

THE UNIVERSITY OF MANITOBA

COMPARATIVE ECOLOGY OF INTRODUCED *CLETHRIONOMYS GAPPERI PROTEUS* (BANGS)  
AND NATIVE *MICROTUS PENNSYLVANICUS TERRAENOVAE* (BANGS) ON CAMEL ISLAND,  
NOTRE DAME BAY, NEWFOUNDLAND

by

LORNA ELIZABETH PAYNE

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## ABSTRACT

An introduced population of *Clethrionomys gapperi proteus* and a native population of *Microtus pennsylvanicus terraenovae* were studied from May 1969 to July 1971 on Camel Island, Notre Dame Bay, Newfoundland. Both genera were found in all available habitats (except burn which *Microtus* strongly avoided), although not all habitats were utilized to the same degree. In some instances *Microtus* and *Clethrionomys* were trapped at the same sites and were found to use the same runways.

Conventional home range concepts were found to be inadequate in analyzing movements of animals and were replaced by a movement index. A limited number of swimming experiments were performed, in which *Clethrionomys* compared favourably with *Microtus*.

Analyses of winter conditions in Notre Dame Bay indicate that the entire maritime winter in this region is a critical period for small mammals. A number of critical factors, their frequency of occurrence in the winters of 1969-70 and 1970-71, and their effect on the *Microtus* and *Clethrionomys* populations are examined.

The existence of competitive exclusion between *Microtus* and *Clethrionomys* is considered and, in terms of the data from Camel Island, it is concluded that differential dispersal and establishment abilities should be given more emphasis and competitive exclusion less in explaining the absence of *Clethrionomys* from Newfoundland and its



offshore islands.

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## INTRODUCTION

Islands, because of their geographic isolation, tend to have fewer species of plants and animals than do nearby mainland areas; among the species present on islands it is not unusual to find morphological and behavioural characteristics that are different from those of the mainland counterparts. The factors singled out as being responsible for these peculiarities, *i.e.*, isolation, space restriction, and special insular climates (Hesse, 1937), determine which species will cross water barriers and, once across, which will become established and which will become extinct on an island. Obviously the situation differs from island to island, and whether or not a species becomes established once it has crossed the water barrier must depend to a large extent on its ability to adapt to conditions prevailing on the island. The mode of interaction of the various extrinsic and intrinsic factors affecting insular colonizers is as yet largely theoretical, particularly with respect to small mammals.

The research reported here deals with an introduced population of *Clethrionomys gapperi proteus* and resident *Microtus pennsylvanicus terraenovae* on an island off the northeast coast of Newfoundland. *M. pennsylvanicus* is the only small microtine to have colonized successfully the main island of Newfoundland and many of the smaller offshore islands, a phenomenon which has aroused much speculative interest. In 1965

Cameron postulated that *Microtus*, as the first invader, set up a "beachhead," thus preventing *Clethrionomys* from successfully colonizing there. Furthermore, there are no islands off the coast of Great Britain, Denmark, or western Canada where both genera occur together in the absence of a third genus -- either *Peromyscus* or *Apodemus* (Cameron, 1965; Corbet, 1961; Grant, 1970). Cameron (1965) considered this to be evidence that *Clethrionomys* and *Microtus* exhibit ecological competition of considerable severity on islands where suitable habitat is at a premium, and that one can effectively exclude the other.

In 1966, Dr. W. O. Pruitt, Jr. introduced *C. gapperi* to Camel Island in an attempt to find answers to the following questions:

1. Do *Clethrionomys* and *Microtus* exhibit habitat segregation on Camel Island? (Camel Island lacks meadows.)
2. Do *Clethrionomys* establish typical home ranges and, if so, where? Is the size of the home range limited by the presence of *Microtus*?
3. How do *Clethrionomys* and *Microtus* compare in their reactions and/or adaptations to maritime Newfoundland winter conditions?
4. Do *Microtus* set up a "beachhead" as Cameron (1965) predicted? Do *Clethrionomys* and *Microtus* exhibit competitive exclusion on Camel Island and, if so, which genus excludes the other? On the basis of Cameron's (1965) "beachhead" hypothesis, *Microtus* should exclude *Clethrionomys*; on the basis of suitable habitat, *Clethrionomys* should exclude *Microtus*.
5. Grant's (1970) paper implied that *Microtus* and *Clethrionomys* should be unable to co-exist on a relatively small island in the absence of *Peromyscus* or *Apodemus*. Does this appear to be borne out?

This thesis presents the results of a 23-month study on the *Microtus pennsylvanicus* and *Clethrionomys gapperi* populations on Camel Island as related to the above questions.

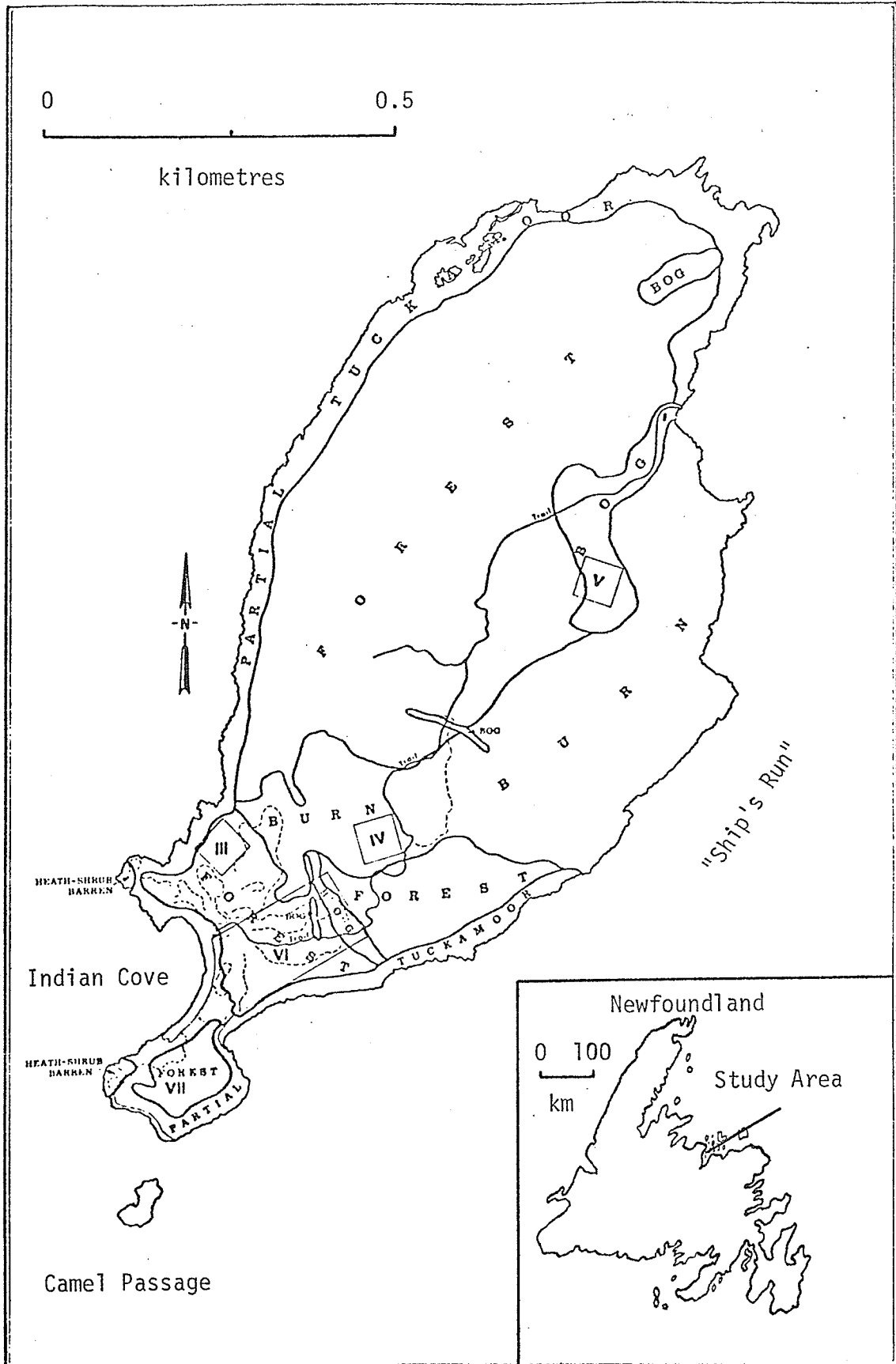
## STUDY AREA

### Location

A map of the study area is shown in Fig. 1. Camel Island, with an area of approximately 61 ha ranks as one of the medium-sized islands in Notre Dame Bay. It is separated from Sivier and Birchy islands by Camel Passage which is about 100 m at its deepest, and even on calm days exhibits a fairly strong current. The shortest distance across the passage is 1.2 km, from the southern tip of Camel Island to the eastern tip of Sivier Island. On the east, Camel Island is separated from the mainland (Comfort Cove Peninsula) by the "Ship's Run" which varies in depth from about 84 to 160 m and is 2.4 km wide at its narrowest point. Knights Island, to the north, is also 1.2 km distant, but here the sea is only about 44 m at its deepest and has numerous shoals, rocks (some of which protrude at low tide), and a small, rocky island. Although it is possible that small mammals could traverse the stretch of water between Knights Island and Camel Island, Knights Island itself is something of a dead end, being 1 km from the nearest small island and about 3 km from the nearest large island. The relative isolation of Camel Island was one of the primary factors in choosing it as a site for the introduction of *Clethrionomys gapperi*.

Besides being isolated, the island is very rugged; beaches are few and are composed of cobbles and boulders worked by the sea. Generally

Fig. 1. Map of the study area showing habitat types and location of plots (III-VII) and trap lines (----).





the shoreline consists of steep cliffs and jagged rocky outcrops (Fig. 2). There are two distinct types of bedrock; the west and northwest sides of the island are primarily mafic and intermediate volcanic rock, while the east and south sides are mainly shaly greywacke and conglomerate with some limestone or dolomite (Patrick, 1956). The highest elevation is 97.7 m above sea level, and there are four smaller hills whose elevations are unknown.

### Habitats

Camel Island has five basic habitat types as defined by the growth-form of the dominant vegetation.<sup>1</sup> With the exception of the description of burn habitat, the following are from Riewe (1971):

1. Spruce-fir forest (Fig. 3): closed canopy forest of 6 to 12 m in height, dominated by *Abies balsamea*, *Picea mariana*, and *P. glauca*. The herb layer is characterized by *Dryopteris spinulosa*, *Cornus canadensis*, *Pyrola secunda*, *Galium* spp., and *Monotropa uniflora*. The ground is usually covered by lichens (such as *Cladonia* spp. and *Peltigera* spp.), mosses (such as *Pleurozium schreberi*, *Dicranum* spp., and *Polytrichum* spp.), and needle litter. Some parts of the forest are so dense that the herb layer is absent, and only needle litter is present on the forest floor. The spruce-fir forest is the dominant habitat on Camel Island.

2. Partial tuckamoor (Fig. 4): relatively dense, wind-pruned *Abies balsamea* and *Picea mariana*. Since Camel Island is never exposed to the full force of a wind from any direction due to the presence of neighbouring

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<sup>1</sup>Vascular plant nomenclature follows Rouleau (1956) and non-vascular follows Polunin (1947).

Fig. 2. Typical rocky shoreline of Camel Island.



Fig. 3. Spruce-fir forest in the interior of Camel Island.



Fig. 4. Partial tuckamoor along the shoreline of Camel Island.



islands, dense tuckamoor as described by Riewe (1971) is rarely found. What I am calling partial tuckamoor corresponds to what Riewe (1971) called "shoreline ecotone;" I am changing the terminology in the context of this thesis as I feel "shoreline ecotone" does not adequately describe the habitat in question.

Partial tuckamoor lacks the ericaceous shrub layer of true tuckamoor; and ground cover consists primarily of needle litter with occasional mosses and lichens. In some areas, particularly the more sheltered ones, entangled branches of *Abies balsamea* and *Picea mariana* extend to the ground and often mingle with shoreline species.

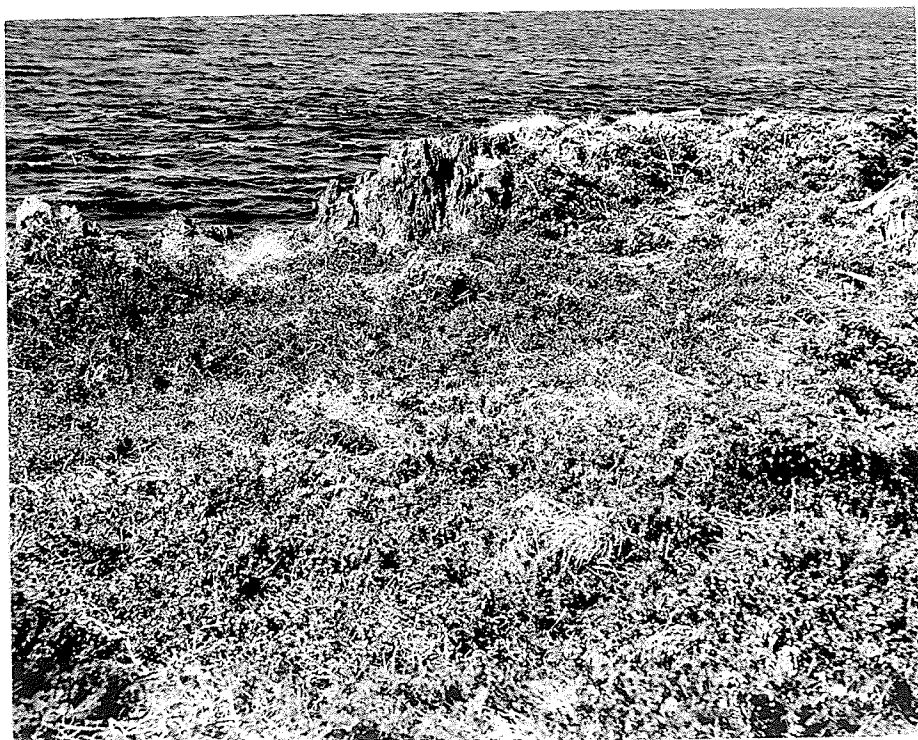
3. Heath (dwarf)-shrub barren (Fig. 5): low, prostrate shrubs dominated by *Empetrum nigrum*, *Vaccinium Vitis-Idaea*, and *Juniperus communis* interspersed with a few herbs such as *Cornus canadensis* and *Potentilla tridentata*. On Camel Island heath-shrub barrens are restricted to the exposed tops of sea-cliffs and are bordered by partial tuckamoor.

4. Bog: ground cover is primarily *Sphagnum* spp. and *Carex* spp. Open bog contains numerous *Sphagnum* hummocks with a shrub layer dominated by *Ledum groenlandicum*, *Andromeda glaucophylla*, *Chamaedaphne calyculata*, *Betula Michauxii*, and *B. pumila*. Some *Picea mariana* and *Larix laricina* are also present. Open bog on Camel Island is restricted to one small area on the northeast end of the island.

Coniferous bog differs from open bog in being restricted to a few low-lying areas within the spruce-fir forest. The ground cover is usually *Sphagnum* spp. growing on rotting, fallen logs. A shrub layer is generally absent, and the bog itself is shaded by the adjacent forest. Shrubby *Acer spicatum* are not infrequent in this habitat.



Fig. 5. Heath-shrub barren on exposed cliffs of Camel Island.



Due to the very restricted area occupied by bogs on Camel Island, coniferous bog and open bog are considered as one habitat.

5. Burn (Fig. 6): characterized by dense clumps of regenerating *Picea glauca*, *P. mariana*, and some *Abies balsamea*, interspersed with a few mature specimens of these species and numerous young *Prunus pensylvanica* and *Betula papyrifera*. In most areas there is no herb layer; needle litter overlies exposed soil while outcrops of rock remain bare. Partially burned logs, branches, and root systems are the single most dominant characteristic of this habitat.

In the preliminary survey in 1968, B. J. Lincoln and D. Watkins established two plots: Plot I at the northwest end of Camel Island in the spruce-fir forest and Plot II in the interior in the burn. These plots were 1 acre (approximately 0.4 ha) and consisted of a 10-line x 10-line grid, giving a total of 100 trap sites. In 1969 these plots were abandoned due to being inaccessible in inclement weather. To replace them I established Plot III, situated in the spruce-fir forest within easy walking distance of base camp; Plot IV, situated in the burn and to which a trail was cut to facilitate trap setting and checking (it was later discovered that Plot IV overlapped, in part, the original Plot II); and Plot V, situated in a boggy area at the northeast end of the island. Plot trapping was supplemented by trap lines, particularly in habitats which were too small for plot trapping. In July 1970 Plots VI and VII were established in an attempt to encompass all habitat types on a grid. Trap lines situated in this area were subsequently abandoned as plot trapping took precedence; trap lines in other areas continued to be checked.

Fig. 6. Burn on Camel Island showing dead trees and regenerating spruce-fir forest.



## Climate

The climate of Newfoundland has been described in detail by Hare (1952); the following is a summary of that description. The Newfoundland climate is dominated by the cold Labrador Current which, in its southward flow, encircles the whole island. As a result, coastal waters remain cold (in comparison with the Gulf of St. Lawrence) throughout the spring and summer. In August and early September the relative coldness of the Newfoundland waters becomes less pronounced, and by the end of November temperatures are comparable with those of the Gaspe Current. From December to May all the sea areas remain close to freezing or become covered with ice.

The sea in Notre Dame Bay varies considerably from year to year with respect to ice; in some years the bay never freezes over, in others the ice is sufficiently thick to permit vehicular transport, and in still other years there is ice formation but it covers only isolated areas of the bay and shifts with the wind and water currents. The presence or absence of ice noticeably affects the climate of nearby land masses; open seas have a moderating effect, while a consolidated ice cover may cool the air above it almost as quickly as a continental land mass (Hare, 1952).

Ice formation and the closure of harbours in Notre Dame Bay usually occur around the end of December-beginning of January; breakup occurs toward the end of April, but as the local ice begins to disappear, pack ice from the Labrador Current usually moves in and continues to exert a cooling influence on ambient temperatures into June and sometimes early July (Hare, 1952).

The mean air temperature for the Notre Dame Bay region in January

is  $-9.4$  to  $-6.7^{\circ}\text{C}$ . however there is usually considerable day to day variation; temperatures remain near freezing until late May, then climb slowly throughout June and into July (mean  $15.6^{\circ}\text{C}$ ) (Hare, 1952). The duration of the growing season is approximately 150 days and is also characterized by great variations due to winds off the Labrador Current bringing hot and cold spells (Hare, 1952).

The mean annual precipitation is approximately 87.5 to 100.0 cm; mean annual snowfall is 312.5 to 375.0 cm, with small amounts falling in October, more in November, and the snows of December becoming relatively permanent (Hare, 1952). These values are much higher than those of the Comfort Cove Meteorological Station for the year of 1970 (annual snowfall = 194.2 cm). The discrepancy can possibly be explained by the numerous reports of residents that winters for the past 10 to 15 years have been characterized by a greatly decreased snowfall. Mean winter maximum snow accumulation is 79 cm (the maximum recorded is 177 cm), while the average depth of snow at the end of each month from December to April is 30 cm, with the greatest accumulation occurring in January and February (Riewe, 1971). Frequent thaws, rains, and freezing rain create numerous ice layers within the snow cover besides causing frequent changes in the density and consistency of it.

From June to October the prevailing winds are southwesterly; from November to May, west to northwesterly. They are lightest during spring and summer (July mean velocity = 57.7 cm/sec. and mean maximum velocity = 161 cm/sec.) and strongest during autumn and winter (January mean velocity = 93 cm/sec. and mean maximum velocity = 255 cm/sec.) (Riewe, 1971). One of the most noticeable characteristics of winds in the study

area is their gustiness.

### Seasons

During the course of this study it became obvious that much of the data needed to be interpreted on a seasonal basis. However, the demarkation and length of conventional seasons did not always coincide with climatological phenomena affecting the animals. For this reason I have discarded the conventional season concept and have subdivided the year on the basis of snow cover (the factor that appears to have the greatest effect on small mammals). This sort of subdivision is not new: Galakhov (1940, cited by Rikhter, 1945) divided the winter into four periods according to the "life" of snow, but since Galakhov was dealing with a continental type of winter, his classification is almost meaningless in terms of a maritime winter.

While it must be borne in mind that the length of each of my subdivisions varies from year to year, I feel that the dates I have chosen best represent the parameters of my climatological subdivisions. They are as follows:

1. 1 September-15 November. Pre-snow Cover Period: at the beginning of this period, leaves of deciduous trees are already changing colour and starting to fall from the trees; by the end of the period, all deciduous trees are bare. Minimum ambient temperatures intermittently fall below the freezing point and rise above it; falling snow is not uncommon and may remain on the ground for several days before melting. Rain is still the major form of precipitation.

2. 16 November-15 March. Period of Greatest Snow Cover: melting



of fallen snow is retarded as maximum ambient temperatures now frequently remain below freezing point. The snow cover is usually greater than during the previous and subsequent periods, but is by no means stable due to frequent thaws. Snow now becomes the major form of precipitation.

3. 16 March-15 June. Period of Ebbing Snow Cover: ambient temperatures begin to rise although the minimum is usually still below freezing point. Rain again becomes the major form of precipitation, particularly toward the end of this period. The snow cover begins to disappear around the middle of this period; photosynthesis begins and by the end of the period deciduous trees and shrubs again have leaves.

4. 16 June-31 August. Period of No Snow Cover: the major form of precipitation is rain; maximum and minimum ambient temperatures are usually well above freezing. This is the period of greatest primary productivity.

#### Human Occupation

Due to the rocky nature of Camel Island, it never has been a place of year-round habitation as have some of the neighbouring islands such as Sivier Island and Birchy Island. It is, however, a favoured lunching and picnic spot of fishermen and "day-trippers" from Lewisporte and Little Burnt Bay. There are two abandoned cabins (one at Indian Cove and one on the northeast end of the island) which formerly served as camps for fishermen who came out for several days at a time. Someone once had a potato patch in a low-lying area above Indian Cove, but other than that no attempt has been made to cultivate the land (local fishermen, pers. comm., 1971).

The island is fairly sheltered and consequently some of the trees have grown large enough to be logged commercially. A logging road was cut from the northeast end of the island to the interior to facilitate removal of logs, while in the Indian Cove area cutting was done just above the high tide line and logs presumably were hauled through the forest to the beach. Although logging operations were terminated before this study commenced, slash piles can still be found. The island was partially burned (Fig. 1), probably as a result of human carelessness, between ten and twenty years ago. I was unable to establish a precise date for the burning.

## MATERIALS AND METHODS

### Preliminary Work

On 8 July 1967 Dr. W. O. Pruitt, Jr. introduced two male and one female *Clethrionomys gapperi* onto Camel Island; these were supplemented by a further 17 animals on 6 August 1967. This island was chosen for the introduction primarily because of its relatively isolated location, because it was a forested island, and because *Microtus* were present on the island prior to the introduction of *Clethrionomys*. The introduction of *C. gapperi* was concurrent with introductions of *C. glareolus* on Yellow Fox Island and *C. rufocanus* on Big Cranpot Island with the intention of using these populations as stock colonies for further introductions of various combinations of the four species on other islands. Although the subsequent demise of the *C. rufocanus* population eliminated several combinations, it became increasingly obvious that it was impractical to study more than one island at a time, hence the decision to concentrate on the Camel Island population.

During the summer of 1968 a preliminary investigation was made by Miss B. J. Lincoln and Mr. D. Watkins who set up and sampled two plots (previously described). Harvey Payne and I began field operations on 12 May 1969 and remained in the field more or less continuously until December 1970. Trapping was resumed in April 1971 and terminated in July 1971. A permanent camp was established at Indian Cove on the

southwest end of Camel Island and it was from here that all field operations were carried out.

### Live Trapping

In an attempt to elucidate answers to the questions posed in the Introduction, an intensive live-trapping programme was initiated in May 1969.

During May and June 1969 only trap lines were utilized. In general, sites were 3 to 5 m apart and were marked with flags to ensure that they remained permanent throughout the study. Traps were set within a circle of 1-m radius centred on markers.

Plots III, IV, and V (described earlier) each had an area of 1 acre (0.4 ha) and consisted of a 7 x 7-line grid, giving a total of 49 trap sites. Trap sites were located at intervals of 8.8 m and were also marked with flags. Traps again were set within a circle of 1-m radius centred on markers.

Plots VI and VII together comprised about 12 acres (about 4.8 ha) containing approximately 1200 trap sites (100 sites/acre). I originally intended to trap these plots once a month, but due to the large area encompassed and the rugged terrain, I found this impossible and consequently resorted to trapping by habitat, utilizing the trap sites of these plots. As with the other plots and trap lines, traps were set within a circle of 1-m radius.

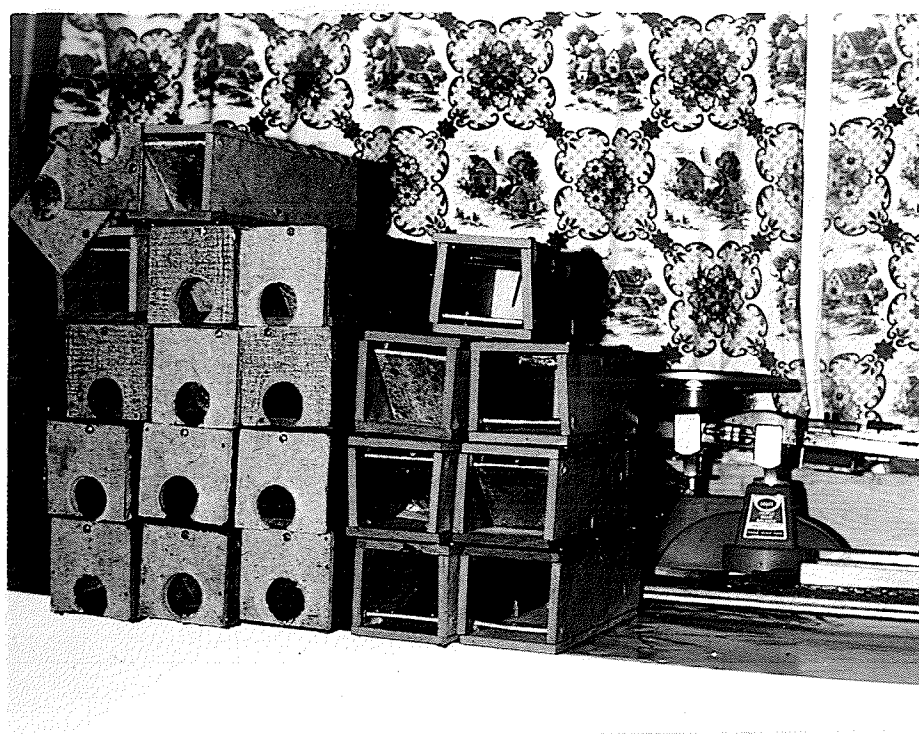
No regular system of trapping was established, primarily due to the necessity of making frequent trips to Lewisporte for supplies and the probability of being stormbound for anywhere from one to seven days.

Collapsible Sherman and non-collapsible Masonite traps were utilized; the Masonite traps were used primarily during the winter as I felt they would provide more heat retention for the voles than would the metal Sherman traps.

My biggest problem proved to be trap-raiding by squirrels (and probably some of the larger voles). The squirrels could enter a Sherman trap, stand on the treadle while eating the bait, then back out leaving the trap still set but baitless. I tried a variety of baits (dried apricots, dried apples, prunes, and raisins) in the hope of finding something that was not attractive to squirrels; in the end I settled for raisins as they could be slipped behind the back of the treadle, thus making it more difficult for squirrels to find them, as well as ensuring that a trapped vole would not find himself in a baitless trap. (Voles, once inside the trap, could reach under the treadle for the bait.)

The problem with the Masonite traps was more complicated: the doors for these traps were at the back, and originally were removed by pulling upwards. This posed no problem for the squirrels who soon discovered that, although they were too large to enter the traps, they could pull the doors out. I remodelled some of the traps so that the doors pulled out from beneath, but the squirrels easily flipped the traps over, opened them as usual, and ate the bait. Eventually I added a screw-on front end with a vole-size opening in it (Fig. 7), and made the back doors fit more snugly. This did not entirely eliminate trap-raiding, but it did reduce it considerably. (Subsequent raiding was probably attributable to larger voles who could enter the trap and eat the bait while straddling the treadle and door, then back out.)

Fig. 7. Masonite traps showing screw-on front ends which were added as a squirrel deterrent.



Live traps generally were operated on a three-night basis to ensure that all habitats would be sampled within a reasonable length of time. Traps were set on the evening of the first night, checked morning and evening of days two and three, then removed on the morning of the fourth day. Captured animals were transported to base camp where they were identified, weighed (to the nearest 0.1 g on an Ohaus triple beam balance), sexed, and in the case of unmarked animals, toe-clipped. They then were released at the site of capture or detained either for observation or for later release in a specific area.

Animals that succumbed in the traps were autopsied as described under Snap Trapping.

#### Snap Trapping

Museum Special and Schuyler's No. 3 Folding Animal Killers were set intermittently on neighbouring rocks and islands to check for the presence of *C. gapperi* or marked *M. pennsylvanicus*. Frequency of checking these traps depended on the weather; when feasible they were checked daily.

Snap-trapped animals were removed from the traps, placed in paper bags, and transported to base camp for examination. Here a few drops of chloroform were placed in each bag, and after a short wait animals were combed for ectoparasites which were preserved in 70% alcohol. The carcasses were then weighed and measured (total length, tail length, hind foot, and ear) before being opened. Length and width of testes were recorded for males; visible embryos and placental scars for females. Reproductive tracts were saved for later examination. Skins, skulls, skeletons, and viscera were preserved for all animals not too badly



damaged, and records of autopsies were kept.

## HABITAT SELECTION

### Microtus pennsylvanicus

Although *Microtus pennsylvanicus* is considered to be typically a grassland species (Cameron, 1965; Grant, 1970; Smith and Foster, 1957; Zimmerman, 1965), the literature contains numerous reports of its occurrence in other habitats. Getz (1963) found *M. pennsylvanicus* to be characteristic of low, marshy areas; Findley (1954) found that this species preferred lush, hydrosere communities but was not found at all in aspen consocieties or alder-willow swamps. Buckner (1957), Clough (1964), Dice and Sherman (1922), and Dice (1925a) found meadow voles to be present, but in small numbers, in bogs. Findley (1954) and Soper (1946) considered *M. pennsylvanicus* to be typical of eastern deciduous and northern coniferous forests and their attendant grasslands, while Smith and Foster (1957) found meadow voles to be common in open woods with grass and sedges. Getz (1970), however, stated that *M. pennsylvanicus* occurs in forests only when graminoid stands are not present. Clough (1964) and Dice (1925a) found *M. pennsylvanicus* to occur infrequently in hardwood and spruce-fir forests.

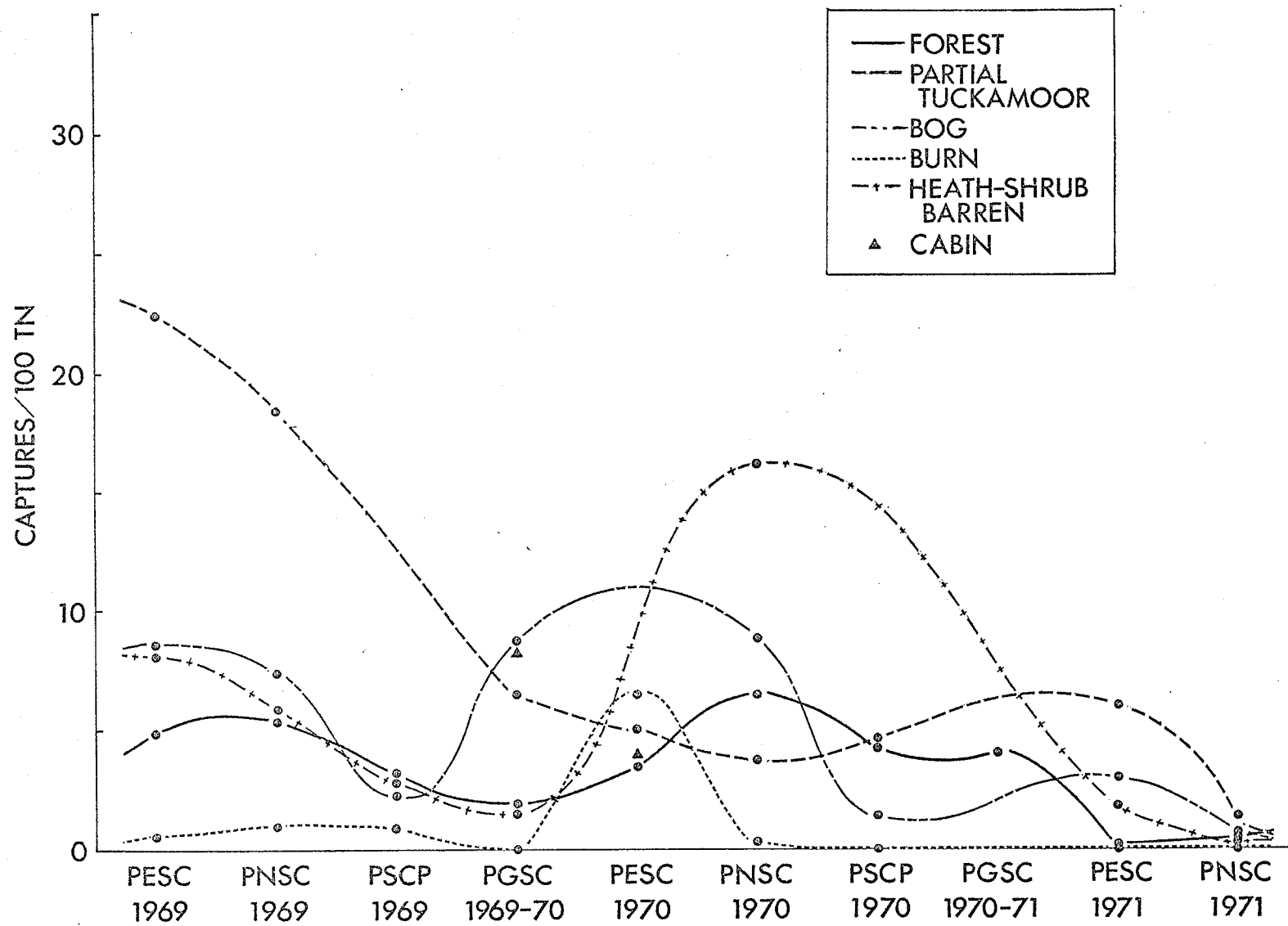
The apparent discrepancy between *M. pennsylvanicus* being typically a grassland species and the numerous reports of its presence in other habitats possibly may be explained by Cameron's (1965) and Grant's (1970) observations that during periods of peak population density,

*M. pennsylvanicus* invaded woodlands, isolated grassy areas, and scrubby areas such as swamps. Alternatively, Morris (1969) has shown that in the absence of a presumed competitor (*Clethrionomys gapperi*), *M. pennsylvanicus* entered woodland more frequently than when *C. gapperi* was present.

In island situations *M. pennsylvanicus* appears to show an even greater propensity for utilizing habitats other than grassland. Dice (1925b) found *M. pennsylvanicus* in hardwood forests on Marion Island and commented on the unusual nature of this occurrence. Webb (1965) found meadow voles in forested areas on islands in the Adirondack Lakes. Cameron (1958a, 1965) reported that *M. pennsylvanicus* on the main island of Newfoundland occurred more frequently in forested areas than in grassland; however, the work of Folinsbee *et al.* (1973) indicated that, on the main island of Newfoundland, *M. pennsylvanicus* responded to available habitat much as it did on the mainland of North America; it occurred primarily in grassy situations and was captured only occasionally in forests. Riewe (1971) found that habitat selection by *M. pennsylvanicus* appeared to be random on small grassy or barren islands whereas, on completely forested islands, shoreline, shoreline ecotone (partial tuckamoor), or tuckamoor were preferred to the interior spruce-fir forest.

Since Camel Island lacks meadows, *Microtus* inhabiting the island must choose amongst the available habitats. Of these there is no one habitat that was favoured during all seasons (Fig. 8), nor does the choice of habitat appear to be consistent either with season or with population density.

Fig. 8. Seasonal habitat selection of *Microtus pennsylvanicus* on Camel Island. PESC = Period of Ebbing Snow Cover, PNSC = Period of No Snow Cover, PSCP = Pre-snow Cover Period, PGSC = Period of Greatest Snow Cover. TN = trap nights



Captures of *Microtus* in partial tuckamoor never were significantly lower than would be expected (Table I), and were often considerably higher. The low value for the Pre-snow Cover Period of 1969 was based on only 12 TN and is probably a biased estimate. Riewe (1971) noted that tuckamoor proper was utilized at a relatively high level throughout the year, and the same appears to hold true for partial tuckamoor. It is difficult to determine what properties of the partial tuckamoor habitat would be so appealing to a vole that is supposed to prefer meadow. Foraging in the partial tuckamoor is not particularly good; it has already been noted that few herbaceous plants grow here.

This habitat would, however, offer good cover from avian predators, such as rough-legged hawk (*Buteo lagopus*), common raven (*Corvus corax*) and common crow (*C. brachyrhynchos*). The trees are twisted and very bushy and often form an almost impenetrable cover at the 1 to 1.3-m level. Also there are many places which mammalian predators would have difficulty penetrating, although in general the tangled branches would form a canopy over anything fox-size or smaller. Getz (1970) found that *M. pennsylvanicus* did not particularly seek out areas with cover rather than areas without, but he felt the presence of adequate cover did contribute to higher population densities. Eadie (1953) and LoBue and Darnell (1959), however, found that *Microtus* did exhibit a positive response to vegetative cover.

In most instances the band of partial tuckamoor adjoins either a shoreline that supports a number of succulent plants such as *Sedum Roseae* and *Plantago juncooides*, or a heath-shrub barren. On the heath-shrub barren innumerable runways were always present, and often there was

TABLE I

## Period of Ebbing Snow Cover 1970

Forest

Partial tuckamoor

506

81

17

4

1

22.2

3.6

0.2

20

3

0

19.6

3.2

0.2

$$\chi^2 = 31.491$$

$$P < 0.001$$

$$\chi^2 = 10.105$$

$$P < 0.95$$

## Period of No Snow Cover 1971

Forest

Partial tuckamoor

Bog

Burn

Heath-shrub barren

Forest-bog

Forest-burn

Bog-burn

Shore

Rocks

293

168

63

248

260

75

6

21

60

635

1

1

1

0

1

1

0

0

0

0

0

—

5

0.8

0.5

0.2

0.7

0.7

0.2

0.0

0.1

0.2

1.7

15

9

2

27

3

4

0

3

0

5

—

68

10.9

6.3

2.3

9.2

9.7

2.8

0.2

0.7

2.2

23.6

Totals:

1829

$$\chi^2 = 3.908$$

$$P < 0.95$$

$$\chi^2 = 29.570$$

$$P < 0.001$$

evidence that some small mammal had recently been eating *Empetrum* or *Juniperus* bark. Riewe (1973) found the bark and leaves of *Empetrum nigrum* to be accepted as food by *M. pennsylvanicus* during all seasons. He did not list the fruit of this plant as being utilized, but in the limited feeding experiments I performed, I found that all test animals ate the fruit completely. The heath-shrub barren on Camel Island also supports a good growth of *Juniperus communis* which Riewe (1973) found was utilized in fall and winter by *M. pennsylvanicus*. Trapping success in the heath-shrub barren was usually slightly below the expected value with the exception of the Period of Ebbing Snow Cover in 1969 when captures were slightly higher than expected, and the Period of No Snow Cover in 1970 when captures were much higher than expected (Table I).

The relatively high year-round utilization of the partial tuckamoor and the fresh clippings of *Empetrum nigrum* and *Juniperus communis* on the heath-shrub barren suggests that *Microtus* might have been using the partial tuckamoor as a sheltered area from which forays were made to the heath-shrub barren and possibly also the shoreline for food. The lower trapping success on the heath-shrub barren might be explained by the suggestion of Robinson *et al.* (1965) that *M. pennsylvanicus* showed a low response to traps when the animals were beyond a certain radius from their centre of activity. As most *Microtus* individuals on Camel Island were very wide-ranging (see section on Observations on Movement of Animals), it is difficult to establish any well-defined centres of activity for them, but the trapping record indicates that captures were more frequent in the partial tuckamoor than in any other habitat.

Beer *et al.* (1954) found that *M. pennsylvanicus* did not enter traps



as readily as *Clethrionomys gapperi*, while Butsch (1954) noted that *C. gapperi* usually investigated the traps before entering. During one of our cage observations, Harvey Payne placed a trap in a cage holding a *Microtus* and a *Clethrionomys*. The *Microtus* investigated the trap at intervals for almost two hours before finally getting caught, while the *Clethrionomys* was caught and released several times during this period. Both animals investigated the trap before entering, but the *Microtus* was by far the more wary of the two. If *Microtus* individuals spend much time investigating traps in the woods, they would probably be more inclined to do so in a reasonably protected area (such as the partial tuckamoor) rather than in a more exposed area (such as the heath-shrub barren).

The bog was probably the next most-favoured habitat. Captures here were usually very close to the expected values or higher (Table I), with the exception of the Period of Ebbing Snow Cover in 1969 and the Pre-snow Cover Period in 1970. As mentioned previously, *Microtus* is known to inhabit bogs and low, marshy areas on the mainland of North America so it is hardly surprising that, in the absence of meadow and grassland, *Microtus* should inhabit boggy areas on Camel Island. Riewe (1971) found that *M. pennsylvanicus* occupied bog throughout the year, but at very low levels during the winter and spring. My data do not corroborate Riewe's results since I found that meadow voles utilized bogs more heavily during the Period of Greatest Snow Cover and the Period of Ebbing Snow Cover than during the remainder of the year. Riewe, however, was dealing almost exclusively with open bogs, whereas my data include both open and coniferous types.

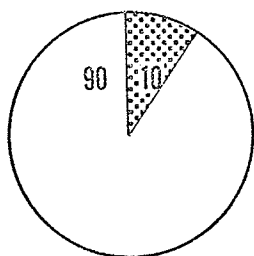
In the mature spruce-fir forest, which is the dominant habitat on

Camel Island, captures of *Microtus* generally were very close to the expected values (Table I). Riewe (1971) found that *M. pennsylvanicus* appeared actively to avoid the interior spruce-fir forest, and although Table I indicates that on Camel Island the number of captures in this habitat closely approximates the number expected, I feel there is an upward bias due to data from Plot III.

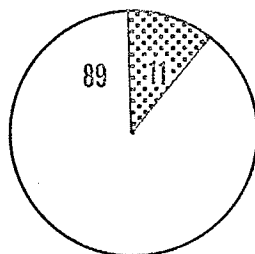
Plot III is unique in having 23 of its 49 trap sites situated in a damp, low-lying area which supports an alder thicket and a stand of young *Abies balsamea*. Alder thickets are rare on Camel Island, and I found in analyzing Plot III data that between 80 and 100% of the *Microtus* captures from this plot were in the low-lying area (Fig. 9). This, I think, is more closely indicative of the reaction of meadow voles to the forest: i.e., in low-lying areas (such as this portion of Plot III), the bog-forest ecotone, and that part of the forest adjacent to the partial tuckamoor, captures of *Microtus* were higher than in the interior spruce-fir forest. In the latter, captures were infrequent and probably were accounted for by transients on the move from one of the more-favoured habitats to another, and forced to pass through the forest to accomplish the move.

Of all habitats, the burn was the one most actively avoided by *Microtus*; in the burn proper only seven animals were captured. The reason for this active avoidance may possibly be related to food and cover. Koshkina (1957) felt that burns afforded little cover, but while this is undoubtedly true of recent burns, the one on Camel Island is several years old, and there are now thick stands of regenerating *Picea glauca* and *Abies balsamea*, not to mention brush piles, burned-out

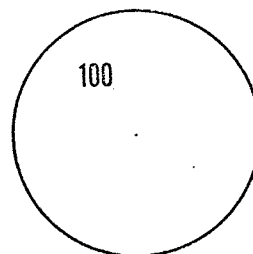
Fig. 9. Percentage of *Microtus pennsylvanicus* present in dry spruce-fir forest (stippled) and in damp spruce-fir forest (unstippled) on Plot III, Camel Island. PESC = Period of Ebbing Snow Cover, PNSC = Period of No Snow Cover, PSCP = Pre-snow Cover Period, PGSC = Period of Greatest Snow Cover.



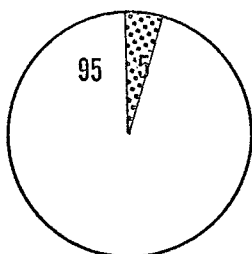
PNSC  
1969



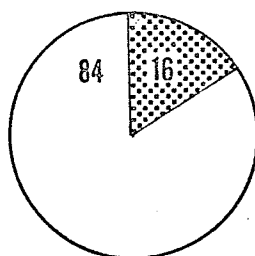
PSCP  
1969



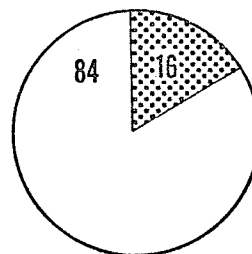
PGSC  
1969-70



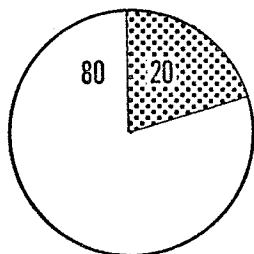
PESC  
1970



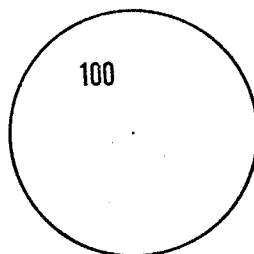
PNSC  
1970



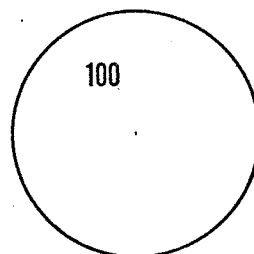
PSCP  
1970



PGSC  
1970-71



PESC  
1971



PNSC  
1971

logs, and tangles of branches. Getz (1967a) noted that *M. pennsylvanicus* actively avoided wooden sticks placed 10 cm apart on a grid. This, he felt, was probably because the stems hindered runway construction rather than because of the woody nature of the stems. It is possible that *Microtus* on Camel Island are reacting to the deadwood tangles of the burn in the same manner for the same reason.

Furthermore, the burn has little to offer meadow voles in the way of food. Herbaceous plants are almost non-existent here, and while there is usually a good crop of *Prunus pensylvanica* berries in autumn, I have been unable to find any citations in the literature regarding the preference of *Microtus* for these berries. In general, meadow voles preferred the vegetative parts of grasses and forbs (Thompson, 1965; Zimmerman, 1965), both of which are virtually non-existent in the burn.

#### *Clethrionomys gapperi*

The red-backed vole, *Clethrionomys gapperi*, inhabits primarily forest and scrubby areas (Cameron, 1965). Morris (1969) and Soper (1946) found it to be the predominant species in coniferous forests and mixed wood stands. Dice (1925a) and Dice and Sherman (1922) found it to be common in hardwood forests but relatively infrequent in second-growth spruce-fir forests (Dice and Sherman, 1922). Clough (1964) found the species to be present in wet spruce woods, mature spruce-fir woods, open spruce woods, and dry spruce woods. According to Butsch (1954), *C. gapperi* was most common in moist subclimax situations and ecotones where heavy ground cover occurred.

Both Butsch (1954) and Getz (1963) found that *C. gapperi* required a

moist habitat so it is not surprising to find numerous reports of its presence in black spruce-tamarack bogs (Buckner, 1957; Dice, 1925a; Dice and Sherman, 1922; Smith and Foster, 1957). Clough (1964) found it to be absent from open and coniferous bogs in Nova Scotia, while Smith and Foster (1957) found it to be more frequent in bogs than in forest.

The data from Camel Island indicate, rather surprisingly, that *Clethrionomys* shows only a slight preference for the interior spruce-fir forest over the other available habitats (Table I and Fig. 10). Table I indicates that in the Pre-snow Cover Period and in the Period of Greatest Snow Cover in 1969, they even exhibited a certain amount of avoidance of the forest; this coincided with habitat shifts to the burn and the cabin respectively. With the exception of the Pre-snow Cover Period in 1969, the highest preferences of *Clethrionomys* for the forest coincided with the highest number of captures of this species (*i.e.*, Period of Ebbing Snow Cover and Period of No Snow Cover, 1969) which suggests that the forest is capable of supporting more red-backed voles than were usually found there, but that the animals themselves did not exhibit a preference for forest over other habitats at times when intraspecific pressures presumably were low.

Data from Plot III (Fig. 11) indicate that *Clethrionomys*, while often showing a preference for the low, damp areas of the forest, do not exhibit the same negative reaction to the higher, drier areas that *Microtus* do. Butsch (1954) showed that the highest concentrations of *C. gapperi* in his study area coincided with the highest densities of herbaceous cover. I attempted to analyze my data in a similar fashion, but could find no such correlation. Morris (1955) noted that slash from cutting

Fig. 10. Seasonal habitat selection of *Clethrionomys gapperi* on Camel Island. PESC = Period of Ebbing Snow Cover, PNSC = Period of No Snow Cover, PSCP = Pre-snow Cover Period, PGSC = Period of Greatest Snow Cover. TN = trap nights.

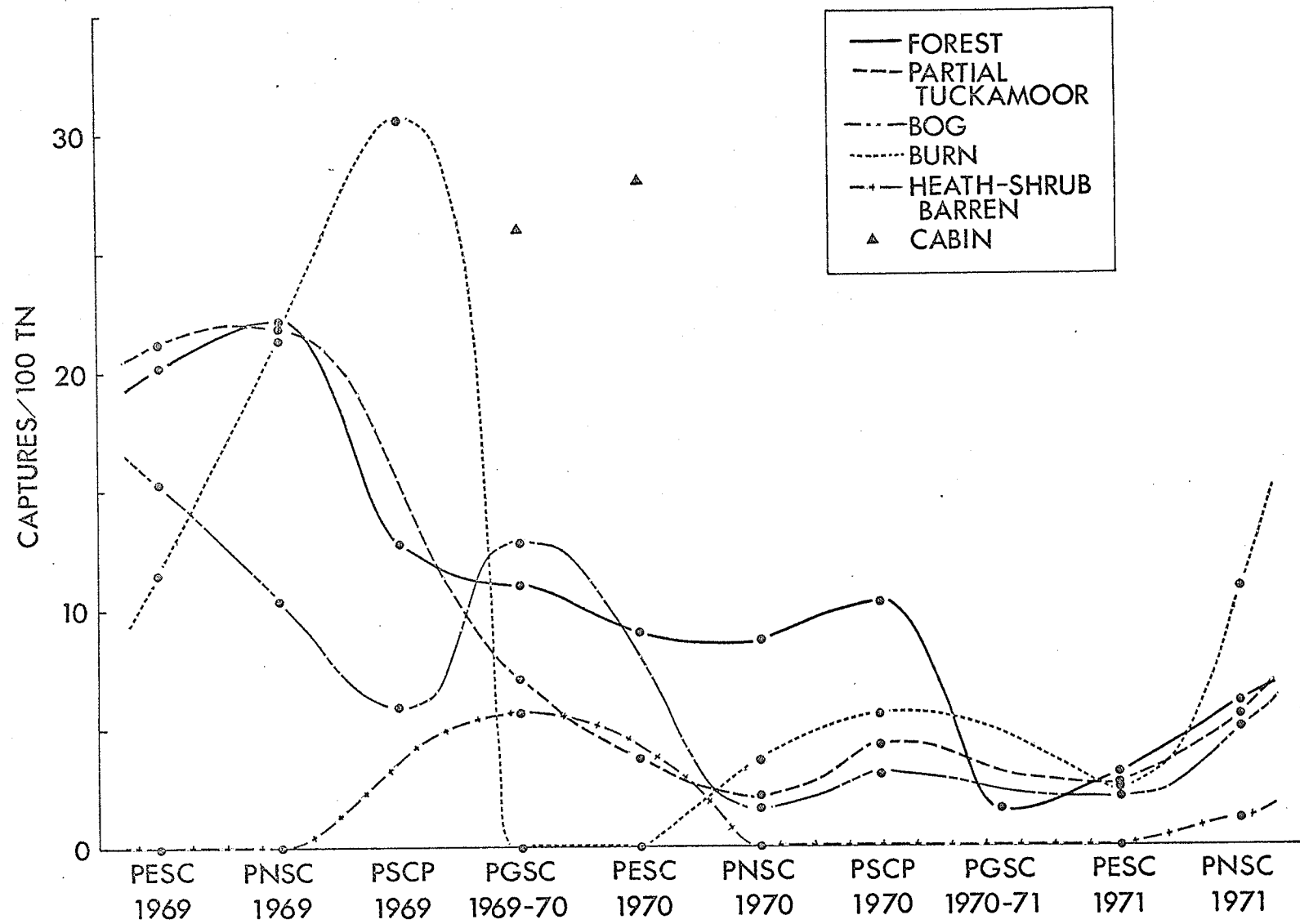
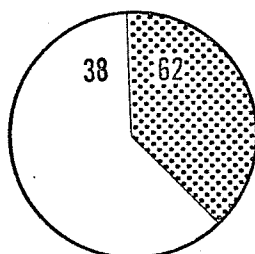
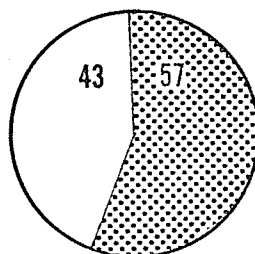




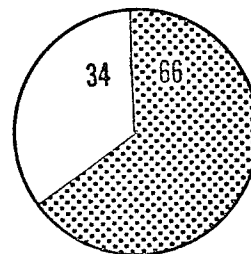
Fig. 11. Percentage of *Clethrionomys gapperi* present in dry spruce-fir forest (stippled) and in damp spruce-fir forest (unstippled) on Plot III, Camel Island. PESC = Period of Ebbing Snow Cover, PNSC = Period of No Snow Cover, PSCP = Pre-snow Cover Period, PGSC = Period of Greatest Snow Cover.



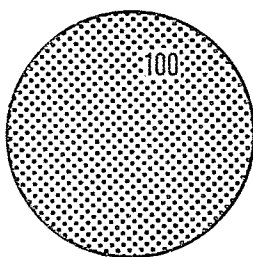
PNSC  
1969



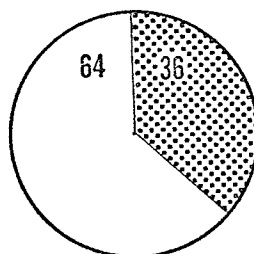
PSCP  
1969



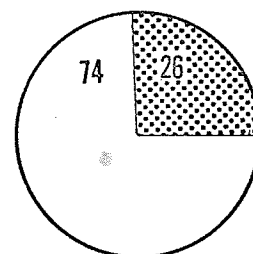
PGSC  
1969-70



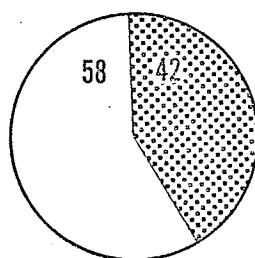
PESC  
1970



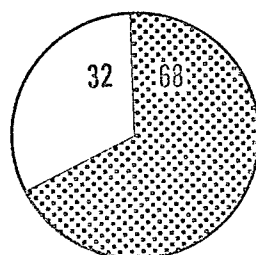
PNSC  
1970



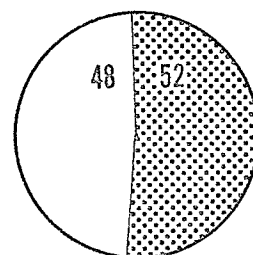
PSCP  
1970



PGSC  
1970-71



PESC  
1971



PNSC  
1971

operations was particularly favourable for *C. gapperi*. Slash piles were abundant throughout much of the forested area on Camel Island, and traps set near them usually yielded a good catch of *Clethrionomys*.

In general, *Clethrionomys* appeared to treat the partial tuckamoor in much the same manner as the forest. The avoidance of partial tuckamoor was more marked in the Pre-snow Cover Period of 1969 than was the avoidance of forest, less marked in the Period of Greatest Snow Cover. As with the forest, the highest preferences coincided with the highest number of captures, but when the latter was low, the forest was slightly preferred to the partial tuckamoor (Table I).

Towards the end of the Period of No Snow Cover and during the Pre-snow Cover Period, *Clethrionomys* preferred the burn, the degree of preference corresponding well with the number of captures. Koshkina (1957) observed a small increase in the number of voles in burn areas during the summer, but found the animals there were exterminated in the autumn due to the burns affording little cover from predators which were numerous that year. She considered burns to be unfavourable habitat for this reason; however, on Camel Island, where there were few predators, the burn apparently was optimum habitat at this time of year. Krivosheev (1961) found *C. rutilus* in relatively high numbers in burns during the autumn, but never found *M. oeconomus* or *M. gregalis* in this habitat. This observation corresponds with the situation on Camel Island.

Krivosheev (1961) found that in autumn, *C. rutilus* was abundant in old plantings that had an abundance of berries, while Koshkina (1965) observed that berries were important food sources for *Clethrionomys*. It has been stated already that the burn on Camel Island supported a heavy

growth of young *Prunus pensylvanica*, and I believe that the fruit from these trees was the main attraction for *Clethrionomys* in the last part of the Period of No Snow Cover and in the Pre-snow Cover Period. During the Period of Greatest Snow Cover in 1969-70, red-backed voles were absent from the burn; there are no data from the Period of Greatest Snow Cover the following year, but as the animals were present when trapping resumed in the Period of Ebbing Snow Cover in 1971, I think it not unlikely that some animals, at least, overwintered in this habitat. There was a particularly good crop of berries in 1970, whereas in 1969 there was not, and all indications point to the Period of Greatest Snow Cover of 1970-71 as having a much better snow cover than in the previous year (see section on The Maritime Winter and its Effect on *Microtus* and *Clethrionomys*).

The bog generally was avoided by *Clethrionomys* except during the Period of Greatest Snow Cover in 1969-70, the Pre-snow Cover Period in 1970, and the Period of Ebbing Snow Cover in 1971, the presence of red-backed voles in the latter two seasons indicating that they probably were present in the bog during the Period of Greatest Snow Cover in 1970-71 as well (Table I). The reasons for this winter preference of bog are obscure, but may be related to the presence of *Rubus* and *Viburnum edule*, the seeds from *Acer spicatum*, and the numerous remains of forbs which would have provided easier foraging under the snow than would have been found in the forest or partial tuckamoor.

The only habitat consistently avoided by *Clethrionomys* was the heath-shrub barren (Table I). As previously noted, the dominant plant of this association is *Empetrum nigrum*, the berries of which captive *Clethrionomys* ate with full acceptance. Since this habitat offers apparently good

foraging and herbaceous cover, its lack of crown cover may have been critical in the red-backs' avoidance of it.

## OBSERVATIONS ON MOVEMENT OF ANIMALS

### Movement Indices

Home range is defined as the "area traversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt, 1943). Over the years a number of techniques have been employed to calculate the home range size of voles, those most frequently used being the minimum area, inclusive boundary strip, and exclusive boundary strip (see Van Vleck, 1969, for explanation of techniques). Depending on the technique employed and the area studied, the average home range for *Microtus pennsylvanicus* varies between 0.012 to 0.384 ha (0.029 to 0.95 acres; see Riewe, 1971, for review). For *Clethrionomys gapperi*, average home range varies between 0.028 to 0.48 ha (0.07 to 1.2 acres; see Butsch, 1954, for review).

While the above definition of home range and the various techniques for estimating it may be applicable to most populations of *Microtus* and *Clethrionomys*, I found them to be too restricting in analyzing the movements of the Camel Island animals. Although my plots encompassed a total of 6 ha and were supplemented by trap lines, I found that individuals frequently were trapped at widely separated sites within a couple of days, or even on the same day. This implies that even the 4.8-ha plot was too small to give an estimate of the home ranges of these individuals if, indeed, they have home ranges in the generally

accepted definition of that term. For this reason, and because I was trapping only part of the area over which the animals were moving, I have abandoned the home range concept in analyzing my data, and instead have used a movement index similar to that used by Riewe (1971) in analyzing Pyke Island data. Riewe (1971) calculated movement indices by dividing the sum of the distances between successive capture sites by the total number of days between the first and last captures. However, as Riewe's trapping on Pyke Island was conducted daily over a 12-week period rather than over many months, as mine was, I have modified his method to the extent of only considering successive captures that were less than four days apart. (The usual trapping rota was three days.) I feel this gives a more accurate estimate of actual movement than considering successive captures that were several weeks or months apart. A lapse of more than four days could have been due to trapping not being conducted during that time, or to traps being set in an area which the vole was not visiting during that particular rota.

The maximum, minimum, and mean movement indices for both sexes of both genera are shown in Table II. It is immediately apparent that, in all categories, considerable individual variation exists, some animals frequently covering long distances, others appearing to be more restricted in their movements. For instance, on 26 May 1969, *Microtus* 0131 (male) travelled 212.7 m in 12 hours; on 10 June 1970, *Microtus* 0040 (male) travelled 136.4 m in 15 hours. To illustrate restricted movements, *Clethrionomys* 1040 (female) was captured four times in three days at one trap site.

Between these two extremes there are many individual patterns which

TABLE II

Maximum, minimum, and mean movement indices by season  
for *Microtus pennsylvanicus* and *Clethrionomys gapperi* on Camel Island. All measurements are in metres.

Season	Male movement index			Female movement index		
	Maximum	Minimum	$\bar{x}$	Maximum	Minimum	$\bar{x}$
<i>Microtus</i>						
Period of Ebbing Snow Cover 1969	117.3	27.3	64.6	28.6	3.4	17.6
Period of No Snow Cover 1969	74.2	0.0	23.1	39.4	2.1	13.7
Pre-snow Cover Period 1969	----	----	----	----	----	----
Period of Greatest Snow Cover 1969-70	38.2	0.8	20.3	21.6	0.0	8.5
Period of Ebbing Snow Cover 1970	47.3	12.4	35.1	12.1	0.0	5.4
Period of No Snow Cover 1970	75.6	6.8	33.5	130.9	0.0	36.7
Pre-snow Cover Period 1970	15.2	11.5	13.4	35.5	9.3	20.5
Period of Greatest Snow Cover 1970-71	----	----	----	----	----	----
Period of Ebbing Snow Cover 1971	32.7	10.9	22.3	16.8	13.0	14.9
Period of No Snow Cover 1971	----	----	----	----	----	----
<i>Clethrionomys</i>						
Period of Ebbing Snow Cover 1969	75.9	5.5	26.5	40.9	5.5	17.4
Period of No Snow Cover 1969	60.0	0.0	27.1	47.9	1.7	19.1
Pre-snow Cover Period 1969	24.5	17.6	21.1	48.8	0.0	25.4
Period of Greatest Snow Cover 1969-70	20.2	5.5	11.5	29.1	0.0	12.3
Period of Ebbing Snow Cover 1970	----	----	----	30.2	12.3	21.3
Period of No Snow Cover 1970	72.3	20.5	45.0	125.5	32.8	79.2
Pre-snow Cover Period 1970	70.9	2.7	18.0	15.8	0.0	7.6
Period of Greatest Snow Cover 1970-71	----	----	----	----	----	----
Period of Ebbing Snow Cover 1971	50.5	0.0	22.3	38.2	9.5	25.4
Period of No Snow Cover 1971	37.6	16.4	25.8	34.1	5.5	21.4



I have arbitrarily broken into three categories:

1. Long movements: movements greater than 50 m in length. May be interspersed with short movements, but the overall pattern is that of a wide-ranging individual.

2. Shifting areas of concentration: short movements in a small area interspersed with a few long movements.

3. Restricted movements: movements less than 50 m and confined to a small area.

Categories 2 and 3 are similar to (or perhaps identical with) conventional home range concepts, however, since not all the animals studied appeared to have home ranges, I have avoided using this terminology.

Due to the absence in the literature of concrete criteria concerning what constitutes a long or short movement for these genera, I have chosen 50 m as the cut-off point. Movements of Category 3 animals were invariably less than 50 m; movements of Category 1 animals usually far greater. Due to the small number of *Microtus* for whom more than one or two captures were available, the data include all animals with three or more captures.

While three captures are undoubtedly too few to give an accurate indication of where and how far the animal is moving, the same case could be made against any number that might be chosen. Voles inhabit a three-dimensional (the third dimension being depth, *i.e.*, underground tunnels) environment, of which we are sampling only two dimensions; furthermore, it has already been noted that these animals do not appear to enter traps indiscriminately. On paper, convoluted movements are diminished, as are movements up or down a hillside, while movements underground are

completely ignored. Other than being able to say that animal so-and-so was trapped here and here at such-and-such times, we have virtually no idea where he goes or what he does. I attempted to employ tracking stations to rectify this situation partially, but found I could tell little from the tracks other than that a vole had passed by during the last few hours. It was impossible to distinguish between *Clethrionomys* and *Microtus*, and the tracks usually were blurred so that even the individual's number was indistinguishable.

Burt (1943) has said, "A calculated home range based on trapping records . . . is no more than a convenient index to size," and I think the same case can be made for the movement index. Despite limitations on the actual figures, the relationships indicated appear to be valid. (When animals with only three captures are removed from Table III, the number of individuals in each category drops, but when calculated on a percentage basis, the numbers remain remarkably stable.)

Riewe (1971) found that *M. pennsylvanicus* on Trump Island more than doubled the size of their home ranges in spring. Analyses of the Camel Island data show that this is not the case with the movement indices of either sex of *Microtus* or *Clethrionomys*. The mean distance covered per day appears to be independent of season.

Table II indicates that, in general, *Microtus* males have greater movement indices than *Microtus* females, but when a Student's "t" test is applied to the data, the difference is statistically significant only in the Periods of Ebbing Snow Cover of 1969 and 1970. For all other seasons, the differences are negligible. *Clethrionomys* males have greater movement indices than females in only four of the eight

TABLE III

Number and percentage  
of male and female *Microtus pennsylvanicus* and *Clethrionomys gapperi*  
in each movement category (May 1969 to July 1971 inclusive)

Movement type	Males		Females	
	Number	Percentage	Number	Percentage
<i>Microtus</i>				
Long	12	41%	2	6%
Shifting	9	31%	9	27%
Restricted	8	28%	22	67%
<i>Clethrionomys</i>				
Long	13	23%	5	9%
Shifting	28	50%	18	34%
Restricted	15	27%	30	57%

seasons for which comparable data are available (Table II), and of these, the difference is significant only in the Period of No Snow Cover of 1969. It appears, then, that sexual differences in mean movement index are more-or-less negligible for both genera.

White (1964) found an inverse correlation between population level and range of movement of *Peromyscus leucopus*. When the mean movement indices of male and female *Microtus* and male and female *Clethrionomys* are plotted against densities of either genus or both genera together, no well-defined relationship is apparent. There does, however, appear to be a direct relationship between the mean movement index of *Microtus* males and the density of *Microtus* males. Fig. 12 ( $0.2 > P > 0.5$ ) shows this relationship for the periods for which data are available. Due to the paucity of information on social relationships between *Microtus* males, it is impossible to say whether the correlation has biological meaning or whether it is an artifact. It does, however, suggest some interesting possibilities for further research, particularly as no such relationship is apparent between mean movement index and population density of *Microtus* females, or of *Clethrionomys* males or females. (Similar tests made on these three groups showed no significant correlations.)

Table II indicates that for female *Microtus* and both sexes of *Clethrionomys*, the greatest mean movement indices are in the Period of No Snow Cover of 1970. The main difference between this Period of No Snow Cover and the Periods of No Snow Cover of 1969 and 1971 appears to be the rather high amount of precipitation that fell in 1970 (Fig. 13). Furthermore, this was preceded by the wettest Period of Ebbing Snow

Fig. 12. Relationship between movement indices and density of *Microtus pennsylvanicus* males. TN = trap nights.

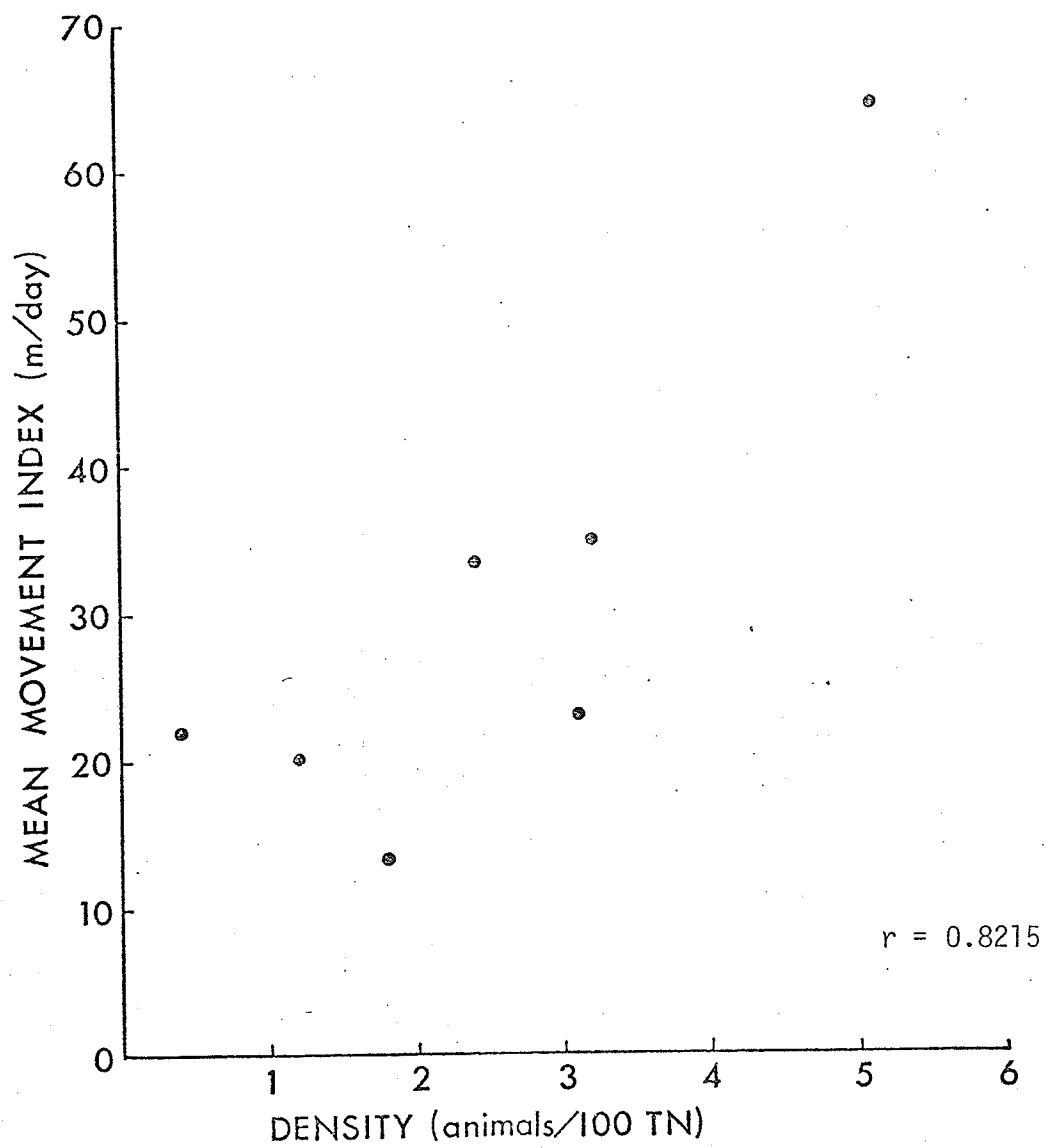
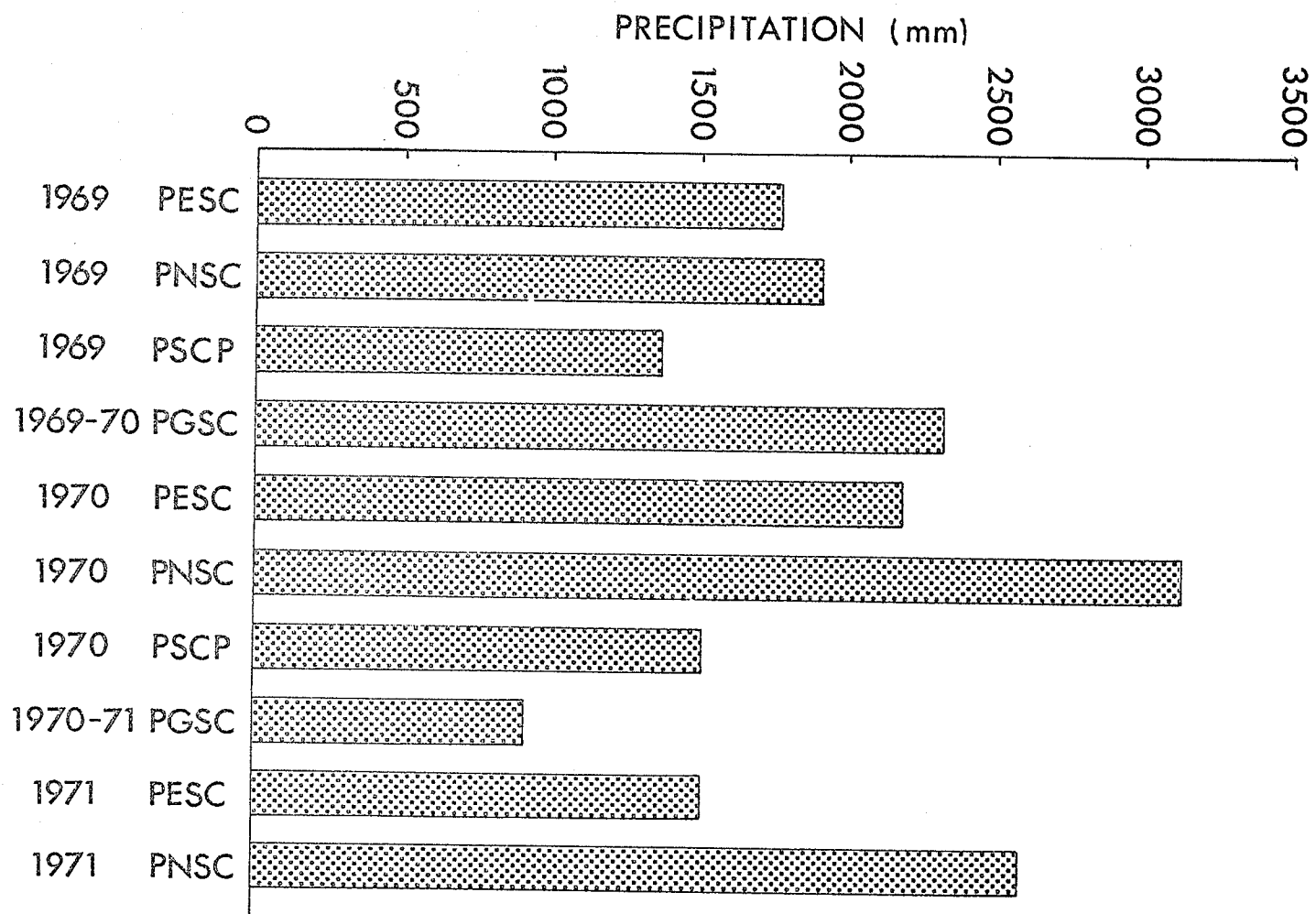


Fig. 13. Seasonal precipitation values recorded at Comfort Cove Meteorological Station during the study period. PESC = Period of Ebbing Snow Cover, PNSC = Period of No Snow Cover, PSCP = Pre-snow Cover Period, PGSC = Period of Greatest Snow Cover.



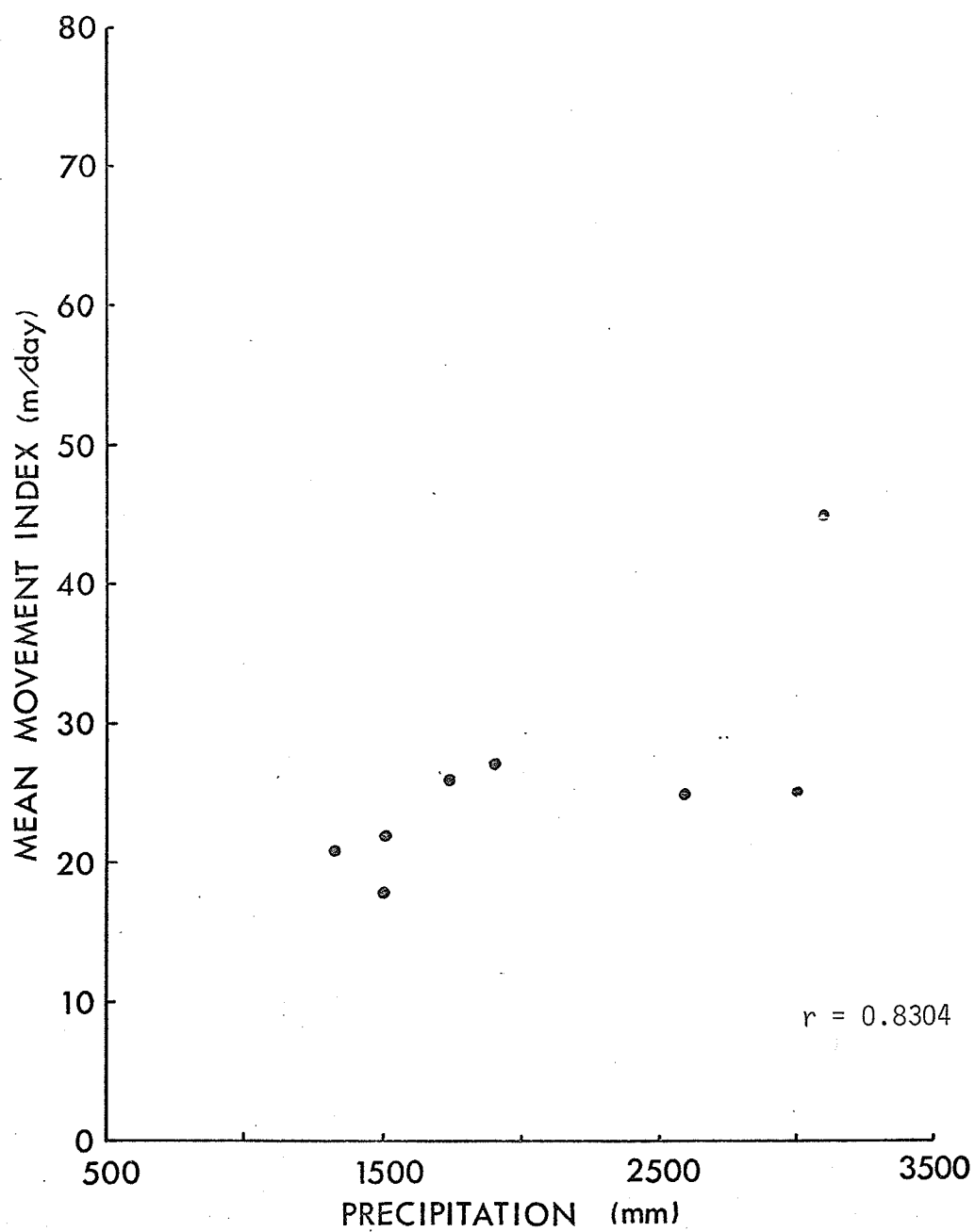


Cover of the three under consideration. When precipitation values for the Pre-snow Cover, Ebbing Snow Cover, and No Snow Cover periods are plotted against mean movement indices of *Clethrionomys* males (Fig. 14), a positive correlation ( $0.02 > P > 0.05$ ) is evident. However, similar tests done on *Microtus* males and on *Microtus* and *Clethrionomys* females indicate no correlation between mean movement index and amount of precipitation. (I have considered precipitation values only from Pre-snow Cover, Ebbing Snow Cover, and No Snow Cover periods in these calculations since precipitation in the Period of Greatest Snow Cover consists primarily of snow, the properties of which are very different from those of rain, the predominant form of precipitation in the seasons considered.)

Borowski and Dehnel (1952, cited by Sidorowicz, 1960) found that temperature and precipitation have a distinct effect on the captures of small forest mammals, and that the amount, quality, and duration of rainfall may increase the results of trapping tenfold or more. The authors (Sidorowicz, 1960) explained these results by the increase in the activity of small mammals caused by rain. Sidorowicz (1960) himself found that rain (or probably rather the changes caused by it in the microclimatic conditions of the habitat) affected the numerical results of trapping. As Sidorowicz (1960) did not analyze his data on a sexual basis, there is no way of knowing how closely my results parallel his.

The apparent correlation between movement index and rainfall needs to be investigated more thoroughly (I lack the data for a detailed analysis). Spot checks on such data as I do have indicate that there is wide individual variation in the distance moved on any one day, and on days with similar amounts of rainfall. Further research is necessary

Fig. 14. Relationship between movement indices of *Clethrionomys gapperi* males and seasonal precipitation values (exclusive of Periods of Greatest Snow Cover).



to elucidate this relationship, and to determine to what extent and in what manner rainfall does influence movement of these animals.

It appears that movement of females of both genera are unaffected either by density or rainfall. The restrictions imposed by bearing and raising young may well be the main factors governing their movements, but since I lack data on nest sites and litter sizes, such speculation cannot be tested at this time.

Table III and Figs. 15 and 16 show the breakdown of individuals into the three type-of-movement categories: Table III includes all individuals for whom sufficient data are available, while Figs. 15 and 16 show the breakdown on a yearly basis. Not all animals fit neatly into one category; for example, *Clethrionomys* 1022 (female) and *Clethrionomys* 1301 (male) exhibited long movements in the Period of No Snow Cover, and shifting areas of concentration during the Period of Greatest Snow Cover, while *Microtus* 0111 (male) had long movements interspersed with restricted ones in a pattern intermediate between long and shifting movements. In such cases as these I have chosen the predominant movement as being most characteristic of the individual.

Another type of problem arises with trap-happy individuals, the best example being *Clethrionomys* 0315 (male). This animal appeared to exhibit shifting areas of concentration, but a closer look at the trapping record shows that he probably was following the traps; when traps were moved to a different area, he would appear in the new area after a lapse of a day or so.

Although the number of individuals with sufficient number of recaptures is small, there are differences between the sexes and between

Fig. 15. Number of individual *Microtus pennsylvanicus* males (top) and females (bottom) in each of the three movement categories. 1 = long movements, 2 = shifting areas of concentration, 3 = restricted movements. Stippled indicates adults, plain indicates young animals.

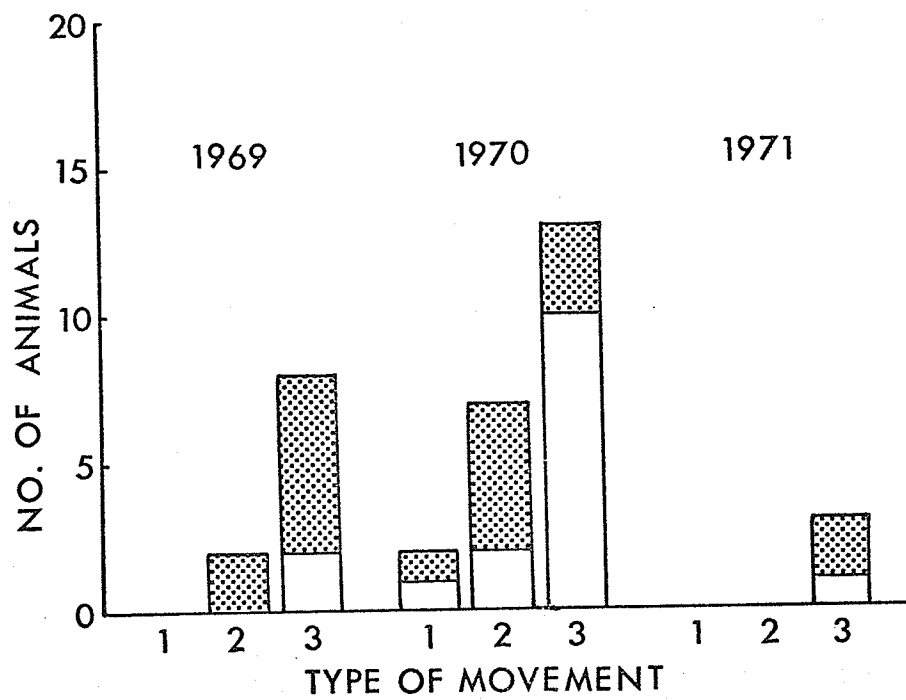
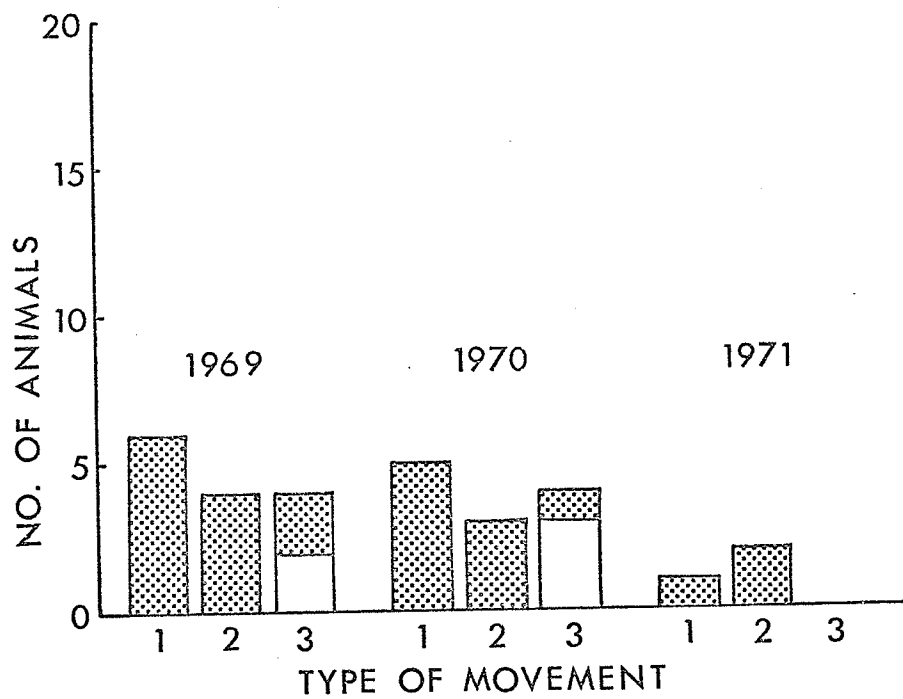
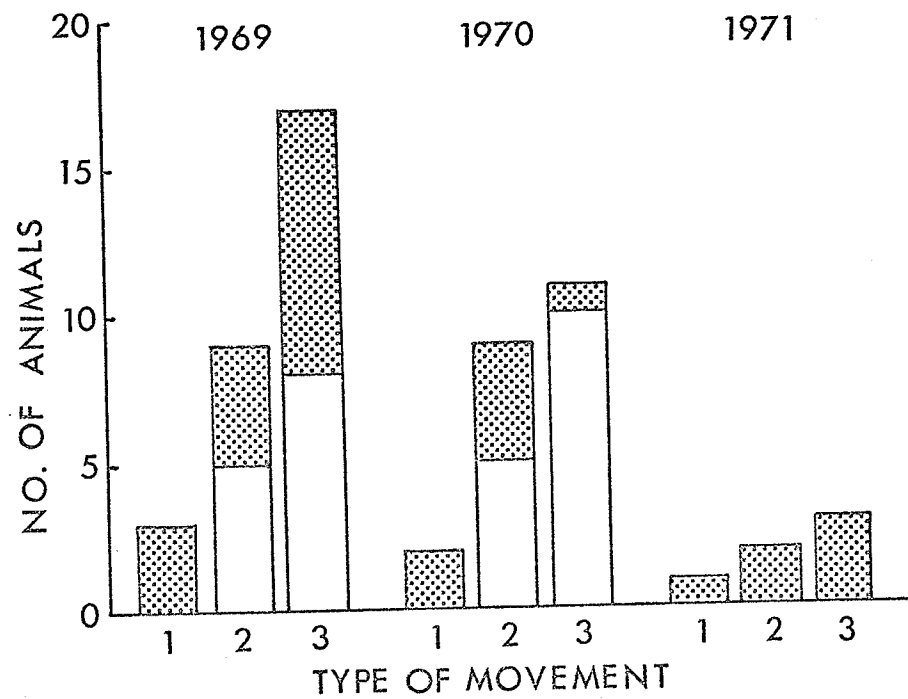
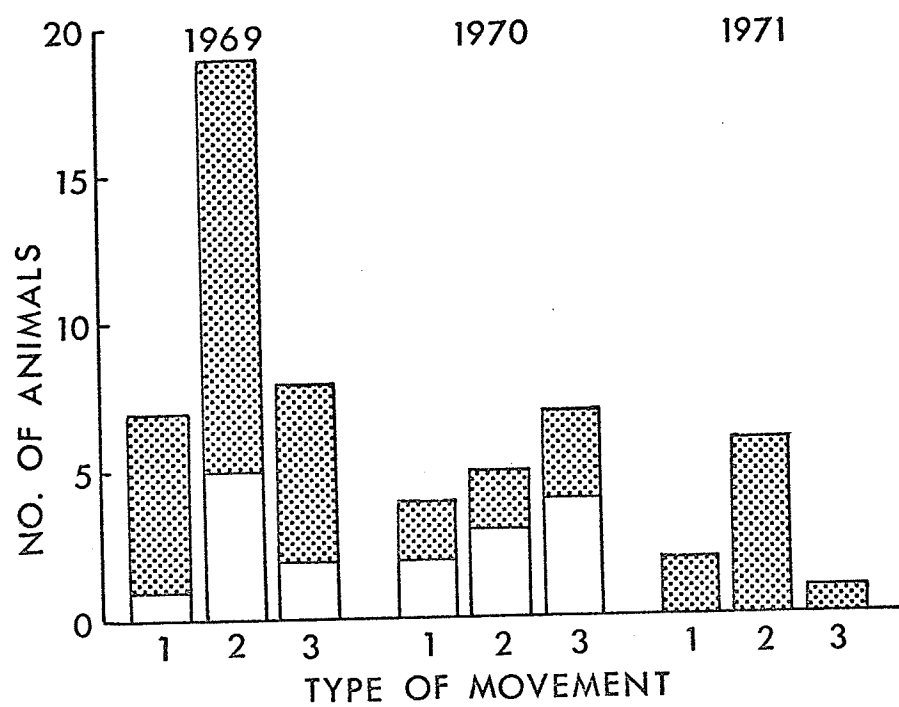


Fig. 16. Number of individual *Clethrionomys gapperi* males (top) and females (bottom) in each of the three movement categories. 1 = long movements, 2 = shifting areas of concentration, 3 = restricted movements. Stippled indicates adults, plain indicates young animals.





the genera that may be indicative of general population trends. Females of both genera seem to prefer restricted movements or shifting areas of concentration; in mature animals, at least, this probably is due to the restrictions of raising a family. However, among the females exhibiting long movements, all but two (one adult and one young-of-the-year) were pregnant and/or lactating while making their longest movements. For example, *Clethrionomys* 0330 was caught and noted to be visibly pregnant on 16 June 1969. She then disappeared from the trapping record until 26 June 1969, at which time she was reported to be aggressive and lactating and presumably had had a litter. She was then captured daily until 4 July 1969, with an average movement index for this period of 52 m/day. This pattern is typical of the few females that exhibited long movements; females with shifting areas of concentration, however, generally covered the longest distance after lactation had ceased. Among the young-of-the-year females for both genera, even those that matured over the first Period of No Snow Cover seemed to prefer restricted movements to long ones, with a few preferring shifting areas of concentration.

Among the males, *Microtus* appeared to show a slight preference for long movements, while *Clethrionomys* males in 1969 showed primarily shifting areas of concentration and in 1970 restricted movements. It is interesting to note that *Clethrionomys* young-of-the-year males were present in all three categories, while *Microtus* young-of-the-year males appeared to exhibit only restricted movements. Again, more data are necessary to determine whether this reflects different social and/or environmental reactions, or whether it merely reflects the small number

of young *Microtus* males.

### Swimming Tests

Unlike Riewe (1971), I did not detect inter-island movements by either *Clethrionomys* or *Microtus* but, as stated in the description of the study area, Camel Island is reasonably isolated. Snap traps set on Sivier Island, Tinker Island, and the rocks off Knights Island yielded no animals at all. On 25 June 1971 three *Clethrionomys* and three *Microtus* were released on the rock off the south coast of Camel Island, but by the time trapping was terminated on 30 July 1971, none had been recaptured on the island even though the area opposite the rock had been continuously inundated with traps.

There are, in the literature, numerous reports of *Microtus* swimming (see Riewe, 1971, for review), but I have been unable to find any field observations of *Clethrionomys* swimming. Getz (1967b), in experiments using aquaria and aquatic tables, found *C. gapperi* to be better swimmers than *M. pennsylvanicus* of comparable size, but *Microtus* treated the water as less of a barrier than did *Clethrionomys*. Butsch (1954) also remarked that *Clethrionomys* did not readily enter water. On several occasions I noticed that, when animals were released in the bog, *Microtus* would swim across pools of standing water with no hesitation, but *Clethrionomys* invariably made straight for the nearest hummock. Even in laboratory cages, when water bowls were used in place of water bottles, *Microtus* could occasionally be seen running through the water in the bowls, and the water had to be changed daily due to the accumulation of feces therein. I have never seen *Clethrionomys* splashing about in their water.

bowls, and the accumulation of feces there was always minimal.

To gain some indication of how the swimming abilities of *Clethrionomys* compared with those of *Microtus*, I performed a limited number of swimming tests in the cove off Camel Island (Figs. 17 and 18 and Table IV). The number of tests performed was too small to allow any conclusions to be drawn, however it does indicate that *Clethrionomys* compared favourably with *Microtus*. *Clethrionomys* 1442 (male) swam rapidly in a straight line for shore so that I was unable to retrieve him from the water. He escaped onto the rocks and was retrapped two days later. *Clethrionomys* 1452 (male) would have reached shore had I not managed to net him while he was still swimming. The only *Microtus* (1340, male) to swim a comparable distance was pulled from the water when he showed signs of foundering.

The tests with *Microtus* indicate that there may be some difference between the swimming abilities of the males and those of the females; alternatively it may indicate only individual differences, especially as Riewe (1971) found no significant difference between the sexes. As no *Clethrionomys* females were tested, it is impossible to say whether or not there might be sexual differences in swimming ability.

Grant (1970), in discussing the comparative dispersal abilities of *Microtus* and *Clethrionomys*, has said that the absence of *Clethrionomys* from most offshore islands in North America might reflect a lowered dispersal ability for this genus, but that at present our knowledge is incomplete. There is certainly a lack of information on the comparative dispersal abilities of these animals, however, I suspect that the biggest difference lies not in the actual swimming abilities but in the psycholo-

Fig. 17. *Clethrionomys gapperi* 1444 (male) swimming in Indian Cove.



Fig. 18. *Clethrionomys gapperi* 1444 (male) recuperating after the swimming experiment. The fur on this animal became wet, consequently he had to be taken from the water after two minutes.



TABLE IV

Swimming tests conducted on *Microtus pennsylvanicus* and *Clethrionomys gapperi* in Indian Cove, Camel Island

Vole number, sex, and weight	Date	Weather conditions	Sea conditions	Shortest distance from shore	Time in sea	Distance swum	Comments
<i>Microtus</i>							
1 0302 ♀ 45.1 g	3-vii-70	Air temp. 64°F; hazy; about 85% cloud cover	Water temp. 54°F; wave action almost nil; current slight	~170 m	4 min.	Headway nil	Zig-zagged and circled, never moving far from boat.
2 0340 ♂ 50.9 g	3-vii-70	As above	As above	~150 m	4 min.	100 m	Swam in zig-zags toward south point of island. Retrieved when he began to drown.
3 0331 ♀ 46.8 g Black	3-vii-70	As above	As above	~150 m	9 min.	Headway nil	Her course alternated between swimming around boat and making a few attempts to swim to south point of island; after about 10 feet, she would return to boat.
<i>Clethrionomys</i>							
4 1442 ♂ 29.8 g	23-vi-71	Winds NW at 2 mph	Wave action slight	~100 m	8 min.	100 m	At first attempted to climb boat, then headed for south point of island. Escaped on rocks.
5 1444 ♂ 29.2 g	23-vi-71	As above	As above	~100 m	2 min.	Headway nil	He became wet at entry. Attempted to climb boat and never swam far from boat. Removed after 2 min. when he looked as if he was drowning. Released again 8 feet from boat, but had to be removed after 1 min. Exhausted.
6 1452 ♂ 17.7 g	1-vii-71	Winds N/NE at 15-20 mph	Wave action slight	~150 m	5 min.	120 m	Swam to bow of boat, then headed straight for shore. Pulled from water after 5 min. He was reluctant to be recaptured. Left alone, he would have swum to shore.



gical attitude toward water: *i.e.*, that *Microtus* treat it as less of a barrier than do *Clethrionomys*.

## THE MARITIME WINTER<sup>1</sup> AND ITS EFFECT ON *MICROTUS* AND *CLETHRIONOMYS*

The role of winter in the ecology and survival of small mammals has, in recent years, been recognised as being a very important one, and work is slowly progressing toward unravelling the individual effects of the physical and meteorological factors involved. To date, however, most work has been done in tundra and continental taiga regions (Formozov, 1946; Fuller, 1969; Pruitt, 1957), and little attention has been paid to maritime areas.

Pruitt (1970) considered the snow of the interior Alaska taiga to be "typical" snow, *i.e.*, snow that is least modified by external factors. The following is a description of supranivean winter conditions in the interior Alaska taiga (Pruitt *et al.*, 1961): temperatures fall steadily through October and November to around  $-17.8^{\circ}\text{C}$  at the end of November. In December they drop below  $-17.8^{\circ}\text{C}$ , the air is noticeably dry, and there is little wind. January is the coldest month with, usually, the heaviest snowfall. The ambient air temperatures begin to climb in February, and this month has less precipitation than January. Precipita-

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<sup>1</sup>In this section the terms "winter" and "Period of Greatest Snow Cover" are not used synonymously. "Period of Greatest Snow Cover" refers, as in other sections, to the period from 16 November to 15 March. "Winter" is used in a general sense and includes part of the Pre-snow Cover Period and part of the Period of Ebbing Snow Cover as well as the whole of the Period of Greatest Snow Cover.

tion is still less in March, by which time the minimum temperature is usually above  $-17.8^{\circ}\text{C}$ , and April is the driest month of the year.

This pattern of winter conditions is very different from that of the maritime Newfoundland taiga (Figs. 19 and 20). Here the winters are characterized by mild temperatures throughout most of October and November, and alternating freeze-thaw thereafter, with temperatures seldom dropping below  $-20^{\circ}\text{C}$ . From an anthropocentric viewpoint, maritime winters would appear to be very mild, however, from a small mammal's point-of-view, the picture is probably very different.

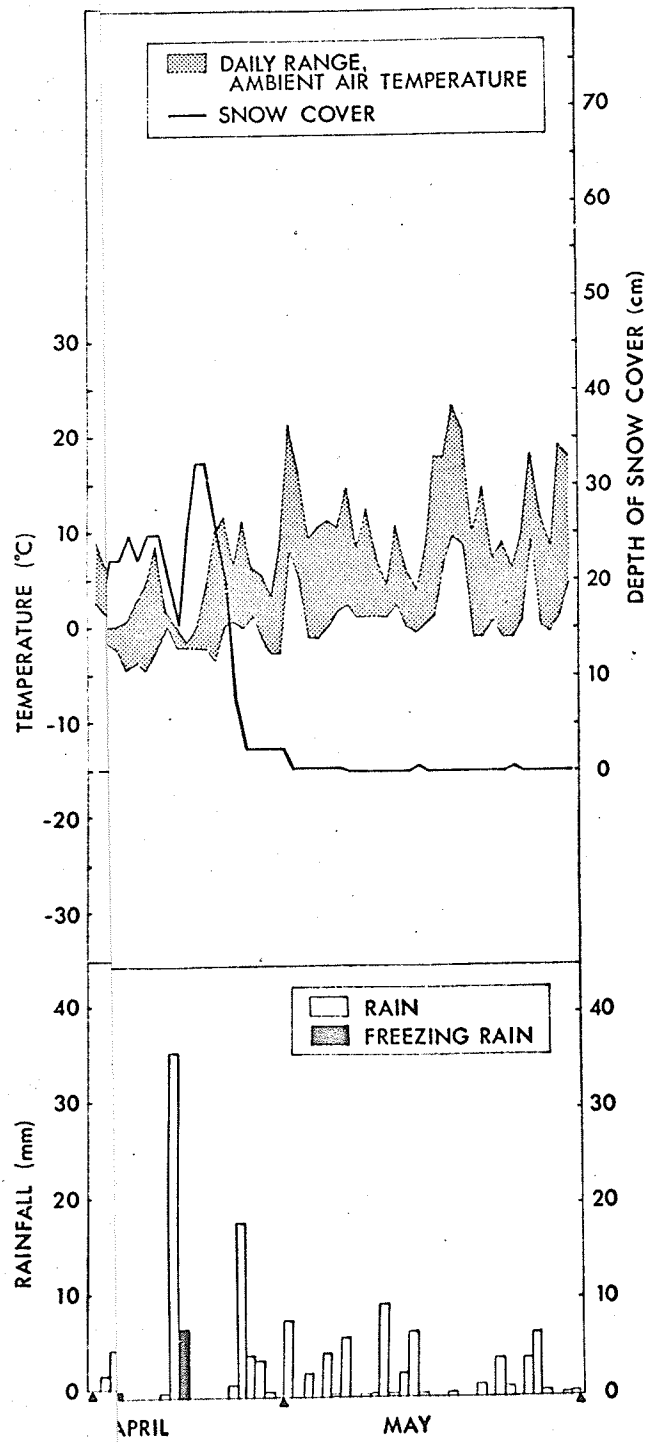
Pruitt (1957) has shown that the period between the thermal overturn<sup>1</sup> and the time when the snow cover reaches a thickness of 15-20 cm (the hiemal threshold) is a critical one for small mammals since the temperature of the upper moss layers closely follows the ambient air temperature fluctuations. Once the hiemal threshold has been reached, however, the bioclimate of the small mammals becomes quite stable: the temperature seldom drops below  $-6.7^{\circ}\text{C}$ , the air beneath the snow is calm and essentially saturated with moisture, and the environment is a dark and silent one (Pruitt, 1957). The data of Pruitt (1957) and of Fuller *et al.* (1969) indicate that in the subarctic taiga, once the hiemal threshold has been reached, the snow cover continues to build up throughout the winter until ablation begins in the spring, followed by the final disappearance of the snow.

Such is not the case in the maritime Newfoundland climate. Figs. 19

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<sup>1</sup>Thermal overturn: the date at which the air temperatures fall below those of the substrate and the moss surface temperatures fall below those of the deeper areas.

Fig. 19. Depth of snow cover, daily range of ambient air temperature, and occurrence of rain and freezing rain during the winter of 1969-70 as measured by the Comfort Cove Meteorological Station near Camel Island.



and 20 show that in both the Period of Greatest Snow Cover of 1969-70 and 1970-71, the hiemal threshold was reached on several occasions, following which the snow cover dropped below this critical level. Although I was unable to take thermistor readings below the snow, data collected by R. R. Riewe (pers. comm., 1972) indicate that, on the whole, subnivean temperatures do not vary significantly from those of the ambient air. Furthermore, I suspect that there is no definite date at which the thermal overturn can be said to have been reached, thus indicating that, in the Newfoundland maritime taiga, the whole winter is a critical period for small mammals.

Table V is a summary of what I consider to be critical factors operating singly or in combination with each other throughout the winter. The table is obviously not complete since important factors such as density and presence or absence of ice layers in the snow have been omitted, and of the factors included it is impossible to say which are operating most effectively, but it does give some indication of the variety and frequency of critical factors with which small mammals in this environment must cope.

Probably the most obvious critical factor is rainfall. Fig. 21 shows the rainfall from April 1969 to August 1971 as measured by the Comfort Cove Meteorological Station. Being in a maritime climate, the magnitude of rainfall here is significantly higher than for interior taiga areas (compared with Fuller's (1969) precipitation data, Camel Island receives approximately ten times more rain during the Period of No Snow Cover). Heavy rain during the Period of No Snow Cover probably is not too serious: temperatures are warm, and intermittent sunny periods give both the ground

Fig. 20. Depth of snow cover, daily range of ambient air temperature, and occurrence of rain and freezing rain during the winter of 1970-71 as measured by the Comfort Cove Meteorological Station near Camel Island.

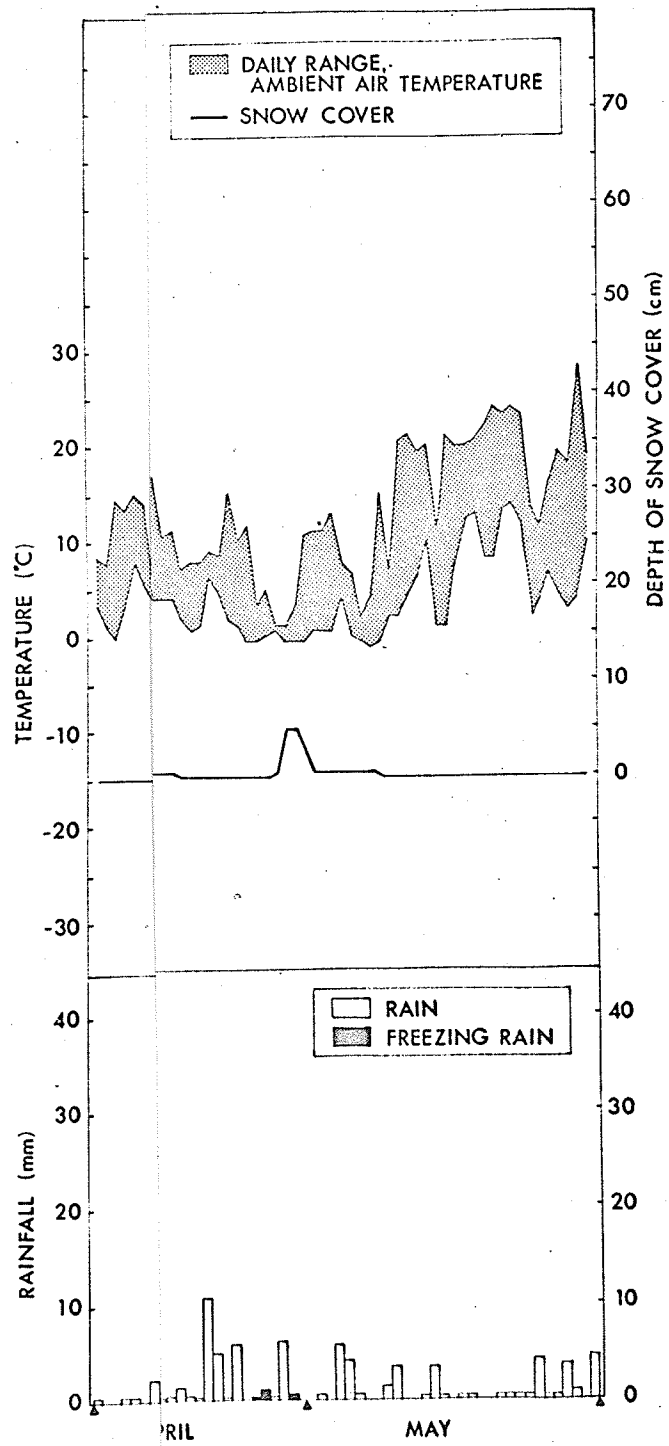




Fig. 21. Rainfall by half-months from April 1969 to August 1971 as measured by the Comfort Cove Meteorological Station near Camel Island. Clear bars present rainfall during the first half of the month (1-15) and dark bars represent rainfall during the last half of the month.

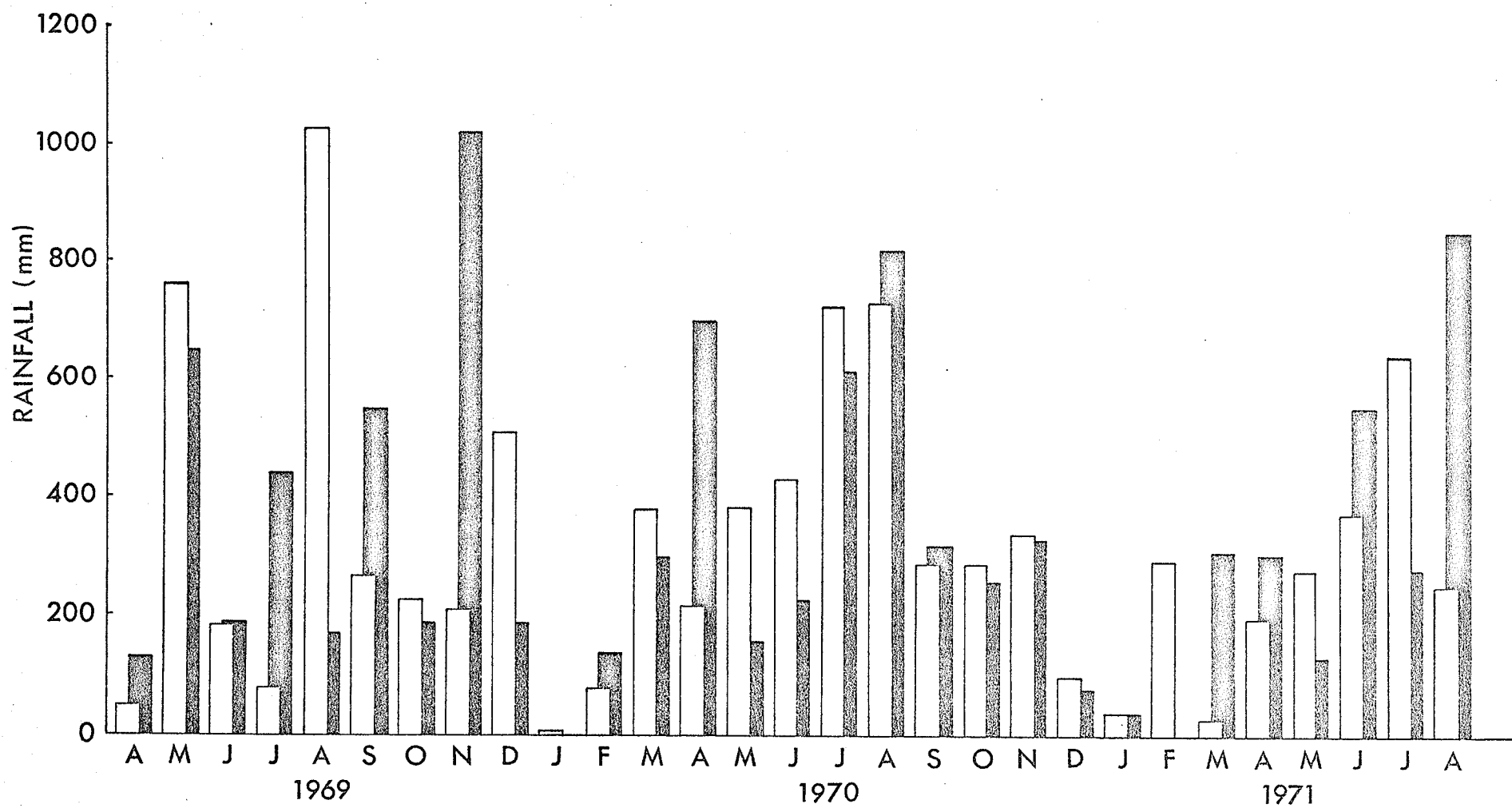


TABLE V

Frequency of occurrence (in days) of critical factors affecting the microhabitat of *Microtus pennsylvanicus* and *Clethrionomys gapperi* during the winters of 1969-70 and 1970-71 on Camel Island

		Rain with minimum temperatures above 0°C	Rain with maximum temperatures below 0°C	Snow cover absent or trace with temperatures below 0°C	Snow cover less than 15 cm with temperatures below 0°C	Snow cover less than 15 cm with temperatures above 0°C	Snow cover greater than 15 cm with temperatures above 0°C	Freezing precipitation	Preceding factors absent	Snow cover greater than 15 cm at all temperatures
October	1969-70 1970-71	12 17	3 2	5 3	6 2	0 0	0 0	0 0	7 10	1 0
November	1969-70 1970-71	9 12	7 8	18 9	1 7	0 1	0 1	0 1	2 6	0 2
December	1969-70 1970-71	10 2	7 11	9 0	8 5	0 4	2 7	3 9	2 17	3 26
January	1969-70 1970-71	0 0	1 11	11 0	2 0	2 0	3 10	6 9	15 21	18 31
February	1969-70 1970-71	1 0	6 4	8 0	12 14	7 3	3 6	5 3	3 8	6 14
March	1969-70 1970-71	0 1	19 10	0 0	5 20	5 18	20 10	16 8	6 0	26 10
April	1969-70 1970-71	6 13	8 8	0 9	2 9	5 10	22 0	7 4	3 0	25 0
May	1969-70 1970-71	16 19	5 2	8 7	1 1	1 1	0 0	0 0	6 6	0 0
TOTAL	1969-70 1970-71	54 64	56 56	59 28	37 58	20 37	50 34	37 34	44 68	79 83

and the animals a chance to dry out. At this time of year there is also the added benefit of moisture inducing greater plant growth, thus increasing the food supply. In the Pre-snow Cover Period, however, heavy rain combined with temperatures near freezing places far more stress on the animals. October and November are usually wet months (Fig. 21), with water lying on the ground for days and sometimes weeks at a time. Rikhter (1945) said that fine and frequent rainfall at temperatures near freezing caused the formation of a thin ice-glazed frost, which would indicate that for most of the Pre-snow Cover Period in the maritime Newfoundland climate the environment of small mammals is either saturated with water or ice-coated. In 1969 intermittent rain in one form or another, often coupled with subzero temperatures, continued until mid-January (Fig. 21) when the hiemal threshold was reached for more than a few days at a time. Throughout this wet period animals were trapped most frequently in or near the cabin (where food and dry shelter presumably were more readily attainable). Captures from other trapping areas dropped dramatically during this time. The October to January period of 1970 had significantly less rainfall than in 1969 (Figs. 19 and 20), but was still greater than usually occurs in continental taiga regions.

The occurrence of rain or freezing precipitation after the hiemal threshold has been reached also has adverse effects on small mammals due to the formation of ice crusts (*sigulik*). Bashenina (1956), Formozov (1946), and Pruitt (1957) have pointed out that there is often a build-up of carbon dioxide in small mammal tunnels under the snow, and to counteract this the animals build "ventilator shafts" by tunnelling to the surface. Obviously, the presence of *sigulik* at the snow surface, or

anywhere below it, is going to make the building of such shafts difficult, if not impossible. The need for ventilator shafts is probably even greater for animals in this maritime climate than in "typical taiga" since the thawing that occurs throughout the winter causes the snow to become very dense and to take on a large, granular structure. Such snow is only slightly permeable to air, but as compensation, thaw channels which serve as canals for the admission of air usually form around bushes, tree trunks, clumps of grass, and branches (Rikhter, 1945). These thaw channels are probably very important for voles overwintering in a maritime climate, but following a period of freezing precipitation (Fig. 22), even they would be frozen over and the snow at the base would be further compressed (Bader *et al.*, 1939), thus creating another stress factor.

Fuller (1969) has observed that a prolonged period of snow melt means that melt water appears under the snow and a large proportion of the total habitat is unavailable to the animals. In a maritime climate this factor operates intermittently throughout the winter, with increasing frequency from March until the disappearance of the snow cover in late April or early May. Even after this time, temperatures usually remain low (hovering just above or below freezing point) until late May or early June due to the presence of pack ice in the bay. Rainfall in May is usually well above the amount that Fuller (1969) considered as having an adverse effect on small mammals: he considered a May rainfall of 34 mm to affect small mammals adversely. The maximum May rainfall in the Camel Island region during the period of this study was 762.5 mm and the minimum was 162.5 mm. This magnitude of rainfall combined with the

Fig. 22. Freezing precipitation on branches of trees. In this instance, the weight of the ice has broken a branch. Freezing precipitation creates ice crusts (*sigulik*) in the snow cover and probably seals off thaw channels around bushes, tree trunks, etc.



low temperatures could only prolong the already lengthy critical period.

Although on Camel Island the winters of 1969-70 and 1970-71 were both quite different from the more typical winters dealt with by Fuller *et al.* (1969) and Pruitt (1957), there are, nevertheless, several significant differences between the two. In both 1969 and 1970 minimum ambient temperatures began to fall below freezing in the latter part of October. In 1969 minimum and sometimes maximum ambient temperatures fluctuated about the freezing point for 73 days, until a cold snap set in on 31 December. During this time the hiemal threshold was reached for one day in October and for three days in December (Fig. 19). From 31 December until 2 February, maximum ambient temperatures remained below 0°C with only a few digressions above the freezing point. During this 34-day cold snap, the hiemal threshold was reached for 20 days. On 3 February the maximum ambient temperature rose above 0°C and the snow began to melt. Snow cover remained below the hiemal threshold for 22 days while another cold snap was experienced (Fig. 19). On 27 February the hiemal threshold again was attained and remained more or less continuously until 25 April (57 days) when the snow cover began its final disappearance.

In 1970 ambient temperature fluctuations about the freezing point lasted for only 41 days (from 19 October to 28 November). On 29 November the ambient temperatures fell, marking the beginning of a 91-day cold period (maximum temperatures rose above 0°C on several occasions for a day or two, then dropped below freezing again). The hiemal threshold was reached on 30 November and was present almost continuously for 71 days until 15 February. Between 16-28 February a cold snap occurred in



the absence of the hiemal threshold, following which maximum ambient temperatures rose above freezing and, except for a few deviations (Fig. 20), remained there. The hiemal threshold again was reached for 10 days in March, after which the snow cover rapidly melted and was virtually non-existent by 8 April. It is interesting to note that the total precipitation during the winter of 1970-71 was approximately half that of the winter of 1969-70 (Fig. 13).

The winter of 1970-71, then, appears to be the more favourable of the two as far as small mammals are concerned. In 1970-71 the hiemal threshold was reached on 29 November and, except for a five-day lapse, remained continuously for 71 days during December, January, and February, which are the coldest months. In 1969-70 during these months there were only 27 days on which the hiemal threshold was present and these were not continuous. The critical periods occurring during the Pre-snow Cover Period and Ebbing Snow Cover Period of 1970-71 were also much shorter than those of 1969-70 (Figs. 19 and 20).

Figs. 23 and 24 show captures per 100 trap nights for *Microtus* and *Clethrionomys* for the months I was in the field. Unfortunately, there are no trapping data for the winter of 1970-71. It is interesting to note, however, that the number of captures of *Clethrionomys* (Fig. 24) was high throughout the Period of No Snow Cover of 1969, then crashed over the Period of Greatest Snow Cover. The number of captures remained low throughout the periods of Ebbing Snow Cover and No Snow Cover of 1970 and increased slightly in the Pre-snow Cover Period. Captures in the Period of Ebbing Snow Cover of 1971 were only slightly lower than in the Pre-snow Cover Period of 1970, thus indicating a high survival rate over

Fig. 23. Captures per 100 trap nights of *Microtus pennsylvanicus* from May 1969 to July 1971. Stippled portion of bar indicates captures/100 TN in all habitats; stippled plus unstippled portion indicates captures/100 TN when burn trap nights are not included. (*Microtus pennsylvanicus* were seldom captured in the burn.)

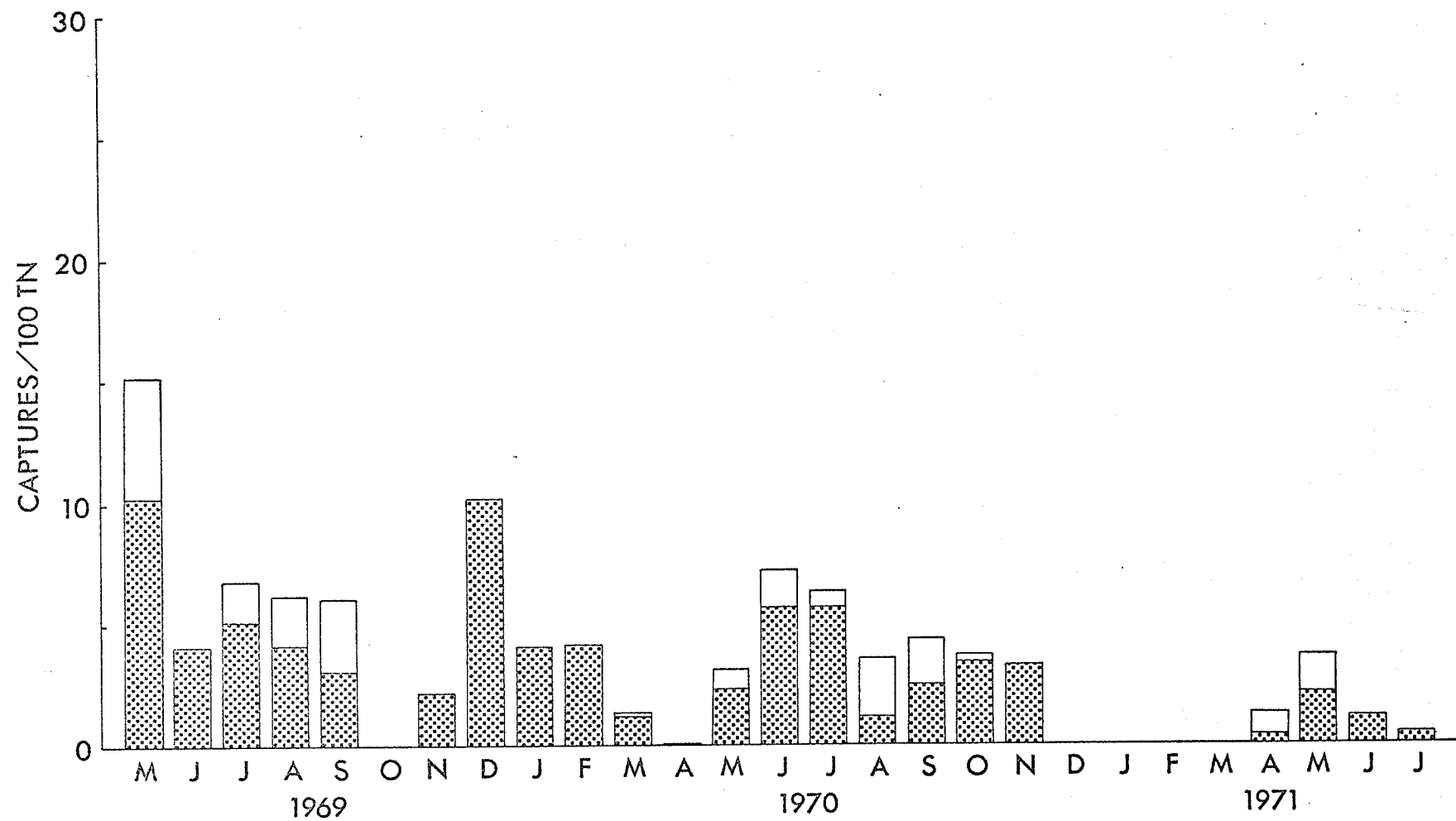
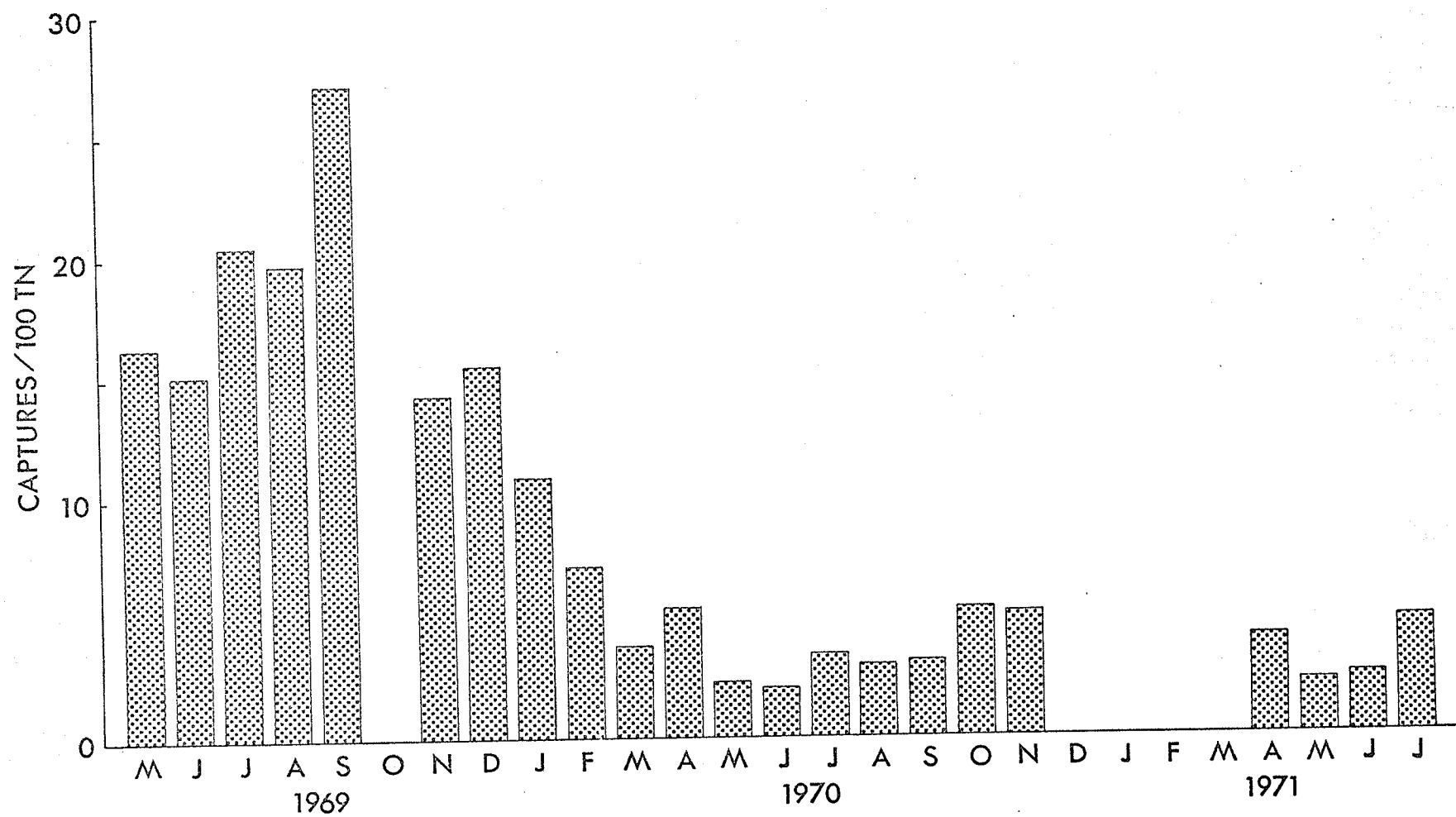


Fig. 24. Captures per 100 trap nights of *Clethrionomys gapperi* from May 1969 to July 1971.



this winter. *Microtus*, on the other hand, showed little fluctuation in the number of captures per 100 trap nights, with no distinct build-ups or crashes in either winter (Fig. 23).

Day by day winter captures on a per trap night basis are shown for the cabin (Fig. 25) and for other areas of the island (Fig. 26). Cabin trapping was done only sporadically, mainly with a view to removing the animals from our food supply. On nights when cabin trapping was carried out, however, the number of *Clethrionomys* caught in the cabin was almost invariably higher than the number caught on the trap lines. Only in February and early March was this true for *Microtus* (Figs. 25 and 26 and Table VI), and this situation was primarily caused by 0322 who accounted for 9 of the 12 *Microtus* captures during this period.

Occasionally animals were captured by accident in the cabin: in November I found six *Clethrionomys* and one *Microtus* dead in a slop bucket on my return from a trip to town; this happened again in January, but this time only two animals could be identified. Occasionally captures were made by hand or in traps that inadvertently had been left set. Adding these accidental captures to the figures in Table VI gives a total of 42 *Clethrionomys* and 8 *Microtus* individuals captured in the cabin over the winter. Of these, 2 *Clethrionomys* had been caught previously on Plot V at the far end of the island; 3 had been trapped on Plot IV in September; 23 had not been marked before the winter; while the remaining 14 were from nearby partial tuckamoor and forest. Of the eight *Microtus* captured in the cabin, five had not been marked before the winter, while the remaining three came from nearby partial tuckamoor and forest. It appears, then, that both species either had high immigration rates or else

Fig. 25. *Microtus pennsylvanicus* and *Clethrionomys gapperi* captures per trap night in the cabin on Camel Island in 1969-70.

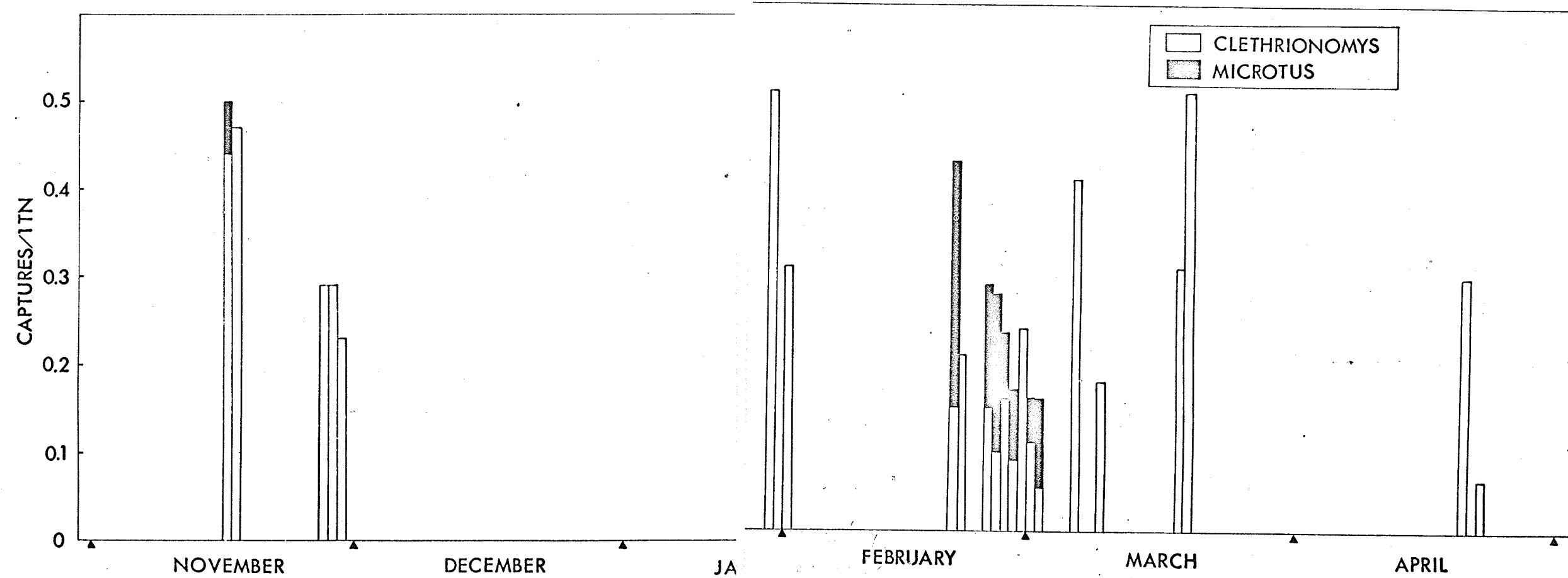




Fig. 26. *Microtus pennsylvanicus* and *Clethrionomys gapperi* captures per trap night on plots and trap lines on Camel Island in 1969-70.

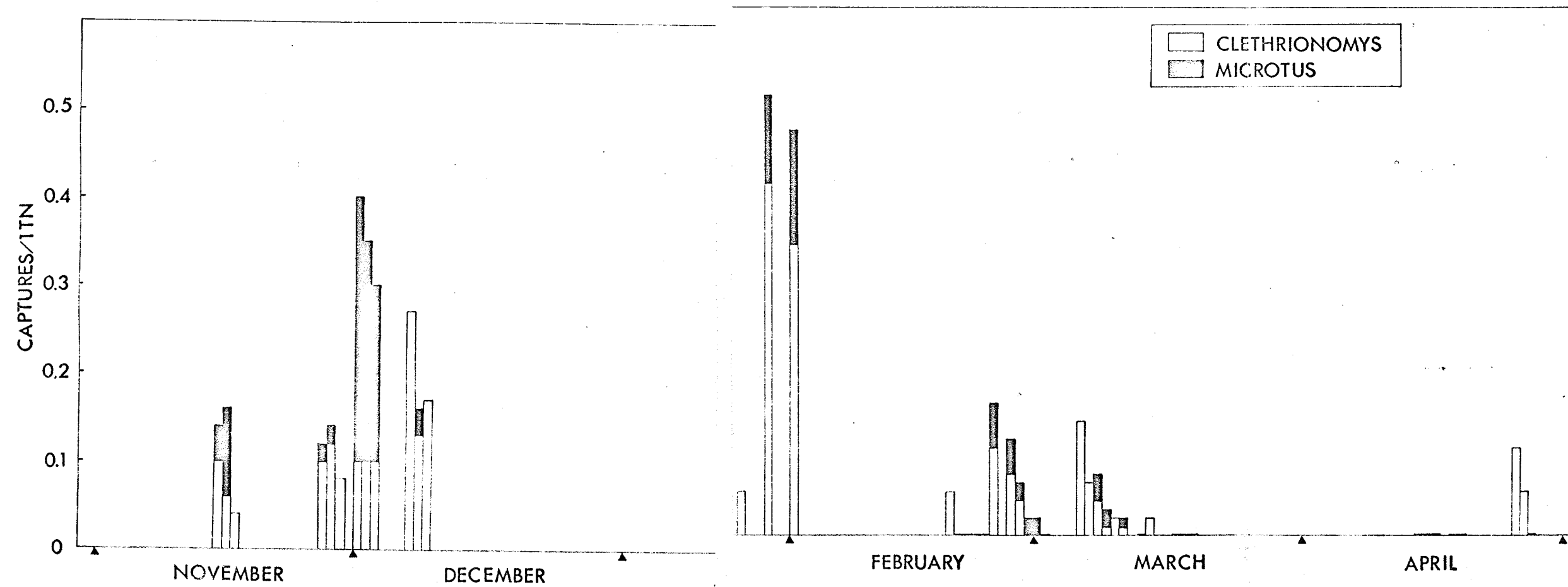


TABLE VI

Captures of *Microtus pennsylvanicus* and *Clethrionomys gapperi*  
in the cabin on Camel Island in the winter of 1969-70

Month	TN in cabin	Number of captures in cabin	Number of animals in cabin	Cabin animals as percent of total
<i>Microtus pennsylvanicus</i> :				
November	50	1	1	7.1%
December	0	-	-	----
January	33	1	1	7.1%
February	63	9	3	30.0%
March	49	3	1	14.3%
April	25	0	0	0.0%
	TOTAL:	14	6	
<i>Clethrionomys gapperi</i> :				
November	50	25	14	32.6%
December	0	--	--	-----
January	33	3	3	12.5%
February	63	12	8	38.0%
March	49	9	4	26.7%
April	25	5	5	62.5%
	TOTAL:	54	34	

a large number of trap-shy individuals began to be caught once the winter set in. While the answer probably lies somewhere between these two alternatives, I think that most of the influx is accounted for by immigration: for *Clethrionomys* there are five records of known emigration from Plots IV and V; for *Microtus* there are no records of known emigration from far-off trap sites, but in general individuals of this species were very far-ranging and throughout the trapping period unmarked adult individuals were often picked up. Table VII shows the number of unmarked individuals from all habitats on a monthly basis over the winter. For *Clethrionomys* the percentage of unmarked animals dropped dramatically as the population declined; for *Microtus*, with the exception of February and March when no new animals were caught, the percentage of unmarked individuals was high throughout the winter.

Table VIII shows the mortality rates for the two species over the winters of 1969-70 and 1970-71. It is interesting to note the extremely high mortality rate of *Clethrionomys* during the first winter and the lower mortality rate in the second. These figures suggest that the more adverse the winter, the higher the mortality rate of this species, but, before any hard and fast rule can be laid down, more work needs to be done studying the response of an introduced population such as this to winters, over an extended period of time. The same holds true for *Microtus* who, on the basis of this study, appear better adapted to the inconsistent maritime winters than are *Clethrionomys*. Crowell (1973) found *C. gapperi* to be a poor colonizer and unable to maintain populations when introduced to islands in Penobscot Bay, although one population did succeed for five years before becoming extinct (pers. comm., 1972). Perhaps maritime

TABLE VII

Number of individual *Microtus pennsylvanicus* and *Clethrionomys gapperi*  
captured in the winter of 1969-70

Month	Number of new animals caught	Total animals caught	New as percent of total
<i>Microtus pennsylvanicus</i> :			
November	8	14	57%
December	5	13	38%
January	5	14	36%
February	0	10	0%
March	0	7	0%
April	1	3	33%
<i>Clethrionomys gapperi</i> :			
November	20	43	47%
December	11	27	41%
January	5	24	21%
February	3	21	14%
March	2	15	13%
April	0	8	0%

TABLE VIII

Overwintering mortality rates for *Microtus pennsylvanicus* and *Clethrionomys gapperi*  
on Camel Island in 1969-70 and 1970-71

	<i>Microtus pennsylvanicus</i>		<i>Clethrionomys gapperi</i>	
	1969-70	1970-71	1969-70	1970-71
Number of animals present in Pre-snow Cover Period	47	36	98	79
Number of overwintered animals present in Period of Ebbing Snow Cover	23	10	19	45
Mortality	51.1%	66.7%	80.7%	43.1%

winters play an important role in the exclusion of *C. gapperi* from coastal islands, as my data suggest they might. Furthermore, if *M. pennsylvanicus* is better adapted than *C. gapperi* to surviving in a maritime climate, the reasons for this need to be investigated. The *Microtus* population on Camel Island did not appear to exhibit the extreme increases and crashes that the *Clethrionomys* showed. Is this a unique situation or an adaptation on the part of *Microtus* to ensure that a few far-ranging individuals will have less intraspecific competition during the months when foraging is most difficult? McCabe and Cowan (1945), discussing *Peromyscus maniculatus* on islands off the coast of British Columbia, suggested that the marginal conditions which kept the numbers of *Peromyscus* down and the distribution sparse could be, at the same time, a safeguard against epidemic maladies. They further suggested that such marginal conditions may, in this one respect, be more favourable than those of environments which otherwise approach the optimum. Evans (1942) put forward a similar suggestion for a wide-ranging, low density population of *Apodemus sylvaticus* in Berkshire.

Jewell (1966) found that populations of *C. glareolus* on Skomer Island and *Apodemus sylvaticus* on St. Kilda were larger than their mainland counterparts. The *Microtus* on Camel Island also exhibited this phenomenon: it was not uncommon to find adult males and adult, non-pregnant females weighing between 50 and 60 g. Is this, perhaps, an adaptation to capricious winter conditions? Larger size would mean a lowered body surface-mass ratio so that less body heat would be lost to the atmosphere; it might also allow the animal a longer period of weight loss before a critical minimum was reached (see Discussion for further comments on size

of animals).

On the basis of the data I have collected from Camel Island, I cannot say why *Microtus* appears to be better adapted to a maritime climate than *Clethrionomys*, but I suggest the foregoing as factors that may be important and that should be studied over an extended period of time during all seasons.



## DISCUSSION

In 1965 Cameron published a paper on competitive exclusion between the genera *Microtus* and *Clethrionomys*, based in large measure on results of sporadic trapping on islands off the eastern coast of North America. Cameron also included British representatives, *C. glareolus*, *M. arvalis*, and *M. agrestis*, but since I have not had first-hand experience with these, I shall restrict the discussion to the North American genera. He found *Clethrionomys* to be absent from all eastern North American offshore islands; *Microtus*, however, not only appeared to be firmly established, but was found in woodland as well as grassland habitat (Cameron, 1958a). *Clethrionomys* was also absent from all small coastal islands (less than 2 miles offshore), except those connected to the mainland by some sort of land bridge (Cameron, 1965). This Cameron interpreted as evidence of "severe competition" between the two genera: on isolated islands the two genera would be incapable of co-existing, so that the first to arrive and establish a population on an island would not only utilize unusual habitat but would be capable of preventing its competitor from colonizing by establishing a "beachhead"; on islands connected to the mainland by a land bridge, competition would increase in severity after the bridge had disappeared until *Microtus* eventually replaced *Clethrionomys*. This, Cameron said, suggests that *Microtus* is the more aggressive of the two, or that it has some slight advantage over its rival under the particular

conditions that obtain in a restricted area.

Other researchers have considered the possibility of competitive exclusion between these two genera, but the number of studies is still small, and the conclusions reached are not always in accord. Morris (1969), studying *M. pennsylvanicus* and *C. gapperi* in an aspen parkland situation in Saskatchewan, found a strong habitat separation in summer, but in late autumn both genera co-existed in approximately equal numbers in aspen stands. He thought that the summer habitat separation was probably due to competitive exclusion of *Microtus* by *Clethrionomys*, and that their co-existence later in the year suggested a lowered competitive interaction in winter. Clough (1964), in Nova Scotia, found that *M. pennsylvanicus* and *C. gapperi* were both able to live in certain habitats but usually did not co-exist there. He felt that this spatial separation might be due to a partial behavioural incompatibility between the two genera. In enclosure experiments in Quebec, Grant (1969) found that *C. gapperi* occupied only woodland when *M. pennsylvanicus* were present in adjoining grassland but, where *Microtus* were absent, *Clethrionomys* were trapped in both habitats; *Microtus* were trapped almost exclusively in grassland, regardless of the presence or absence of *Clethrionomys*. Grant (1969) felt that the exodus of *Clethrionomys* to the grassland was due to density of *Clethrionomys* exceeding the carrying capacity of the woodland, but that the presence of *Microtus* in the grassland of one enclosure inhibited *Clethrionomys* movement to this habitat.

On the basis of these and other studies, Grant (1970) hypothesized that because *Microtus* and *Clethrionomys* are closely related systematically, and have similar dentition, body form, temporal activity, and diet, they

find it difficult to co-exist on islands.

In postulating that competitive exclusion operates between the genera *Clethrionomys* and *Microtus*, Cameron (1965) and Grant (1970) appear to have ignored the cautionary comments of Gause (1934) and Gilbert *et al.* (1952) that the intensity of competition is determined *not by the systematic or taxonomic likeness* (italics mine), but by the similarity of the demands of the competitors upon the environment. To my knowledge, no one has yet demonstrated either that the demands of *Clethrionomys* and *Microtus* on the environment are sufficiently limited that these genera would be competing on a "life-or-death" basis, or how such limited commodities vary from season to season, year to year, or place to place.

There is a further difficulty involved in the usage of the term "competitive exclusion", and that is that there exists some controversy over the meaning of the phrase. Numerous definitions of the principle of competitive exclusion have appeared in the literature over the past 40 or so years (see Gilbert *et al.*, 1952), but there seems to be no unanimity of agreement over which will be used. Some authors, such as Allee *et al.* (1949) and Lack (1947) state their own interpretations of Gause's hypothesis (the previously accepted name for the competitive exclusion principle); Lack (1947) has actually used three different definitions, all of which he attributed to Gause! At the other extreme, Cameron (1965) and Grant (1970, 1972) have included no definition, leaving the reader to make up his own mind as to what they mean not only by "competitive exclusion", but by "competition" as well (see Birch, 1957, regarding examples of use and misuse of the term "competition").

Hardin (1960) has put forward an erudite case for the following

definition of competitive exclusion: ". . . Complete competitors cannot coexist." He claims that every one of the four words is deliberately ambiguous, not out of perversity but to emphasize the fact that we still do not comprehend the exact limits of the principle. Hardin (1960) further maintained that the "truth" of the principle is and can be established only by theory, not being subject to proof or disproof by facts, as ordinarily understood. However, Cole (1960) has pointed out that the very ambiguity of Hardin's (1960) definition makes the principle almost dogma so that it can be summarily used to dismiss a variety of field observations without the observer ever having to think too deeply about alternate hypotheses.

That Cole's (1960) fears in this respect are being realized is evident from Cameron's (1965) and Grant's (1970) work, as I will show later in this discussion. Grant, however, has not been content to confine his application of the competitive exclusion principle to *Microtus* and *Clethrionomys*, but has extended it to account for the distribution patterns of a variety of rodents (Grant, 1972). While all-inclusive hypotheses are a necessary part of the scientific method, I feel that Grant (1972) is premature in attributing a competitive exclusion relationship to so many genera not only because, as Grant himself said, the majority of the experiments did not have adequate controls, but also because so little is yet known about the requirements of these animals and their plasticity in adapting to suboptimal situations.

Cole (1960) has pointed out that two of the major problems associated with the term "competitive exclusion" are the lack of a definition of the word "competition", and the semantic vagaries that make any reasoning of

the principle a circular process. I agree with Cole (1960) that ecologists are already wasting too much time debating about semantics rather than ecological principles, but if observers are going to continue using the competitive exclusion principle to explain field observations, perhaps we should call a symposium to define precisely what we mean by the term, in what respect it differs from niche segregation, to what extent it is part of the process of ecological replacement, and to outline the boundary between competition and competitive exclusion.

As mentioned previously, neither Grant (1970) nor Cameron (1965) has defined what he means by competitive exclusion although both authors stress the importance of the theory in explaining the lack of *Clethrionomys*-*Microtus* combinations on islands; they differ only in that Cameron (1965) postulated the establishment of a "beachhead" by the first arrivals. Both authors suggested alternate explanations such as differential dispersal and establishment abilities, but placed very little emphasis on these alternatives.

The occurrence of *M. pennsylvanicus* in woodland on small islands has been well-documented (Cameron, 1958a, 1965; Dice, 1925b; Hatt *et al.*, 1948; Webb, 1965; Werner, 1956), and both Cameron and Grant interpret such reports as implying that, on the mainland, *Microtus* is excluded from forests by *Clethrionomys* and only in the absence of this genus can *Microtus* inhabit woodland. While this may or may not be true on the mainland (*cf.* Clough, 1964 and Morris, 1969), it does not appear to be the case on Camel Island where both *Clethrionomys* and *Microtus* were trapped in four of the five available habitats (forest, partial tuckamoor, bog, and heath-shrub barren). Not only did the two genera appear to co-exist in these

habitats, they often used the same runways and both frequently were caught at the same trap sites. This situation obviously contradicts Cameron's (1965) "beachhead" hypothesis (according to which *Microtus* should have prevented *Clethrionomys* from becoming established), and the competitive exclusion hypothesis (by which *Clethrionomys* should have ousted *Microtus* from the forest and partial tuckamoor at least). Nor is this the only example of the co-existence of these genera on islands since Crowell (pers. comm., 1973) found a similar situation in introduction experiments on two islands off the coast of Maine. On the other hand, however, Morse (1973) found that there appeared to be a distinct line of demarcation between the two genera in spruce forests on an island off the coast of Maine, with *Microtus* tending to avoid the forest.

The question that arises from the observation that both genera co-exist in certain habitats on Camel Island is: if competitive exclusion does operate to keep *Clethrionomys* and *Microtus* in different habitats on the mainland, why does it appear to break down in an island situation? There are two inferences that can be drawn from this question. First, competitive exclusion may not be operating in mainland situations. I do not propose to answer this suggestion one way or the other, however, I do think that until parameters such as the food requirements and preferences of these genera and the productivity of various habitats have been established, it is somewhat presumptuous to state that competitive exclusion exists in a particular situation. Second, the situation on islands is probably quite different from that on the mainland and drawing parallels between the two may be a delicate business.

Islands, because of their geographic isolation, tend to have fewer

species of plants and animals than do nearby mainland areas. Furthermore, the species that do manage to establish themselves on islands have, as a result of this isolation, a restricted gene pool. Although it is not known when Newfoundland became inhabited by mammals, it was probably less than 10 to 13 thousand years ago (Prest, 1969). Whatever the time span involved, it has been long enough for 10 of the 14 species of mammals native to Newfoundland to evolve well-defined subspecies (Cameron, 1958b). The Newfoundland *Microtus* is one of the ten; in fact, it was originally classified as a separate species, *Arvicola terraenovae*, in 1894 (Bangs, 1894) and not until 1936 was it designated a subspecies of *Microtus pennsylvanicus* (Davis, 1936). There still exists some controversy as to the precise status of Newfoundland *Microtus*, since animals from offshore islands may differ not only from animals from the main island of Newfoundland, but from those of other offshore islands as well (Pruitt, pers. comm., 1973 and Riewe, 1971).

That the *Microtus* in Newfoundland have been classified as an identifiable subspecies, primarily on the basis of cranial and dental characteristics, indicates a certain amount of genetic change in the population. There are, however, other differences between Newfoundland *Microtus* and their mainland counterparts that may indicate genetic change, or that may simply reflect the plasticity of the animals in adapting to an island situation. The presence of *Microtus* in woodland habitat on islands has been mentioned already, however Riewe and Folinsbee (pers. comm., 1971) found that *Microtus* from offshore islands in Notre Dame Bay were trapped more frequently in forests than were *Microtus* from the main island of Newfoundland. As Riewe (pers. comm., 1973) suggested, this

indicates that not only is there a difference between island and mainland situations, but also between large and small islands, with large islands tending toward a "continental" influence. Foster (1965) reached much the same conclusion about Vancouver Island.

Another difference between mainland and island *Microtus* is the apparent absence of a conventional home range for many of the island animals. On Camel Island, only 28% of all *Microtus* males had what could be interpreted as conventional home ranges, 31% exhibited shifting areas of concentration, while 41% traversed distances of 50 m or more daily. Riewe (1971) found a similar situation on another forested island in Notre Dame Bay. Whether these long movements are the result of genetic changes or represent responses to forested islands or something not yet determined, is unclear, however it is interesting to note that among the *Clethrionomys* introduced to Camel Island, only 27% appeared to have conventional home ranges, 50% exhibited shifting areas of concentration, and 23% travelled long distances.

It has often been commented upon that small mammals on islands tend to obtain a larger size than their mainland counterparts (Corbet, 1961; Foster, 1965; Wheeler, 1956) and the *Microtus* from Camel Island fit this pattern. Here again, there appears to be a difference between large and small islands since *Microtus* from the islands of Notre Dame Bay not only were larger than mainland *Microtus*, but usually were larger than *Microtus* from the main island of Newfoundland as well (Riewe, 1971). Foster (1965) discussed at length the question of change in size of island forms and concluded that it was due to some aspect of the insular environment, possibly climate.



According to Bergmann's rule (Allee *et al.*, 1949), homoiothermal animals from colder climates tend to be larger in size and hence to have less surface in proportion to body weight than do their relatives from warmer regions. However, Mayr (1963) said: "Burrowing mammals almost consistently fail to obey Bergmann's rule. They are well protected against the cold, particularly in areas with snow cover, and for them the amount of food available in winter seems to be the decisive factor determining body size." As an example, Mayr (1963) cited *Microtus*.

In northern regions, once the snow cover has passed the hiemal threshold (15 to 20 cm), the subnivean environment of small mammals remains relatively constant and they are able to exist quite well under the insulating blanket of snow; the animals have only two, usually brief, critical periods to contend with, one during the autumn and one during the spring (Pruitt, 1957). Winter conditions in a temperate maritime climate, however, are usually characterized by repeated freeze-thaws so that, in essence, the whole winter is a critical period for small mammals. This being the case, it would seem that, by attaining larger size on islands, small mammals are actually conforming to Bergmann's rule.

This appears to be borne out by Foster's (1965) results: he found that, in general, small isolated islands have large mice, and large islands, small mice, with the largest mice occurring on the most distant islands, *i.e.*, those which have the most severe climates. Foster (1965) also found that insular British Columbia *Peromyscus* (excluding those from the Queen Charlotte Islands) averaged 14% larger than their relatives on the adjacent mainland, while insular California and Mexico *Peromyscus* averaged only 8% larger than their nearby relatives. Assuming that the

British Columbia winters are more severe than California and Mexico winters, these results also fit Bergmann's rule.

There are other advantages to being large besides heat conservation: intrauterine competition puts a premium on speed of development and large size (since smaller embryos may be resorbed) which continues after birth; there may be an organizational advantage in having more nerve cells; larger animals are more efficient metabolically, thereby tending to have a longer life; and, by living longer, the animals have more time to accumulate antibodies and to gather experience (Rensch, 1959, cited by Foster, 1965). Disadvantages to attaining large size might include an increased vulnerability to predation since the animals would be easier to see and, presumably, easier to catch (Foster, 1965). How important this factor would be in an island situation depends, of course, on the number of predators present.

Whatever the reason, large size, abandonment of home range, ability to utilize all habitats (except burn), or a combination of the three, *Microtus* on Camel Island appear to have adapted quite well to the insular situation, and particularly to the critical maritime winters. The Period of Greatest Snow Cover in 1969-70 was characterized by repeated freeze-thaws, with the hiemal threshold being exceeded for only 20 continuous days. During this period the *Clethrionomys* population crashed dramatically. I have two records of *Clethrionomys* movement from the northeast end of the island to the cabin at the southwest end, and three records of movements from the burn to the woods to, eventually, the cabin (where foraging would presumably be easiest). Cabin trapping was conducted sporadically over this time, primarily with a view to

removing the animals from our food supply, however, a total of 42 *Clethrionomys* were trapped in the cabin compared to 8 *Microtus*. Although *Clethrionomys* mortality over the Period of Greatest Snow Cover in 1969-70 was 80.7%, *Microtus* mortality was only 51.1%. By comparison, the Period of Greatest Snow Cover in 1970-71 was characterized by fewer freeze-thaws and 71 continuous days with snow cover above the hiemal threshold. The mortality rate for *Clethrionomys* over this period was 43.1% and, for *Microtus*, 66.7%. A comparison of the two seasons indicates that *Microtus* are better adapted to withstanding the maritime critical period than are *Clethrionomys*, but during a winter that more closely resembles a typical northern winter (as described by Pruitt, 1957), *Clethrionomys* might have the advantage over *Microtus*.

During the period of this study, the *Clethrionomys* population peaked, crashed, and had begun to build up again when trapping was terminated in 1971. The *Microtus* population, on the other hand, was characterized by low numbers throughout the trapping period. Whether the number of *Microtus* was small as a result of competition (Birch, 1957, definition #1) or as a result of some other factor, such as intrinsic population control, is unclear, however, given the relatively large size of Camel Island and the small number of both *Microtus* and *Clethrionomys* after the Period of Greatest Snow Cover in 1969-70, I rather suspect that competition is not the decisive factor in depressing the numbers of *Microtus*.

As an alternate hypothesis for explaining the lack of *Clethrionomys*-*Microtus* combinations on islands, Grant (1970) suggested that it might reflect unequal abilities of these two genera to disperse and establish

themselves, but that at present our knowledge of their abilities in this respect is incomplete. If, as Grant implied, dispersal to islands means swimming, then the indications are that *Clethrionomys* and *Microtus* differ considerably in their abilities to cross water barriers. As mentioned previously, Getz (1967b) found *C. gapperi* to be better swimmers than *M. pennsylvanicus* of comparable size, but *Microtus* treated the water as less of a barrier than did *Clethrionomys*. This fits in well with my own observations; in swimming experiments in Indian Cove, *Clethrionomys* covered a greater distance in less time than *Microtus*; one red-back actually swam ashore and escaped on the rocks before it could be recaptured. However, when animals were released in standing water in a bog, *Clethrionomys* made for the nearest hummock while *Microtus* swam the length of the pool of water before clambering onto dry land. Butsch (1954) also commented on *Clethrionomys*' disinclination to enter water: "*Microtus* under similar circumstances would have taken to the water without hesitation, but *Clethrionomys* would climb up my leg or walk over my feet rather than enter the water. . . . The animals would swim only as a last resort."

While the foregoing comprise the only references I was able to find regarding the swimming ability of *Clethrionomys*, there are numerous reports of *Microtus* crossing open water (see Riewe, 1971, for review). To my knowledge, no one has yet determined the maximum distance that *Microtus* can swim, although several authors have found *Microtus* on islands more than 1 km from shore (Beer *et al.*, 1954; Hatt *et al.*, 1948; Jackson, 1920). Riewe (1971) found that several *Microtus* homed across open stretches of water, with some even including two or more nearby

islands in the areas they regularly visited.

On the basis of our knowledge to date, it would appear that *Microtus* and *Clethrionomys* differ considerably in their dispersal abilities: although *Clethrionomys* appears to be more highly adapted for swimming than *Microtus* (Getz, 1967b), the negative response of *Clethrionomys* to water appears to prevent this genus from fully utilizing its capacity for swimming. It has not colonized a single offshore island in eastern North America (Cameron, 1965) and few in the west, all of which are fairly large and only short distances from the mainland (Grant, 1970), while off the coast of Maine, Crowell (pers. comm., 1973) thought that all colonization by *Clethrionomys* had been via land bridges.

With respect to establishment abilities, fewer studies have been conducted but they, too, indicate considerable difference between the two genera. Crowell (1973) found that *Clethrionomys* was a poor colonizer and unable to maintain populations even when introduced, while Werner (1956) found *Microtus* to be adaptable to small islands, readily maintaining itself both as an individual and as a species under such situations. Winter survival rates for the two genera on Camel Island also suggest that *Microtus* is better able to withstand a lengthy maritime critical period than is *Clethrionomys*, an asset that would be invaluable in colonizing an island.

Grant's (1970) third hypothesis for explaining the lack of *Clethrionomys*-*Microtus* combinations on islands was that these genera may exhibit differential compatibility with *Peromyscus*. No *Peromyscus* were involved in the Camel Island study, however it is notable that Cowan and Guiget (1965) referred to *P. maniculatus* as "perhaps the most plastic of

all North American species", occurring in almost any area habitable by terrestrial mammals and feeding on a wide variety of plant and animal foods. The species is capable of swimming (Beer *et al.*, 1954), although its capacities for active dispersal have not been clearly defined: Crowell (1973) found *P. maniculatus* only on islands with land bridges in his study area, while Foster (1965) felt that passive dispersal by Indian canoes most adequately explained their wide insular distribution off the coast of British Columbia. Whatever the method of dispersal, *Peromyscus* appears to be able to take advantage of insular situations to establish itself, probably as a result of its "plastic" generalist nature.

In the absence of any precise information on the overlap of diet between *Peromyscus*, *Microtus*, and *Clethrionomys*, the responses of these genera to food not normally eaten, and the carrying capacity of islands with particular respect to food and space available to small mammals, it seems somewhat unjustified for Cameron (1965) and Grant (1970) to place so much emphasis on competition and the likelihood of competitive exclusion.

The more widespread occurrence of *Microtus* on islands in relation to occurrence of *Clethrionomys* is not unique. In 1856, *Zosterops lateralis*, the small white-eye, colonized New Zealand and its outlying islands from Tasmania (a 2000-km gap) while a close relative, *Z. rendovae*, refused to cross barriers only a few kilometers wide although the flying equipment of both species is essentially the same (Mayr, 1963). To my knowledge, no one has yet suggested the absence of *Z. rendovae* from islands occupied by *Z. lateralis* to be evidence of competitive exclusion.

Mayr (1970) has said that if a colonizing organism is unable to find a habitat or ecological niche equivalent to that which it has left, it will not be able to establish itself unless it has the capacity for a shift in its ecological requirements or its niche, but if a species has the ability to change its habitat preference, it not only can expand its range but also can change genetically under the pressure of the new environment in the newly established geographical isolate. From the foregoing discussion it would appear that *Microtus* has been able to adapt to a new environment, perhaps to the degree that drawing parallels between insular and continental *Microtus* is not justified. In the absence of any evidence of competitive exclusion between *Microtus* and *Clethrionomys* on Camel Island, it appears that, using Occam's Razor, differential dispersal and establishment abilities would provide a more fruitful avenue of research for explaining the absence of *Clethrionomys* from so many offshore islands.

## CONCLUSIONS

Consideration may now be given to answering the questions posed at the beginning of this thesis.

1. With the exception of the burn, *Clethrionomys* and *Microtus* utilized all habitats on Camel Island, although not to the same extent. *Microtus* appeared actively to avoid the burn while *Clethrionomys* were found there only during the Pre-snow Cover Period of 1969 and 1970 and in the Period of Ebbing Snow Cover in 1971, which indicates that they probably overwintered in the burn in 1970-71. Both genera utilized the spruce-fir forest, although *Microtus* captures there were more frequent in low-lying areas than in the drier interior. *Clethrionomys*, surprisingly, did not exhibit a high preference for forest over the other habitats. Unlike *Microtus*, *Clethrionomys* did not appear to distinguish between forest and partial tuckamoor; *Microtus* were captured more frequently in partial tuckamoor than in forest. In general, *Clethrionomys* avoided bog, whereas *Microtus* favoured this habitat second only to partial tuckamoor. Captures of both genera were low in the heath-shrub barren. In many instances *Clethrionomys* and *Microtus* were captured at the same trap sites and utilized the same runways, although *Microtus* appeared to be more restricted to runways than did *Clethrionomys*.

2. Attempted analyses of home ranges revealed that some animals of both genera did not have typical home ranges but instead made relatively



long, linear movements. A greater segment of the *Microtus* population (41% of males, 6% of females) made long movements than did *Clethrionomys* (23% of males, 9% of females). Other movement patterns included restricted movements and shifting areas of concentration (restricted movements, interspersed with a few long ones). There appears to be a direct relationship between length of movement and density of *Microtus* males. For *Clethrionomys* males, length of movement correlates directly with amount of rainfall. No such correlations were apparent for females of either genus.

No inter-island movements by either genus were detected. In a limited number of swimming experiments, *Clethrionomys* compared favourably with *Microtus* although observations from animals released in the bog indicate that *Clethrionomys* does not enter water as readily as *Microtus*.

3. The maritime Newfoundland winter is characterized by intermittent freeze-thaws so that the subnivean environment usually does not remain stable for long. Frequent rain and freezing rain create crusts within the snow, and it is not unusual for a cold snap to occur when the snow cover is below the hiemal threshold. The *Clethrionomys* population peaked during the Pre-snow Cover Period of 1969 and crashed during the Period of Greatest Snow Cover 1969-70. Captures remained low until the Pre-snow Cover Period of 1970 and had dropped only slightly by the Period of Ebbing Snow Cover 1971, indicating a high survival rate over the second winter. The *Microtus* population showed little fluctuation throughout this period, remaining consistently low. *Microtus* appear to be better adapted to withstanding maritime winters than do *Clethrionomys*, possible adaptations being: low population densities, larger than

average body size, and at least partial abandonment of home range.

4. *Microtus* did not establish a "beachhead" on Camel Island, nor did *Microtus* and *Clethrionomys* appear to exhibit competitive exclusion. In postulating the operation of competitive exclusion between these genera, proponents of the principle appear to have ignored the cautionary comments of Gause (1934) and Gilbert *et al.* (1952) that intensity of competition is determined not by the systematic or taxonomic likeness but by the similarity of the demands of the competitors upon the environment. Until the demands of *Clethrionomys* and *Microtus* on the environment are better known, it seems somewhat presumptuous to explain away the situation as competitive exclusion. Furthermore, there still exists considerable controversy over the meaning of the term "competitive exclusion" and until a satisfactory definition is decided upon, usage of the term should be held in abeyance. The Camel Island study indicates that, in future, more attention should be paid to differential dispersal and establishment abilities of these genera.

5. *Clethrionomys* and *Microtus* have co-existed on Camel Island from 1967 to 1971 in the absence of a third genus (*Peromyscus* or *Apodemus*). Whether or not the *Clethrionomys* population on Camel Island can maintain itself over the years depends, I think, not so much on the presence or absence of a third (intermediary?) genus as on the ability of *Clethrionomys* to adapt to maritime meteorological and environmental conditions.

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