seemed to disperse rather than die (Krebs et al. 1976). Clark (1956) noted vigorous aggression among Microtus females that were nursing young or were in the late stages of pregnancy. This aggression might serve to drive away other mature females, males, or young of previous litters, but may also result in infanticide and cannibalism. Friesen (1972) observed 75% and 20% losses among C. rutilus and C. gapperi litters respectively. Small mammal and researcher interference at nests may be important factors in breeding success. Gliwicz (1975) noted compensating mortality between early and late summer litters.

Identified negative feedback mechanisms do not act consistently to regulate populations. While Batzli and Pitelka (1970) found high Microtus populations affecting the abundance of preferred food plants, apparent food limitation or high mouse densities are not sufficient to bring about population declines (Krebs and Myers 1974). If the hypothesis of a single common mechanism of population regulation is to be pursued with any success, a greater emphasis must be placed on eliminating or controlling factors that do not consistently regulate numbers as critically high densities are approached. Isolated but adjacent populations of the same and different species should receive increased attention. Sources of variability between study areas such as predation, disease, food supply, weather and winter deaths may be considered controlled in adjacent populations, and thus allow examination of factors varying with population density. However, habitat and microhabitat of such comparative studies cannot be ignored. West (1977) suggested that habitat was a significant factor in winter survival.

Because the present study was located on islands, the dispersal hypothesis favored by Errington (1956), Lidicker (1962) and Krebs and Myers (1974) may not be applicable. Regulatory mechanisms of island populations are of interest in light of the Krebs effect (MacArthur 1972). MacArthur proposed that density might be inversely related to island size. However, Dickinson (1976) studied <u>Clethrionomys rutilus</u> on islands, including those of the present study, and was not able to demonstrate a negative relationship between animal density and island size. Herman (1979) studied island populations of <u>Peromyscus</u> <u>maniculatus</u> and did not find evidence of a Krebs effect.

The islands used in this project are located in a 21 km section of the Mackenzie River northwest of Fort Providence, Northwest Territories (Fig. 1). Previous work on these islands by Canham (1969) and Dickinson (1976) suggested relatively consistently high densities of _Clethrionomys_ _rutilus_ and _Peromyscus_ _maniculatus_ and densities usually higher than found on the mainland. The live-trapping and snap-trapping of the present study were done to determine whether numbers are nearly constant on an island from year to year and whether or not densities are the same on different islands. If numbers are high and constantly high on islands and if dispersal is not a useful means of population regulation, how are numbers controlled or regulated? This study examines the demographic parameters of natality (litter size, recruitment, maturation) and mortality (intra -uterine, pre-maturation, post-maturation, winter) in two species of small rodent on two superficially similar islands, and attempts to identify those parameters that may act to bring about regulation through negative feedback.

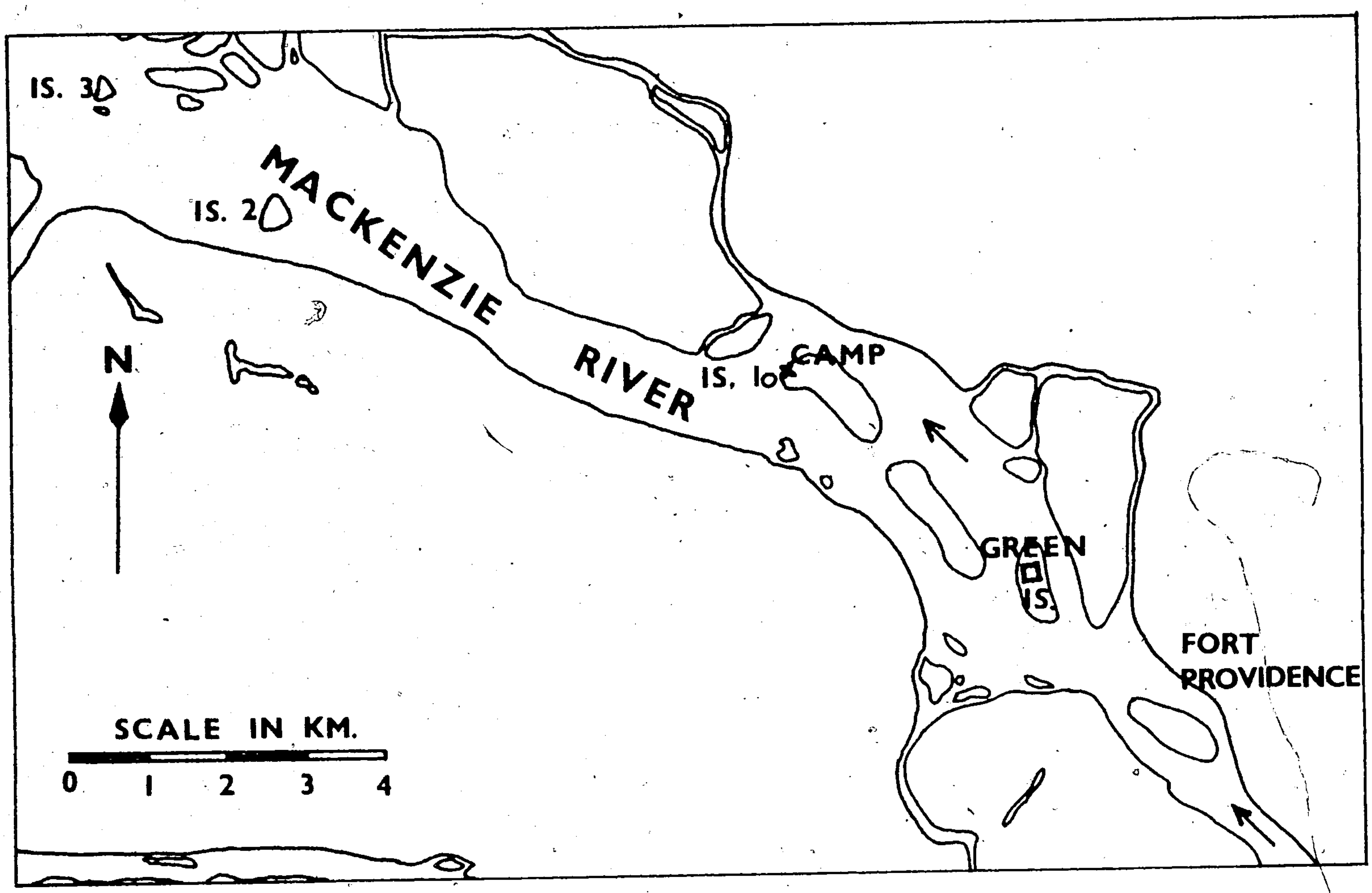


Figure 1. Map of study area.

Paper 1

Population Dynamics of Island Populations of Subarctic *Clethrionomys rutilus*

Abstract

Populations of Clethrionomys rutilus were studied on two islands (Island 2 and Green Island) in the Mackenzie River during the summers of 1977 and 1978 primarily by live-trapping but also by snap-trapping and autopsy.

The number of voles on Island 2 in 1977 increased until late June and then remained nearly constant until trapping ceased in late August. On Green Island in 1977 and 1978 and Island 2 in 1978, populations grew all summer and even in August had not reached the densities found during the 1977 high on Island 2. Island 2 in 1977 had an unusually low number of maturing young voles. Litter size, the number of young recruited per overwintered female, prenatal mortality, sex ratios and body length and weight showed no correlation with differences in population density. Higher wounding rates and shorter adjusted range lengths were associated with higher population densities. Overwinter survival rates (0.87 to 0.90 for 14 days) exceeded those of summer (0.50 to 1.00 for 14 days) and did not differ between islands.

Although high densities of voles were reached early in the summer of 1977 on Island 2, expansion of population size was observed to stop before the end of the breeding season. Restraint of growth potential was seen in poor maturation of the young and in declining juvenile survival and recruitment of young through summer.

Introduction

Studies of island populations of small mammals have led to a number of interesting observations. Lidicker (1973) noted 2-year cycles in Microtus californicus populations on islands concurrent with mainland cycles of three or more years, and attributed the shorter cycle length to lack of mammalian predators. Variations in body size were seen in Apodemus by Delany (1970) and in Peromyscus by Foster (1964). Berry (1968) found island populations of Mus to have larger litters and bodies than mainland populations. Berry and Jakobson (1975) attributed differing body sizes on islands to founder effects while Redfield (1976) associated increases in Peromyscus body size with "isolation itself". Sullivan (1977) compared Peromyscus populations and found differences in growth rates and dispersal tendencies between mainland and island populations. Crowell (1973) investigated factors contributing to the success of three small mammal species in colonizing and occupying islands and concluded that Microtus was the most successful insular species. Clethrionomys, which have poor dispersal abilities, and Peromyscus, which require large population sizes to prevent extinction (Redfield 1976), were less successful as island colonists. Crowell found significant positive correlations for Peromyscus and Clethrionomys between population growth rate and island size and concluded that density-dependent effects were observed sooner with the lower overall numbers of small islands. From his observation of asynchrony between populations, he concluded that the populations were regulated by unknown intrinsic controls. Bujalska (1970, 1975) sought factors stabilizing population size in an island population of Clethrionomys glareolus. She found that territoriality among mature females affected the number of females reaching reproductive status. Thereby the reproductive capacity of the population was limited. Survival of young was important in determining the island's peak population size. Redfield (1976) suggested that mouse populations on very small islands maintain very high densities. He found that islands below a critical size could not support a population, that trapping success was high on small islands and that island populations had different schedules of recruitment and generally heavier animals than adjacent mainland populations of Peromyscus.

Krebs et al. (1969) observed habitat destruction in a fenced population of Microtus and concluded that dispersal was necessary for normal population regulation. MacArthur (1972) extended this "Krebs effect" to geographic islands to explain why higher densities are often found in island populations than in mainland populations. He noted that the Krebs effect disappears as island size increases. In the summers of 1967, 1973 and 1976 small mammal populations from a number of islands in the Mackenzie River near Fort Providence, Northwest Territories showed high densities of animals in comparison with the nearby mainland (Canham 1969; Dickinson 1976). No habitat destruction was observed.

If dispersal from islands is minimal, these findings appear to be contrary to expectation, which suggests that these populations may be regulated below levels that would result in habitat destruction. The population dynamics of these island populations became the subject of the present study.

The present experimental design allowed consideration of two general questions in population biology - why does population density vary over time and why does density vary between isolated populations? Although Krebs and Myers (1974) state that cyclic microtine populations are the rule and that non-cyclic populations are the exception, the available historical information on the upper Mackenzie River populations of Clethrionomys rutilus on islands suggests constantly high numbers - an exception to the rule.

The islands used in this study are located in the Mackenzie River near Fort Providence, Northwest Territories (61°21'N 117°40'W). Islands became accessible by boat in spring from mid-May to early June after ice had cleared. The start of river travel was on May 27 in 1977 and June 7 in 1978. The later starting date in 1978 than in 1977 was indicative of a later spring in 1978. The islands are dominated by white spruce (Picea glauca) but locally important patches of trembling aspen (Populus tremuloides) and black spruce (Picea mariana) are also found. Green Island (30.6 ha) is largely covered by white spruce. Island 2 (7.7 ha), while its cover is dominated by white spruce, has large areas covered by black spruce and aspen. Cover dominated by white spruce was interpreted as climax vegetation which has been undisturbed for some time. From this climax condition on study islands and a general appearance of similarity, it was concluded that the islands had superficially similar habitat. Other islands with recent fire history are dominated by trembling aspen, are in different stages of succession and therefore cannot be considered to have similar habitats.

Methods

One grid was surveyed for capture-mark-release studies of rodents and shrews on each of two islands. Intersections of grid lines were separated by 25 m and a Longworth trap was placed within 2 m of each intersection. If it is assumed that each trap samples an area 25 m square, the suitable habitat on Island 2 (6.44 ha) was covered by 103 traps in lines of varying length. An 8 x 8 array (4.00 ha) of 64 traps was placed on Green Island in 1977 and expanded in 1978 to a 10 x 10 array (6.25 ha). Thus, only about one-eighth (1977) or one-fifth (1978) of Green Island, which has an area of 30.6 ha, was sampled.

Longworth traps caught both Clethrionomys rutilus and Peromyscus maniculatus on both islands. In addition, a few shrews (Sorex cinereus) were taken on Green Island only. Traps were equipped with terylene fibre for nesting material and a supply of sunflower seed for food. One trapping period, or rota, began with the opening of traps, generally, late on Saturday afternoon. Animals were cleared from traps in the morning and evening starting on Sunday and continuing until after the Thursday morning clearance. Individuals were toe-clipped for identification. Population estimates for each rota included previously marked animals missing that rota but recaptured later. Records of pregnancy, condition of the vagina, prominence of nipples, position of testes, body weight and location were recorded. In the first two rotas, voles weighing more than 18.0 g at first capture were designated as overwintered but thereafter were considered as mature young-of-the-year. Rotas began on Island 2: June 19, July 3, July 17, July 31, August 13, 1977; June 18, July 2, July 16, July 30, August 13 and August 25, 1978. Starting dates for Green Island rotas were: June 12, July 10, August 19, 1977; June 25, July 9, July 23, August 6 and August 20, 1978. Trapping began as soon as the river was clear of ice and safe for boat travel and after the completion of grid surveying.

Island 1 (1.5 ha) and Island 3 (2.0 ha) were chosen for an ill-fated experiment to test the prediction that limitation of winter food would affect survival. To mark all animals, lines of Longworth traps were distributed on Island 1 (40 traps) and Island 3 (37 traps). A rota of marking and releasing animals was started on August 7, 1977. In the same week, an attempt was made to remove all berries of <u>Geocaulon</u> <u>lividum</u>, <u>Vaccinium</u> <u>vitis-idaea</u> and <u>Viburnum</u> <u>edule</u> from Island 1. During the week of June 12, 1978, Museum Special snap traps baited with peanut butter were used to recover marked animals. One hundred traps were set for three nights on Island 1 and for five nights on Island 3. The experiment failed with respect to <u>C</u>. <u>rutilus</u> because no voles were found on Island 1 in 1977.

Animals for autopsy came from two sources. One was from trap lines consisting of 100 Museum Special snap traps, baited with peanut butter and set at 10-pace intervals. One such line was run for one night (August 10, 1976) on Island

2 and others were set on June 26, July 24 and August 21, 1977 on Green Island and run for three nights. The second source of animals was from the live-trap grids on Island 2 and Green Island at the end of the study in 1978. During the last two days (August 23, 24) of the fifth rota on Green Island, captured animals were kept for autopsy rather than released. Then the Longworth traps were replaced by snap traps for three nights. On Island 2, the Longworth traps were opened to start a sixth trapping period (August 25) and animals taken during the first three days were kept for autopsy. Live traps were then replaced by snap traps for two additional nights.

Autopsy procedure consisted of noting wounds, taking body weight and embryo weight, measuring total length and tail length, noting testis size, counting follicles, corpora lutea, corpora albicantia, embryos and placental scars and removing skulls for ageing. The morphology and development of roots on the second upper molar (M^2) were used as indices to age (Tupikova _et al_ 1968).

Results

Numbers

Increases in total numbers of voles and decreases in numbers of overwintered voles were for the most part exponential (Fig. 1). The maximum number of voles on Island 2 in 1977 was reached in early July and the slope of the growth curve was not significantly different from zero due to slow growth in July and August. The breeding season of 1978 began with half as many overwintered animals as in 1977 and maximum numbers were only attained at the end of the sampling season. While new recruits were still appearing at the termination of live trapping in 1978, it is not likely that by mid-September numbers could have equalled or exceeded those of 1977. Extrapolating numbers in 1978 to mid-September, a population of 41 voles was predicted, well below the 90 - 100 voles found in August 1977. Rates of increase in total numbers and decrease in numbers of overwintered voles did not differ significantly between years.

Initial densities of overwintered voles on Green Island were higher in 1977 on the smaller grid than in 1978. Growth in population size resulted in similar August densities in 1977 and 1978 on Green Island. A single short-tailed weasel (<u>Mustela erminea</u>) was captured on Green Island in August of both years. Weasel predation may have kept numbers down, but should have had no differential effect between years. Numbers of overwintered voles declined more rapidly on Green Island than on Island 2 in the summer of 1978 as shown by a significantly ($P<0.05$) different slope in the overwintered population curves.

Breeding

Spring densities of overwintered female voles were similar on both islands each year but were about 2.5 times as great in 1977 as in 1978 (Table 1). The number of young known alive in August per overwintered female was similar both years on Island 2 and on Green Island in 1978 but Green Island females appeared to be only about half as successful as Island 2 females in 1977. Density of young in August was greatest on Island 2 in 1977 and identical in both years on Green Island.

Half the females and less than half the males taken in the first two rotas on Island 2 in 1977 matured in the summer of birth (Table 2) whereas all young appearing in Rotas 1 and 2 matured in the other populations. In these populations only a few animals first caught during Rotas 3 and 4 failed to mature in their first summer. For Rotas 1 and 2, Island 2 in 1977 differed in the number of mature females ($P<0.05$, χ^2 test) and mature males ($P<0.005$) from the other populations pooled. For Rotas 3 and 4, the same population differed from the rest pooled in both sexes ($P<0.005$). The difference between 1977 and 1978 on Island 2 was significant for both sexes ($P<0.01$). Reduced maturation of young-of-the-year voles coincided with high population density on Island 2.

Estimates of litter size from embryo counts did not differ significantly from estimates based on counts of the most recent placental scars (Table 3). This was true for populations treated separately as well as pooled. Estimates of litter size based on combined embryo and placental scar counts did not vary significantly between islands or years. Dickinson (1976) also found no differences in litter sizes for voles on Island 2 and Green Island. Although she found significantly larger litters in overwintered females than in young females, the differences found in the present study were not significant. Based on embryos alone, overwintered females had litter sizes of 7.00±0.50 (5) and young females had litter sizes of 5.92±0.36 (13) embryos. Based on both embryos and placental scars, overwintered females had litter sizes of 5.92±0.79 (12) and young females had litter sizes of 5.86±0.32 (22) embryos. There was no significant difference between the larger litter size estimate based on embryo counts and the smaller estimate based on placental scar counts.

Survival and Recruitment

Survival of juveniles (trappable young) from one rota to the next was generally higher through the summers on Island 2 than on Green Island (Fig. 2a). In 1977, survival rates of young voles declined through the summer. In 1978, survival rates generally increased over time on Island 2 whereas they fluctuated erratically between 50% and 100% on Green Island.

Krebs and Myers (1974) (and elsewhere) used a 30-day survival rate of 0.707 (14-day rate of 0.841) to separate periods of "high" and "low" survival. Monthly survival was close to or exceeded 0.707 on Island 2 except in July 1978 and August 1977. On Green Island, monthly survival was below 0.707 except for late July 1978.

Recruitment of young into the trappable population declined steadily on Island 2 in 1977, but showed a general tendency to increase in 1978 (Fig. 2b). Recruitment increased over time in both years on Green Island. Both juvenile survival and recruitment appeared to be reduced in a regulatory response to high population densities on Island 2. Recruitment of young on Green Island on the smaller grid in 1977 was similar to that on the larger grid in 1978. However, the number of young known alive in August per overwintered female was lower in 1977 than 1978. Low 14-day survival rates (0.62 - 0.72, Fig. 2a) may explain the low numbers of young found in August.

Where overwinter survival rates did not fall to zero, they were comparable to or higher than summer survival rates (Table 4). Ratios of numbers of voles surviving from August 1977 to June 1978 to numbers not surviving show no difference between islands (χ^2 test). Although the 14-day survival rates were high, overall mortality was heavy. Spring counts revealed one to three survivors from counts of 10 to 53 individuals in the previous August. Given the possibility of repopulating dispersal on the Green Island grid, the possibility of extinction is low.

Extinction does appear to be a real possibility for small mammal populations such as on Island 1 or Island 3. Snap trapping, preliminary to this project, revealed the presence of voles on Island 1 in 1976. Live trapping on Island 1 in 1977 revealed no voles while snap trapping in 1978 revealed one vole. Of the 54 voles marked on Island 3 in 1977, only one marked vole was recovered in 1978.

More unmarked voles were captured in spring 1978 on Green Island than Island 2 in spite of a later end to trapping on Green Island in 1977. This suggests either that recruits were still appearing on Green Island in late August 1977 or that dispersers reached the grid from elsewhere on Green Island over the winter. Slow increase in total numbers through the summer on Green Island in 1977 (i.e. outward dispersal) and the high number of unmarked animals peculiar to the small grid favor the dispersal explanation.

Nestling Mortality

To estimate the number of young born on the grid, the estimated number of litters dropped was multiplied by the mean litter size based on combined embryo and placental scar counts. Number of litters dropped on the trapping grid was estimated from weight changes of individual females captured repeatedly in live traps and from the number of sets of placental scars in autopsied females. This estimate was then compared with the number of young surviving to trappable age. Green Island in 1978 showed the highest survival to capture (number of young captured/estimated number of young born) (Table 5), which may have contributed to the apparent difference between years on that island in the success of overwintered females in producing a large number of August young (Table 1) in spite of poor survival as juveniles (Fig. 2a). A higher proportion of the potential number of young was captured on Green Island than Island 2 in 1978 ($P < 0.005$, χ^2 test). Mortality among nestlings (young which have not reached trappable age) appeared to be an important source of loss of young but it did not seem to be consistently related to population density.

Considering all populations together, prenatal mortality did not contribute significantly to mortality (Table 6) but 83% of the total observed loss occurred on Green Island in 1978. The observed losses probably have little significance for population regulation. In 1973, incidence of resorption of embryo~~s~~ was very low (Dickinson 1976). One case of monozygotic twinning was observed on Green Island in 1977.

Body Weight and Length

Live weights were compared only for reproductive young males because there were too few overwintered voles to reveal differences and female weights were influenced by repeated pregnancy. Green Island voles were lighter ($P < 0.05$, Fig. 3) than those on Island 2 in early July 1977 but the difference disappeared after the second rota and was probably related to a later start of the breeding season on Green Island. Weights of voles on Island 2 in 1977 and Green Island in 1978 exhibited similar declines from mid-July to early August followed by increases in late August. The declines may represent a time of heavy recruitment of small young from the second litter or a general trend for animals to lose weight through summer. Increasing mean weight may represent decreasing recruitment and the growth of second litter young.

August samples of kill-trapped overwintered voles showed no difference between samples in body length or weight (Table 7).

August samples of kill-trapped young without roots on M^2 were subdivided according to whether or not the anterior labial groove was open. There were no significant differences in weights either between islands or between years in either category (Table 7). Body lengths (total length - tail length) of young with closed grooves were significantly ($P < 0.05$) longer on Green Island than on Island 2 in 1976. Young with open M^2 grooves were significantly ($P < 0.05$) shorter on Island 2 in 1976 than those of Green Island in 1977 and 1978, and in 1978, voles from Island 2 were shorter ($P < 0.05$) than those from Green Island. The 1976 sample was taken 13 days earlier than any other sample and this may explain the smaller size, but the longer animals on Green Island may also be related to lower densities of animals there than on Island 2 which may have led to faster growth rates because of a lower level of competition. No significant differences appeared in lengths or weights between years on the same island.

Sex Ratios

There were more young males than females recruited on Green Island in 1978 ($P < 0.01$, Table 8). More young males than females were recruited in Rota 3, ($P < 0.05$) and Rota 5, ($P < 0.025$) on Green Island in 1978. The imbalance on Green Island in 1978 led to a significant ($P < 0.05$) difference between islands in the sex ratio of recruits in that year.

The male:female sex ratio for the total population in all rotas combined on Green Island in 1977 was 20:16 and in 1978 was 33:15. On Island 2, the sex ratio was 78:85 in 1977 and 29:29 in 1978. There were significantly ($P < 0.01$) more males than females on Green Island in 1978 in all rotas combined. Among overwintered animals on Green Island, the male:female sex ratio in all rotas combined was 6:6 in 1977 and 5:4 in 1978. On Island 2, the sex ratio was 11:15 in 1977 and 4:4 in 1978. No imbalance in sex ratios of overwintered animals was found from live trapping.

The male:female sex ratio in all snap trap samples from Green Island in 1977 (all ages - 16:19, overwintered animals only - 3:6) and from Island 2 in 1976 (all ages - 17:17, overwintered animals only - 1:1) suggests no imbalance among overwintered voles or in whole samples.

Spacing Behavior

Spatial patterns were examined in a nearest neighbor analysis (Clark and Evans 1954) of centers of activity (arithmetic mean of capture locations).

Centers of activity of all sex and age classes tended to be uniformly distributed on Island 2 in 1977 (Table 9). Mature females were also uniformly distributed in 1978, but the mature male pattern changed to predominantly random. With the one exception of Rota 4 in 1978, aggregation was not apparent in the period of study. Lacking an abundance of data for Green Island, only a few patterns could be determined. Mature males in Rota 3 of 1977 and Rotas 3 and 4 of 1978 and mature females in Rota 5 of 1978 were all distributed randomly. It appears that uniform dispersion is the best way of accommodating peak numbers.

There was a sufficient number of overwinter survivors on Island 2 to examine loyalty to a territory between years. The distance moved from the center of activity established in 1977 to that of 1978 was significantly less ($P<0.01$) for females (27.3±9.6 m) than for males (123.3±28.2 m).

There was a significant difference ($P<0.01$) in adjusted range lengths between overwintered and young males on Island 2 in 1977 (Table 10). Consistent with expectations based on generally lower densities, range lengths were larger in 1978 than in 1977 on Island 2, where both overwintered and young males showed a significant difference ($P<0.01$) between years, and on Green Island, where ranges were significantly different ($P<0.05$) between ~~years~~ except for overwintered females. Interisland comparisons of range lengths were, however, contrary to expectation since they were consistently larger on Island 2 than on Green Island, but this difference was significant ($P<0.01$) for young females of 1977 only. This anomaly may result from an earlier decline in seasonal territoriality or it may indicate a higher social tolerance peculiar to small island populations or it may reflect the difference in grid size on Green Island between years.

Analysis of variance showed that sex, year, age and island were all important factors in determining adjusted range lengths of voles (Table 11).

Wounding

There was no significant difference in the amount of wounding in August between male and female or between adult and young (χ^2 test, Table 12). There was more wounding of immature voles (sexes combined) on Green Island in 1977 than in 1978 ($P<0.01$). Immature voles of Green Island in 1977 showed significantly ($P<0.01$) more wounding than those of Island 2 in 1976 and in 1978. Differences in wounding between years on Green Island can be related to differences in population density but density cannot explain the observed variation between islands. Due largely to immatures of 1977, there was more wounding on Green Island than on Island 2 ($P < 0.01$). The extent of wounding observed was only one or two bites per wounded individual.

Trapping Success

Because 103 traps on Island 2 captured 104 Clethrionomys and 85 Peromyscus in Rota 4 of 1977, and given the high proportion of traps per rota filled by an animal (Table 13), I examined my data for the sufficiency of traps. Table 14 shows that on average a single rota was effective in recording the presence of resident voles. One vole missed capture in two consecutive rotas and six missed one rota.

The attempt to remove all animals from the live-trap grid at the end of the 1978 trapping season allowed another measure of the success of live-trapping. Based on mean summer survival rates, I expected to capture 84% of the voles known alive during the previous trapping period on Island 2 and the removal trapping took 83% of those animals. All overwintered animals and most of the mature young were recaptured and removed from both grids in the first two days of removal trapping. Since none of the overwintered and mature young were unmarked, I conclude that few, if any, individuals consistently avoid capture in the live traps. Three unmarked mature young males were found on Green Island but they were probably immigrants. No marked animals that had disappeared earlier in the summer reappeared on the Green Island grid during the removal phase, which suggests that they did not simply shift their ranges off the trapping grid. Hilborn and Krebs (1976) observed that disappearing individuals located in evacuated areas and marginal habitat. Space adjacent to the Green Island grid was either fully occupied through the summer or of inferior habitat quality as no marked and presumably dispersed individuals returned to the grid during the removal phase.

Discussion

Overwinter survival rates, litter size and sex ratio did not appear to be related to differences in densities of voles between islands or to the limited population growth on Island 2 in 1977. Reduction in survival of juveniles and reduction in the maturation of young voles suggest regulated population growth. Generally lower densities of voles on Green Island than on Island 2 may be explained by the dispersal option, lower survival to trappable age and/or lower juvenile survival or differences in suitability of the two islands.

The gap between numbers of nestlings and numbers of young recruited into the trappable population revealed a large source of mortality. This substantial area of loss did not vary sufficiently between years to completely account for population fluctuations, but it did vary between islands in 1978 when densities were similar, suggesting that nestling mortality cannot be the only source of population regulation for voles. Whitney (1976) recognized large and variable nestling mortality and Okulova (1975) recorded 60% to 80% nestling mortality in C. rutilus. Crowcroft and Rowe (1957), referring to nestling Mus, and Krebs et al. (1969), referring to untrappable weaned young Microtus, argued that survival was not correlated with population size. Nestling mortality was called the primary control of population size in Mus (Southwick 1955a). Food supply (Calhoun 1949; Christian 1961), breakdown in maternal behavior

(Koshkina 1966; McPhee 1977) and interference at the nest (Brown 1953; Southwick 1955b; Friesen 1972; Savidge 1974) have been proposed to explain nestling mortality.

Kalela (1957) found little annual variation in litter size of fluctuating populations of _C_. _rufocanus_, while Pitelka (1957), Koshkina (1966) and Fuller (1969) observed that litter sizes appeared to be inversely related to population size. Litter size varied directly, but not significantly, with population density in this study. Green Island had both a higher density of overwintered females and larger litters in 1977 than 1978.

Prenatal mortality was generally not an important source of loss with the exception of Green Island in 1978. The observed losses on Green Island are of questionable significance because of the small sample size. Okulova (1975) found insignificant levels of resorption in _C_. _rutilus_. Kalela (1957) demonstrated low levels of prenatal mortality in _C_. _rufocanus_, which did not vary between years. Pre-implantation and post-implantation mortalities each ranged from 6% to 12% in _Microtus_ and _Peromyscus_ (Beer _et_ _al_. 1957; Keller and Krebs 1970).

Among young born in late summer, there were no differences between years in body weight, but there were differences in length with Green Island voles being larger than those on Island 2. If the larger size of Green Island voles is associated with greater viability of the young, in accordance with Chitty's hypothesis, then one would predict superior survival of young on Green Island with respect to Island 2, but this was not the case. Foster (1964) correlated large body size with island isolation, but Island 2, smaller and more isolated than Green Island, has the smaller animals, not the larger ones. An explanation involving a founder effect could be implemented but one would expect the long trip through cold water to Island 2 would select against smaller colonizers.

Densities on Green Island were higher in 1977 than 1978, except for the last rota when densities were similar, and more immature voles had wounds in 1977 than in 1978. Thus one might postulate that amount of wounding is positively correlated with density. But vole densities were higher on Island 2 in 1976 and 1978 than on Green Island in 1977, yet Green Island voles were more frequently wounded. Given the small number of wounded animals even in 1977, it seems unlikely that aggression resulting in wounds has any significance in the limitation of population growth. A low rate of wounding was also found in an island population of <u>Mus</u> (Lidicker 1966), and McPhee (1977) suggested that <u>C</u>. <u>rutilus</u> seldom exhibit aggressive encounters in the wild. In studies of <u>Microtus</u> <u>breweri</u> on an island and <u>M</u>. <u>pennsylvanicus</u> on the mainland, Tamarin (1977) found more wounding in the mainland species than in the island species. Lloyd and Christian (1967) saw a decreasing trend in aggressive behavior in two confined populations of <u>Mus</u>.

With the decline in vole density on Island 2 between

1977 and 1978, dispersion of centers of activity shifted from uniform to random except for mature females. Mature females also did not show a significant increase in adjusted range length as was shown by males. Thus mature females appear to maintain stable, probably exclusive, territories with no change in size over at least a 2-fold change in density. These distinct territorial requirements suggest that mature females play a major role in population regulation. Bujalska (1970) regarded the constancy of territoriality among adult females as the key to regulation of reproductive capacity in _C_. _glareolus_. She observed uniform dispersion, and little change in the degree of overlapping of home ranges, for adult females. Immature females were observed in aggregated distributions and exhibited variable amounts of home range overlap.

The island location of study populations is of interest in the context of population regulation. Mazurkiewicz (1972) observed an annual population maximum in mainland populations of _C_. _glareolus_ in October, whereas on an island, the peak was reached in early to late summer and peak density was 2 to 2.5 times higher than for the unrestricted mainland population. Gliwicz _et al_ (1968) found an early peak of numbers in an island population of _C_. _glareolus_ and a later peak for mainland animals. The difference was attributed to either the specific character of the years or to the specific ecological nature of the island. In years of rapid population growth, individuals born in later litters had a lower capacity for survival than those born in spring litters (Gliwicz 1975). This was observed on Island 2 in 1977 when there was a continuous decline in survival of young through summer and essentially no population growth after late June.

Three observations can be made about these island populations of C. rutilus. First, densities reached by August of each breeding season, while generally high in comparison with mainland population densities (Fuller, pers. comm.), were not constant between islands or years. Second, consistently lower densities of voles were found on Green Island than on Island 2. Third, the vole population on Island 2 in 1977 increased little after late June and recruitment thereafter was limited to replacement levels, whereas other populations appeared to be still increasing in size in August.

In terms of the number of young present per overwintered female in August, there was little difference between the two years on Island 2 or between the two islands in 1978, but in terms of absolute numbers (or density) of young, Island 2 in 1977 stands out. The large crop of young, despite decreasing recruitment and survival and poor maturation of young, points to a highly productive first breeding in 1977.

I had no way to predict the unusual success of the first breeding and I can only suggest that it was dependent on favorable weather. Unfavorable weather may affect breeding by delaying its start generally, by lowering the percentage of females that participate in breeding or by reducing the survival of young. Koshkina (1966) and Martell (1975) thought that the start of breeding was climate-dependent although Fuller (1969) considered C. rutilus to be insensitive to spring weather and did not find a delay in breeding in a year with a late spring. That the date of initiation of breeding in spring varied between islands or years could not be directly determined from the present study because of late starts in trapping. Recruitment of the first young-of-the-year occurred at different times on Green Island and Island 2, and in 1973, populations on these islands began breeding on different dates (Dickinson 1976). Weather cannot simply explain different starting dates for breeding on adjacent islands in the same year. But since young of the first litter mature and breed, they can have a strong effect on the season's output.

Contributing to the consistently lower densities of voles on Green Island with respect to Island 2 was poor recruitment of young into the trappable population in June (later start of breeding), a lower rate of recruitment generally, a lower juvenile survival rate, the possibility that animals dispersed from the grid and the presence of a weasel. Because only one weasel was captured, and only in August, in both 1977 and 1978, differences between years in the success of mature females in building an autumn population are probably not due to differential predation loss. The difference in population density between islands and mainland is consistent with MacArthur's prediction regarding the Krebs effect (MacArthur 1972). However, Dickinson (1976) with data on seven islands (including Island 2 and Green Island) was unable to demonstrate the Krebs effect.

The levelling off of growth in 1977 on Island 2 is of interest because it occurred at a time when other populations were still expanding. Several factors contributed to this early stabilization of numbers. Survival of both nestlings and juveniles declined through summer and many early-born young voles failed to mature. In contrast, both recruitment and subsequent survival increased through the summer in 1978, and almost all early-born young matured. Each of these factors could, therefore, have been responding in a negative feedback way to overall density. On Green Island, where densities were much lower, recruitment and maturation rates were both high while juvenile survival was erratic. Taken together, the evidence suggests that the summer maximum in 1977 on Island 2 was set by negative feedbacks, i.e. the population was regulated.

Table 1. Initial spring breeding populations of *C. rutilus* as predictors of annual population growth.

	Island 2		Green Is.*	
	1977	1978	1977	1978
Number of Overwintered Females	10	4	4	3
Density of Overwintered Females (/ha)	1.6	0.6	1.0	0.5
Number of Young Alive in Last Rota	92	39	17	27
Density of Young Alive in Last Rota (/ha)	14.3	6.1	4.3	4.3
Young Per Overwintered Female	9.2	9.8	4.3	9.0

*Grid increased from 64 to 100 traps in 1978.

Table 2. Percentage of young C. rutilus maturing in the year of birth.

			Time of Initial Capture in:					
			Rotas 1+2		Rotas 3+4		Rotas 5+6	
			% Mature	N	% Mature	N	% Mature	N
Island 2	1977	Male	39	33	0	17	0	10
		Female	50	28	11	19	0	11
	1978	Male	100	7	67	3	0	13
		Female	100	6	100	2	25	16
Green Is.	1977	Male	-	0	60	5	0	5
		Female	100	1	100	2	20	5
	1978	Male	100	2	100	9	100	4
		Female	100	2	100	4	50	4

Table 3. Litter size of *C. rutilus* from counts of embryos and placental scars of the latest pregnancy.

		Litter Size Derived From:		
		Embryo Count $\bar{X}\pm$S.E. (N)	Placental Scar Count $\bar{X}\pm$S.E. (N)	Embryo and Scar Counts $\bar{X}\pm$S.E. (N)
Island 2	1976	7.00±1.41(2)	4.00±0.00(2)	5.50±1.11(4)
	1978	5.75±0.48(8)	5.60±0.67(5)	5.69±0.36(13)
Green Is.	1977	7.25±0.55(4)	5.86±1.38(7)	6.36±0.87(11)
	1978	5.75±0.55(4)	5.50±0.71(2)	5.67±0.37(6)
	Totals:	6.22±0.31(18)	5.50±0.60(16)	5.88±0.32(34)

Table 4. Overwinter survival rate and numbers of marked and unmarked animals surviving winter.

	Sex	Number Known Alive in mid-Aug. 1977	mid-June 1978 Recapture	mid-June 1978 New	14-day Survival Rate
Green Is.	M	9	0	4	<0.91
	F	10	1	3	0.90
Island 2	M	53	3	1	0.88
	F	51	2	2	0.87
Island 3	M	20	1	1	0.87
	F	34	0	0	<0.84

Table 5. Comparison of C. rutilus potential versus observed numbers of young. (Potential young predicted from reproductive parameters and live-trap observations)

	Observed No. of Litters	Number of Young Potential	Number of Young Captured	Survival to Capture
Island 2				
1977	35 - 40	198-226	137	0.61-0.69
1978	14	81	50	0.62
Green Is.				
1977	5 - 8	32-51	24	0.47-0.75
1978	8	45	39	0.87

Table 6. Pre-implantation and post-implantation mortality in August samples of pregnant _C_. _rutilus_.

		No. of Litters	No. of Embryos	No. of Corpora Lutea - No. of Embryos	No. of Dead Embryos	Total Losses
Island 2	1976	2	14	0	0	0
	1977*	1	5	0	0	0
	1978	8	47	1	0	1
Green Is.	1977	4	28	-1**	0	0
	1978	4	26	3	2	5
Totals:		19	120	4**	2	6

Pre-implantation loss = 4/120 = 3.33%
Post-implantation loss = 2/117 = 1.71%,
*trap death on live-trap grid **monozygotic twinning not considered to offset part of losses.

Table 7. Comparison of August samples of *C. rutilus* for body length (mm) and weight (g) by Duncan's multiple range test. (sexes combined). Values underlined by the same line are not significantly different at $P < 0.05$.

OVERWINTERED VOLES

Length	Green '78	Is. 2 '76	Is. 2 '78	Green '77
N	1	1	3	2
$\bar{X}$	95.0	99.0	103.3	104.0

Weight	Green '78	Is. 2 '78	Green '77	Is. 2 '76
N	1	3	2	1
$\bar{X}$	18.4	23.0	25.1	25.3

YOUNG WITH GROOVES OF SECOND UPPER MOLAR CLOSED

Length	Is. 2 '76	Green '77	Is. 2 '78	Green '78
N	3	5	6	12
$\bar{X}$	88.0	90.2	90.8	94.5

Weight	Is. 2 '76	Green '77	Is. 2 '78	Green '78
N	3	5	6	12
$\bar{X}$	16.4	16.7	17.3	18.1

YOUNG WITH GROOVES OF SECOND UPPER MOLAR OPEN

Length	Is. 2 '76	Is. 2 '78	Green '77	Green '78
N	27	26	4	13
$\bar{X}$	82.7	84.8	88.8	88.8

Weight	Is. 2 '78	Green '78	Is. 2 '76	Green '77
N	26	13	27	4
$\bar{X}$	14.3	15.0	15.4	16.1

Table 8. Numbers of young male and female _C_. _rutilus_ entering the trappable population. (Tested by 2 x 2, 3, 5 or 6 χ^2).

		1977		1978	
	Rota	M	F	M	F
Island 2	1	23	14	3	3
	2	12	21	6	4
	3	8	13	1	1
	4	14	11	2	1
	5	10	11	3	4
	6			10	12
	Σ	67	70	25	25
	2 x 5 or 6 χ^2	6.24		1.06	
	Sig.	NS		NS	
Green Is.	1	1	1	2	2
	2	5	2	2	1
	3	8	7	7	1^{*}
	4			2	3
	5			15	4^{**}
	Σ	14	10	28	$11^{\dagger}$
	2 x 3 or 5 χ^2	1.35		11.40	
	Sig.	NS		NS	

$^{*}P < 0.05$ $^{\dagger}P < 0.01$

$^{**}P < 0.025$

Table 9. Dispersion of centers of activity for _C_. _rutilus_ on Island 2. Animals with single appearances excluded. (U = uniform, R = random, A = aggregated)

	1977					1978					
Rota:	1	2	3	4	5	1	2	3	4	5	6
Mature Male	R	U	U	U	U			R	A	R	R
Female	U	U	U	U	R		R	U	U	U	U
Immature Male	R	U	U	U	R			R			
Female		U	R	U	R						

Table 10. Adjusted range length (m) for C. *rutilus* having four or more captures.

			Overwintered $\bar{X}$±S.E. (N)	Young $\bar{X}$±S.E. (N)
Island 2	Male	1977	182±17.5 (11)††	128± 9.4 (45)
		1978	266±16.9 (4)**	212±17.9 (11)**
	Female	1977	106±11.2 (10)	87± 4.8 (43)†
		1978	121± 7.2 (4)	106±10.9 (6)
Green Is.	Male	1977	136±28.7 (5)	122±16.6 (6)
		1978	213±35.8 (2)*	195±21.2 (7)*
	Female	1977	84±11.4 (4)	54± 8.3 (5)
		1978	112±16.2 (2)	102±18.4 (4)*

*significantly different from 1977 (P < 0.05)

**significantly different from 1977 (P < 0.01)

†significantly different from Green Is. (P < 0.01)

††significantly different from young (P < 0.01)

Table 11. Analysis of variance of Adjusted Range Length by sex, year, age and island in _Clethrionomys rutilus_.

Source of Variation	Sum of Squares	DF	Mean Square	F	Significance of F
Main Effects	292783.500	4	73195.875	29.209	0.000
Sex	157762.938	1	157762.938	62.955	0.000
Year	104776.938	1	104776.938	41.811	0.000
Age	22367.723	1	22367.723	8.926	0.003
Island	13604.957	1	13604.957	5.429	0.021
Explained	323329.000	15	21555.266	8.602	0.000
Residual	383410.125	153	2505.948		

No higher level interactions were significant with the exception of the 2-way interaction between sex and year (F=5.700, P=0.018).

Table 12. Proportion of August samples of C. rutilus showing one or more recent wounds.

			Mature Proportion (N)	Immature Proportion (N)
Island 2	1976	Female	0.50 (2)	0.00 (15)
		Male	0.50 (2)	0.07 (15)
	1978	Female	0.00 (10)	0.00 (13)
		Male	0.00 (6)	0.00 (13)
Green Is.	1977	Female	0.00 (2)	0.60 (5)
		Male	0.50 (2)	0.50 (4)
	1978	Female	0.00 (6)	0.00 (2)
		Male	0.20 (10)	0.00 (9)

Table 13. Mean number of C. rutilus captures per trap per rota. (9 trap checks per rota).

	Island 2		Green Is.	
Rota	1977	1978	1977	1978
1	1.59	0.87	0.55	0.50
2	3.60	1.30		0.28
3	3.40	1.61	1.22	0.65
4	4.07	0.99		0.57
5	3.91	1.23	0.97	0.70

Table 14. Number of times at risk of capture needed to recapture a vole. Count of number of times at risk begins with the first day of next rota and continues, spanning rotas if necessary, until the vole is recaptured. A rota consisted of 9 trap clearances. Interval between clearances was ±12 hours. Data for _C_. _rutilus_ on Island 2 in 1977.

Recovery after Rota No.	No. of Times at Risk of Capture Needed for Individual Recovery range	mean	S.E.	N
1	1-10	2.02	0.31	51
2	1-27	3.83	0.47	72
3	1-14	2.29	0.28	72
4	1-9	2.12	0.19	76

Figure 1. Minimum number of <u>Clethrionomys</u> <u>rutilus</u> known to be alive.

● Total Population

○ Overwintered Population

Statistics for prediction equations based on exponential model.

$\ln(N_t) = \ln(N_o) + bx$ where t_o = June 1 and x is in days.

Island	Year	Population	Constant	Slope±S.E.	r^2	P
2	1977	Total	ln(58.22)	0.009±0.004	0.63	NS
		Overwintered	ln(38.73)	-0.022±0.007	0.78	<0.05
	1978	Total	ln(12.00)	0.012±0.004	0.65	<0.05
		Overwintered	ln(11.51)	-0.015±0.002	0.96	<0.01
Green	1978	Total	ln(6.55)	0.015±0.006	0.65	NS
		Overwintered	ln(16.19)	-0.032±0.007	0.88	<0.05

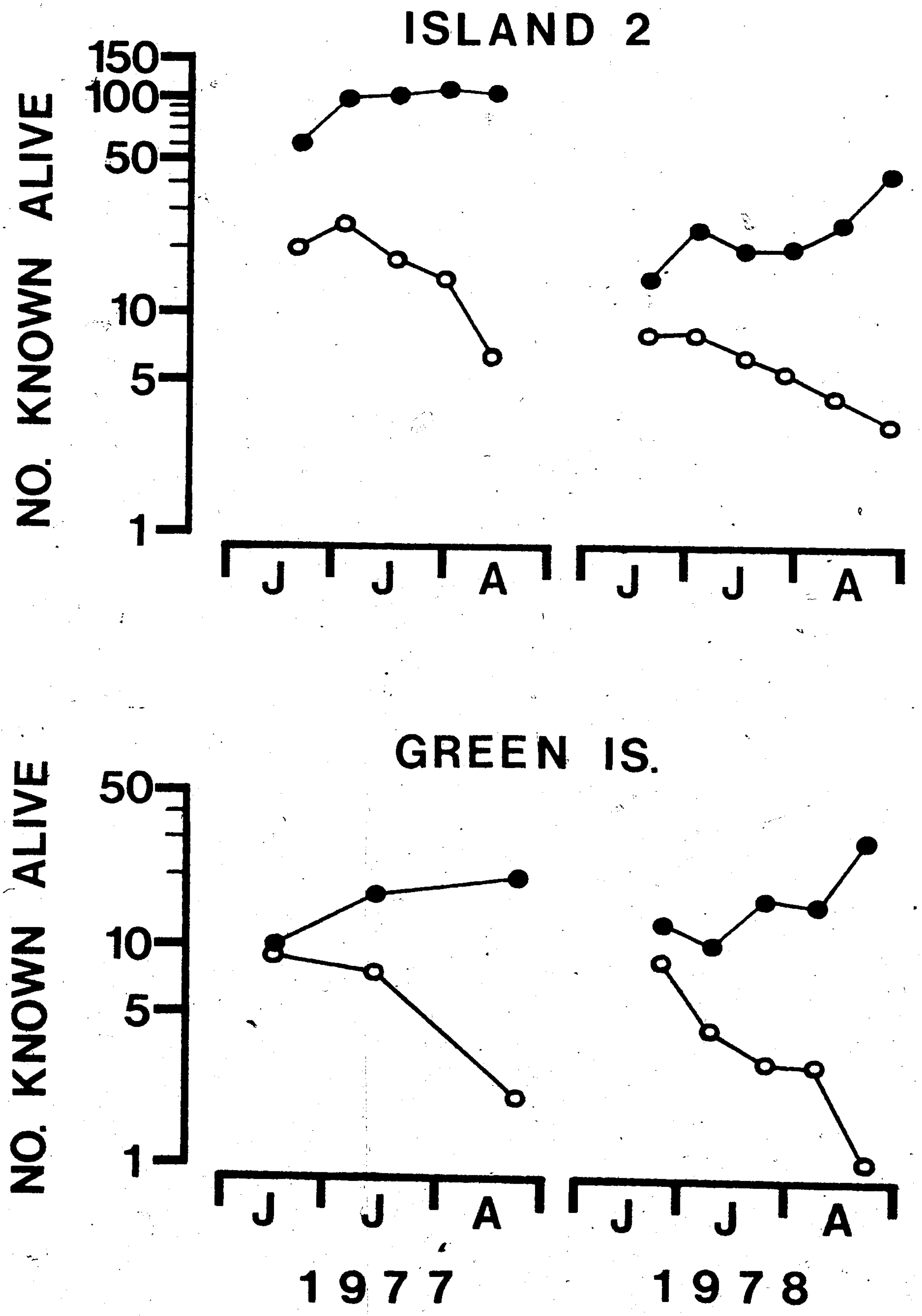

ISLAND 2
NO. KNOWN ALIVE
150
100
50
10
5
1
J
J
A
J
J
A
GREEN IS.
NO. KNOWN ALIVE
50
10
5
1
J
J
A
J
J
A
1977
1978

Figure 2. Survival from previous rota and numbers of young *C. rutilus* entering the trappable population. Dashed line is the 14-day equivalent of Krebs' monthly 0.707 used to separate "high" and "low" rates of survival.

● 1977 ○ 1978

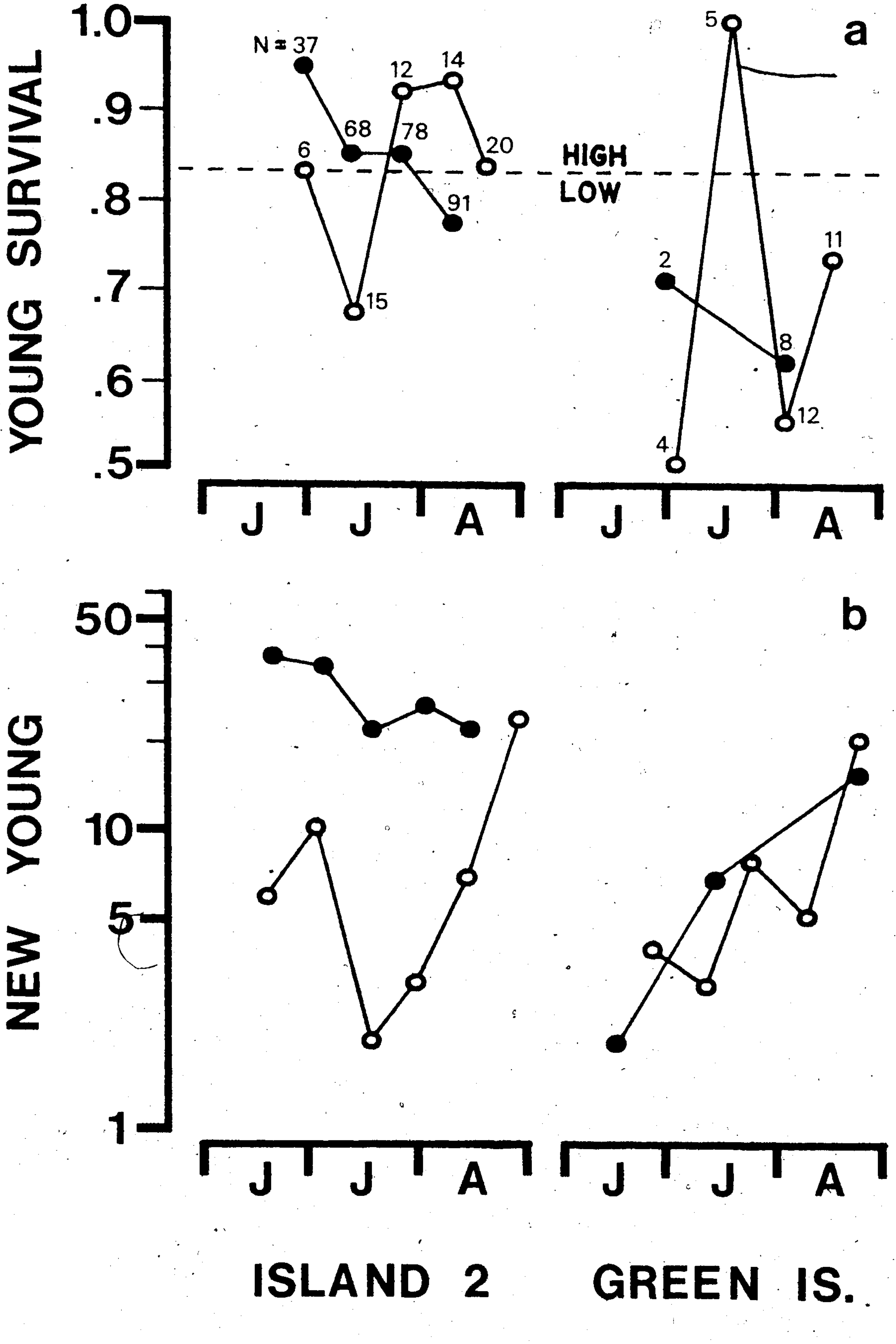
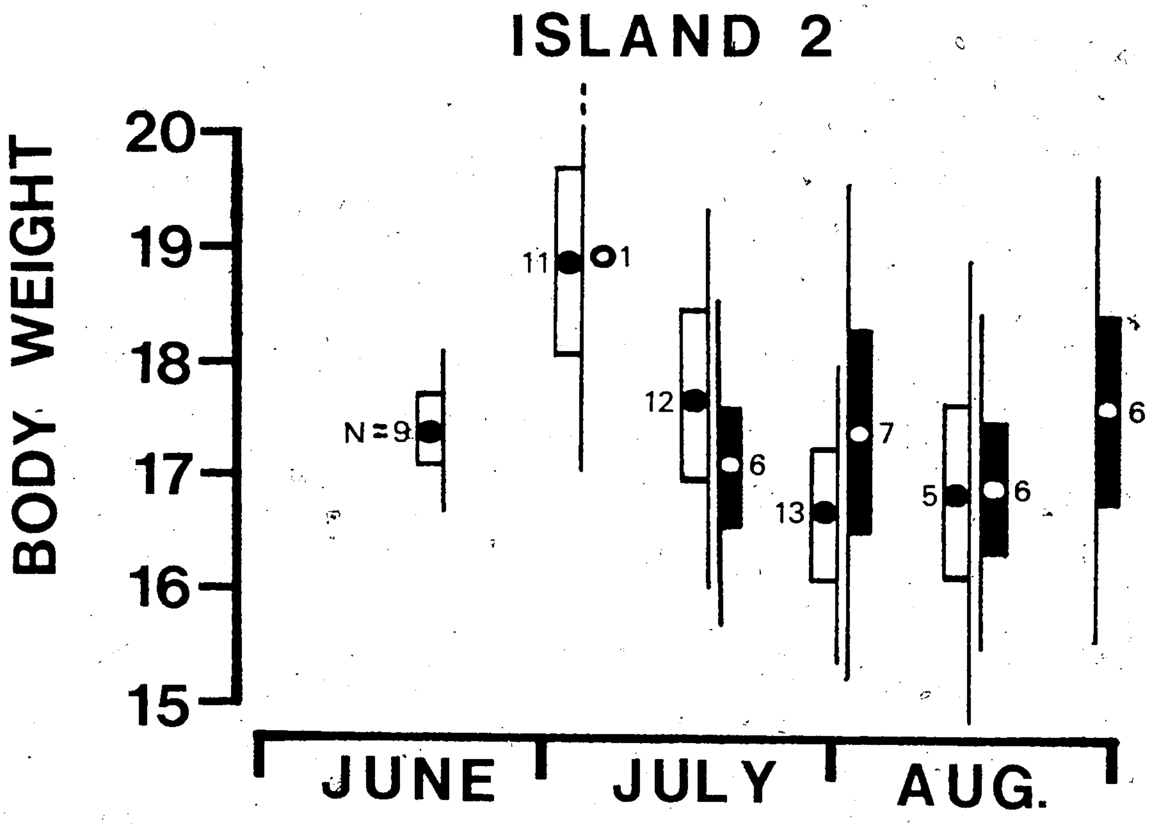

a
YOUNG SURVIVAL
1.0
.9
.8
.7
.6
.5
N = 37
68
78
91
6
15
12
14
20
HIGH
LOW
5
2
8
4
12
11
J
J
A
J
J
A
b
NEW YOUNG
50
10
5
1
J
J
A
J
J
A
ISLAND 2
GREEN IS.

Figure 3. Mean weight (g) of reproductive young male C. rutilus. (± 1 S.E. (bar), 95% C.I. (line)).

● 1977 ○ 1978


ISLAND 2
BODY WEIGHT
20
19
18
17
16
15
N=9
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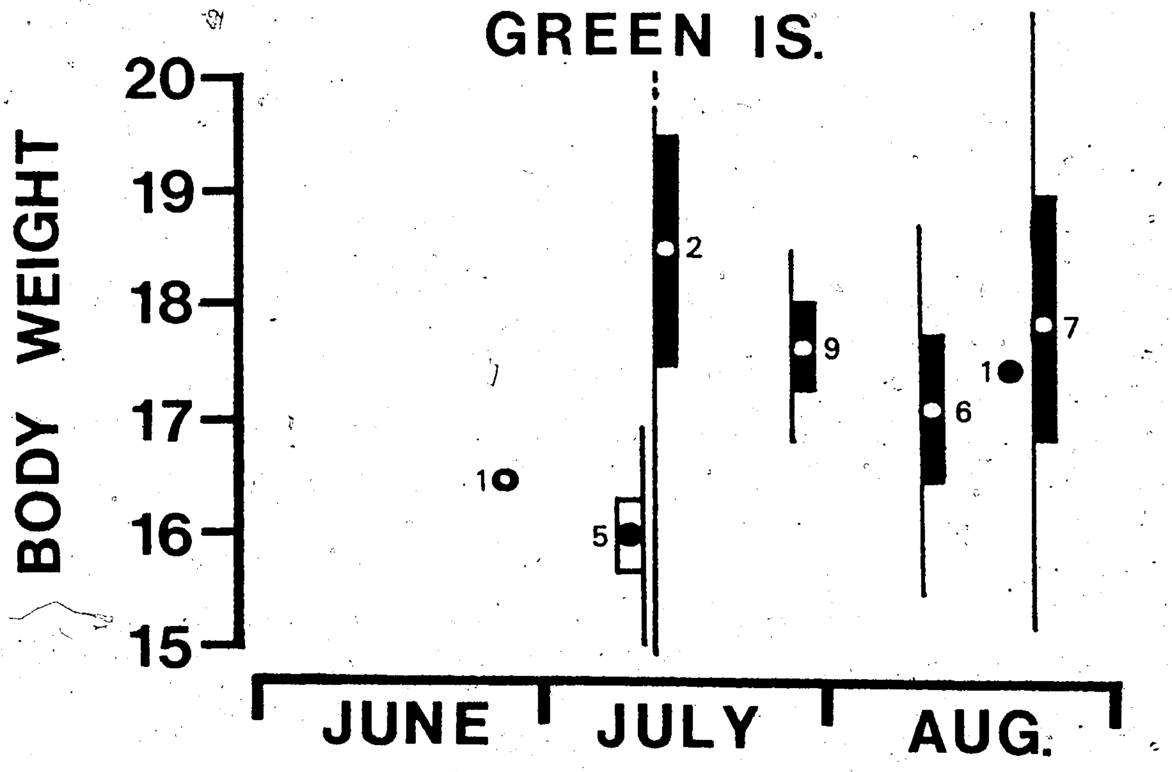
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Paper 2

Population Dynamics of Island Populations of Subarctic *Peromyscus maniculatus*

Abstract

Numbers of deer mice on Island 2 in 1977 were already high in late June. Density increased insignificantly thereafter. Populations on Green Island in 1977 and 1978 and Island 2 in 1978 showed growth throughout the summer. Higher densities were reached on Island 2 than on Green Island. The stable population on Island 2 in 1977 suffered a declining number of young entering the trappable population through summer and decreasing survival of trappable young. The mean number of August young per breeding female varied between islands and years. Overwinter survival rates did not differ between islands and were higher than survival rates in summer. Litter sizes, sex ratios and body weights and lengths did not show any relationship with population density. Adjusted range lengths and wounding rates were consistent with expectations of a territorial species - larger ranges at lower population density and more wounding with high numbers of mature animals. Higher wounding levels on Green Island than on Island 2 were not consistent with expectation.

Survival of nestlings and juveniles was negatively related to the spring density of breeding females. This relationship, along with a positive correlation between wounding and density, suggests that numbers may be limited, at least in part, by negative feedbacks.

Introduction

Preliminary observations of populations of Clethrionomys rutilus and Peromyscus maniculatus on several islands in the upper Mackenzie River near Fort Providence, Northwest Territories (61°21'N 117°40'W) showed numbers consistently higher than on the adjacent mainland (Canham 1969; Dickinson 1976). Burns (1979a) described the demography of C. rutilus on two of the same islands and found some evidence that numbers were limited by negative feedbacks. The present paper describes the demography of P. maniculatus and permits consideration of the following questions: (1). Does Peromyscus regulate its numbers below levels that would result in destruction of its food supply? (2). If so, how is regulation brought about? (3). Why does population density vary over time and why does population density vary between isolated populations? (4). How does population regulation differ between Peromyscus maniculatus and Clethrionomys rutilus?

Krebs et al (1969) observed habitat destruction in a fenced population of Microtus and concluded that dispersal was necessary for normal population regulation. MacArthur (1972) noted that small islands have much in common with Krebs' fenced plot, and suggested that they ought to have dense populations and consequent habitat destruction. He further noted that, since continents are merely very large islands, the "Krebs effect" ought to diminish with increasing island size. Herman (1979), while finding suggestions of relationships between wounding and aggressiveness and island size, found no consistent relationship between density and island size.

Islands used in the present study became accessible by boat in spring from mid-May to early June after winter ice left the river. The start of river travel was on May 27 in 1977 but was not until June 7 in 1978, as a result of a later spring in 1978.

Green Island (30.6 ha) is mainly covered by white spruce (_Picea glauca_). Island 2 (7.7 ha) is largely covered by white spruce but also has large areas covered by black spruce (_P. mariana_) and trembling aspen (_Populus tremuloides_). Relationships between small mammals and habitat types on the islands are explored in another paper.

Methods

Peromyscus maniculatus (and sympatric *Clethrionomys rutilus*) populations were studied on live-trap grids and by autopsy of snap-trapped samples. The live-trap grid on Green Island occupied 4.00 ha (8 x 8 array of 64 Longworth traps at 25 m intervals each assumed to sample 625 m^2) in 1977 and was extended to 6.25 ha (10 x 10 array of 100 traps) in 1978. Suitable habitat on Island 2 was covered by a grid of 103 traps (6.44 ha) in both years. Animals for autopsy came from snap-trap lines on Island 2 in August 1976 and on Green Island in June, July and August 1977. Additional animals for autopsy were taken from both grids at the end of live trapping in 1978. Standard methods used in live trapping, snap trapping and autopsy are described in Burns (1979a). Overwintered and young-of-the-year deer mice, both dead and alive, were separated primarily on the basis of pelage. Secondarily an arbitrary 18.0 g boundary for body weight was used to distinguish between young and overwintered mice.

An ill-fated experiment was designed to test the hypothesis that limited food resources in winter would affect survival. Lines of Longworth traps were distributed on Island 1 (40 traps) and Island 3 (37 traps) in August 1977 and animals were marked during one trapping period or rota (4.5 days). Simultaneously, an attempt was made to remove all berries from Island 1. One hundred snap traps were set on Island 1 (3 nights) and Island 3 (5 nights) in June 1978 to recover surviving marked animals. The experiment failed because there was evidence of predation by *Lynx canadensis* during winter on Island 3 but not on Island 1.

Results

Numbers

Spring numbers of overwintered deer mice on Island 2 were about twice as high in 1977 as in 1978 (Fig. 1). Numbers were already high in June as trapping began in 1977. Increases in total numbers and decreases in numbers of overwintered animals over the summer of 1977 were minimal (slopes of lines did not differ significantly from zero). In 1978, total numbers exhibited exponential increase and numbers of overwintered animals showed exponential decline. Slope of the increase in 1978 was significantly ($P<0.01$) greater than that in 1977 and slope of the decline in overwintered mice in 1978 was significantly ($P<0.001$) greater than that in 1977. The summer maximum was apparently reached in early August 1977, but numbers may still have been increasing in late August 1978. If so, September numbers of 1977 could have been exceeded in 1978.

On Green Island, numbers increased exponentially through the summer of 1978 and were probably still growing in late August each year. Overwintered animals declined in 1977, but increased in 1978 as a result of immigration onto the grid.

The rate of growth in numbers on Green Island was greater than that on Island 2 in 1978. Slopes of growth curves differed significantly ($P<0.02$). Extrapolations of these curves suggest that numbers on the Green Island grid (125 mice) would have just surpassed those on the Island 2 grid (120 mice) in mid-September.

Breeding

The population on Island 2 consisted mainly of young as early as mid-June 1977, whereas only one young was taken in mid-June 1978. This suggests that breeding began earlier in 1977 than in 1978, probably as a result of earlier disappearance of the winter snow cover. (The river was ice free about 11 days earlier in 1977 than in 1978.)

Breeding behavior of Peromyscus appeared to be inflexible. Overwintered mice all matured, and females surviving to the end of summer produced two litters. There was no evidence that young deer mice participated in breeding in the year of their birth. However, on Island 2 in 1977 a small number of young showed some indications of maturing (perforate vagina, body weights reaching 18 to 20 g, enlarged testes). As none of the mice on Island 2 were autopsied in 1977, I could not confirm that no young had attained sexual maturity. Young mice were snap-trapped in 1977 on Green Island and no males had sperm and no females had placental scars or embryos. Thus breeding appeared to be carried out by overwintered animals only.

The density of overwintered females was about one per hectare on Island 2 in 1977 and on Green Island in both years, but it increased by a factor of three on Island 2 in 1978 (Table 1). In spite of the differences in initial spring density, the August density of young on Island 2 was virtually identical. This suggests an inverse relationship between initial density and production of young, which could act in a regulatory manner. Densities of breeding females and August young on Green Island did not differ between years. Spring densities were the same as on Island 2 in 1977 but the density of August young was smaller in both years. Dispersal from the grid to some other part of Green Island may account for some of the apparent difference between islands in breeding success, but there is probably also a real difference in carrying capacity.

Mean litter sizes of *Peromyscus* sampled in August were determined, in the absence of pregnant females, from placental scar counts only (Table 2). Litter sizes found on Island 2 in 1976 were significantly ($P < 0.05$) different from those from Green Island in 1977 and 1978. Because the 1976 sample was taken earlier in the month than the Green Island sample, there was more contrast between early and late scars in 1976. The 1976 figure agrees with the mean litter size based on embryo and placental scar counts for June to August 1973, which were 5.31±0.36 (13) on Green Island and 5.89±0.62 (9) on Island 2 (Dickinson, unpublished data). I therefore consider the Green Island estimates for 1977 and 1978 to be unreliable and conclude that there is probably little variation in litter size between islands or years.

Survival and Recruitment

Ratios of numbers of mice surviving from August 1977 to

June 1978 to numbers not surviving (overwinter survival) did not differ significantly between islands (χ^2 test, Table 3). Rates of overwinter survival were generally higher than summer rates. Although Green Island was sampled later than Island 2 in 1977, there were more unmarked animals on Green Island in 1978 which suggests that animals were recruited into the population on the grid after trapping ended in 1977 or that there was immigration onto the Green Island grid. Declining numbers of new young in August 1977 on Island 2, and increasing numbers on Green Island at the same time, point to later breeding and recruitment on Green Island than on Island 2 in 1977, but immigration cannot be ruled out.

On Island 1, one male and one female survived to June 1978 after 14 males and 12 females were marked in the previous summer. This represented an average 14-day survival rate of 0.89 even though their food supply had been reduced.

Survival rates of juveniles (trappable young) on Island 2 decreased through the summer of 1977 (Fig. 2a). Excluding a drop in early July, survival was high in 1978. Young survived well on Green Island in 1978 to late July when survival declined. Because the grid covered only part of Green Island, the apparent drop in survival may have been caused by emigration.

Recruitment of young into the trappable population was delayed on Island 2 in 1978 and on Green Island in 1977 presumably as a result of delayed onset of breeding (Fig.

2b). Young appeared on Island 2 in large numbers in June 1977 but recruitment declined thereafter. Recruitment into the trappable population increased over summer for the other populations.

Nestling Mortality

The calculated survival of nestlings (young which have not reached trappable age) for both islands in 1977 suggests that I underestimated litter size, or number of litters dropped on the grid, or both (Table 2). If placental scar counts tend to overestimate litter size (Lidicker 1973), then my estimate of the number of litters dropped must have been low. Because number of litters for 1977 was based only on observations of weight changes in breeding females, small litters (little weight change) and insufficient trapping frequency may have led to the underestimate.

Survival to capture (number of young captured/estimated number of young born) was high on both islands in 1977, but in 1978 survival to capture was 79% on Green Island and only 55% on Island 2. Nestling survival appears to be inversely related to spring density of overwintered females. Spring density of breeding animals and survival of young to trappable age may be parts of a negative feedback that regulates population size.

Body Weight and Length

Live weights of immature young males did not vary between islands (Fig. 3). Early July weights on Island 2 were higher in 1977 than 1978 reflecting the earlier appearance of young in 1977. Weight appeared to rise to a peak in late July and then drop in August in both years. The same trend appeared on Green Island in 1978. The rise was caused by growth of the first litter young and the decline was caused by the appearance of lighter young of the second litter.

Lengths and weights of snap-trapped samples from different islands, years and age-classes showed no significant difference between males and females, so sexes were combined for further analysis (Table 4). Data from the present study were supplemented with unpublished data from Dickinson.

Among overwintered mice, those from Green Island were significantly ($P < 0.05$) shorter than mice from Island 2 in 1973 and 1978 and from Green Island in 1977. Overwintered mice from Island 2 in 1976 were significantly ($P < 0.05$) shorter than those from the same island in 1978 and from Green Island in 1977. Animals from Green Island in 1978 were significantly ($P < 0.05$) lighter than all other island-year samples and overwintered mice from Island 2 in 1973 were significantly ($P < 0.05$) heavier than those from the same island in 1976 and 1978 and from Green Island in 1973. Because the size of overwintered animals varied from year to year, interisland differences in body size probably have no significance in relation to island size.

Among young mice, those from Green Island in 1973 were significantly ($P<0.05$) shorter than mice from the same island in 1977 and 1978 and from Island 2 in 1978. Young of 1978 from Green Island and Island 2 were lighter ($P<0.05$) than mice from Green Island in 1977 and Island 2 in 1976. As with the overwintered deer mice, there were no consistent differences between islands in the size of young mice. Samples of young mice were generally ordered by mean size in the same way as the overwintered mice of the same island and year were ordered.

Larger or small body size could not be consistently associated with one island or one year or with population size.

Sex Ratios

Sex ratios of young recruits, although showing an overall female bias, showed no significant imbalance by single rota or by island and year (Table 5).

Among overwintered mice enumerated on Island 2 in 1978, there were fewer males than females (9:21) ($P<0.05$, χ^2 test) but Island 2 in 1977 (male:female = 4:7) and Green Island in 1977 (0:4) and in 1978 (6:7) showed no significant imbalance. The male:female sex ratios in total populations showed a significant imbalance ($P<0.025$) on the Island 2 grid in 1978 (43:69) but not on that grid in 1977 (53:56) or the Green Island grid in 1977 (15:18) or in 1978 (34:33).

Snap-trap samples from Green Island in 1977 (all ages - 18:21, overwintered population - 4:6) and Island 2 in 1976 (all ages - 13:10, overwintered population - 3:3) showed no sex ratio imbalance.

Sex ratios of young recruits (rotas pooled) did not differ between islands or years.

Spacing Behavior

Spatial patterns were examined in a nearest neighbor analysis (Clark and Evans 1954) of centers of activity (arithmetic mean of capture locations).

Dispersion of centers of activity of mature male mice was predominantly uniform (Table 6). Other classes were dispersed randomly more often than uniformly. No aggregated pattern of dispersion was observed during the period of study.

Island 2 provided sufficient overwinter survival to examine loyalty to location from year to year. The distances between 1977 and 1978 centers of activity were significantly ($P < 0.01$) greater for males than females. Females shifted their centers an average of 48.5±13.3 m and males moved an average of 135.3±13.5 m.

On Island 2, adjusted range lengths of overwintered males were significantly different from those of overwintered females in 1977 ($P < 0.01$) and 1978 ($P < 0.02$, Table 7). Young males and females showed very similar range lengths. Overwintered males generally had longer range lengths than young males (significant ($P < 0.01$) on Island 2 in 1977). Range lengths of females varied erratically with age. Young males and females and overwintered females on Island 2 had slightly shorter range lengths in 1977 than in 1978 which is consistent with the hypothesis that range size varies inversely with density. However, overwintered males on Island 2 had longer range lengths in 1977 than in 1978. None of the differences was significant.

On Green Island, adjusted range lengths of young males and females were slightly shorter in 1977 than in 1978. Overwintered females showed a more marked, but still insignificant difference. The general increase in range length was probably due to the increase in grid area between 1977 and 1978. There were no significant differences in range length between overwintered and young or between males and females, although, as expected, adults had larger ranges than juveniles and male ranges were larger than those of females.

There were no significant differences in range length between islands in spite of differences in grid size, population density, island size and whether or not a dispersal option was available.

Analysis of variance showed that among the factors of sex, year, age and island, only sex was found to affect adjusted range length (Table 8).

Wounding

Frequency of wounded animals in August samples was low (Table 9).

Mice on Island 2 experienced almost no wounding with no differences between sexes or years. Mature animals, however, had significantly ($P < 0.05$, χ^2 test) more wounds than immature animals.

Mice on Green Island showed no differences in wounding frequency by age, sex or year.

A 23% wounding rate among immature female mice on Green Island in 1978 played a large role in interisland comparisons. Young from Green Island showed more wounds than young from Island 2 in 1978 ($P < 0.05$) and in both years combined ($P < 0.05$). Overwintered mice showed a significantly ($P < 0.05$) higher frequency of wounding than young mice (sex, island and year classes combined). A significantly ($P < 0.05$) higher wounding rate was found on Green Island than on Island 2 when sex, age and year classes were combined.

Trapping Success

The sufficiency of trap density and trapping success was examined. Island 2 in 1977 at Rota 4 was critical, with peak numbers of 85 Peromyscus and 104 Clethrionomys known to be alive and vulnerable to 103 traps. Nocturnally active deer mice were only vulnerable to capture five times per rota. Given an average of 2.68 captures per trap (Table 10), animals may have avoided capture in some rotas. However, a single rota was found to be effective in demonstrating the presence of most resident trappable animals (Table 11).

Overall, two deer mice missed capture in two consecutive rotas, and six missed a single rota.

Continuous removal of animals from the grids at the end of live trapping in 1978 permitted further evaluation of live-trapping success. Based on survival rates through the summer on Island 2, I expected to capture 86% of the mice from the previous trapping session, and I actually took 90%. All overwintered mice and 85% of the marked young ultimately recovered were captured in the first two days of removal trapping on Island 2. Sixty-eight per cent of all unmarked animals captured were taken from the third to fifth trapping days. Social subordination and lack of open traps may have prevented earlier appearance of unmarked young in traps. No marked animals that had disappeared earlier were recovered from the "biological vacuum" created by removal trapping on the Green Island grid, which suggests that those animals that disappeared had either died or dispersed over a considerable distance.

On Island 2, the snap-trapping phase of removal trapping caught no unmarked adults or subadults, i.e. animals that might have been living on the grid yet evaded capture in live traps. On Green Island, two adults (one of each sex) were caught in snap traps on the second and fourth days of removal trapping. They may well have been immigrants but even if they were residents that had not entered the live traps, trap avoidance was not a major source of error.

Discussion

Previous sampling by Canham (1969), Dickinson (1976) and the preliminary sampling in this study indicated consistently high populations of small mammals on several islands in the Mackenzie River. That situation was confirmed in the present study although the population on Island 2 in late June and July of 1978 was probably lower than in any previous sample. Early spring populations consisting only of overwintered animals would reveal little difference between islands because of similar numbers of overwinter survivors. Populations diverged following birth of the first litter. Timing and fate of that litter therefore affects capture rates in late June and July samples. Survival of juveniles was relatively high at the time of the first litter in the present study. Fairbairn (1977a), however, found low survival of young at the start of the breeding season and increased survival at the end of breeding.

Reproductive effort was not a variable in the demography of <u>Peromyscus</u>. Young-of-the-year mice did not mature in the year of birth. All overwintered females that lived long enough had two litters.

Although individual reproductive effort was not a variable, growth in numbers of mice was not consistent. There was little or no increase in numbers after early July on Island 2 in 1977. (Slope of the growth curve did not differ significantly from zero.). Numbers grew rapidly throughout the breeding season in 1978 on Island 2 and

Green Island.

Recruitment, or survival of nestlings to trappable age, increased through summer on both islands in 1978 and on Green Island in 1977. Recruitment on Island 2 in 1977 was high in June but declined thereafter. Survival of trappable young on Island 2 in 1977 also declined through the breeding season while survival of juveniles from Island 2 and Green Island in 1978 remained generally high during summer.

Dispersion of centers of activity of mature males was predominantly uniform whereas it was usually random for other deer mice. Adjusted range lengths of deer mice varied only by sex. Males had longer range lengths than females. Year, island and age did not affect range length.

Wounding was more prevalent among overwintered than young mice. If aggression by adults against juveniles is involved in population regulation, one would expect to find many young with bite wounds unless every animal attacked was killed or driven out, and few survivors received any bites. The low incidence of wounding, especially on Island 2, therefore, probably reflects a low level of aggression on the part of adults. Juvenile survival is apparently not related to the density of resident adults during the breeding season (Sadleir 1965) or the aggression directed against juveniles by breeding males (Fairbairn 1977a). Green Island animals showed more wounding than Island 2 animals among the young and all ages combined. Generally low levels of wounding may be an adaptation reflecting the lack of a real dispersal option. Dispersal from the Island 2 grid was probably negligible, however, the possibility of limited dispersal may have played a minor role on Green Island. Animals probably moved onto the grid over winter, and some of the disappearance of young during summer was probably due to emigration from the grid, but dispersal to and from Green Island must have been severely limited.

Changes in various demographic parameters can be interpreted, in their apparently appropriate timing in relation to changes in density, to indicate regulation of numbers. The conditions of population growth on Island 2 in 1977 (little increase in numbers in July and August) contrasts with conditions on Island 2 and Green Island in 1978 (rapid growth in numbers through summer). Reproduction, adjusted range lengths, dispersion of centers of activity, litter size, sex ratios and body length and weight showed either no variability or no relationship to population growth in either year, or on either island. Both nestling and juvenile survival declined on Island 2 in 1977 when the density of mice was high. Nestling and juvenile survival appear to be adversely affected by high population density. If so, they constitute an important mechanism for population regulation.

Differences between densities achieved at peaks on Green Island and Island 2 cannot be satisfactorily explained by trends seen in the present study. Overwinter survival did not differ significantly between islands. Breeding populations were similar in size in 1978 but the peak density for the summer was lower on Green Island than on Island 2. Survival was only slightly lower on Green Island than Island 2 during summer and little difference was evident in recruitment of young into the trappable population. Dispersal from the Green Island grid was probably insignificant.

Wounding was more prevalent on Green Island than on Island 2. Dickinson (1976) found low wounding rates on small islands with high densities. Herman (1979) found an inverse relationship between wounding among Peromyscus maniculatus and island size but not between density and island size. High density may reduce the threat of extinction on small islands (Redfield 1976) but why there was almost no wounding is not clear. It is especially puzzling in light of the apparent positive relationship between numbers and the proportion of wounded young on Green Island.

Under the conditions imposed by the island location, Peromyscus maniculatus and Clethrionomys rutilus populations must regulate their population densities. How do the demographies of Peromyscus and Clethrionomys compare?

(1). Overwinter survival (ratio of number of animals surviving winter to number not surviving) was significantly higher for deer mice than for voles ($P < 0.001$, χ^2 test). Voles are winter-active but deer mice go into torpor. Overwintered females on the live-trapping grids showed higher densities for deer mice in 1978 on both grids, lower densities for mice on Island 2 in 1977 and the same density as for voles on Green Island in 1977.

(2). August densities of voles were more variable than those of deer mice. On Island 2, voles were more numerous than deer mice in 1977 but the reverse was true in 1978. On Green Island, deer mice were more numerous than voles in both years. Growth rates of populations did not differ significantly between species on Island 2 in 1977 and 1978 and on Green Island in 1978. Rates of growth in numbers of both Clethrionomys and Peromyscus were lowest on Island 2 in 1977 (slopes: 0.009 and 0.004 respectively); were intermediate on Island 2 in 1978 (slopes: 0.012 and 0.016 respectively); and were highest on Green Island in 1978 (slopes: 0.015 and 0.029 respectively). This suggests an overriding influence on population growth of both species by conditions peculiar to certain islands or years but the fate of overwintered voles and mice refutes this idea. Declines in overwintered voles were highest on Green Island in 1978 (slope: -0.032) but immigration of mice caused an increase in their numbers. The intermediate rate of decline of voles (slope: -0.022) occurred on Island 2 in 1977 where deer mice experienced their lowest rate of decline (slope: -0.001). Voles declined at their lowest rate (slope: -0.015) and deer mice declined at their highest rate (slope: -0.012) on Island 2 in 1978. Declines in numbers of overwintered animals over the breeding season appeared to be more rapid in the voles than the mice (significantly so on

Island 2 in 1977 - slopes of declines different at $P < 0.025$). Declines in numbers of overwintered voles were consistently rapid leaving 25% or less of June numbers by mid-August.

(3). The breeding pattern of deer mice is inflexible - only overwintered animals mature and mature females surviving long enough produce two litters. Among the voles, an overwintered female may survive long enough to have three litters. Young-of-the-year females may drop zero, one or two litters depending on the date of their birth and whether or not they mature. Maturation of young voles was negatively correlated with numbers of mature animals (e.g. Island 2 in 1977).

(4). Estimates of survival to trappable age ranged from 55% to 100% in Peromyscus and from 47% to 87% in Clethrionomys. Extent of nestling mortality appeared to be more variable among deer mice than among voles.

(5). Trends in survival after recruitment were similar in both species on Island 2 in both years. On Green Island, vole survival fluctuated widely and appeared to be generally lower than mouse survival.

(6). Weight did not differ between populations of young voles (M^2 grooves open or closed) or overwintered voles. There were no differences in weight of small samples of overwintered voles but young voles showed some differences between samples by weight. Few differences in length were found among populations of young and overwintered deer mice. Mouse populations also showed few differences by weight, however, overwintered mice on Green Island in 1978 were significantly lighter than all other samples of overwintered mice. There was no correspondence in size between <u>Clethrionomys</u> and <u>Peromyscus</u> (rank order of island and year samples).

(7). The territorial sex in <u>Peromyscus</u> is the male while it is the female in <u>Clethrionomys</u>. Mature female voles and mature male deer mice showed uniform dispersion during the study period generally. Mature male voles and mature female deer mice were uniformly distributed at high density but were otherwise randomly distributed.

(8). Adjusted range length was correlated with sex, year, age and island in the voles but correlated only with sex among the deer mice. As expected, range lengths were greater for mature males than for mature females, and for overwintered animals than for young in both species.

(9). <u>Peromyscus</u> sex ratios showed a female bias while <u>Clethrionomys</u> showed a balanced or slightly male-biased sex ratio. There was no significant difference in sex ratios in comparisons of the two species by island and year.

(10). Wounding rates did not differ between species among young or overwintered animals on Island 2 or on Green Island (χ^2 test).

Table 1. Numbers of overwintered female P. *maniculatus* as predictors of annual population growth.

	Island 2		Green Is.*	
	1977	1978	1977	1978
Number of Overwintered Females	7	21	4	6
Density of Overwintered Females (/ha)	1.1	3.3	1.0	1.0
Number of Young Alive in Last Rota	65	68	25	41
Density of Young Alive in Last Rota (/ha)	10.1	10.6	6.3	6.6
Young Per Overwintered Female	9.3	3.2	6.3	6.8

*Grid increased from 64 to 100 traps in 1978.

Table 2. Comparison of _P_. _maniculatus_ potential versus observed numbers of young. (Number of litters from observations of the live populations. The weighted mean of 1973 (Dickinson 1976) and 1976 litter sizes (based on latest set of placental scars) was used to calculate the potential number of young.)

	Litter Size	Observed	Number of Young		Survival
	$\overline{X} \pm$S.E. (N)	No. of Litters	Potential	Captured	to Capture
Island 2					
1976	5.50±0.33 (4)*				
1977		12 - 16	68-91	98	1.08-1.44
1978	6.67±0.54 (6)	26	148	82	0.55
Green Is.					
1977	7.33±0.67 (6)	4 - 6	23-34	29	0.85-1.26
1978	8.00±0.85 (6)	12	68	54	0.79

*significantly different from Green Island in 1977 or 1978 ($P < 0.05$).

Table 3. Overwinter survival rate and numbers of marked and unmarked P. maniculatus surviving winter. (Survival rate based on recovery of marked animals only.)

	Sex	Number Known Alive in			14-day Survival Rate
		mid-Aug. 1977	mid-June 1978		
			Recapture	New	
Green Is.	M	14	1	5	0.89
	F	13	2	5	0.92
Island 2	M	38	7	2	0.93
	F	47	15	5	0.96
Island 3	M	14	0	0	<0.89
	F	10	3	1	0.95
Island 1	M	14	1	1	0.89
	F	12	1	0	0.89

Table 4. Comparison of August samples of P. *maniculatus* for body length (mm) and weight (g) by Duncan's multiple range test. (sexes combined). Values underlined by the same line are not significantly different at $P < 0.05$. Data for 1973 from Dickinson (unpublished data). No young were found on Island 2 in 1973.

OVERWINTERED MICE

Length	Green '73	Is. 2 '76	Green '78	Is. 2 '73	Is. 2 '78	Green '77
N	19	9	11	15	15	6
$\bar{X}$	85.0	87.7	88.4	89.6	93.5	93.7

Weight	Green '78	Is. 2 '78	Green '73	Is. 2 '76	Green '77	Is. 2 '73
N	11	15	19	9	6	15
$\bar{X}$	17.5	19.3	20.0	20.1	20.8	22.3

YOUNG MICE

Length	Green '73	Is. 2 '76	Green '78	Is. 2 '78	Green '77
N	12	14	40	66	18
$\bar{X}$	76.9	79.7	80.0	82.4	82.4

Weight	Green '78	Is. 2 '78	Green '73	Green '77	Is. 2 '76
N	40	66	12	18	14
$\bar{X}$	13.6	13.8	14.3	15.2	15.6

Table 5. Numbers of young male and female *P. maniculatus* entering the trappable population. (Tested by 2 x 2, 3, 5 or 6 χ^2).

		1977		1978	
	Rota	M	F	M	F
Island 2	1	25	28	0	1
	2	2	3	7	4
	3	10	9	4	10
	4	8	7	10	16
	5	4	2	9	7
	6			4	10
	Σ	49	49	34	48
2 x 5 or 6 χ^2		1.16		8.60	
	Sig.	NS		NS	
Green Is.	1	0	1	3	3
	2	5	6	1	3
	3	10	7	6	1
	4			14	9
	5			4	10
	Σ	15	14	28	26
2 x 3 or 5 χ^2		1.62		8.23	
	Sig.	NS		NS	

Table 6. Dispersion of centers of activity for P. *maniculatus*. Animals with single appearances excluded. (U = uniform, R = random, A = aggregated)

		1977					1978					
	Rota:	1	2	3	4	5	1	2	3	4	5	6
Island 2	Mature Male		U	R	U		U	U	U	U	U	
	Female	R	R	R	R		R	R	U	U	U	
	Immature Male	R	R	U	U	U		R	U	R	R	
	Female	R	U	R	R	U			R	R	R	
Green Is.	Immature Male					R			R	R		
	Female					R		U	U	U		

Table 7. Adjusted range length (m) for P. maniculatus having four or more captures.

			Overwintered X̄±S.E. (N)	Young X̄±S.E. (N)
Island 2	Male	1977	225±20.4 (4)*	130±10.1 (35)
		1978	171+20.5 (9)**	136±13.6 (21)
	Female	1977	119±20.3 (7)	121± 6.8 (41)
		1978	123± 8.9 (17)	127± 9.7 (32)
Green Is.	Male	1977	(0)	106±17.2 (7)
		1978	169±28.7 (5)	134±12.7 (16)
	Female	1977	114±14.0 (2)	104±19.1 (7)
		1978	157±14.5 (6)	129±11.9 (16)

*significantly different from females and from young ($P < 0.01$).

**significantly different from females ($P < 0.02$).

Table 8. Analysis of variance of Adjusted Range Length by sex, year, age and island in <u>Peromyscus maniculatus</u>.

Source of Variation	Sum of Squares	DF	Mean Square	F	Significance of F
Main Effects	52744.930	4	13186.230	1.741	0.142
Sex	41557.414	1	41557.414	5.487	0.020
Year	74.293	1	74.293	0.010	0.921
Age	11889.406	1	11889.406	1.507	0.212
Island	2763.054	1	2763.054	0.365	0.547
Explained	100679.000	14	7191.355	0.949	0.507
Residual	1590600.000	210	7574.285		

No higher level interactions were significant.

Table 9. Proportion of August samples of P. *maniculatus* showing one or more recent wounds.

			Mature	Immature
			Proportion (N)	Proportion (N)
Island 2	1976	Female	0.00 (3)	0.00 (7)
		Male	0.00 (3)	0.00 (10)
	1978	Female	0.33 (6)	0.03 (40)
		Male	0.14 (7)	0.00 (28)
Green Is.	1977	Female	0.33 (3)	0.13 (8)
		Male	0.67 (3)	0.10 (10)
	1978	Female	0.00 (6)	0.23 (22)
		Male	0.17 (6)	0.06 (17)

Table 10. Mean number of P. maniculatus captures per trap per rota. Deer mice were at risk of capture five times per rota.

	Island 2		Green Is.	
Rota	1977	1978	1977	1978
1	1.33	1.31	0.03	0.29
2	1.86	1.52		0.34
3	2.34	1.76	0.56	0.90
4	2.68	2.18		1.73
5	2.48	2.85	1.36	1.77

Table 11. Number of times at risk of capture needed to recapture a deer mouse. Count of number of times at risk begins with first day of rota following capture and continues, spanning rotas if necessary until the mouse is recaptured. Mice were vulnerable to capture 5 times per rota or once per day. Data for P. *maniculatus* on Island 2 in 1977.

Recovery after Rota No.	No. of Times at Risk of Capture Needed for Individual Recovery			
	range	mean	S.E.	N
1	1-12	2.44	0.27	59
2	1-12	2.05	0.29	55
3	1-5	1.82	0.14	65
4	1-7	1.72	0.12	67

Figure 1. Minimum number of <u>Peromyscus</u> <u>maniculatus</u> known to be alive.

● Total Population

○ Overwintered Population

Statistics for prediction equations based on exponential model.

$\ln(N_t) = \ln(N_o) + bx$ where t_o = June 1 and x is in days.

Island	Year	Population	Constant	Slope±S.E.	r^2	P
2	1977	Total	ln(59.53)	0.004±0.002	0.54	NS
		Overwintered	ln(10.07)	-0.001±0.002	0.03	NS
	1978	Total	ln(21.76)	0.016±0.002	0.97	<0.05
		Overwintered	ln(33.50)	-0.012±0.001	0.98	<0.05
Green	1978	Total	ln(5.62)	0.029±0.004	0.95	<0.05

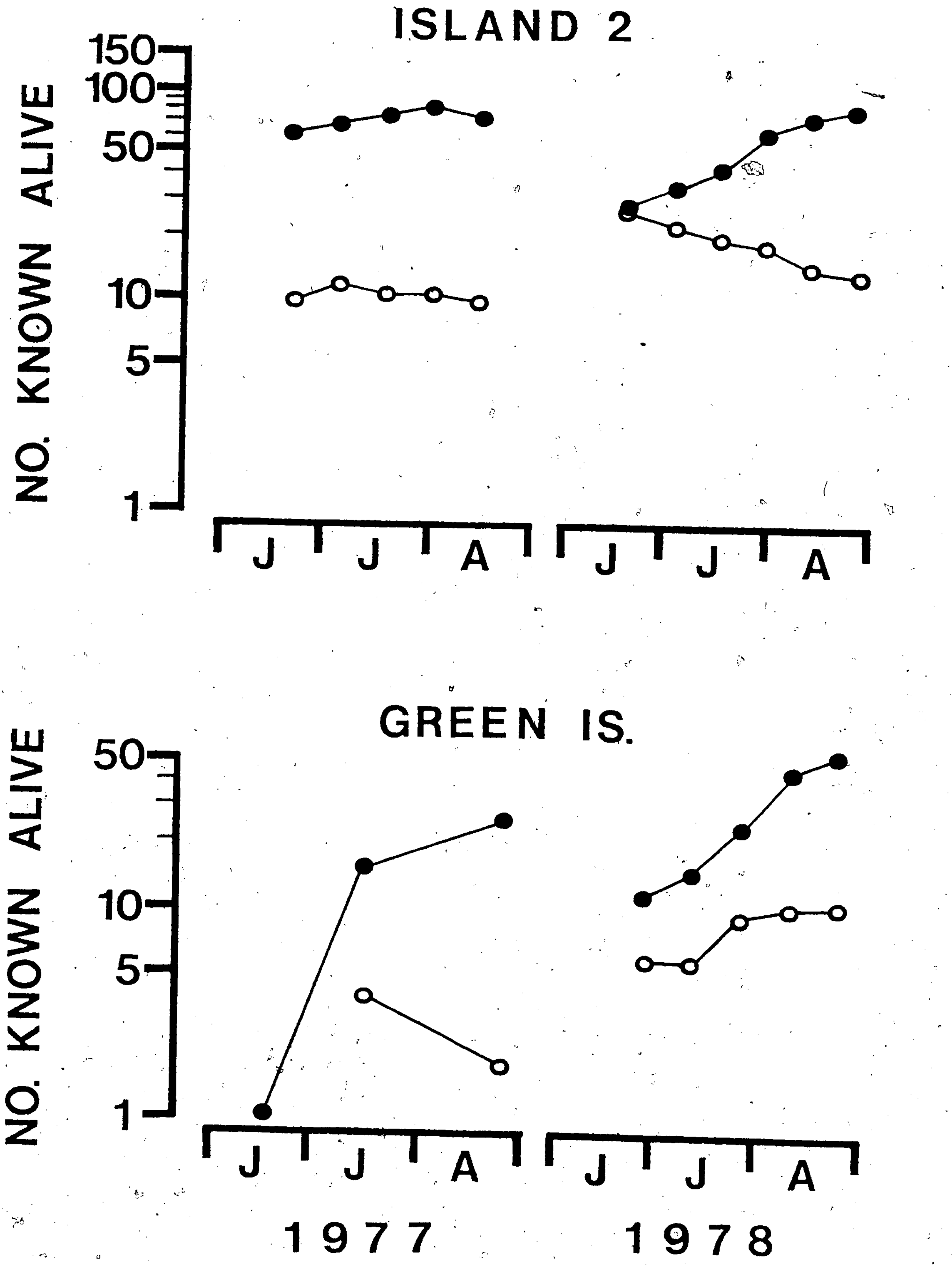

ISLAND 2
150
100
50
10
5
1
NO. KNOWN ALIVE
J
J
A
J
J
A
GREEN IS.
50
10
5
1
NO. KNOWN ALIVE
J
J
A
J
J
A
1977
1978

Figure 2. Survival from previous rota and number of young *P. maniculatus* entering the trappable population. Dashed line is the 14-day equivalent of Krebs' monthly 0.707 used to separate "high" and "low" rates of survival.

● 1977 ○ 1978

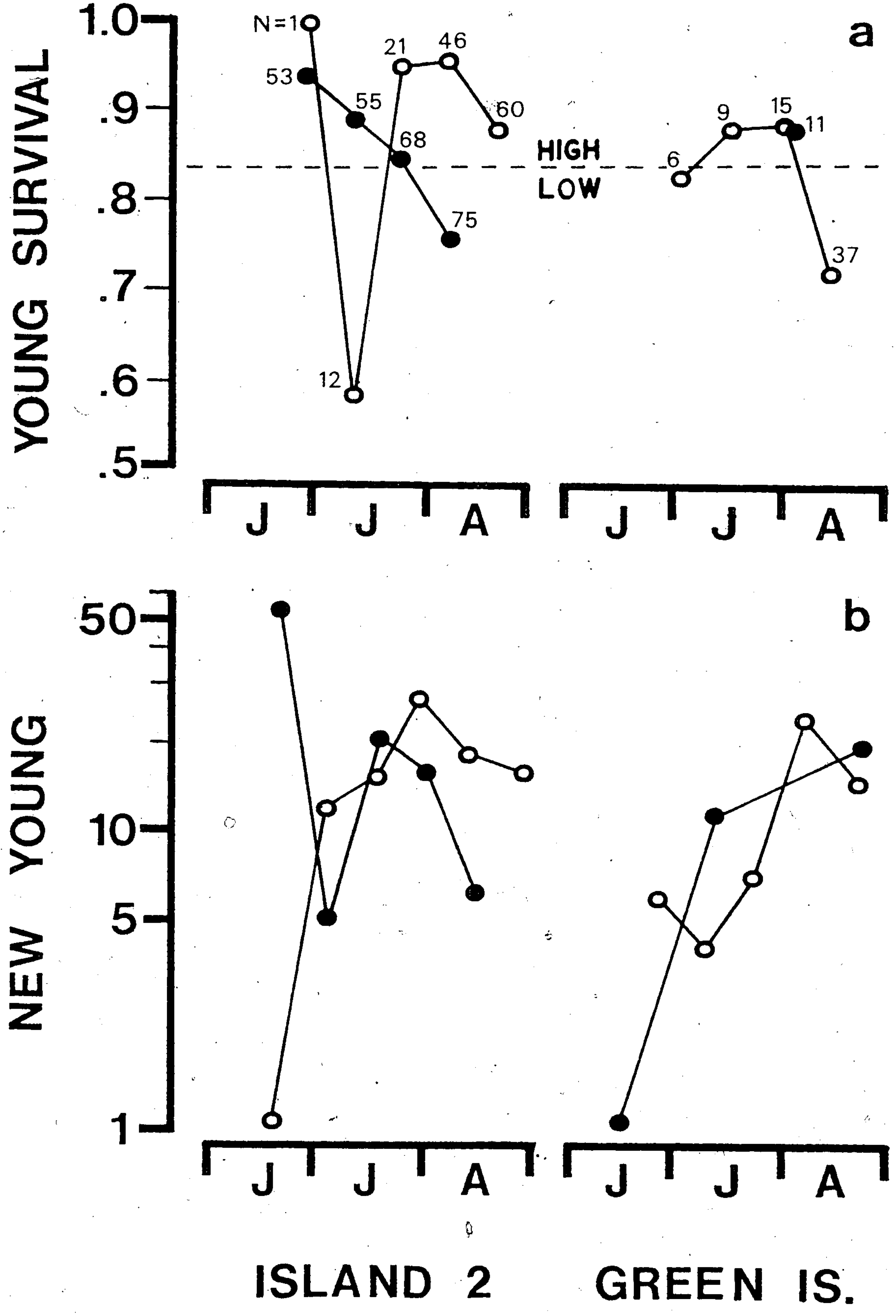
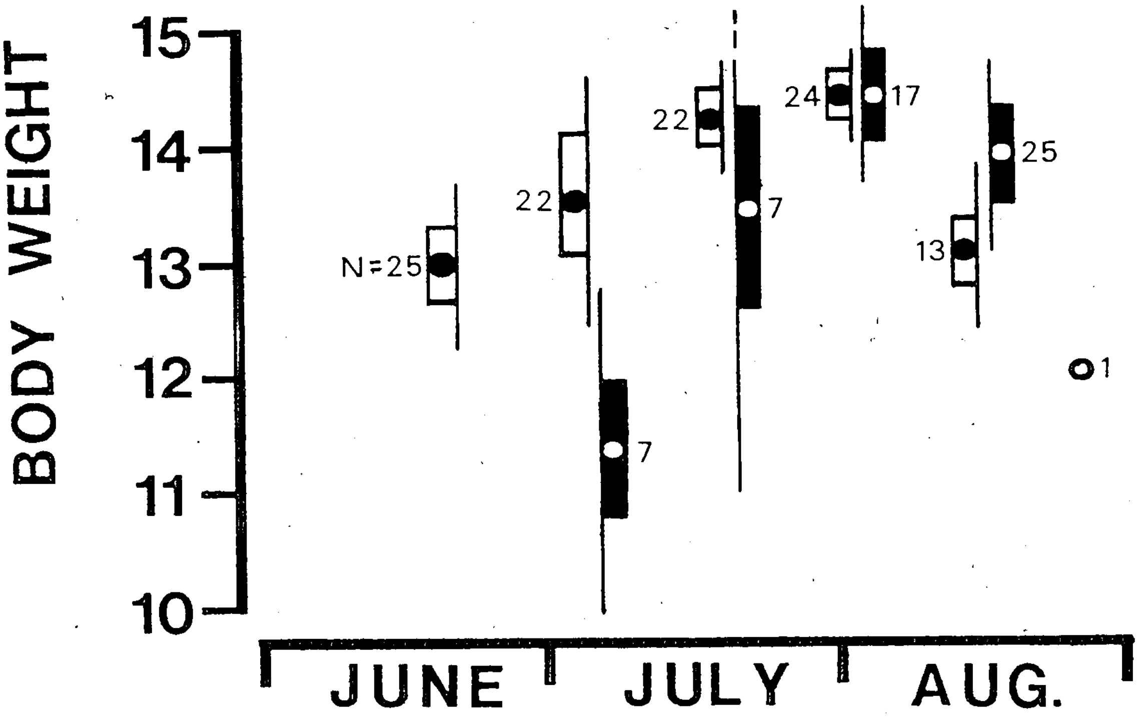
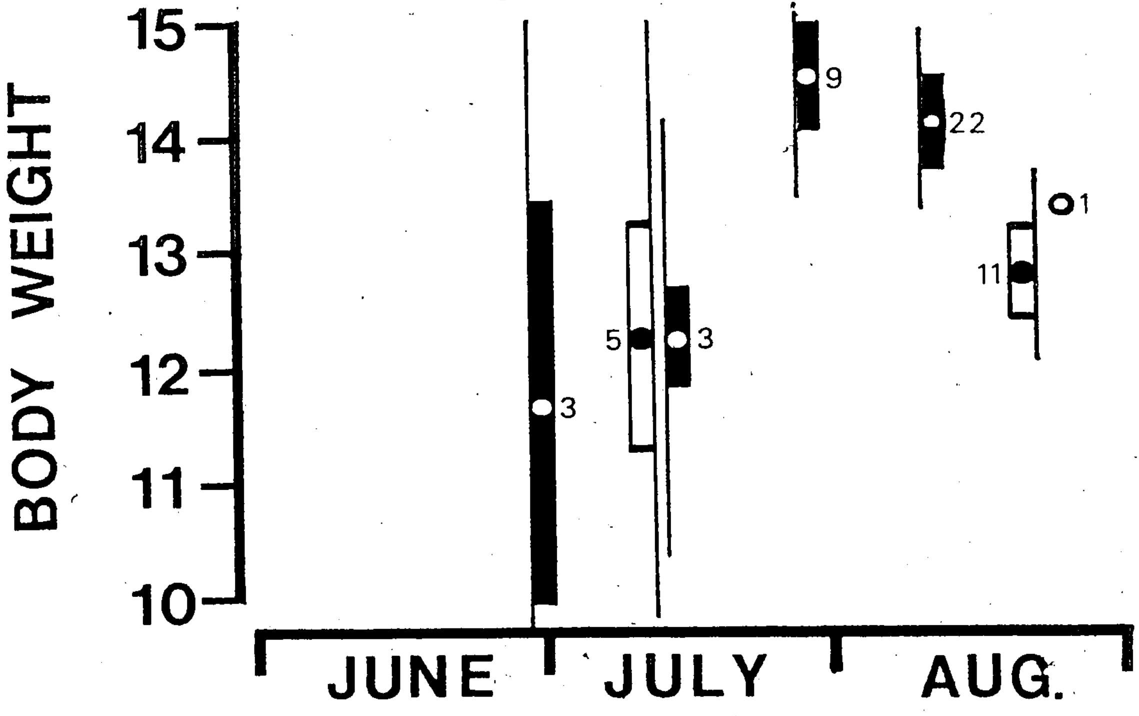

a
YOUNG SURVIVAL
1.0
.9
.8
.7
.6
.5
N=1
53
55
12
21
46
68
60
75
HIGH
LOW
6
9
15
11
37
J
J
A
J
J
A
b
NEW YOUNG
50
10
5
1
J
J
A
J
J
A
ISLAND 2
GREEN IS.

Figure 3. Mean weight (g) of immature young male *P. maniculatus*. (± 1 S.E. (bar), 95% C.I. (line))

● 1977 ○ 1978



ISLAND 2



GREEN IS.

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Paper 3

Habitat and Spatial Variation in Densities of Small Mammals

Abstract

In July of 1978, a vegetation analysis was carried out on two islands in the Mackenzie River on which I had observed different densities of two species of small mammal. Three major habitat types were identified by multivariate statistical methods. Distributions of measured habitat characteristics and habitat types were compared with distributions of Clethrionomys rutilus and Peromyscus maniculatus captures.

Cover in the form of logs appeared to have some importance for Peromyscus distribution and groups of water-associated plants suggested some significance of moisture for Clethrionomys distribution but there was no correlation between abundance of known food plants and animal distribution.

Two of the major habitat types were poorly represented on Green Island but were well represented on Island 2. Given that both voles and mice showed preference for those two types of habitat, it was not surprising that Green Island had lower overall densities of both mammal species than Island 2. The third habitat type, common to both islands, harbored fewer animals on Green Island than Island 2 and this difference is without explanation.

Introduction

Annual peak densities reached by island populations of <u>C</u>. <u>rutilus</u> and <u>P</u>. <u>maniculatus</u> were observed to vary between islands (Burns 1979a,b). This begs the question - can habitat differences account for the spatial variation in density?

Habitat can be examined in terms of the food resources and cover it provides and the competitors and predators it supports. Lack (1954) considered food shortage to be a significant source of rodent mortality. Fluctuations in overwintering weight and the size of spring populations of <u>Microtus</u> <u>oeconomus</u> were associated by Tast (1972) with variations from winter to winter in abundance of the main diet item. Getz (1969), Goszczynski (1970), Miller and Getz (1977) and Flowerdew <u>et</u> <u>al</u>. (1977) provided evidence for habitat selection by small mammals on the basis of food selection and need for, or avoidance of, water.

I studied habitat characteristics of two islands. Green Island (30.6 ha) is covered by white spruce (<u>Picea</u> <u>glauca</u>) with some patches of black spruce (<u>P</u>. <u>mariana</u>) and scattered white birch (<u>Betula</u> <u>papyrifera</u>), trembling aspen (<u>Populus</u> <u>tremuloides</u>) and willow (<u>Salix</u> spp.). Island 2 (7.7 ha) is dominated by white spruce, has significant portions covered by black spruce and trembling aspen and a scattering of white birch and willow. Upstream ends of both islands show the strong influence of ice action at spring break-up. The east side of Green Island consists of a 5 m high vertical mud bank whereas the west shoreline is rocky and slumping. Island 2 has an average height of 2 - 3 m. Its upstream end is pushed up to 4 m by ice and its downstream end tapers first to marsh and then to submerged sandbars. The islands are separated by a distance of 12 km, and are subject to the same macroclimatic regime. Both islands have escaped fire and other disturbance for long enough to develop a typical climax vegetation in contrast to nearby islands covered by aspen that are in earlier seral stages.

Burns (1979a,b) dealt with temporal variations in _Clethrionomys_ _rutilus_ and _Peromyscus_ _maniculatus_ populations on islands. In the present paper, the spatial variations of these populations are examined. The spatial pattern of captures (Burns 1979a,b) is compared with distributions of habitat variables for food and cover and of captures of "competitor" species.

Methods

Grid points established on two islands in small mammal capture-mark-release studies (Burns 1979a,b) were used as sampling points for a vegetation survey in July 1978. This provided 103 sample points on Island 2 and 100 on Green Island although only 64 sites on Green Island were used in 1977 for live trapping. At each sample site, vegetation was examined in a circle of 1 m radius. Vascular plants were identified according to Moss (1959). Stem counts were used for vascular plant species, but an estimate of per cent cover was applied to leaf litter, <u>Cladonia</u> spp., <u>Peltigera</u> spp., <u>Sphagnum</u> spp. and "other mosses". Also recorded in each sample area was the mean diameter at breast height (DBH.) of all trees (species combined), the number of logs larger than 2 cm in diameter and ~~the~~ distance to, and the species of, the nearest tree. Records for species of plants appearing at fewer than three sample sites were deleted before data were analyzed.

I used the data to answer four questions: (1). Is the habitat on Green Island different from that on Island 2? (2). Which habitat variables influence the distribution of animals as reflected by the distribution of captures? (3). Do groups of habitat variables or habitat types correlate with animal captures? (4). Do capture distributions show correlations between years or between species and thereby demonstrate the significance of habitat to animal distribution? (If certain habitat variables are important to vole or mouse distribution patterns, the patterns should be similar from year to year and be positively correlated. If certain habitat variables distinguish niche boundaries for sympatric rodents and these habitat variables are not uniformly distributed, then capture distributions of the sympatric species should be negatively correlated.) A computer program for vegetation analysis designed to compute a "plots by species matrix, principal ordination axes and vegetation groupings" (written by Brian Pinchbeck, Computing Services, University of Alberta) was used in treating questions 1 to 3.

The computer program takes the raw data (matrix of sample sites x habitat variables), does a factor analysis (matrix of habitat variables x factors), calculates and plots ratings of the factors for each sample point (matrix of sample sites x factors) and then uses Ward's Discrete Classification (Ward 1963) to merge similar sample points into groups of sample points representing habitat types. As the merging process proceeds, similarity of groups of points being merged declines. The experimenter determines the number of habitat types by stopping the merging process before two very dissimilar groups are brought together.

Results

Plant species found on Island 2 and Green Island are listed in Table 1. Juniperus communis (Pinaceae), Larix laricina (Pinaceae), Mitella nuda (Saxifragaceae), Ribes hirtellum (Saxifragaceae) and Oxycoccus microcarpus (Ericaceae) were found at one or two sites only, do not appear in Table 1 and were dropped from data analysis.

On Island 2, captures of C. rutilus were associated with Picea mariana and Larix laricina in both years. Captures were also strongly associated with Betula papyrifera, Salix spp. and Picea glauca in 1977 but only weakly in 1978 when population density declined (Table 2). Captures of P. maniculatus were associated about equally with Picea glauca, Populus tremuloides and Betula papyrifera. Results for both rodent species on Green Island, probably affected by small sample sizes for some trees, showed no consistency between years nor with Island 2.

The frequency of tree species closest to grid intersections was significantly ($P < 0.01$, χ^2 test) different between grids. The predominance of Picea glauca at the expense of other tree species on Green Island caused this difference. The number of trees per site (all species combined) was used as an index of canopy cover. Clethrionomys showed significant ($P < 0.002$) positive correlation with canopy cover in all samples except on Green Island in 1977. Peromyscus showed significant ($P < 0.02$) negative correlation with canopy cover in all samples except on Green Island in 1977.

A general comparison of habitat between islands by Hotelling's T^2 test showed no significant difference ($T^2 = 266.30$, $P = 0.746$). Failure to demonstrate a difference between between islands may have been caused by the large number of zeros in the habitat data. Although the assumption that plants are normally distributed is questionable if not unlikely, the probability that the null hypothesis is true is too high to question its acceptance.

The strength of relationship between habitat variables and rates of capture was investigated in a stepwise multiple regression. Table 3 shows the first habitat variable to enter each regression against captures per site. *C. rutilus* captures correlated best with a different variable each year on each island: *Picea mariana*, *Sphagnum* spp., *Betula* and DBH., but *P. maniculatus* captures correlated best with numbers of logs on Island 2 and with *Viburnum edule* on Green Island in both years. These habitat variables explained 4 to 21% of variance in captures. Regressions were repeated using all grid points and including captures of the "competing" species as an additional habitat variable. The added captures variable displaced a habitat variable as first variable to enter a regression in three out of four cases in 1977. With both *Clethrionomys* and *Peromyscus* exhibiting high densities on Island 2, the interaction of competitors explained 52% ($r = -0.72$) of variance in captures. The correlation coefficient was positive for *C.*

rutilus on Green Island in 1977 suggesting a lack of competition among the two cricetid species under conditions of low density. Habitat was secondary to competition in importance to capture distributions of populations with high densities. Regressions were repeated again using data from grid points where there were fewer than four captures in either year or more than 20 captures in either year. This was done in an attempt to clarify both the positive amd negative relationships between habitat variables and captures. In only three cases did the first variable entering the new regressions explain more than 20% of capture variance. Forty per cent of capture variance in P. maniculatus in 1977 on Island 2 and 56% of capture variance in the same species in 1978 on Island 2 was explained by distributions of Shepherdia (r = -0.63) and Salix spp. (r = -0.75) respectively when grid points with more than 20 captures were used. The distribution of Pyrola spp. (r = 0.81) explained 65% of P. maniculatus capture variance on Island 2 in 1978 when grid points with fewer than four captures were used. There was no clarification of relationships between captures and habitat for Clethrionomys generally and for Peromyscus on Green Island.

Habitat variables such as number of logs, DBH., Equisetum scirpoides, Picea glauca, Salix, Betula, Fragaria, Empetrum, Cornus canadensis, Galium, Linnaea and Viburnum, chosen as good predictors of captures by multiple regression, were not predicted intuitively. For each of those variables, data for grid points having a zero count for the habitat variable were deleted and a linear regression was done. No line was significant. Sites with and without logs were compared for captures. Clethrionomys and Green Island Peromyscus attached no importance to the presence of logs. Island 2 Peromyscus in both years showed significantly ($P < 0.05$) more captures at trap sites with logs than those without logs.

Factor analysis of habitat variables and capture rates, showed that both the plants and the animals were responding to some of these factors. These factors represent a combination of biologically-meaningful variables but unfortunately the identity of variables represented in a factor is not always obvious. Along the factor 1 axis, cover by leaf litter (largely aspen leaves), numbers of logs and numbers of Rosa plants had high positive eigenvalues and cover by Cladonia, numbers of Ledum groenlandicum plants and numbers of Rubus chamaemorus plants had low negative eigenvalues suggesting that factor 1 represents a moisture gradient. The arrangement of habitat variables along the other factor axes did not suggest a single physical or biological interpretation for those factors. Factors 1 and 3 separated captures of Clethrionomys and Peromyscus.

Five habitat groupings or types emerged from analysis of data from both grids combined (Fig. 1). Three points marked "4" or "5" did not closely resemble any of the three major habitat types and were dropped from further consideration. Habitat Type 1 may be described as open Picea glauca - moss forest, Type 2 as mature Populus - Rosa forest and Type 3 as Picea mariana bog. Types 2 and 3 are more common on the Island 2 grid than on the Green Island grid. Preference shown on Island 2 by Clethrionomys for Type 3 and by Peromyscus for Type 2 habitat (Table 4, Fig. 1 - 3) may partly explain the lower capture rates of both species on Green Island than on Island 2 (Tables 2 and 4). While preferences for habitat types were clearly expressed on Island 2, captures on Green Island appeared to be randomly associated with habitat types (Table 5). The low densities of both rodent species on Green Island and a need for high density for habitat selection to be expressed or simply the low number of trap sites classified as Habitat Types 2 or 3 may explain the random association of captures and habitat type on Green Island. Habitat Type 1, used randomly by both Peromyscus and Clethrionomys, had higher numbers of captures on Island 2 than Green Island for both species in both years (Tables 4 and 6). Habitat Type 3, preferred by Clethrionomys, showed higher capture rates of voles on Island 2 in 1977 than on the same island in 1978 and on Green Island in both years.

Grid points from both grids were plotted with respect to the first three factors (Fig. 4). Island 2 exhibited extremes along each axis and thus the outline of Green Island grid points was largely included inside the outline of Island 2 points.

Examination of capture distribution can indicate the degree of importance of habitat to study species. Similar capture distributions from year to year suggest that the animals exhibit some form of habitat selection. Strong negative correlations between captures of sympatric species suggest segregation of habitat between species. *Peromyscus* and *Clethrionomys* on both islands showed strong correlations ($0.001 < P < 0.02$) of preference for trap sites between years (Table 7). Habitat did not act as the primary influence over capture distribution, however, habitat was important in separating distributions of *Clethrionomys* and *Peromyscus* on Island 2 in 1977 and 1978 because ranks of sites showed a significant ($P < 0.001$) negative relationship between species. Generally lower densities of animals on Green Island than on Island 2 and the scarcity of the favored habitats (Types 2 and 3), which contributed at least in part to the lower overall densities of animals on Green Island, may account for the evident lack of differences in site preferences between the two rodent species on Green Island.

Discussion

Two aspects of this comparison of habitat and the capture patterns of two rodent species are of interest. One is the failure to clearly demonstrate an association of capture rates with any measured habitat characteristic. The second is the observation of different capture rates on the two islands in the same type of habitat.

Vegetation has been interpreted in three ways with respect to small mammals. Plants can be seen as a source of food, as cover, or as an arena for definition of niche boundaries.

Seed- and fruit-producing plants such as _Geocaulon_, _Rosa_, _Rubus_, _Empetrum_, _Cornus_ and _Vaccinium_, contrary to expectation, did not appear in data analyses to be attractive food sources. As specimens of _Viburnum_ on Green Island were small and without flowers or fruit and as there were no indications that vegetative parts were being eaten, it is difficult to explain the positive correlation of deer mouse captures with _Viburnum_ distribution on that island.

Winter should be the time to find relationships between plants used for food and capture distribution. The critical nature of winter food was demonstrated by Tast and Kalela (1971) in their association of good _C. rutilus_ survival in winter with profuse flowering of plants in the preceeding summer. Whitney (1976) concluded that _C. rutilus_ has a broad niche and has variable habitat and food preference in the presence of _Microtus_ or _Peromyscus_. Dyke (1971) noted the ability of C. rutilus to survive on foods low in preference and nutritive value such as the vegetative parts of plants which are high in roughage and are available throughout the year. Peromyscus, while showing strong preference in late summer for fruits, reduces overwintering food restrictions by going into torpor (Stebbins 1971). Greater annual variation in fruit production than in overall production, as seen by Dyke (1971), would affect deer mice more than voles. Capture data for the present study come from only the summer months when non-selective consumers are eating the fruit crop of a diversity of plants and therefore it is not too surprising that analysis of capture distribution and plant distribution did not show strong correlations.

I deduced in two ways that food resources were of little significance in the demography and the distribution of captures in summer. First, habitat destruction was not apparent and animals appeared to be in good physical condition and therefore food limitation could not have brought about population limitation. The rodents of the present study were not seen to affect the continuous availability of food supply as Krebs et al. (1969) and Batzli and Pitelka (1970) found with Microtus. Populations did not crash as the consequence of habitat destruction, either with predation (Green Island) or without predation (Island 2) (Murdoch 1966). The second suggestion that food plays a minor role came at the start of the breeding season. Breeding was initiated at approximately the same time on Island 2 and Green Island in 1978 but in 1977 breeding began earlier on Island 2 than on Green Island. Assuming that plant growth began in spring at the same time on both islands, and that initiation of plant growth was a critical factor in the initiation of breeding, it is difficult to explain why breeding did not begin at the same time on both islands in 1977. Andrzejewski (1975) and Watts (1970) considered that the start and end of breeding were not related to food availability.

The pattern of captures showed little correlation with individual habitat components. Appearance of such positive correlates as Sphagnum and number of logs and such negative correlates as DBH. as good predictors of captures suggests a weak relationship with cover. This observation agrees with Dyke (1971) who found correlations between numbers of deer mice and frequency of fallen trees and between vole distribution and habitats with dense cover. Morris (1955), noting the wide omnivorous diets of rodents, decided that cover was a more critical aspect of habitat than foraging possibilities. A close association of vole distribution with ground cover and an increased correlation between distribution and cover in winter was noted by Kikkawa (1964) and West (1977).

Mixed habitats provide an opportunity to demonstrate niche segregation. Miller and Getz (1977) studying Peromyscus leucopus and Clethrionomys gapperi attributed their niche differentiation to food preference and behavioral avoidance of standing water by Peromyscus and the restriction of Clethrionomys to habitats with high water availability due to low kidney efficiency. No interspecific aggression was found. Getz (1969) and Goszczynski (1970) also noted the role of a moisture gradient in Clethrionomys distribution. The preferences of C. rutilus for bog habitat and of P. maniculatus for aspen forest seen in the present study are consistent with the observations of Getz and Goszczynski. Crowell and Pimm (1976) found displacements from habitats shared with competing rodent species as populations fluctuated. Trap sites were significantly different in terms of numbers of captures of Clethrionomys and Peromyscus on Island 2 where rodent densities were higher and availability of water on the island was more variable than on Green Island.

Given the different capture rates associated with each habitat type and the differing distributions of habitat types on the two grids, one would expect that capture rates would differ between grids. Such a difference was found but the capture rate associated with Habitat Type 1, found most commonly on both grids, also differed between islands. Captures of both species in Habitat Type 1 were significantly lower ($P < 0.01$) on Green Island than Island 2. Also, in Habitat Type 3, captures of Clethrionomys in 1977 were significantly lower ($P < 0.01$) on Green Island than Island 2.

My observations are in accord with Redfield's (1976) suggestion that natural selection ought to favor high density in populations living in small confined spaces as a hedge against extinction. Consistent with this idea are the uniform distribution of centers of activity on Island 2 (unfortunately sample sizes were insufficient for Green Island) and the lower rate of wounding among voles and deer mice on Island 2 than Green Island. Populations on Island 2 differed from those on Green Island in several demographic characteristics (Burns 1979a,b) but my data do not allow me to say whether demographic changes caused, or were caused by, differences in density.

While not knowing what habitat variables must be measured to gain some understanding of rodent distribution, the difference between capture rates in some habitat types indicates that the mathematical process of sorting habitat variables did have some meaning in relation to the way the animals perceive their habitat. Summer distribution of voles and deer mice depends primarily on physical characteristics of habitat such as moisture and cover and secondarily on habitat offering food resources. The importance of the food factor may be more evident in diverse habitats under conditions of high numbers and densities of competing species. These factors affect distribution of captures or animal density across continuous space. Differences in density between isolated populations, however, may also be related to enclosure size.

Table 1. Plants enumerated on Island 2 and Green Island. (Based on 103 sample sites on Island 2 and 100 sites on Green Island).

Family	Species	No. Sites Having Plant Island 2	 Green Is.
Equisetaceae	Equisetum arvense	20	0
Equisetaceae	Equisetum scirpoides	0	10
Pinaceae	Picea glauca	65	84
Pinaceae	Picea mariana	23	7
Gramineae	Calamagrostis canadensis	39	7
Salicaceae	Populus tremuloides	16	1
Betulaceae	Betula papyrifera	18	9
Santalaceae	Geocaulon lividum	66	95
Rosaceae	Fragaria virginiania	4	1
Rosaceae	Rosa acicularis	72	60
Rosaceae	Rubus chamaemorus	11	0
Leguminoseae	Lathyrus ochroleucus	10	0
Empetraceae	Empetrum nigrum	0	5
Elaeagnaceae	Shepherdia canadensis	13	0
Onagraceae	Epilobium angustifolium	22	2
Cornaceae	Cornus canadensis	43	16
Cornaceae	Cornus stolonifera	3	1
Pyrolaceae	Pyrola spp.	16	27
Ericaceae	Ledum groenlandicum	27	12
Ericaceae	Ledum palustre	20	4
Ericaceae	Vaccinium vitis-idaea	88	88
Rubiaceae	Galium boreale	3	0
Caprifoliaceae	Linnaea borealis	25	21
Caprifoliaceae	Viburnum edule	11	15
Peltigeraceae	Peltigera spp.	15	28
Cladoniaceae	Cladonia spp.	24	28
Sphagnaceae	Sphagnum spp.	5	1
	"other mosses"	87	98

Table 2. Differences in C. rutilus and P. maniculatus mean capture rates at vegetation sample sites classified by nearest tree species.

	No. of Sites with Nearest Tree sp.		Mean Captures Per Site			
			C. rutilus		P. maniculatus	
			1977	1978	1977	1978
Island 2						
Picea glauca	57		14.8	3.8	12.7	13.3
Picea mariana	22		22.3	10.9	5.9	3.7
Populus tremuloides	7		13.3	6.9	12.4	10.6
Betula papyrifera	13		16.9	7.0	10.5	10.7
Salix spp.	3		15.0	3.3	7.7	8.7
Larix laricina	1		16.0	16.0	1.0	0.0
Green Is.	1977	1978				
Picea glauca	57	86	2.8	2.7	2.0	5.2
Picea mariana	3	7	1.3	2.7	2.0	3.0
Betula papyrifera	1	2	1.0	0.0	1.0	3.5
Salix sp.	3	5	2.7	4.2	1.7	6.2

Table 3. First habitat variable (with r) entered into stepwise multiple regression against captures of _C_. _rutilus_ and _P_. _maniculatus_.

	Trapping		First Habitat Variable			
			Entered into Regression with r			
	Grid	Year	Habitat Variable		*Hab. Var.+"Competitor"	
C. rutilus	Island 2	1977	Picea mariana	+.35	Peromyscus	-.72
		1978	Sphagnum spp.	+.35	Sphagnum spp.	+.37
	Green Is.	1977	Betula papyrifera	+.20	Peromyscus	+.22
		1978	DBH.	-.32	DBH.	-.32
P. maniculatus	Island 2	1977	no. of logs	+.45	Clethrionomys	-.72
		1978	no. of logs	+.46	no. of logs	+.46
	Green Is.	1977	Viburnum edule	+.25	Viburnum edule	+.25
		1978	Viburnum edule	+.23	Viburnum edule	+.23

*number of captures of "competing" species treated as a habitat variable.

Table 4. Mean captures per site by habitat type for C. rutilus and P. maniculatus on Island 2 and Green Island.

			Mean and 95% Confidence Interval for Captures Per Site			
	Habitat Type	No. Sites Per Type	Clethrionomys		Peromyscus	
Island 2 1977	1	62	17.0	14.7-19.3	10.5	8.9-12.1
	2	21	11.8	8.7-14.9	14.7	11.9-17.5
	3	18	21.7	18.0-25.5	5.4	2.9- 8.0
1978	1	62	6.0	4.4- 7.5	10.5	8.5-12.5
	2	21	3.8	1.5- 6.1	16.7	13.4-19.9
	3	18	9.4	5.0-13.9	2.4	0.3- 4.5
Green Is. 1977	1	60	2.9	2.1- 3.6	2.0	1.5- 2.4
	2	1	0.0	----	0.0	----
	3	3	1.3	0 - 5.1	2.0	0 - 6.3
1978	1	92	2.7	1.9- 3.6	5.2	4.2- 6.2
	2	1	0.0	----	0.0	----
	3	6	2.8	0 - 5.8	3.5	0.6- 6.4

Table 5. Observed versus expected total number of captures of <u>Clethrionomys</u> <u>rutilus</u> and <u>Peromyscus</u> <u>maniculatus</u> by habitat type.

		Habitat	No. Sites	Total Number of Captures					
				Clethrionomys			Peromyscus		
		Type	Per Type	Observed	Expected	Use	Observed	Expected	Use
Island 2	1977	1	62	1057	1040.50	random	665	649.47	random
		2	21	247	352.42	avoid	295	219.98	prefer
		3	18	391	302.08	prefer	98	188.55	avoid
			$\Sigma=101$	$\Sigma=1695$		$\chi^2=58.0^*$	$\Sigma=1058$		$\chi^2=69.4^*$
	1978	1	62	369	379.98	random	674	639.64	random
		2	21	80	128.70	avoid	325	216.66	prefer
		3	18	170	110.32	prefer	43	185.70	avoid
			$\Sigma=101$	$\Sigma=619$		$\chi^2=51.0^*$	$\Sigma=1042$		$\chi^2=165.7^*$
Green Is.	1977	1	60	171	164.06	random	119	117.19	random
		2	1	0	2.74	random	0	1.95	random
		3	3	4	8.20	random	6	5.86	random
			$\Sigma=64$	$\Sigma=175$		$\chi^2=5.2^{**}$	$\Sigma=125$		$\chi^2=2.0^{**}$
	1978	1	92	249	249.98	random	475	454.42	random
		2	1	0	2.72	random	0	4.94	random
		3	6	20	16.30	random	14	29.64	avoid
			$\Sigma=99$	$\Sigma=269$		$\chi^2=3.6^{**}$	$\Sigma=489$		$\chi^2=14.1^*$

$^*P < 0.005$ **NS

Table 6. Level of significance of differences in mean number of captures per trap site by island and year in habitat types 1 and 3 (from Table 3). Clethrionomys in upper-right corner, Peromyscus in lower-left corner.

Habitat Type 1

		Island 2		Green Is.	
		1977	1978	1977	1978
Island 2	1977		P<.001	P<.001	P<.001
	1978	NS		P<.01	P<.01
Green Is.	1977	P<.001	P<.001		NS
	1978	P<.001	P<.001	P<.001	

Habitat Type 3

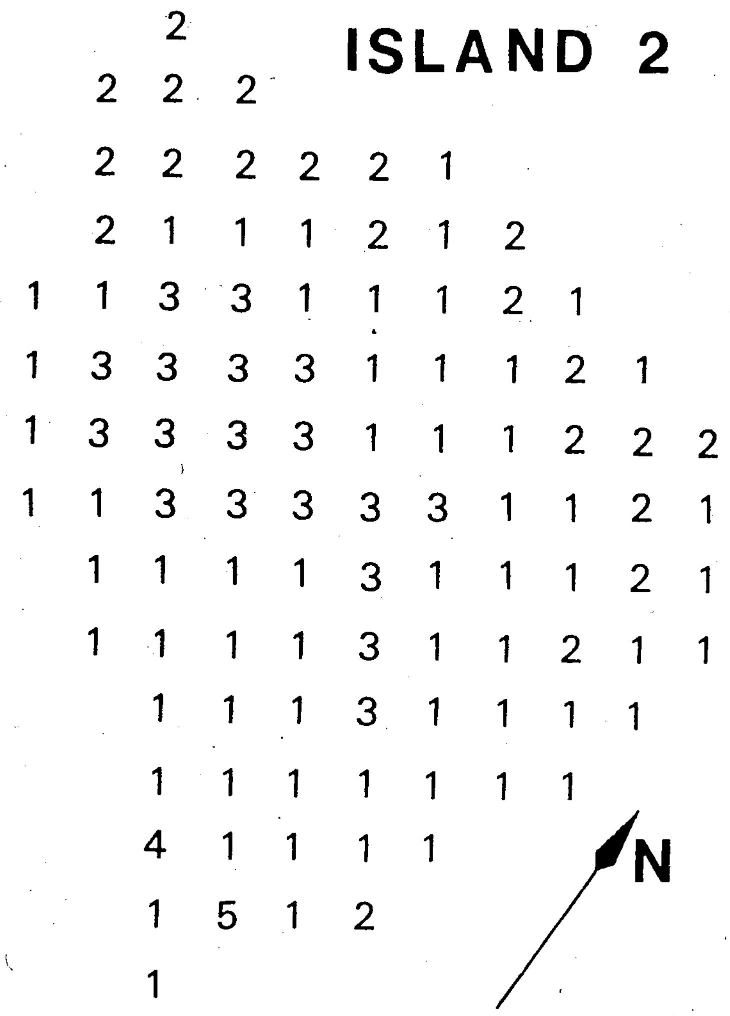
		Island 2		Green Is.	
		1977	1978	1977	1978
Island 2	1977		P<.01	P<.01	P<.01
	1978	NS		NS	NS
Green Is.	1977	NS	NS		NS
	1978	NS	NS	NS	

Table 7. Kendall Rank-order Correlation performed on capture distributions of *C. rutilus* and *P. maniculatus* on Island 2 and Green Island in 1977 and 1978.

	Captures$_1$		Captures$_2$	Tau	Significance
Island 2	Clethrionomys 1977	vs	Clethrionomys 1978	0.50	0.001
	Peromyscus 1977	vs	Peromyscus 1978	0.51	0.001
	Clethrionomys 1977	vs	Peromyscus 1977	-0.54	0.001
	Clethrionomys 1978	vs	Peromyscus 1978	-0.23	0.001
Green Is.	Clethrionomys 1977	vs	Clethrionomys 1978	0.47	0.001
	Peromyscus 1977	vs	Peromyscus 1978	0.20	0.020
	Clethrionomys 1977	vs	Peromyscus 1977	0.15	0.060
	Clethrionomys 1978	vs	Peromyscus 1978	-0.06	0.206

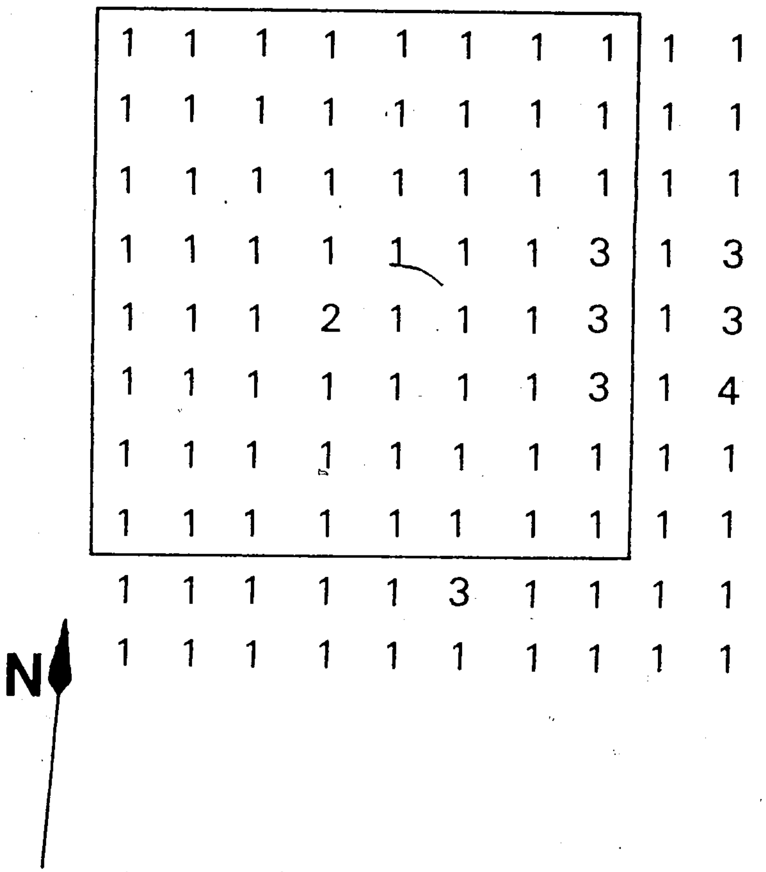
Figure 1. Distribution of habitat types on Island 2 and Green Island. (Box outlines Green Island grid of 1977).

ISLAND 2



		2								
	2	2	2							
	2	2	2	2	2	1				
	2	1	1	1	2	1	2			
1	1	3	3	1	1	1	2	1		
1	3	3	3	3	1	1	1	2	1	
1	3	3	3	3	1	1	1	2	2	2
1	1	3	3	3	3	3	1	1	2	1
	1	1	1	1	3	1	1	1	2	1
	1	1	1	1	3	1	1	2	1	1
		1	1	1	3	1	1	1	1	
		1	1	1	1	1	1	1		
		4	1	1	1	1				
		1	5	1	2					
		1								

GREEN IS.



1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	3	1	3
1	1	1	2	1	1	1	3	1	3
1	1	1	1	1	1	1	3	1	4
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	3	1	1	1	1
1	1	1	1	1	1	1	1	1	1

Figure 2. Distribution of captures of C. rutilus and P. maniculatus on Green Island in 1977 (left bar) and 1978 (right bar).

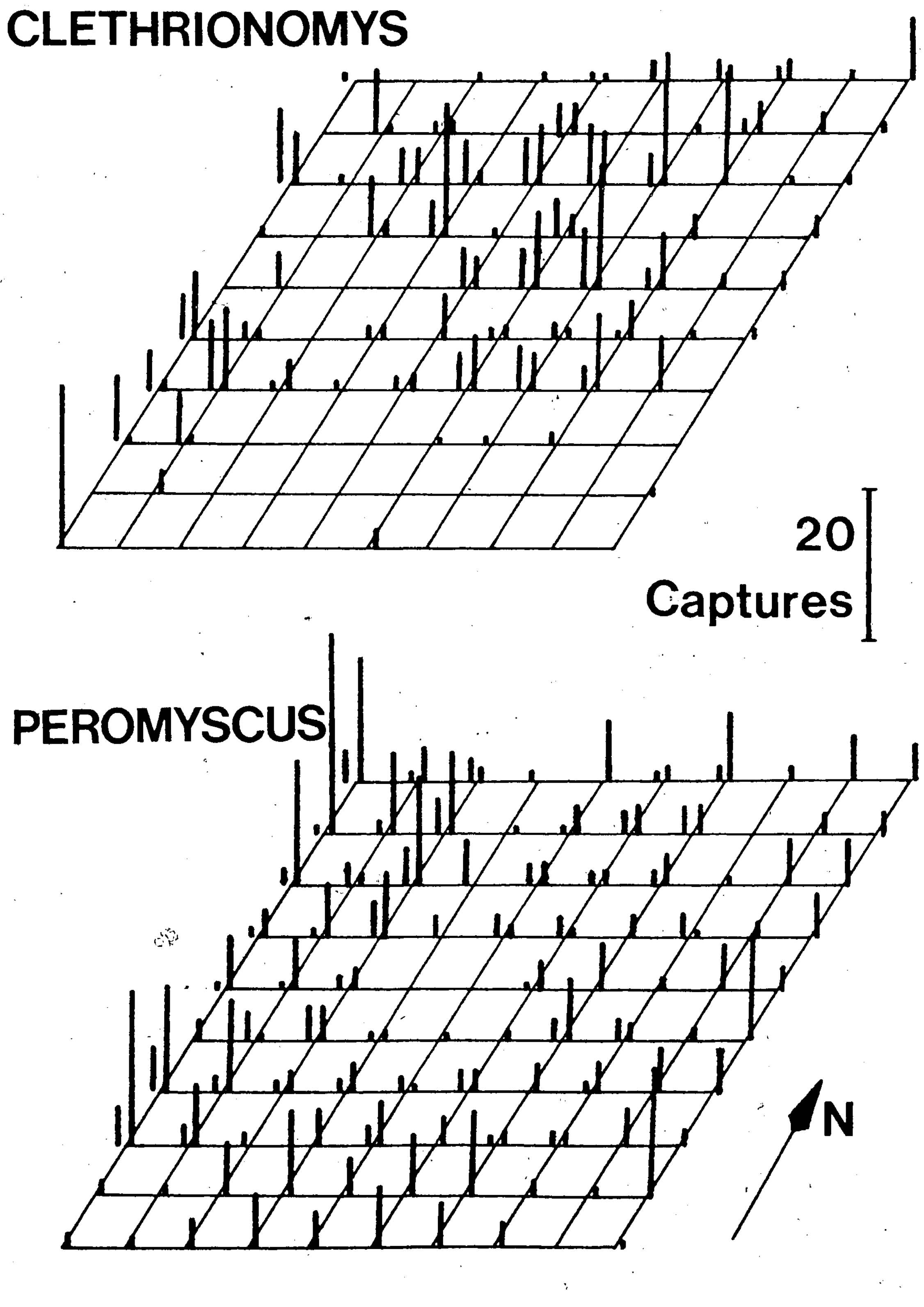

CLETHRIONOMYS
20 Captures
PEROMYSCUS
N

Figure 3. Distribution of captures of *C. rutilus* and *P. maniculatus* on Island 2 in 1977 (left bar) and 1978 (right bar).

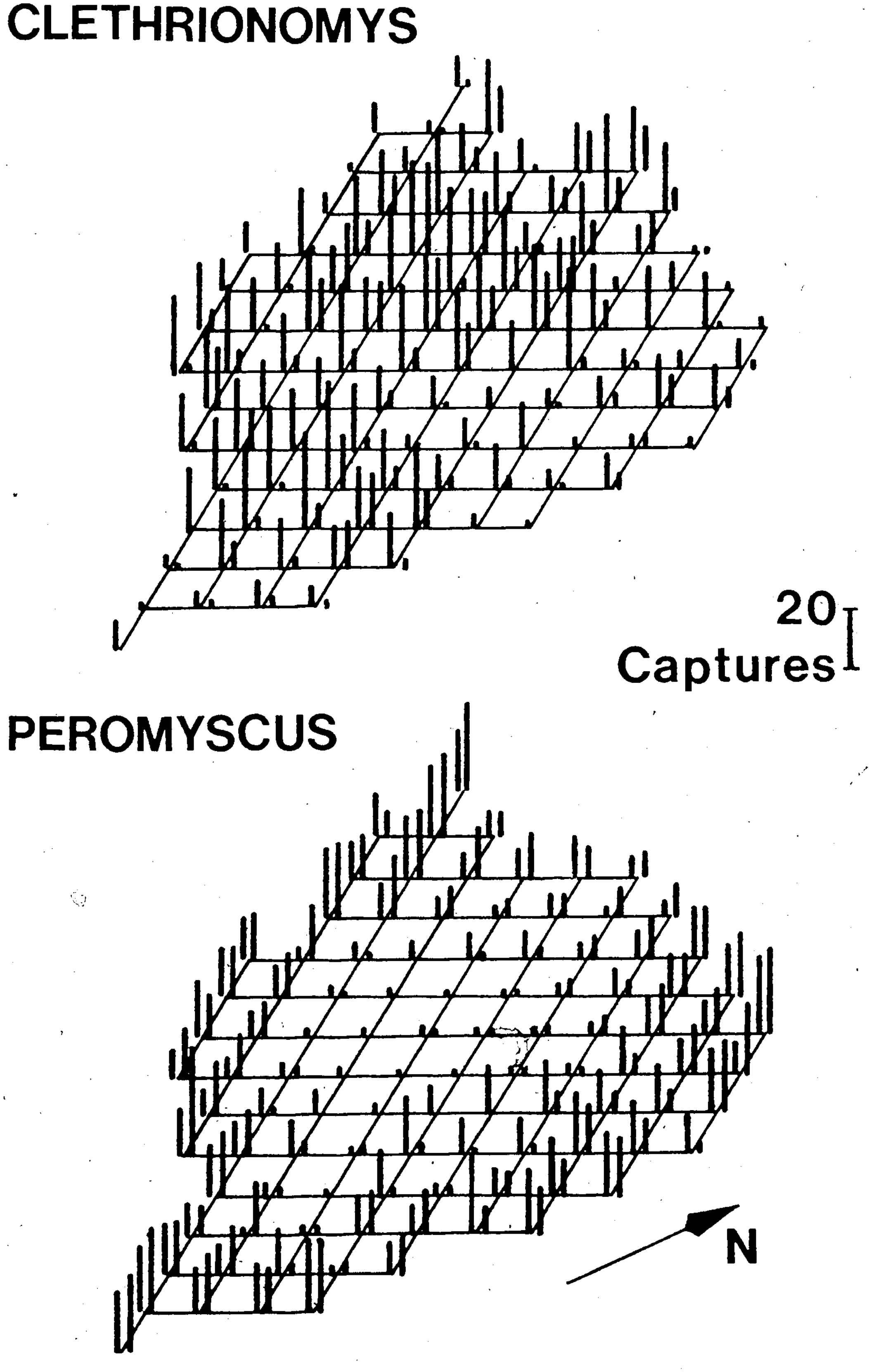
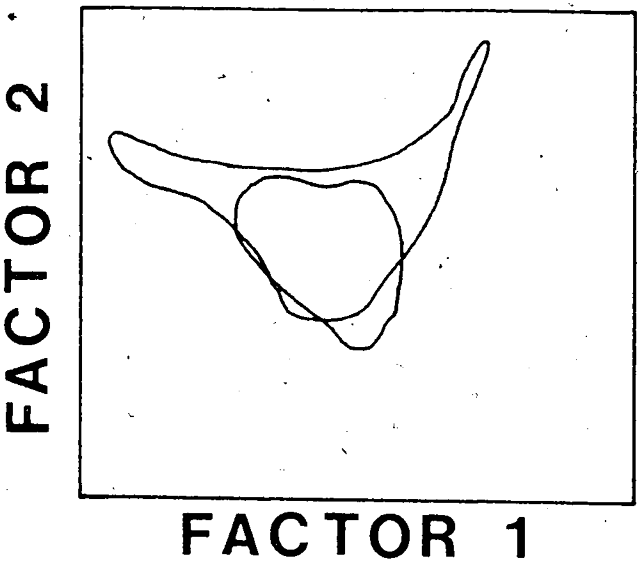
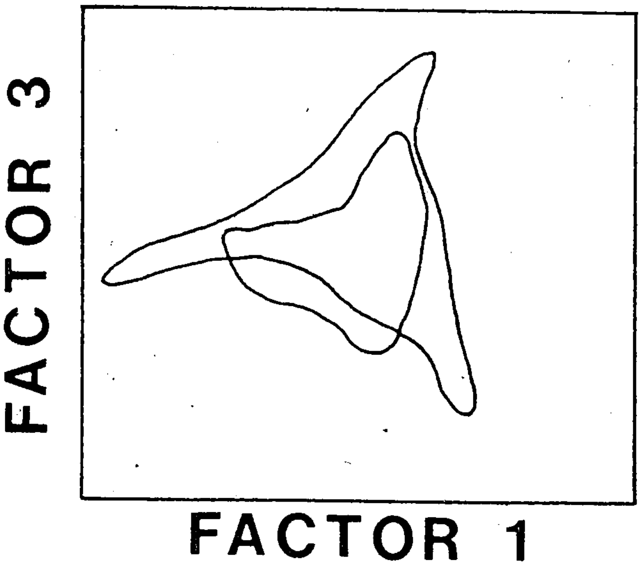
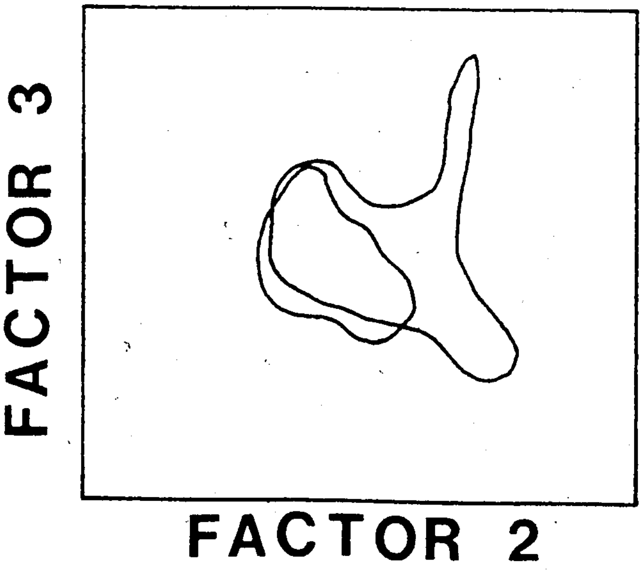

CLETHRIONOMYS
20
Captures
PEROMYSCUS
N

Figure 4. Comparison of distribution of plots of sample points on Green Island and Island 2 on axes rating factors at each point. (Sample points on Green Island outlined by smaller enclosure than Island 2 in all 3 cases).


FACTOR 2
FACTOR 1


FACTOR 3
FACTOR 1


FACTOR 3
FACTOR 2

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Appendix 1. Summary of vegetation data for Island 2 and Green Island. Enumeration was done by estimate of per cent cover (denoted by *) or by stem count at each sample site.

	ISLAND 2		GREEN ISLAND	
	$\bar{X}$	S. D.	$\bar{X}$	S. D.
No. of logs	3.5	2.64	4.0	3.28
Picea glauca	3.3	4.74	5.4	8.27
P. mariana	1.8	4.01	0.6	2.78
Betula papyrifera	0.3	0.70	0.1	0.37
Populus tremuloides	0.2	0.49	0.0	0.10
Salix spp.	0.1	0.69	0.4	1.35
Rosa acicularis	10.3	14.80	4.0	5.51
Ledum palustre	8.0	25.00	3.4	32.01
L. groenlandicum	8.8	21.01	2.7	13.29
Viburnum edule	0.7	3.37	0.8	3.27
Rubus chamaemorus	1.6	5.49	0.0	0.00
Shepherdia canadensis	0.3	1.15	0.0	0.00
Empetrum nigrum	0.0	0.00	4.8	27.28
Vaccinium vitis-idaea	217.6	201.73	248.8	223.57
Linnaea borealis	19.7	58.75	13.2	50.63
Cornus canadensis	13.0	29.18	1.8	6.36
Pyrola spp.	1.8	7.84	1.0	3.09
Lathyrus ochroleucus	0.3	1.22	0.0	0.00
Geocaulon lividum	8.3	12.47	22.2	17.61
Epilobium angustifolium	1.3	4.09	0.1	0.51
Fragaria virginiana	0.1	0.93	0.0	0.20
Calamagrostis canadensis	30.8	121.12	0.7	3.05
Equisetum arvense	0.7	2.27	0.0	0.00
E. scirpoides	0.0	0.00	0.6	2.16
Sphagnum spp.*	0.7	3.73	0.6	5.50
"other mosses"*	43.8	36.86	73.2	28.25
Cladonia spp.*	7.6	19.79	4.8	12.81
Peltigera spp.*	0.9	2.50	2.4	5.43
leaf litter*	46.9	40.66	19.1	25.22

DISCUSSION

The present study dealt with island populations of small mammals for which dispersal is not an option or is only an option of last resort. In the absence of a real dispersal option, higher relative densities have been found on these islands than on the adjacent mainland. Not only was there no evidence of destruction of the food base at high densities, but Peromyscus survived even after the attempt to harvest all berries on Island 1. Therefore these island populations must be limited in some way.

Factors limiting population size can be separated into two types - those that exert random control over numbers, and those that regulate density through negative feedbacks.

Weather may limit density through its effects on various demographic parameters, but it does not function in a regulatory manner. Lower temperatures hinder reproduction (Baker and Ranson 1932). Bergstedt (1965), working with C. glareolus, concluded that spring weather affected spring weight gain, entry of the first litter into the trappable population and the start of the breeding season. Differences in annual juvenile survival as well as duration of breeding of Peromyscus were attributed to yearly environmental variation by Sadleir (1974). Variations in the starting dates for breeding were noted by Whitney (1976) but not by Kalela (1957). In the location of the present study, there was variation between islands in the timing of the first litter in 1977 (this study) and 1973 (Dickinson 1976).

Factors such as epidemics, heavy parasite loads, competition and predation, all of which can act as nagative feedbacks, are not necessarily reliable methods of preventing overpopulation. In the present study, little or no disease was observed and very few internal parasites were found. Therefore, no difference in populations of different densities was found. It is unlikely that competitors (e.g. hares, squirrels, graminivorous birds) or predators (e.g. weasels, marten, hawks and owls) exerted differential effects on Island 2 compared with Green Island. It is possible that lynx on Island 3 during the winter may have exerted higher intensities of predation pressure on Clethrionomys on that island than elsewhere.

Food shortage is ultimately a reliable method of population regulation but it may result in extinction if starving animals destroy their food supply.

Negative feedbacks between density and some demographically-significant variables have been observed. Southwick (1955a) found that nestling mortality increased and natality decreased with increased density in populations of Mus. Sadleir (1965) associated reduced survival and recruitment with aggression by mature Peromyscus males initiated by high density. Petticrew and Sadleir (1974), also in deer mice, observed that breeding seasons were shortened and survival of young was reduced as density increased. Ryszkowski and Truszkowski (1970) found a significant drop in litter size in late summer probably related to age structure changes. Whitney (1976) noted low survival of C. rutilus males during population increases and peaks. Survival of young varied with the size of an island population (Bujalska 1975). Martell (1975) found no differences in survival of young in a fluctuating population of C. rutilus. Errington (1946) thought that heavy mortality of early young of muskrats was offset later by the extension of the breeding season and increased survival. Kalela (1957) observed high mortality of C. rufocanus during the breeding season and noted a negative relationship between juvenile maturation and the number of overwintered animals.

The breeding season for Peromyscus varied in its onset and the number of breeding females. Young appeared on Island 2 in 1977 earlier than on Green Island in 1977 or on the same island in 1978. The number of breeding females ranged from seven in 1977 to 21 in 1978 on Island 2 but on Green Island, density of breeding females did not vary between years.

Deer mice had a fixed breeding pattern. Overwintered females surviving through summer had two litters. There was no maturation of young mice. Litter size did not appear to vary and prenatal mortality was negligible.

Final densities of young were similar between years on the same grid but densities were lower on Green Island than Island 2. Density appeared to have been regulated. Variations in the breeding season, affected by such unpredictable factors as weather, cannot result in a negative feedback for population regulation. Fixed reproductive parameters cannot regulate density. Mortality among nestlings and juveniles, inversely related to adult density, may form a negative feedback to regulate density.

The breeding season for <u>Clethrionomys</u> varied in its onset and numbers of breeding animals. As with the deer mice, an earlier start of breeding was found on Island 2 in 1977. Density of breeding females did not differ between islands but did differ between years.

Overwintered voles exhibited the constant part of vole breeding patterns - all overwuntered voles matured and may have survived to produce three or four litters in the breeding season. The role of the young is variable - few young may mature at high population densities or all early-born young may mature and produce one or two litters at lower densities. Litter size showed no significant variation between islands or years and prenatal mortality was negligible.

August densities of young were variable. On Island 2, changes in numbers of young produced per year can be related to variations in the size of the breeding population. Similar densities of young voles were found in 1977 and 1978 on Green Island. Densities of voles were limited both through mortality and natality changes. As with the deer mice, nestling and juvenile mortality were inversely related to density. Maturation of young voles was also inversely related to density. Negative feedbacks for population regulation may be found in both maturation rates and mortality rates among nestlings and juveniles.

A number of interpretations can be given to the lack of correlation between any food item in the vegetation analysis and the distribution of captures of mice. The measures of plant abundance may be inadequate. Important food items may be geographically widely available. The mice may have wide feeding niches. The assessment of Beer (1961) that cover would be more important than food plants in winter may also be true in summer. That there were differences in capture rates between vegetation types on Island 2 was clear but the reasons for the differences were not clearly demonstrated. Cover, moisture and food availability may all be involved in habitat choice.

The island location for this project was one of its most interesting aspects. Two extinctions (one probably of human origin on Island 1 - cutline widening and snap trapping may have caused Clethrionomys extinction) and one colonization event were observed. Densities of animals found on the islands were consistent with prediction based on the Krebs effect. Island population densities exceeded those on the mainland and density on Island 2 exceeded that on Green Island. Dickinson (1976) noted higher island than mainland rodent densities as did Mazurkiewicz (1972). Mazurkiewicz also saw earlier annual population peaks on islands with respect to mainland populations. Without the option of dispersal or redistribution of surplus animals, populations on islands (particularly smaller islands) reach higher peak densities than those on mainland.

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