

THE UNIVERSITY OF MANITOBA

ECOLOGY OF THE MEADOW VOLE,
MICROTUS PENNSYLVANICUS TERRAENOVAE,
ON THE ISLANDS OF NOTRE DAME BAY,
NEWFOUNDLAND, CANADA

by

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ABSTRACT

ECOLOGY OF THE MEADOW VOLE, *MICROTUS PENNSYLVANICUS TERRAENOVAE*, ON THE ISLANDS OF NOTRE DAME BAY, NEWFOUNDLAND, CANADA

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An investigation into the ecology of the meadow vole, *Microtus pennsylvanicus terraenovae*, inhabiting the islands of Notre Dame Bay, Newfoundland was conducted on 89 islands between May 1966 and August 1969. Information was gathered on habitat utilization, food habits, home ranges, homing ability, colonization, inter-island movements, reproduction, longevity, moult, anatomical variations, parasites and predation.

Data were obtained on habitat utilization from 32,800 trap nights on 56 islands. Meadow voles were found in all major terrestrial habitats (spruce-fir forest, tuckamoor, alder patch, dwarf shrub barren, grassy area, bog, salt marsh and shoreline). On small islands voles were forced to utilize the one or two available habitats or emigrate. On larger islands where a wider diversity of habitats is available voles utilized the forest habitats (particularly tuckamoor and alder patches) throughout the year and grassy areas and bogs during the summer and fall. Snow cover, predation and the scarcity of grassy areas appeared to be the major factors responsible for habitat utilization on larger islands.

From field observations and cafeteria feeding tests it was ascertained that the voles had varied diets which included at least 64 vascular and 7 non-vascular species. Some voles also appeared to scavenge upon animal remains in the inter-tidal zone.

Home ranges of voles inhabiting four islands were delimited by trapping. The largest home ranges (mean minimum area = 2.0436 ha, range = 0.1692 to 8.6601 ha) were recorded in a spruce-fir forest. The smallest home ranges (mean minimum area = 0.0146 ha, range = 0.0004 to 0.1688 ha) were recorded where a variety of forest and grassy habitats occurred. Habitat quality and diversity, population density, season of the year, sex, sexual activity and island size influenced home range size.

Eighteen inter-island movements were recorded for dispersing and homing voles during the summers of 1967 and 1968; these movements were accomplished by swimming. One female vole made two inter-island movements covering a total of 1280 m. The fastest inter-island movement was made by a male vole who covered 610 m in less than 16 hours.

Eight swimming tests were conducted at sea under various environmental conditions. The voles swam for periods of up to 32 minutes at speeds of up to 60 cm/second. Swimming voles oriented to objects on the horizon; the smallest object to which a vole oriented subtended an angle of $2^{\circ}35'$. During calm weather voles could probably have colonized almost any island in the study area by swimming.

The extirpation of insular populations was a common phenomenon. Nineteen of the 89 islands investigated had recently had their vole population extirpated. Predation and adverse weather appeared to be the major causes responsible for the elimination of insular vole populations.

The insular vole populations did not fluctuate in synchrony because colonization and extirpation were fortuitous.

An age classification with five age groups was developed using moult progression and femur length. Maximum age recorded was 21 to 27 months.

Due to a short breeding season, a scarcity of breeding juveniles and a small number of litters/female/year, the insular voles possessed a

relatively low reproductive rate.

Anatomical measurements were made on more than 650 *M. pennsylvanicus* from Newfoundland, Labrador and Nova Scotia. From cranial measurements it appeared that the Newfoundland subspecies is more closely related to the Labrador race than to the Nova Scotia race. Differences in pelage colouration, skeletal measurements and molar tooth patterns were discovered among the Notre Dame Bay populations. These variations were not related to the degree of isolation, to island size or to habitat type, but were most likely the result of genetic drift.

A total of 285 predator scats and pellets were collected and analyzed. The major predators of *Microtus* in Notre Dame Bay were the coloured fox (*Vulpes fulva*), the short-tailed weasel (*Mustela erminea*) and the rough-legged hawk (*Buteo lagopus*).

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INTRODUCTION

Since Darwin's time there has been considerable interest in the evolution of island species. It has often been shown that insular populations differ morphologically and/or behaviourally from other populations on nearby islands or mainlands. Innumerable hypotheses and theories have been postulated to account for these observed differences. Unfortunately, it has often been easier to theorize than it has been to conduct extended research on isolated island populations, and, as a result, hypotheses have been generated at a faster rate than substantiating data. Grant (1968) has pointed out the need for further ecological research to help assess the validity of current theories regarding insular populations.

In 1965 Cameron postulated that interspecific competition is the major factor responsible for the present-day distribution of two genera of voles, *Microtus* and *Clethrionomys*, on the islands off the North Atlantic coasts. On the continents of North America and Europe *Microtus* is essentially a grassland form, and *Clethrionomys* is confined to the forests. On islands this situation changes considerably. On the islands off Europe, according to Cameron, both voles are capable of excluding one another; he suggested that the first genus to invade an island forms a "beachhead" and thereby prevents its rival from becoming established. On the islands off eastern North America *Microtus pennsylvanicus* is supposedly the more aggressive vole and excludes *Clethrionomys gapperi* from both grassy and forested islands.

Cameron gathered much of the information for his hypothesis between

1949 and 1955 while conducting an extensive study on the mammals inhabiting the islands in the Gulf of St. Lawrence (Cameron, 1958). During these years he spent a total of six months collecting specimens on the island of Newfoundland. The data which he obtained from 43 specimens of the Newfoundland meadow vole, *Microtus pennsylvanicus terraenovae*, played a prominent role in the formulation of his hypothesis.

In 1966 W. O. Pruitt, Jr. initiated a long-term project designed to test Cameron's hypothesis. He selected the islands of Notre Dame Bay, Newfoundland for this study. On these islands *M. p. terraenovae* is the only native small rodent.

My study presents information on inter-island variations, habitat utilization, food habits, home ranges, dispersal, colonization, longevity, fecundity, parasites and predation from the insular populations of *Microtus* in Notre Dame Bay. Later studies in Notre Dame Bay will hopefully provide equivalent ecological data on various introduced species of *Clethrionomys*. Comparison of the ecological relations between these two genera of voles may reveal the factors responsible for the voles' distribution on the islands off the North Atlantic coasts.

STUDY AREA

The study area is situated in the southeast portion of Notre Dame Bay, Newfoundland, Canada, between $49^{\circ}21'$ and $49^{\circ}37'$ N. Lat. and $54^{\circ}35'$ and $55^{\circ}10'$ W. Long. These boundaries encompass an area of approximately 1255 sq. km¹ of which more than half is sea (Fig. 1, p. 11). The study area is depicted on National Topographic Series map 2E, edition 1 ASE, Series A 501. The study was restricted to the islands of Dildo Run, Bay of Exploits and Friday Bay (Appendix A, p. 186).

Geology

The geology of the area was examined by Heyl (1936), Patrick (1956) and, more recently, by Horne (1968).

Closely-folded Pre-Cambrian and Paleozoic granites and volcanics are the dominant rock types. The whole region was glaciated by northerly-moving ice in the Pleistocene, leaving a submerged coastline. The occurrence of wave-cut benches and raised beaches indicates that the area has been emerging. Stoss and lee topography is characteristic of the region. Roches moutonnées occur from the highest hilltops to the present strand lines. Erosion has dominated over deposition, leaving fresh striae on the exposed bedrock. Glacial erratics are extremely common and varied in size. Most of the boulders and till are probably of Wisconsin age.

¹I converted all measurements originally taken in English units to metric units.

Physiography

The islands in the study area range in size from a few square metres to about 180 square kilometres. They can be divided into two categories:

1. There are numerous small islands in Dildo Run many of which are only rocks rising a metre or so above the sea. The relief is usually less than 15 m above sea level, and only a few rise above 30 to 45 m. These islands are sheltered from the open sea by New World (No. 89) and Farmers islands on the northwest and are bounded on the southeast by Dunnage (No. 75), Chapel (No. 32) and Coal All (No. 27) islands. Treacherous shoal waters separate most of the islands. The shorelines often slope gently to the sea. Sand or gravel beaches (Fig. 2, p. 12) and mud flats are common, but there are a few sea cliffs that rise to heights of 6 to 30 m.

2. The islands of Bay of Exploits and Friday Bay are fewer in number but larger in size. Elevations of 60 m or more are common, and peaks rise to a maximum of 135 m above sea level. These islands are often widely scattered and isolated by deep water; soundings have been made in the Bay of Exploits which exceed several hundred fathoms (Heyl, 1936). The shorelines are extremely rugged (Fig. 3, p. 12); in the northwest section of the study area, cliffs of 100 to 120 m plunge vertically into the sea. Beaches are rare along the exposed rocky shorelines, but where they do occur they are composed of cobbles and boulders worked by the sea.

Climate

The cold Labrador Current is the dominating influence on the climate.

The Current moderates the continental air masses sweeping off North America and gives Notre Dame Bay its cool maritime climate (mean daily temperature = 4.5°C).¹

The summer temperatures are cool; July is the warmest month with a mean daily temperature of 16.1°C and a recorded maximum of 34.4°C . The winters are mild; February is the coldest month with a mean daily temperature of -5.7°C . The record low of -27.1°C was recorded in the month of January.

The mean annual precipitation of 91.5 cm is evenly distributed throughout the year. The mean total snowfall is 254 cm. The mean winter maximum snow accumulation is 79 cm, and the maximum recorded is 177 cm. The average depth of snow on the ground at the end of each month from December to April is 30 cm, while the greatest accumulation of snow occurs in January and February. Glaze or ice storms are common phenomena during the winter. In spring the coastline is often foggy.

The prevailing winds from June to October are southwesterly; from November to May they are west to northwesterly. The winds are lightest during spring and summer (July mean velocity = 57.7 cm/sec. and mean maximum velocity = 161 cm/sec.) and strongest during fall and winter (January mean velocity = 93 cm/sec. and mean maximum velocity = 255 cm/sec.).

The Labrador Current, laden with arctic pack ice, delays the onset of spring for at least a month. The average frost-free period is 120 days. The vegetative season (daily average temperature above 6.1°C) begins about mid-May and lasts for approximately 155 days (Hare, 1952).

¹I extracted the following climatic data from the Canada Department of Transport's monthly meteorological reports for the Twillingate station (1957 through 1966) or from the normal records for the same station (Canada Department of Transport, 1964, 1967).

The sheltered islands and bays of Dildo Run are not affected by the Labrador Current to the same extent as are the islands in Friday Bay and Bay of Exploits. These sheltered areas have a slightly warmer summer and cooler winter.

Human Occupation

Prior to the seventeenth century, Notre Dame Bay was a stronghold of the Beothuck Indians. In the seventeenth and eighteenth centuries, the region was settled by adventurers and fishermen of British descent, and the extermination of the native people followed (Horwood, 1969).

Until recently, fishermen and their families have resided on many of the offshore islands in Friday Bay and Bay of Exploits (Horwood, 1969; Wadel, 1969). Since the Newfoundland government began its resettlement programme in 1953, the communities on these islands have been gradually abandoned (Skolnik, 1968; Wadel, 1969). On most of the islands the only signs of past human occupation are small meadows and old-fields (Fig. 4, p. 13).

At present the majority of the people are living in settlements which dot the shorelines of New World and Twillingate islands. Prior to 1963 these outports were linked to the rest of the province by steamship from St. John's and Lewisporte (Horwood, 1969; Wadel, 1969). These ships have now been outmoded by a system of causeways, roads and a ferry connecting New World and Twillingate islands with Newfoundland.

Habitats

There are eight basic types of terrestrial habitats in the study area as defined by the growth form of the dominant vegetation:

1. Spruce-fir forest: this habitat consists of closed-canopy forests 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 by needle litter. Some of the forests are so dense that the herb layer is absent, and only needle litter is present on the floor (Fig. 5, p. 14). The spruce-fir forest is the dominant habitat on the islands in the study area.

2. Tuckamoor: this habitat is characterized by dense, wind-pruned *Abies balsamea* and *Picea mariana* interspersed with a closed shrub layer of *Kalmia angustifolia*, *Ledum groenlandicum* and *Vaccinium angustifolium*. These trees and shrubs usually form a barrier one to three metres in height and almost impenetrable by man. The ground cover is dominated by *Cladonia* spp. and *Peltigera* spp. Large boulders covered with crustose lichens (*Parmelia* spp.) often emerge above the shrub layer (Fig. 6, p. 15). Tuckamoor commonly merges with the spruce-fir forest, forming belts around the island peripheries (Fig. 7, p. 16).

Along the supralittoral zones of many of the sheltered islands, tuckamoor is replaced by a shoreline-ecotone. This ecotone forms a dense barrier above five metres wide around the spruce-fir forests. Entangled branches of *Abies balsamea* and *Picea mariana* extend to the ground. The ericaceous shrub zone, characteristic of tuckamoor, is lacking. Needle litter and occasionally mosses and lichens carpet the ground. Species typical of the shoreline habitat are present along the outer edges of the ecotone, sometimes even protruding through the prostrate conifer branches. This narrow band of interwoven evergreens

is in contrast to the more open spruce-fir forest (Figs. 5, 8 and 9, pp. 14, 17 and 18).

3. Alder patch: this habitat consists of dense stands of *Alnus crispa* 1.5 to 4.5 m in height interspersed with a few tree or shrub species such as *Abies balsamea*, *Picea mariana*, *Sorbus decora* and *Lonicera villosa*. A herb layer composed of such species as *Sanguisorba canadensis*, *Thalictrum polygamum* and *Solidago rugosa* is sometimes present, but often this layer is scanty or non-existent. The ground is usually covered with *Alnus* twigs, leaves and cones. This habitat is found on the edges of moist old-fields and bogs (Fig. 10, p. 19), along streams and on islands which have recently experienced forest fires.

4. Dwarf shrub barren: this habitat is characterized by an association of low, prostrate shrubs dominated by *Empetrum nigrum*, *Vaccinium angustifolium*, *V. Vitis-Idaea* and *Juniperus communis* interspersed with a few herbs such as *Cornus canadensis* and *Potentilla tridentata*. On islands of less than 0.5 ha, mats of these species, in places associated with grasses and sedges, may form closed cover (Fig. 11, p. 20). On larger islands, the dwarf shrub barrens are confined to exposed ridge tops and the rims of sea cliffs and are surrounded by tuckamoor on the leeward side.

In some areas *Vaccinium angustifolium*, *V. Vitis-Idaea* and *Juniperus communis* form a dominant community which grows to a height of about 0.5 m; *Empetrum nigrum* is subordinate or absent. This variant of the dwarf shrub barren will be referred to as berry patch.

5. Grassy area: this habitat is characterized by a large variety of grasses such as *Agropyron repens*, *Festuca rubra*, *Deschampsia flexuosa*, *Poa* spp., *Agrostis* spp. and *Phleum pratense*, sedges such as *Carex flava*, *C. interior* and *C. lasiocarpa* and forbs such as *Atriplex patula*,

Ranunculus repens, *Trifolium* spp., *Lathyrus* spp., *Aster* spp., *Solidago* spp. and *Rumex* spp. Scattered shrubs such as *Ribes* spp., *Rubus idaeus*, *Juniperus* spp. and *Lonicera villosa* and small trees such as *Sorbus decora* and *Viburnum cassinoides* may be present. Mosses such as *Racomitrium lanuginosum*, *Dicranum undulatum* and *Polytrichum* sp. and lichens such as *Peltigera* spp. are often associated with the herb layer. The species composition is dependent upon the past history of the area. This habitat category includes disturbed areas such as hay fields, pastures, abandoned gardens, edges of freshwater ponds (other than bog ponds), roadsides and burns. These grassy areas occur only on small islands (Fig. 12, p. 21) or as isolated clearings on the larger forested islands (Fig. 4, p. 13).

6. Bog: this habitat is characterized by a ground cover of *Sphagnum* spp. and *Carex* spp. On *Sphagnum* hummocks there is a shrub layer dominated by *Ledum groenlandicum*, *Andromeda glaucophylla*, *Chamaedaphne calyculata*, *Betula Michauxii* and *B. pumila*. Where the shrub layer is sparse or lacking, *Sarracenia purpurea*, *Drosera rotundifolia*, *Pogonia ophioglossoides*, *Spiranthes Romanzoffiana* and *Habenaria* spp. are abundant. *Nymphaea odorata* and *Utricularia cornuta* are common in the open bog pools, known locally as flashets (Pollett, 1968). *Picea mariana* and *Larix laricina* may or may not be present as dominant elements. Bogs are often present in topographic basins on islands of 60 ha or more (Fig. 13, p. 21).

7. Salt marsh: this habitat is characterized by an assemblage of semiaquatic species of the intertidal zone such as *Hierochloa odorata*, *Eleocharis halophila*, *Limonium Nashii*, *Spartina* spp., *Carex* spp. and *Scirpus* spp. (Fig. 14, p. 22). Except for a few isolated salt marshes in the shoal waters of Dildo Run, they are rare in the study area as they

are throughout the province of Newfoundland (Dr. E. Rouleau, personal communication).

8. Shoreline: this habitat is characterized by a very narrow strip of vegetation along the upper edge of the supralittoral zone. Herbs resistant to the salt spray such as *Elymus mollis*, *Sedum Rosea*, *Lathyrus japonicus*, *Mertensia maritima*, *Ligusticum scothicum*, *Cakile edentula*, *Cochlearia tridactylites* and *Plantago juncooides* are widely scattered over the exposed rocky and sandy shorelines (Fig. 15, p. 23).

Appendix B (pp. 187-193) lists the plant species found in each habitat.

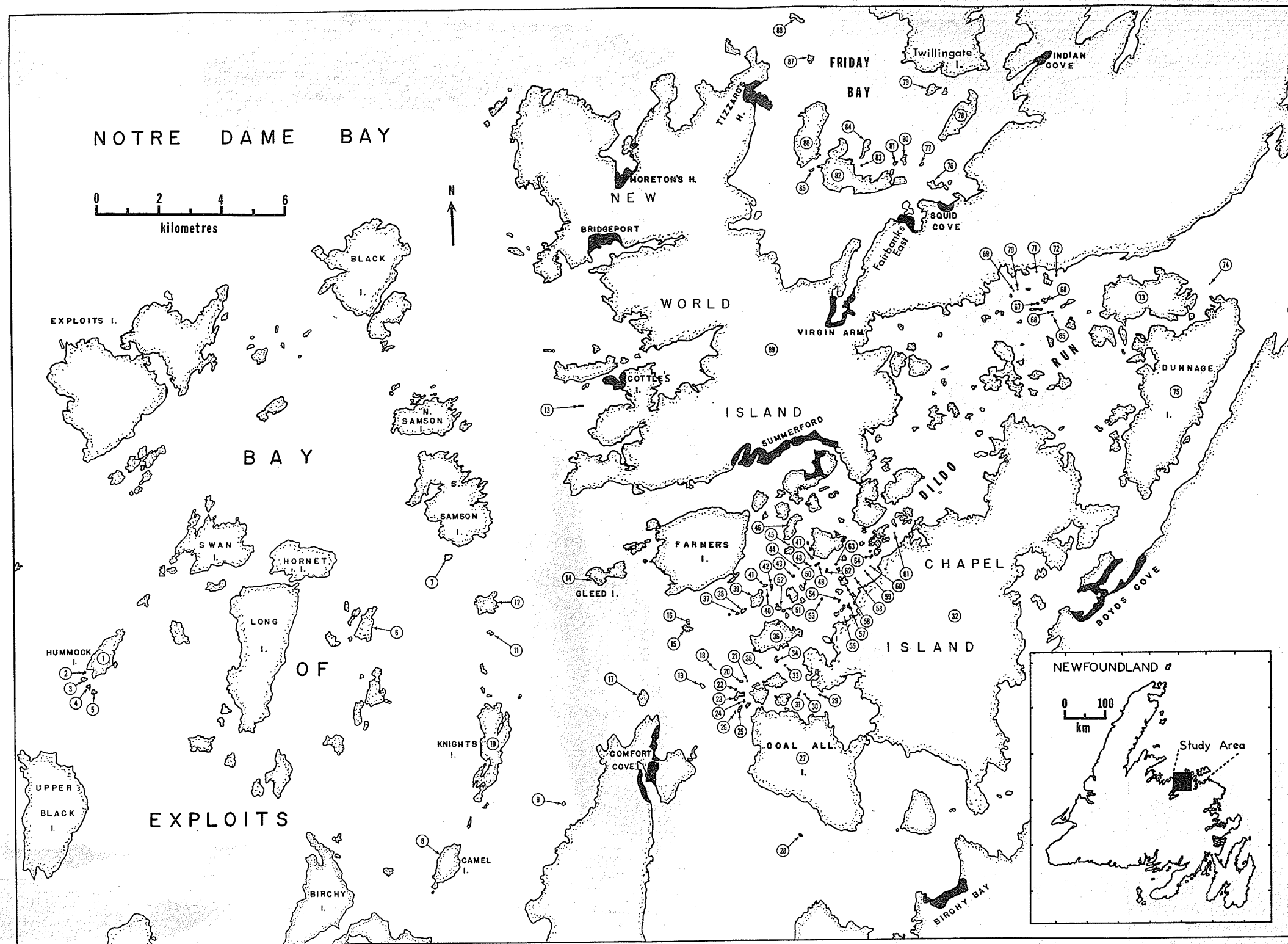


Fig. 1. Map of study area in Notre Dame Bay, Newfoundland. Investigations were carried out on the numbered islands. For information regarding the names and physical characteristics of these islands see Appendix A (p. 186).



Fig. 2. Sand-and-gravel beach on southwest shore of Inspector Island (No. 36), June 1967. Beaches are common on the sheltered islands of Dildo Run but only rarely are they as well developed as this one.

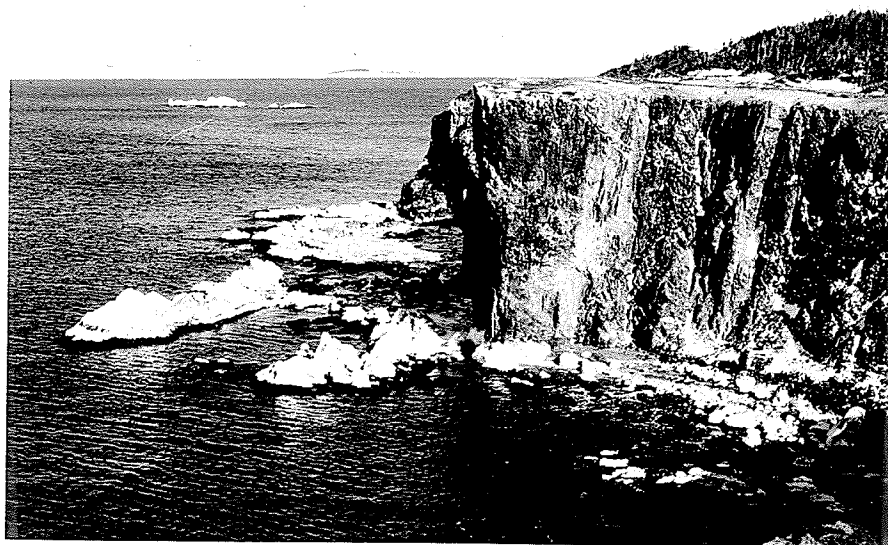


Fig. 3. Sea cliff on the north end of North Trump Island (No. 86), February 1969. Cliffs similar to this are common on the islands in Friday Bay and Bay of Exploits.

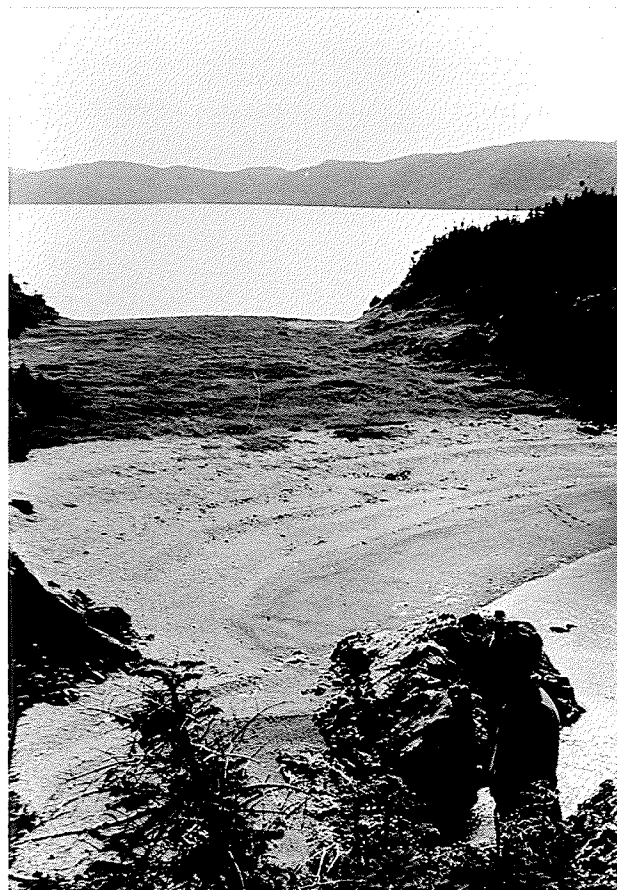


Fig. 4. Small meadow on the northwest shore of North Trump Island (No. 86), July 1968. Many of the larger islands in Notre Dame Bay have small old-fields similar to this one which has been abandoned by the local inhabitants for at least 15 years.

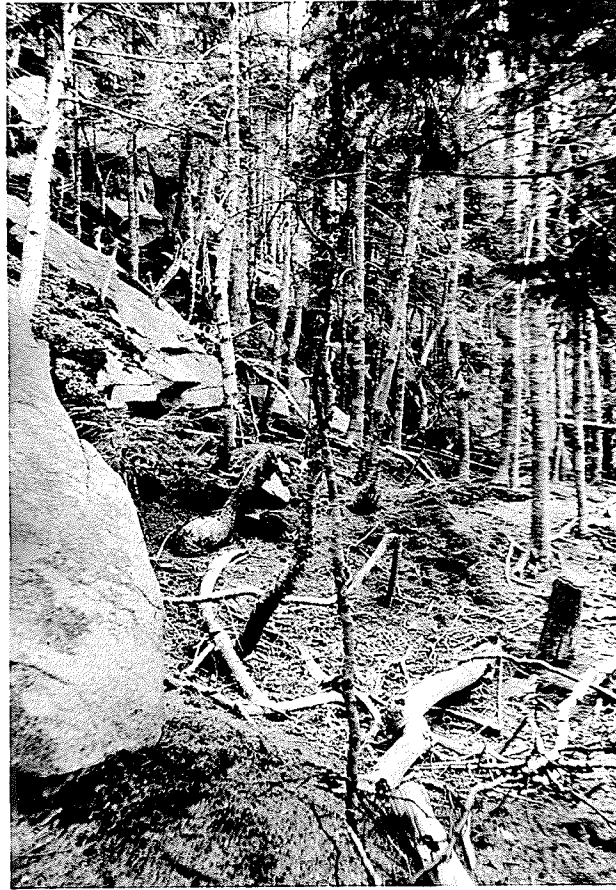


Fig. 5. Spruce-fir forest in the interior of Shag Cliff Island (No. 6), June 1967. The fir trees are approximately 10 to 15 cm diameter breast high. The forest floor is covered predominately by needle litter, mosses and lichens. This habitat type covers most of the islands in the study area.



Fig. 6. Wind-pruned tuckamoor on hilltop on South Trump Island (No. 82), May 1969. This habitat type is present on exposed sites on many of the islands in the study area.

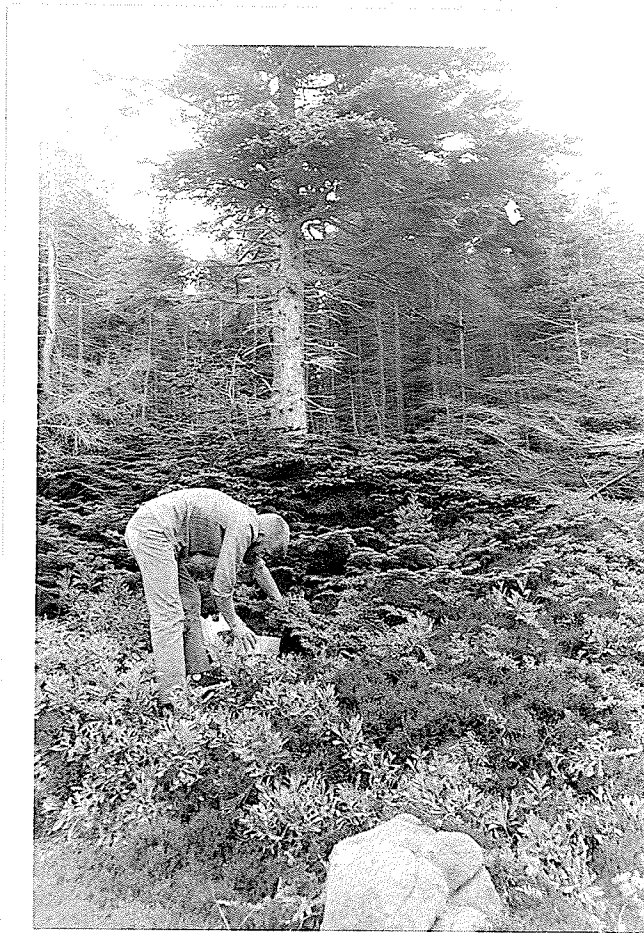


Fig. 7. Low tuckamoor bordering the shoreline of Shellbird Island (No. 42) grades into dense spruce-fir forest, July 1967. Tuckamoor often forms a dense belt around spruce-fir forests in the study area.



Fig. 8. Shoreline-ecotone along the rock-and-gravel beach on Pyke Island (No. 39), July 1967. This habitat is found only in sheltered areas.

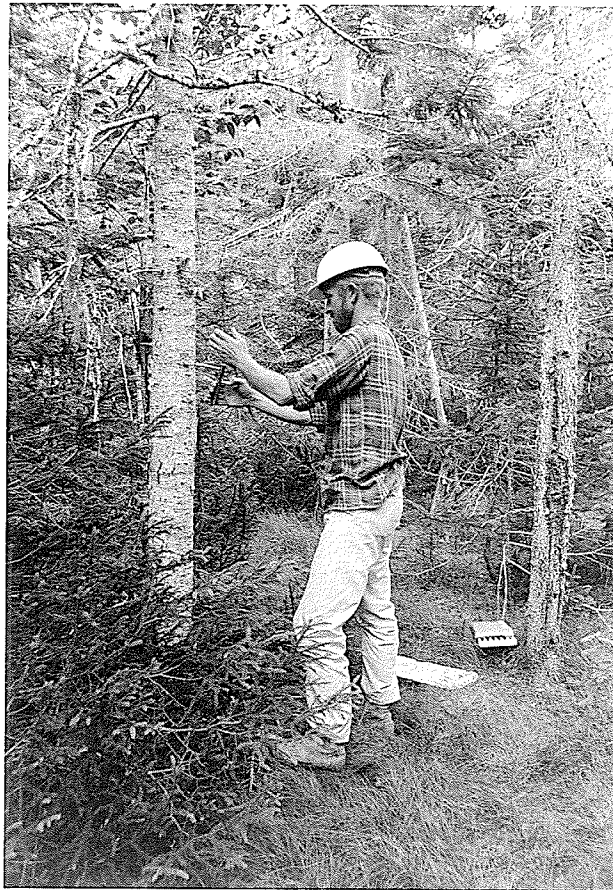


Fig. 9. O. Forsey taking a core sample in an open section of the spruce-fir forest on Pyke Island (No. 39), August 1967.



Fig. 10. Small alder patch bordering a meadow on South Trump Island (No. 82), May 1969. Small alder patches frequently border creeks, moist old-fields or bogs on the larger islands in Notre Dame Bay.

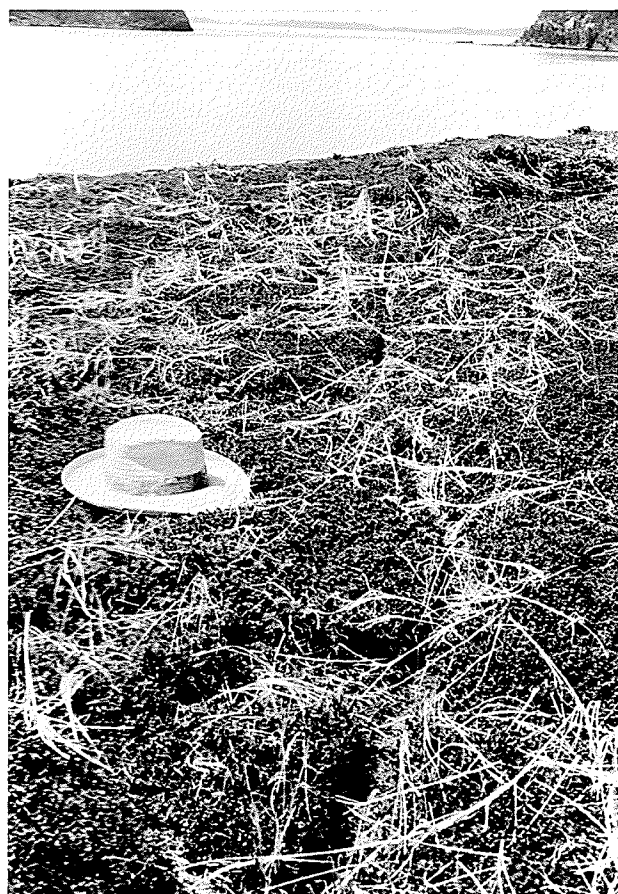


Fig. 11. Prostrate dwarf shrub barren on Mile Island (No. 19), June 1967. In Notre Dame Bay dwarf shrub barrens cover many of the small islands as well as the exposed sites on the larger islands. Note the extensive *Microtus* runway system.



Fig. 12. Grass-and-herb cover on Grassy Rock (No. 37), June 1967. For scale, note the biologist to the left of centre. Cave Island (No. 38) and Pyke Island (No. 39) are the forested islands in the background. Only some of the smaller islands (less than 4 ha) in the study area are completely covered with grassy vegetation.



Fig. 13. Basin bogs on the interior of South Trump Island (No. 82), May 1969. The small clearing near the shoreline in the centre foreground is an abandoned homesite. The larger clearing along the shoreline on the right is the Sam Keefe's Cove meadow and campsite. Note the loose arctic ice on the far side of the island.



Fig. 14. Salt marsh at low tide on the west end of Chapel Island (No. 32), August 1967. Salt marshes are uncommon in the study area.



Fig. 15. Lush growth of *Plantago juncooides* on the rocky shoreline of Grassy Rock (No. 37), July 1967.

METHODS AND MATERIALS

Introduction

A total of 19 months was spent in the field. Dr. Wm. O. Pruitt, Jr. and Mr. O. Forsey made a preliminary investigation during May and June of 1966. In 1967 I was in the field from 25 May to 30 August. In 1968 I began field operations on 30 May and continued them until 22 August 1969. Field operations were conducted from five base camps, on Camel (No. 8), Yellow Fox (No. 12), Inspector (No. 36), Pyke (No. 39) and South Trump (No. 82) islands, and eight outlying camps, on No. 4, Gleed (No. 14), Big Cranpot (No. 15), Little Cranpot (No. 16), Dunnage (No. 75), North Trump (No. 86), New World (No. 89) and Upper Black islands (Fig. 1, p. 11).

Extensive studies were carried out on 89 islands ranging in size from less than 0.08 ha to more than 18,000 ha. Eighty-five percent of these islands, however, are less than 40 ha in size (Appendix A, p. 186).

Two locally constructed boats, one 4.86 m and the other 5.47 m long, powered with 20 and 29 hp Johnson outboard engines, were used throughout the field study.

Trapping

Fifty-six islands were trapped with 32,800 trap nights (TN) and 2116 tracking station nights. A total of 943 *Microtus* was captured.

Throughout the study I used Museum Specials, Schuyler's No. 3 Folding Animal Killers and collapsible, aluminum Sherman live traps (23 cm x 9 cm x 7.6 cm). In 1967 I also used, on a limited basis,

tracking stations similar to those designed by Justice (1961) and Sheppe (1965a).

The kill traps were baited with peanut butter. The Sherman live traps were each baited with a small handful of dried apple which supplied the voles with sufficient food and moisture for periods of up to 18 hours. The tracking stations were likewise baited with dried apple.

I placed live traps in the shade whenever possible. In exposed areas the traps were shaded with small pieces of driftwood or local vegetation. In order to reduce trap mortality I provided the Sherman live traps with terylene fibre during winter and spring (Radvanyi, 1964).

Removal Studies

Removal trapping programmes were conducted from 1966 through 1969 on 53 islands with 13,143 TN. The island populations were periodically sampled with snap traps in order to obtain data on occurrence, longevity and parasites. I live trapped voles and retained them in captivity for experimental studies on food preferences and swimming abilities. Other voles were removed from islands and released on uninhabited islands in the hopes of forming new colonies. I transplanted others in order to test their homing abilities.

In these removal studies it was desirable to secure the maximum number of voles with the least amount of time and effort. Therefore, I always set traps in runways, burrow entrances and feeding sites. On islands of 4 ha or less, traps were set over the entire area whenever the topography permitted.

Kill traps were checked once a day in the morning (unless access to

an island was cut off by high winds or ice). Traps which had been sprung during the night were adjusted and reset at this time. I placed the specimens in paper bags and returned them to camp for examination and preservation.

Live traps were checked twice daily, in the morning and in the evening. Malfunctioning traps were cleaned, rebaited and reset at these times. I took the voles to base camp, where they were toe clipped, sexed, weighed and retained in captivity or released, depending on the nature of the study. Body weights were taken to 0.1 gm on an Ohaus Triple Beam balance.

I conducted snap trapping programmes on widely scattered islands throughout the study area, except during the 1968-69 fall and winter when unpredictable weather and ice conditions forced the confinement of snap trapping to the islands in the vicinity of South Trump Island. Live trapping was conducted only on islands easily accessible from a field camp. During the 1968-69 winter, live trapping was necessarily restricted to South Trump Island where I could reach the traps by foot under all weather conditions.

Mark-Recapture Studies

Mark-recapture programmes were carried out from 1967 through 1969. Seventeen islands were investigated with 19,657 TN and 2116 tracking station nights. I obtained data on dispersal, island colonization, home range, habitat selection, natality, longevity, ectoparasites and blood parasites. All traps and tracking stations were located on mimeographed maps prepared from aerial photograph enlargements.

Initially I designed the studies to be conducted on gridded plots

of 0.5 ha. However, I soon discovered that these plots would be thoroughly inadequate for either home range or dispersal studies on the small islands in Dildo Run. Therefore, plot trapping in this area was abandoned in favor of trap lines set around the periphery of the island, except for certain small, low, grassy islands where traps were spread over the entire island. In the peripheral trapping I set traps among rocks and terrestrial vegetation just above the supralittoral zone. On Pyke Island traps were spaced at 30-m intervals around the entire 11.84 ha. On the smaller islands the trap spacing was reduced to 10 to 30 m. The number and spacing of the traps were dictated by the coastline, terrain and the vegetation.

During a dispersal study I used tracking stations to survey islands which appeared to lack a vole population. The stations were placed in locations most likely to attract voles and were checked for sign about once a week. If I discovered vole sign I would set live traps on the island. The use of tracking stations alleviated the problem of setting live traps on uninhabited islands and having to visit them by boat twice daily.

An extended mark-recapture programme was conducted on South Trump Island from September 1968 through August 1969. A 1.36-ha area, known as Sam Keefe's Cove (SKC), was gridded in 6.4-m intervals with plastic marker flags. There were five different habitats: tuckamoor, alder, berry patch, bog and meadow. I set traps in each of the habitats at those sites where voles were most likely to be caught. By using the marker flags and mimeographed maps, I located the traps accurately to within one metre. Trapping was conducted during four periods: fall (24 September to 2 November), winter (25 February to 13 March), spring (25 April to 11 May) and summer (12-21 August). I sometimes shifted the trap locations slightly in order to delimit the home ranges of particular

animals. The new sites were recorded on the prepared maps each time. During the end of the summer trapping period, I intensively snap trapped the plot and removed as many *Microtus* as possible.

Anatomical Measurements

In order to obtain data on inter-island variation, reproduction and longevity, I made anatomical measurements on 525 *Microtus*. I took the external body measurements in the field. Skeletons were cleaned by dermestid beetles and soaked in a 14% solution of ammonia to remove excess grease (Hall and Russell, 1933). All skeletal measurements were taken on a craniometer similar to the one described by Anderson (1968). Measurements were taken to 0.01 mm under 7x magnification. Paired structures were measured on the right side. The measurements were taken as described below.

Total body length: distance between tip of nose and tip of fleshy part of tail. The specimen was placed on its dorsum on a dissecting board and gently straightened. Dissecting needles were used to mark the end points. The distance was then measured to the nearest 1 mm with a Helios dial caliper.

Tail length: distance between base and fleshy tip of tail. The specimen was hung over the edge of a plastic rule so that the body was at right angles to the tail (Burt, 1957). Measurements were taken to the nearest 0.5 mm.

Hind foot length: greatest distance from heel to end of longest toe, exclusive of toe nail, measured to the nearest 0.5 mm with a plastic rule.

Ear length: distance between base of notch and tip of ear, excluding hair, measured to the nearest 0.5 mm with a plastic rule.

Basioccipital length: greatest distance from most posterior point of occipital condyles to most anterior point on midline.

Palate length: distance from posterior point of palate in midline to posterior edge of incisive alveolus (Anderson, 1954).

Maxillary alveolus length: greatest anterior-posterior distance (Anderson, 1954).

Condylzygomatic length: distance from occipital condyle to most anterior edge of zygomatic process of maxilla (Snyder, 1954).

Incisive foramen length: length of foramen on right side of septum.

Incisive foramen width: greatest width.

Diastema length: distance from anterior edge of maxillary alveolus to posterior edge of incisive alveolus (Snyder, 1954).

Condylbasilar length: distance from posterior edge of occipital condyle to posterior edge of incisive alveolus (Anderson, 1954).

Zygomatic breadth: greatest distance along a line passing through first salient angles of both right and left M^2 .

Interorbital breadth: least distance between orbits as viewed dorsally (Anderson, 1954; Snyder, 1954).

Rostrum length: condylbasilar length minus condylzygomatic length (Snyder, 1954).

Cranial height: perpendicular distance from highest point of parietal to a plane passing from ventral point of auditory bulla along crown of most-prominent molar (Corbet, 1964; Snyder, 1954).

Cranial breadth: distance between squamosal bars at the points where, in dorsal view, they seem to disappear anteriorly behind upper part of squamosal (Corbet, 1964; Snyder, 1954).

Mandibular alveolus length: greatest anterior-posterior distance.

Femur length: distance between dorsal side of head and distal

edge of median condyle in a line parallel to shaft.

Pelvic length: distance from posterior-dorsal edge of ischium to anterior edge of ilium (cf. Dunmire, 1955).

Sacrum width: greatest width of sacral vertebrae.

Moult Progression

As an aid in determining the age of the voles I examined their moult patterns. I prepared flat skins from 340 *Microtus* following the techniques of Ecke and Kinney (1956). The specimens were skinned by making an incision along the venter from the anus to the tip of the lower jaw. The skins were then stretched and pinned to sheets of cardboard. I stripped the excess fat from the skins, but, in order to avoid a change in hair colour or texture, they were not degreased. When thoroughly dried they were stored individually in paper envelopes.

I determined the juvenal and post-juvenal moult progression by laying the skins of 245 summer-caught specimens out on a table and working out a logical continuum. The progression was checked by statistically comparing the lengths of femurs of groups along the continuum. Body weight, skull development and pelvic length were also used as checks on the proposed moult progression.

Parasites

Mites, fleas and lice were collected from 131 snap-trapped and 36 live-trapped voles. I placed the snap-trapped individuals in paper bags upon removal from the traps. At camp I gave each bag a quick spray of ethyl ether which immobilized the ectoparasites (Davis, 1964). They were then removed from the carcass and paper bag with forceps and preserved in 70% ethyl alcohol (Anderson, 1965). Ectoparasites were

removed and preserved from the live-trapped *Microtus* during toe clipping. All ectoparasites were sent to Dr. C. E. Hopla and his staff at the University of Oklahoma for identification.

The viscera of 380 snap-trapped voles were individually wrapped in gauze and preserved in 10% formalin (Davis, 1964). The material was sent to Mr. F. Smith of Memorial University who is making an exhaustive investigation of the helminth burden of Newfoundland mammals.

Blood smears were taken from the live-trapped voles when they were toe clipped. The blood slides were also sent to Mr. F. Smith who will examine them for blood parasites.

Food Preference Tests

In order to ascertain which components of the local flora are important items in the voles' diets, I conducted cafeteria food tests (Drozdz, 1966, 1967; Gorecki and Gebczynska, 1962; Miller, 1954; Thompson, 1965) during the winter (18 March to 4 April 1969) and the summer (16-22 August 1969). Most of the vegetation available to the voles on the SKC plot was tested. I offered 45 species of vascular and 7 species of non-vascular plants to 13 voles captured on the plot. Nineteen of these plant species were tested in both seasons. The vascular plants were identified by Mr. O. Forsey, Mrs. G. Keleher and Dr. E. Rouleau; the non-vascular plants were identified by Drs. I. Brodo, D. Murray and R. Longton.

The voles were caged individually in fiber glass flower boxes (60 cm x 20 cm x 15 cm) with screen tops. Wood shavings and terylene fibre were provided for litter and nest material, respectively. Water in dishes (summer) or snow balls (winter) were supplied *ad libitum*. I

kept the caged animals in an unheated shed where the ambient temperature was close to that of the macroenvironment. At the beginning of each test I placed five to seven species of plants in each cage. Purina laboratory mouse chow was supplied in excess, thereby allowing the subjects to refuse all plant species offered and to subsist on the lab chow. I kept records on the plant species, the amounts and the parts (such as berries, roots, stems, etc.) given to each vole. After three days, I removed the voles from their cages and examined the plant remains. Each species was given a rating of A through D, depending upon the percent consumed (A = 0%, B = 1-30%, C = 31-60%, D = 61-100%).

Swimming Tests

In order to ascertain whether *Microtus* has the ability to swim between islands, I conducted eight swimming tests in the late summer and fall of 1968. During these tests data pertaining to the following environmental parameters were recorded on a Philips portable tape recorder: air temperature, surface water temperature, current, wave action, wind, cloud cover and precipitation. During each test a vole was released from a boat and observations on its behaviour were made with 7 x 50 binoculars and recorded on the tape recorder. I terminated the test when the subject reached shore or drowned.

The exact position of the release site was determined on aerial photographs by triangulation or by a floating rope marked at 3-m intervals which extended from the nearest land to the boat. I gently lowered the animals to the water's surface in an insect net, thereby avoiding excessively wetting their fur.

Average speeds were calculated from the distances covered between

the release site and their landing sites. I calculated an exact speed for a vole which swam parallel to the marker rope for a distance of 12 m.

In an attempt to discover the modality used by the voles to orient at sea, I calculated the contours of the horizons as seen by the swimming voles. By using topographic maps, aerial photographs and trigonometry, I determined the angles subtended by objects (islands, hills, boats, setting sun, etc.) on the horizon in a 360° -circle around each of the eight release sites.

Scat and Pellet Analyses

Two hundred and eighty-five predator scats and pellets were collected in the field, dried and stored in paper bags. In the laboratory I thoroughly moistened each fecal passage and pellet in soapy water, broke it apart and examined it beneath a dissecting scope.

Hairs were identified to species by making plastic impressions (Williamson, 1951) of unknowns and comparing these with impressions of identified hairs from a reference collection (Day, 1966). I identified invertebrate remains with the aid of a reference collection from the study area. I made no attempt to identify fish or bird remains beyond those superficial categories. The small amounts of vegetation found in the scats and pellets were identified only to the categories of grasses or berries, except for the needles of *Abies balsamea* which were easily identified.

Only percent occurrence (Macpherson, 1969; Scott, 1947) was determined in these analyses. The scats and pellets have been saved for a future, more-exhaustive study.

Meteorological Measurements

I made macroclimatic observations from 25 May to 30 August 1967 from the base camp on Pyke Island. Macro- and microclimatic data were collected from 25 June to 28 August 1968 at the base camp on Inspector Island and from 3 October 1968 to 4 July 1969 at the base camp on South Trump Island.

Macroenvironmental temperatures were recorded from a Taylor maximum-minimum thermometer situated 1.2 m above the ground. In 1967 the thermometer was secured to a fir tree in the shade. In 1968 and 1969 the thermometer was sheltered in a ventilated white box (approximately 25 cm x 20 cm x 15 cm) which was located in the centre of a small old-field. Barometric pressures were recorded from an aneroid barometer sheltered in the ventilated box. Wind speeds were taken with a Dwyer wind gauge at 1.5 m above the ground. Rainfall was measured in a Tru-Check rain gauge. I measured snow accumulation with a 2-m pole calibrated in centimetres. Observations were made on the general weather changes which occurred from day to day.

I recorded microenvironmental temperatures in different habitats. The temperatures were sensed by thermistors (same as those described by Pruitt, 1957) at various levels above and below the ground (Appendix C, p. 194).

During the 1968-69 winter I made observations on the snow conditions on the islands in the vicinity of South Trump Island. I recorded and mapped snow depths for all habitats on the SKC plot during January, February and March.

In addition to my records, climatological data were obtained from the Department of Transport's meteorological stations at Twillingate

and Comfort Cove. The Twillingate station is situated approximately 6.5 km north of the study area ($49^{\circ}41'$ N. Lat., $54^{\circ}49'$ W. Long.); the Comfort Cove station is approximately 9.5 km south of the study area ($49^{\circ}16'$ N. Lat., $54^{\circ}53'$ W. Long.). Data from Twillingate for 1957 to 1966 and from Comfort Cove for 1967 to 1969 were examined.

Additional Observations

In addition to the above-mentioned observations and measurements, I observed many other aspects of *Microtus* ecology, particularly food habits, predation, island colonization and habitat selection. Records were kept on the occurrence and status of birds and mammals in the study area. I also gathered natural history data from the local trappers, hunters and fishermen.

RESULTS AND DISCUSSION

Anatomical Variations

Many of the islands in the study area are isolated by water barriers exceeding several hundred metres, and some of the island complexes in Bay of Exploits are separated by several kilometres. Under such circumstances of isolation, insular populations of vertebrates often display phenotypic variations (e.g., Anderson, 1960; Bangs, 1908; Barrett-Hamilton and Hinton, 1913; Berry, 1964, 1969; Berry *et al.*, 1967; Cameron, 1958; Cook, 1961; Corbet, 1961, 1964; Engels, 1936; Foster, 1964, 1965; Grant, 1968; Hall, 1938; Jewell, 1966; Rausch and Rausch, 1968).

During the field study I examined 943 *Microtus* from 30 islands. The only gross morphological variation which I detected was a difference in coat colouration. Some of the voles that inhabited Camel Island (No. 8), Mile Island (No. 19) and Island No. 65 were melanistic; their dorsums were Black¹ (2.5Y 2/0) and speckled with silver hairs, their sides were Very Dark Grey (5YR 3/1) and their venters were Dark Grey (2.5Y 4/1). This was in sharp contrast to the typical colouration of the non-melanistic individuals: Dark Brown (7.5YR 3/2) dorsum, Brown (7.5YR 5/2) sides and Grey (7.5YR 7/1) venter.

A fisherman from Tizzard's Harbour told me that the voles on Mouse Island (No. 87) were a reddish colour and could be distinguished easily

¹The colour terms are those of Munsell (1954).

from all other voles by this fact. Unfortunately, when I attempted to secure specimens from Mouse Island I discovered that the vole population had recently been extirpated (see section on Island Colonization and Inter-Island Movements, pp. 132-134). Thus, I was unable to substantiate or refute the fisherman's statement.

In search of additional inter-island variations, I made anatomical measurements on 525 *Microtus*. I attempted to minimize intrapopulation variation by making the following considerations before arriving at a comparative series of 121 specimens from 10 islands [Matthews (No. 88), South Trump (No. 82), South Berry (No. 84), Fools Harbour (No. 80), Rat (No. 81), Grassy Rock (No. 37), Nos. 2, 3, 4 and 5]:

1. In order to reduce the age variation, I compared only adult and old-age animals (see section on Age Determination and Longevity, pp. 152-163).
2. In the hopes of minimizing seasonal and cyclical variation, all animals were snap trapped during June, July and August 1969, except for the Grassy Rock specimens which were collected 27-30 May 1966.
3. Only those islands which yielded six or more adult specimens were considered.
4. Goin (1943) demonstrated that there is only a slight difference between male and female series of *M. pennsylvanicus*. Therefore, I lumped the sexes together to avoid reducing the already-small samples.
5. The external measurements of the Grassy Rock series were taken by O. Forsey. Since there is considerable variation in the same measurement taken by different persons (Jewell and Fullagar, 1966), these measurements were omitted from the general analysis.

6. Because a total of only 17 adult and old-age animals was collected on island Nos. 2, 3, 4 and 5 and due to the isolated position of these islands (see Fig. 1, p. 11), I lumped the specimens together and referred to them as the Hummock Island sample.

I graphed the anatomical measurements in the format proposed by Hubbs and Hubbs (1953) in Figs. 16-34 (pp. 44-62).

The graphs for hind foot length (Fig. 18, p. 46), incisive foramen length (Fig. 24, p. 52) and incisive foramen width (Fig. 25, p. 53) show extensive overlapping of the standard deviations for all samples and hence indicate relatively little inter-island variation in these structures. For a majority of the measurements, maxillary alveolus length (Fig. 22, p. 50), condylozygomatic length (Fig. 23, p. 51), condylobasilar length (Fig. 27, p. 55), zygomatic breadth (Fig. 28, p. 56), interorbital breadth (Fig. 29, p. 57), rostrum length (Fig. 30, p. 58), cranial height (Fig. 31, p. 59), cranial breadth (Fig. 32, p. 60) and mandibular alveolus length (Fig. 33, p. 61), there are at least two samples which show no overlap in the standard deviations and therefore indicate considerable variation. The remaining measurements, total body length (Fig. 16, p. 44), tail length (Fig. 17, p. 45), ear length (Fig. 19, p. 47), palate length (Fig. 21, p. 49), diastema length (Fig. 26, p. 54) and femur length (Fig. 34, p. 62), show intermediate amounts of variation. If the latter measurements are tested with Student's "t," significant differences are often found to exist between the samples even though their standard deviations are overlapping. For example, statistically there is a highly significant difference in the basioccipital lengths of the Matthews Island and Hummock Island series ($t = 3.39$, $df = 33$, $P < 0.005$) even though their standard deviations overlap on the

graph.

These inter-island variations do not appear to be related to the distances between the islands. For palate length, zygomatic breadth, cranial breadth and femur length, there is as much variation between the specimens from Rat and Fools Harbour islands which are only 100 m apart as there is between the series from South Trump and Hummock islands which are 29,300 m apart. The differences between the specimens from South Trump and South Berry islands, 280 m apart, and between South Trump and Matthews islands, 4050 m apart, are similar for basioccipital length, maxillary alveolus length, condylozygomatic length, diastema length, condylobasilar length and rostrum length.

There also appears to be little or no correlation between habitat type or island size and anatomical variations. For example, the specimens from South Berry Island (8.52 ha), which is primarily covered with tuckamoor, and Matthews Island (4.07 ha), primarily grassy, have similar measurements for basioccipital length, palate length, maxillary alveolus length, diastema length, condylobasilar length and rostrum length. South Trump Island is 172.2 ha whereas Grassy Rock is only 0.28 ha, yet the series from these islands have similar measurements for condylozygomatic length, interorbital breadth and cranial breadth.

While taking the skull measurements, I noticed definite variations among the molar tooth patterns.¹ The specimens show a gradation of

¹The molar crowns of microtines consist of series of alternating enamel loops (Fig. 35, p. 63); the loops are referred to as salient angles and the intervening notches as re-entrant angles. It has been pointed out by many investigators (Corbet, 1964; Goin, 1943; Guthrie, 1965; Hibbard, 1944; Komarek, 1932; Reichstein, 1966; Reichstein and Reise, 1965) that there is considerable variation in the shape and number of the salient angles, particularly those at the anterior end of m_1 and the posterior end of M^3 . According to Guthrie (1965), the microtine molar is rapidly evolving toward a more complex structure by the addition of extra salient angles.

complexity between the two m_1 dental patterns shown in Fig. 35 (p. 63). In the simple form (Fig. 35a), the fifth inner (lingual) salient angle is weakly developed with only a slight indentation anterior to it. The more complex pattern (Fig. 35b) has a strongly developed fifth inner salient angle with a prominent anterior re-entrant angle. The simple pattern is characteristic of the entire Hummock Island sample. The complex form is typical of the other island populations; on some of these other islands, however, the simple pattern is also present but at very low frequencies.

Colouration, skeletal form and molar structure are diagnostic characters of microtine taxa. Characters with the same magnitude of variation that I found in Notre Dame Bay are commonly used by taxonomists to designate new subspecies (e.g., Anderson, 1956; Bangs, 1894, 1896, 1900; Cockrum and Fitch, 1952; Dale, 1940; Komarek, 1932; Youngman, 1967) and even fossil species (Hibbard, 1944). I do not believe, however, that the inter-island variations in my study area are of taxonomic importance. They are not the result of gene pools being isolated for long periods of time (see section on Island Colonization and Inter-Island Movements, pp. 132-151), but probably are only the fortuitous phenotypic expression of variations which can be expected within a rapidly evolving species (Guthrie, 1965; Hooper, 1957).

Several authors have noted that insular forms of rodents tend to be larger than forms on adjacent mainlands (e.g., Berry, 1964, 1968, 1969; Corbet, 1964; Foster, 1964, 1965; Jewell, 1966; Rausch and Rausch, 1968; Wheeler, 1956). In order to determine whether the insular populations of *Microtus* in Notre Dame Bay followed this trend, I examined an additional 100 specimens from the main island of Newfoundland. Since

these specimens had been collected and prepared by other persons, I did not utilize their measurements (see Jewell and Fullagar, 1966) but instead took 14 cranial measurements. Of the 100 specimens examined, only 17 adults (7 males and 10 females) were in a usable condition (skulls intact and cleaned). These specimens had been taken from Manuels River (1), Badger (1), Baie Verte highway (2), Grand Falls (3), North Pond (2), Big Brook (2), St. George's (3) and Codroy Valley (3) (Fig. 36, p. 64).

The cranial measurements from these voles are given in column 3, Table I (p. 65). A visual comparison of the means and standard deviations given in Figs. 20-33 with the data presented in column 3, Table I indicates that some of the island populations in Notre Dame Bay had larger skulls (especially palate length, maxillary alveolus length, zygomatic breadth, rostrum length, cranial height, cranial breadth and mandibular alveolus length) than the voles from the main island of Newfoundland.

I carried this analysis a step further by comparing *M. p. terraenovae* from the main island of Newfoundland with the geographically closest mainland forms, *M. p. enixus* from Labrador and *M. p. acadicus* from Nova Scotia (Hall and Kelson, 1959). Cranial measurements from 10 adult Labrador voles (6 males, 3 females and 1 unknown) and 15 adult Nova Scotia voles (7 males and 8 females) are presented in columns 2 and 4, Table I. The Labrador specimens had been collected from Hawks Harbour (1), Hopedale (1), Red Bay (4) and Cape Diabale (4). The Nova Scotia voles were from Annapolis Co. (1), Kings Co. (10), Halifax Co. (2), Pictou Co. (1) and Cape Breton Co. (1) (Fig. 36).

The "t" tests in columns 1 and 5, Table I indicate that there are no statistically significant differences ($P > 0.10$) between the 14 cranial

measurements for the voles taken from the main island of Newfoundland and the Labrador shore. There are, however, highly significant differences ($P < 0.01$) between the Newfoundland and Nova Scotia specimens for basioccipital length, palate length, condylobasilar length, zygomatic breadth, interorbital breadth and rostrum length; for condylozygomatic length there is a statistical difference between the 1% and 2% level of significance.

The data in Table I also imply that the Newfoundland race is more closely related to the Labrador form than to the Nova Scotia form. This conclusion is in direct contrast to Cameron's (1958) findings: he strongly suggested that the Newfoundland vole is more closely related to the Nova Scotia vole because of a similarity in pelage colouration, and he noted a definite darker colouration in the Ungava form. Although I examined more than 600 *M. p. terraenovae* and 50 *M. p. enixus*, I was unable to separate these two forms using colouration.

Pelage colouration is not an ideal standard to use when comparing museum specimens, because many factors act to alter the original colour of the fur, e.g., the amount of stuffing used to make the study skin, the amount of grease in the skin, the amount of exposure to sunlight and humidity and the type of preservatives used. In addition, the use of colour as a standard is quite subjective.

Since it has been demonstrated that microtines vary in size at different phases of their population cycles (Chitty, 1952; Chitty and Chitty, 1962; Karaseva *et al.*, 1957; Krebs, 1964a; Keller, 1968) and with changes in sexual activity and age (Barbehenn, 1955; Fuller, 1969; Pokrovski and Bolshakov, 1969; see also sections on Age Determination and Longevity and Reproduction, pp. 152-168), it is of the utmost importance that only individuals captured at the same phase of the population cycle

as well as at the same stage of sexual activity and same age be used when comparing different populations. This, however, has rarely, if ever, been done in a taxonomic study for the obvious reason that data would have to be collected over a period of several years before two populations could be compared.

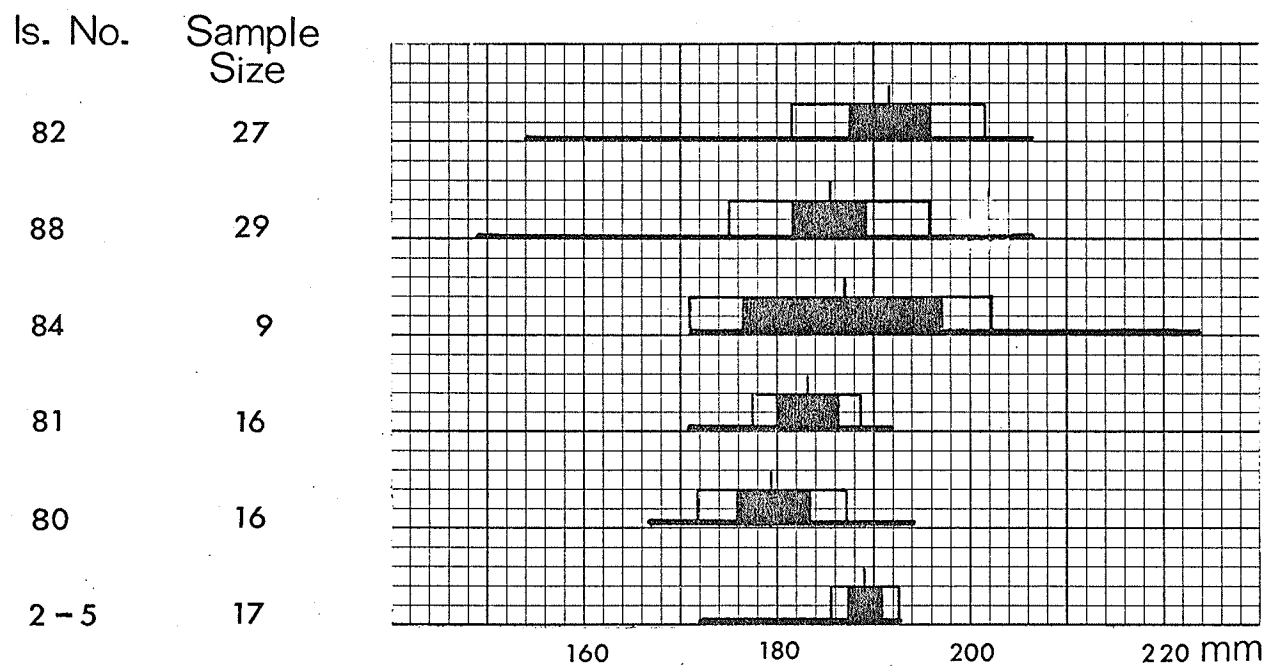


Fig. 16. Variation in total body length of adult *Microtus pennsylvanicus* captured on various islands in Notre Dame Bay. The thick horizontal line indicates the range and the short midline the arithmetic mean. The black bar represents two standard errors of the mean on either side of the mean. The distance from the midline to the end of the white bar represents one standard deviation on either side of the mean.

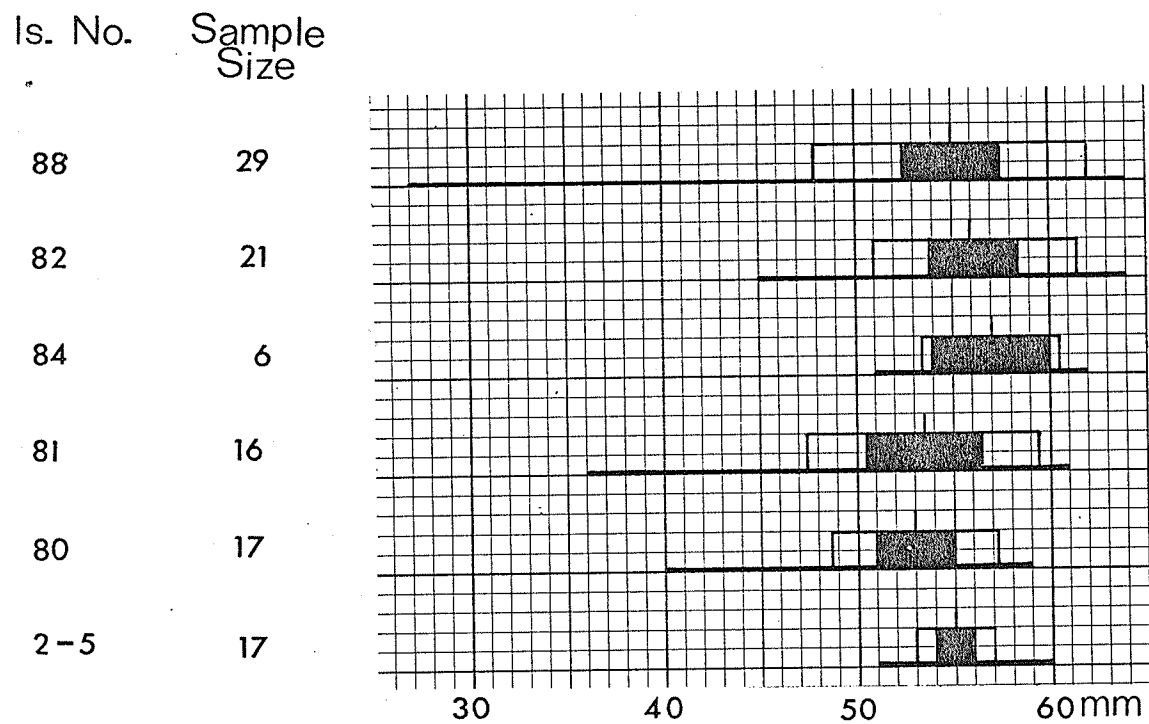


Fig. 17. Variation in tail length of adult *Microtus pennsylvanicus* captured on various islands in Notre Dame Bay. Symbols as in Fig. 16.

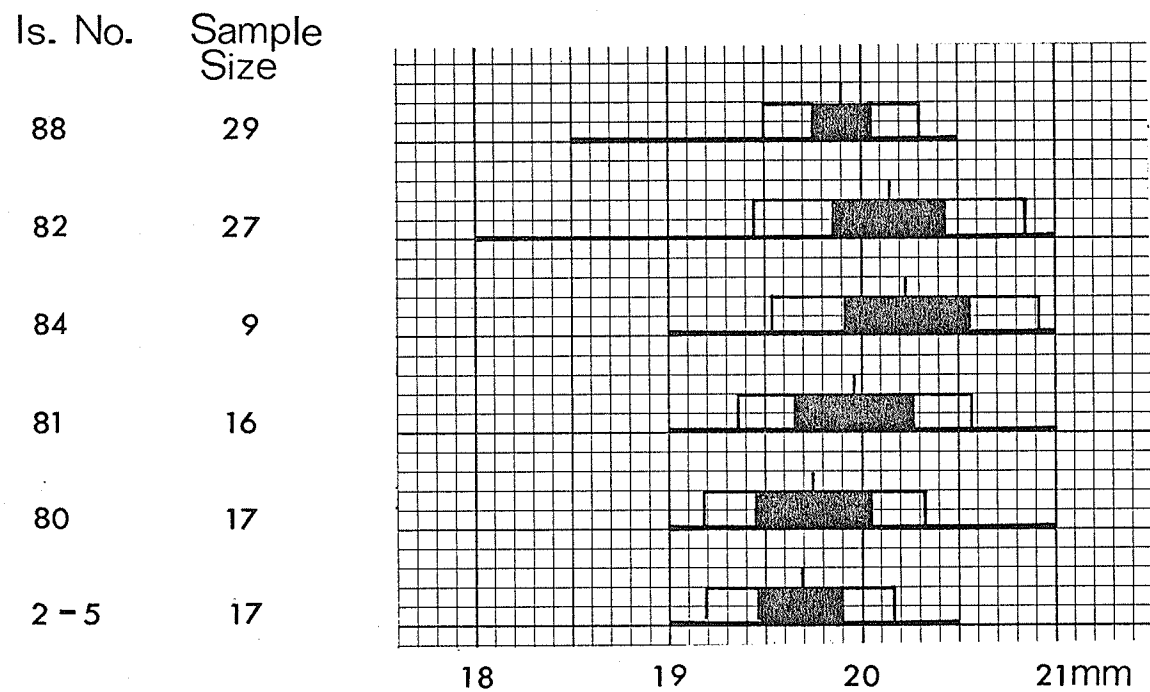


Fig. 18. Variation in hind foot length of adult *Microtus pennsylvanicus* captured on various islands in Notre Dame Bay. Symbols as in Fig. 16.

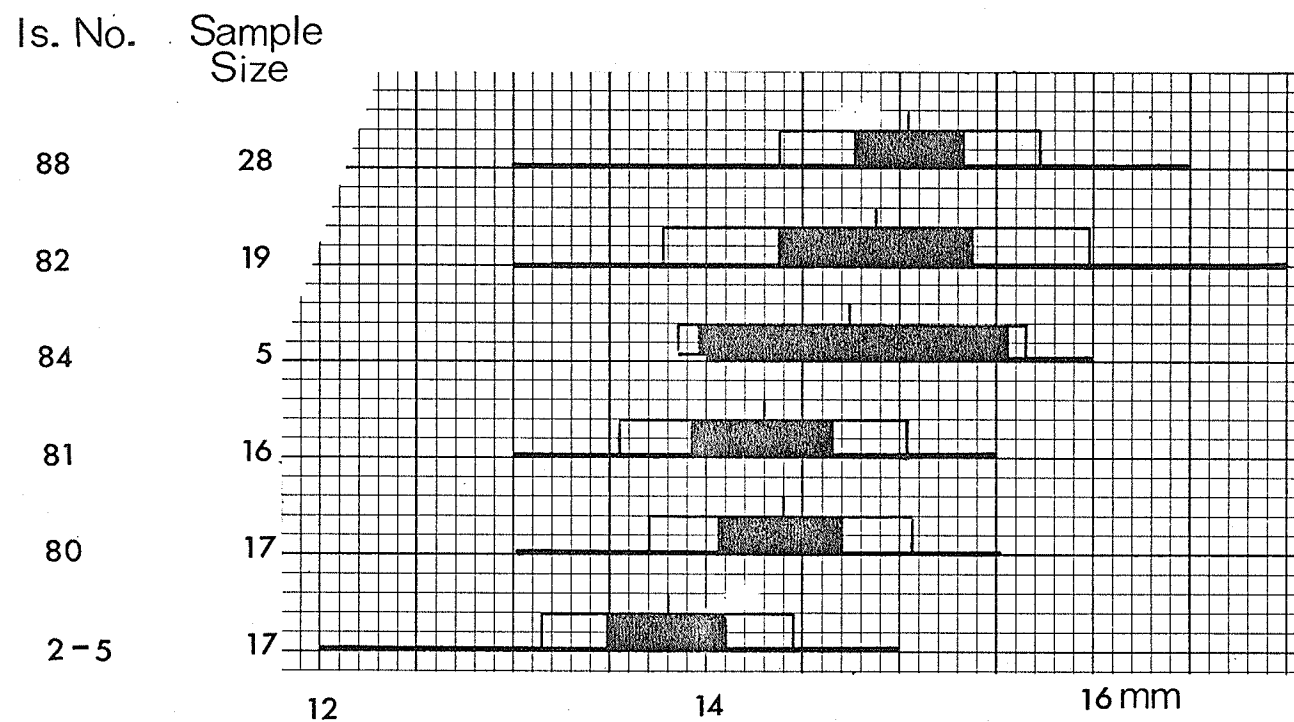


Fig. 19. Variation in ear length of adult *Microtus pennsylvanicus* captured on various islands in Notre Dame Bay. Symbols as in Fig. 16.

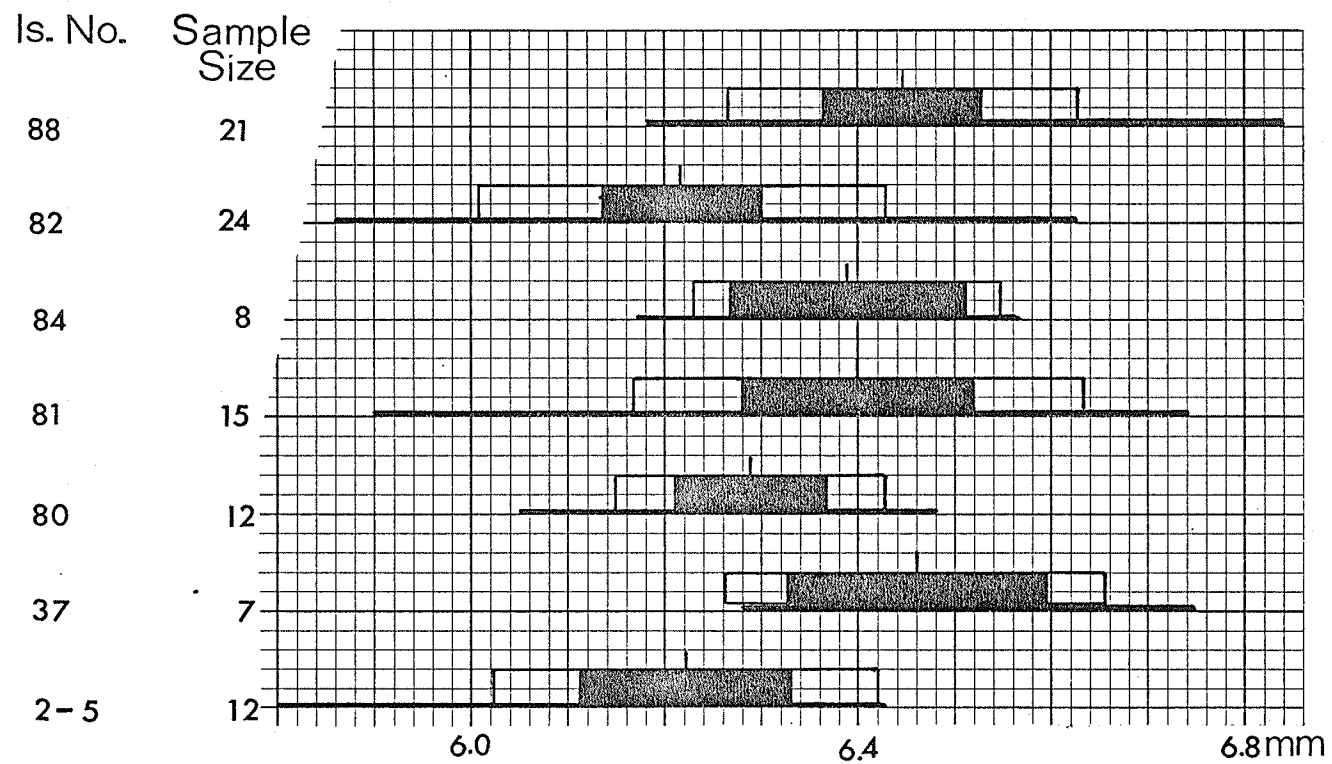


Fig. 20. Variation in basioccipital length of adult *Microtus pennsylvanicus* captured on various islands in Notre Dame Bay. Symbols as in Fig. 16.

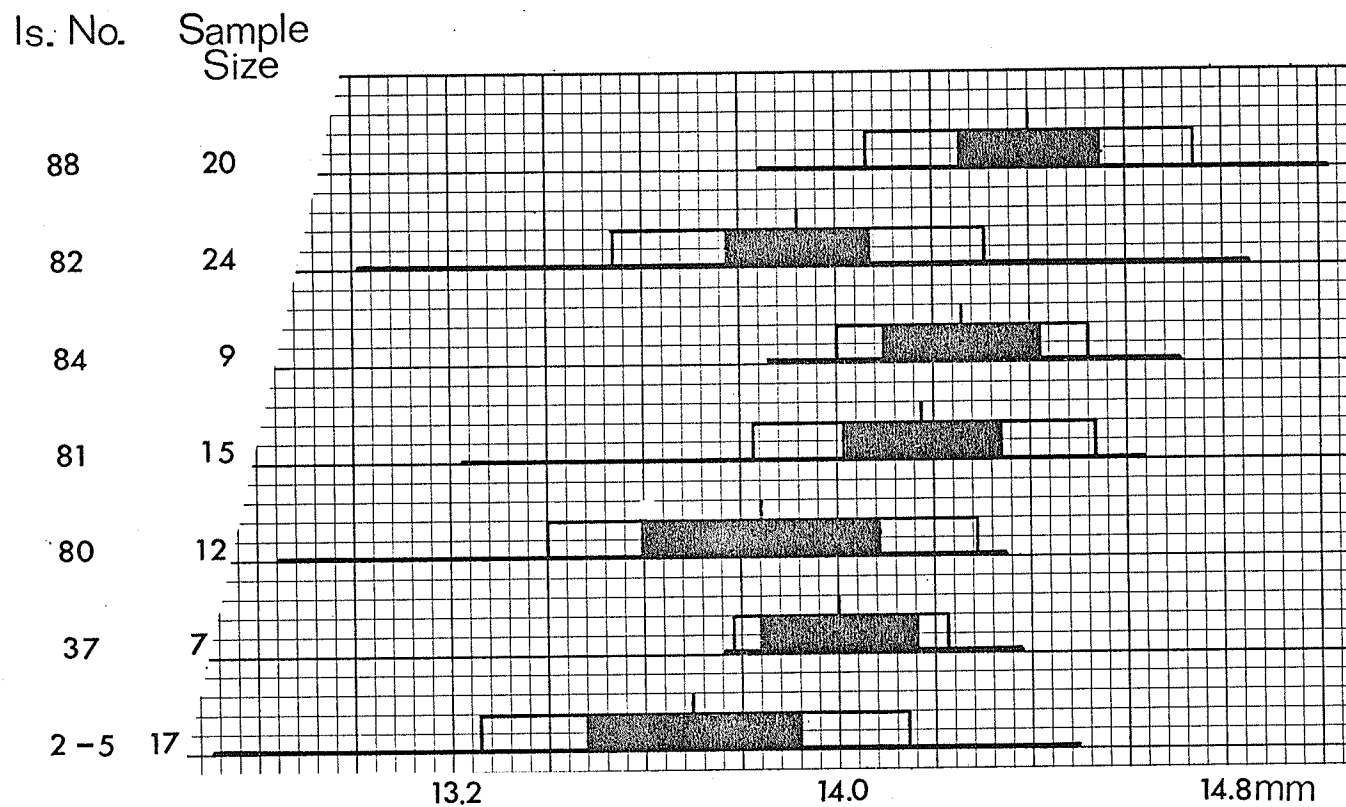


Fig. 21. Variation in palate length of adult *Microtus pennsylvanicus* captured on various islands in Notre Dame Bay. Symbols as in Fig. 16.

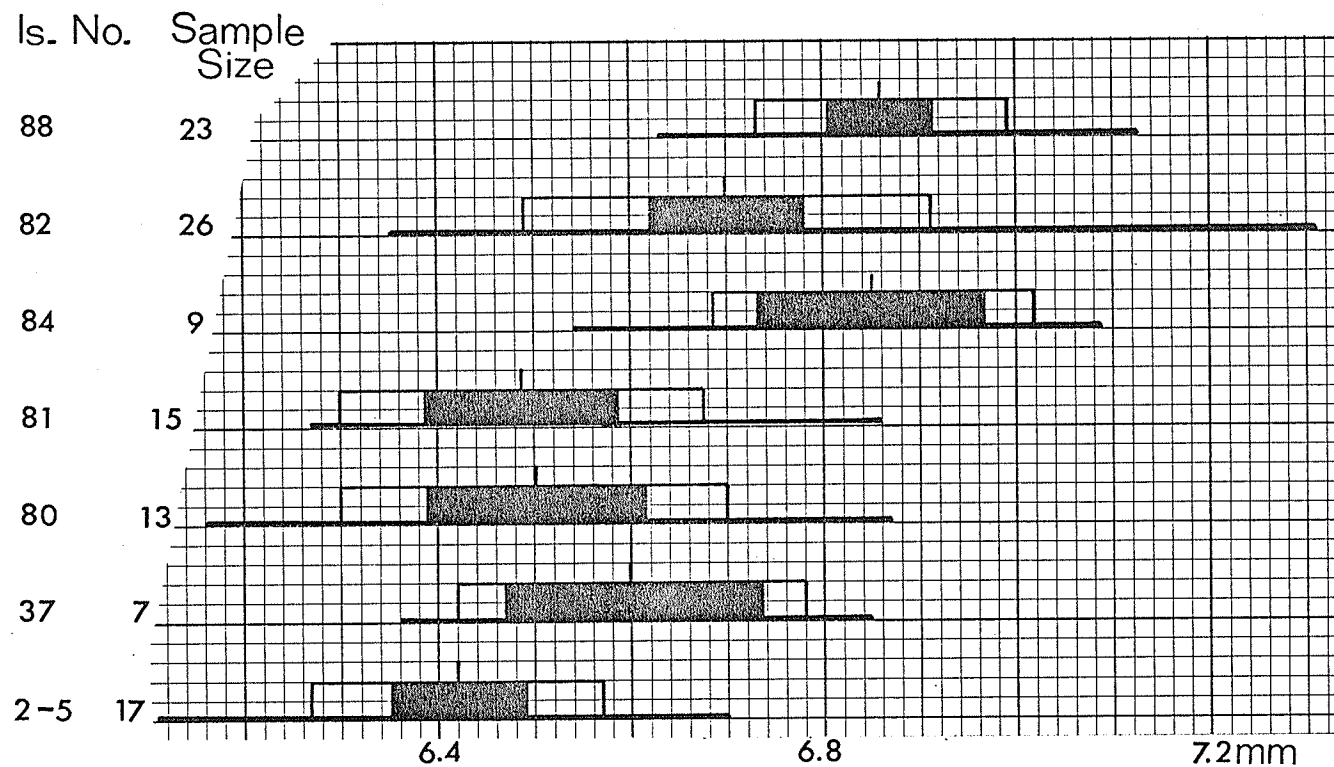


Fig. 22. Variation in maxillary alveolus length of adult *Microtus pennsylvanicus* captured on various islands in Notre Dame Bay. Symbols as in Fig. 16.

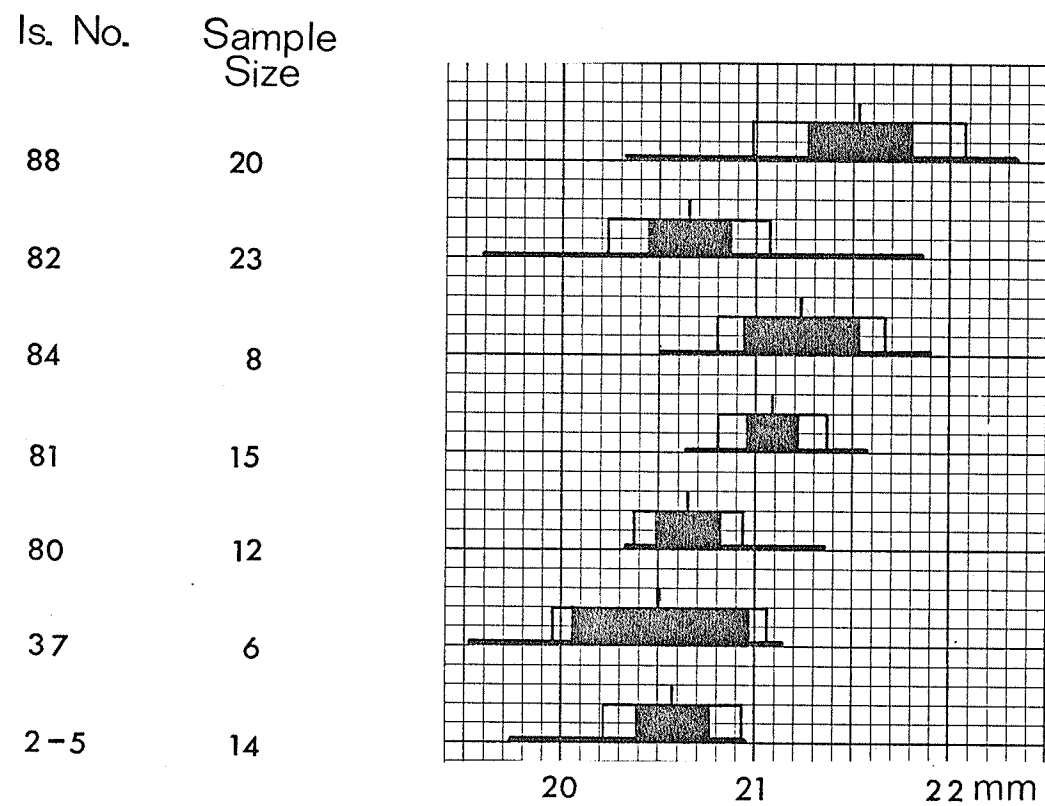


Fig. 23. Variation in condylozygomatic length of adult *Microtus pennsylvanicus* captured on various islands in Notre Dame Bay. Symbols as in Fig. 16.

Is. No.	Sample Size
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88	29
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82	24
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84	9
----	---

81	15
----	----

80	12
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37	7
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2-5	17
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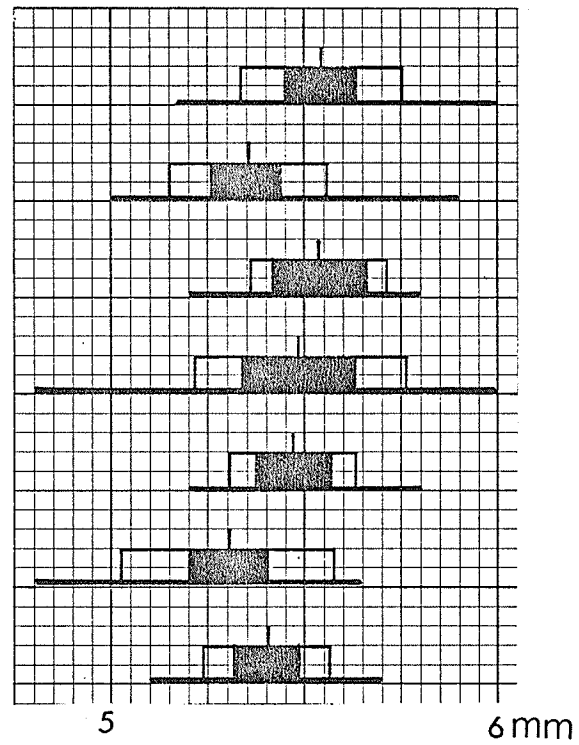


Fig. 24. Variation in incisive foramen length of adult *Microtus pennsylvanicus* captured on various islands in Notre Dame Bay. Symbols as in Fig. 16.

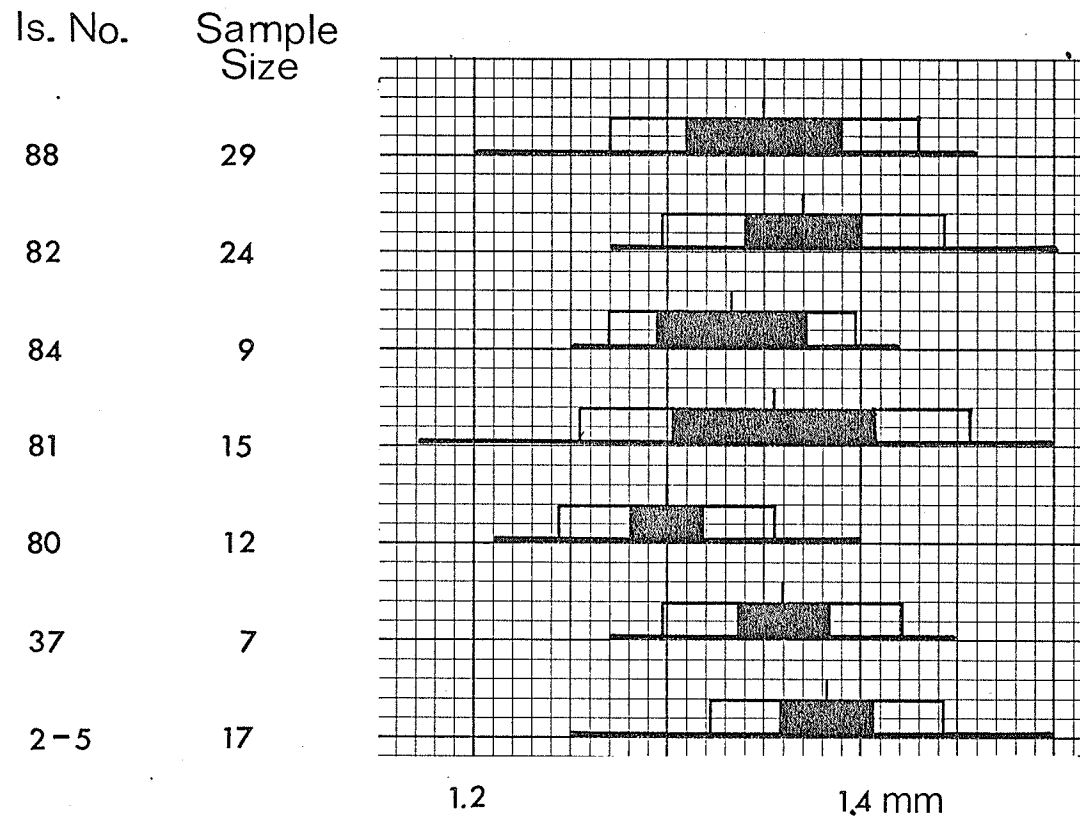


Fig. 25. Variation in incisive foramen width of adult *Microtus pennsylvanicus* captured on various islands in Notre Dame Bay. Symbols as in Fig. 16.

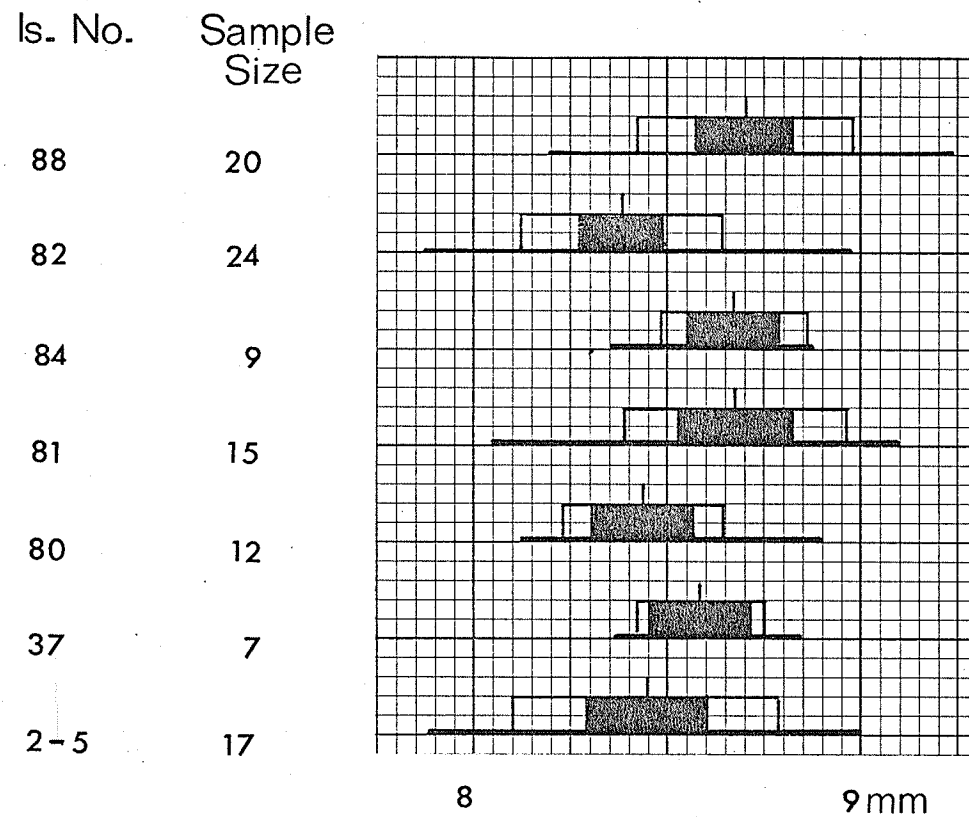


Fig. 26. Variation in diastema length of adult *Microtus pennsylvanicus* captured on various islands in Notre Dame Bay. Symbols as in Fig. 16.

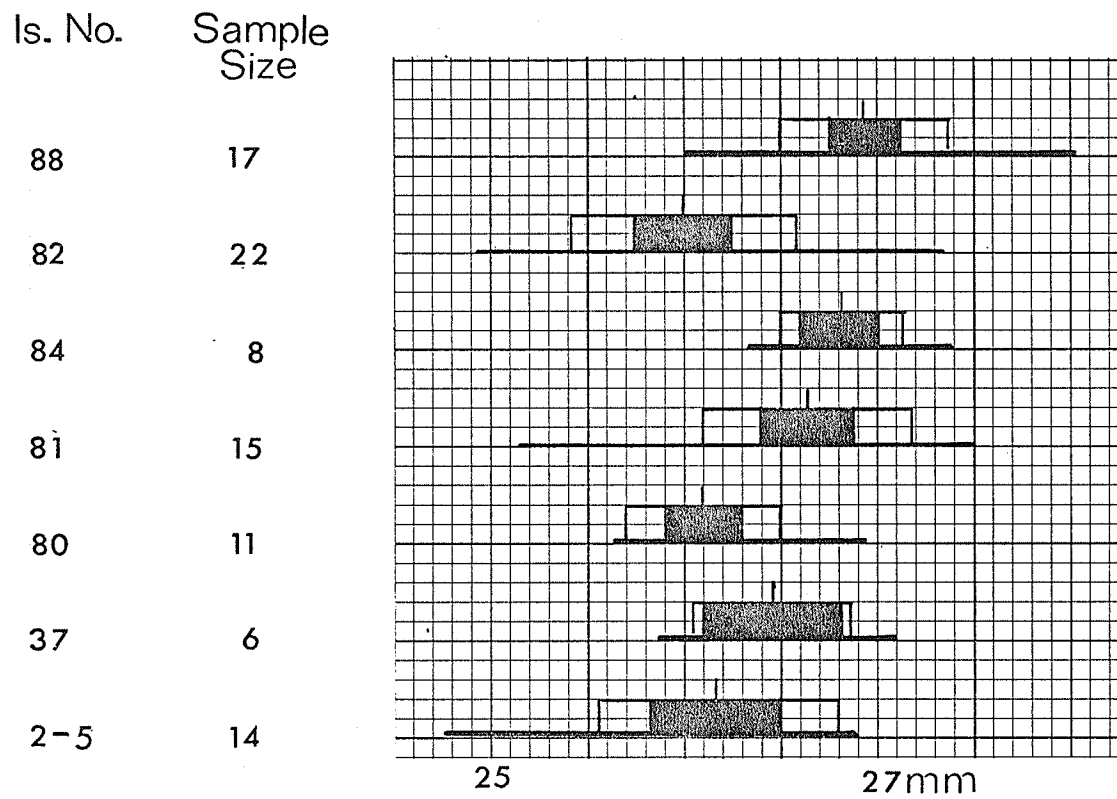


Fig. 27. Variation in condylobasilar length of adult *Microtus pennsylvanicus* captured on various islands in Notre Dame Bay. Symbols as in Fig. 16.

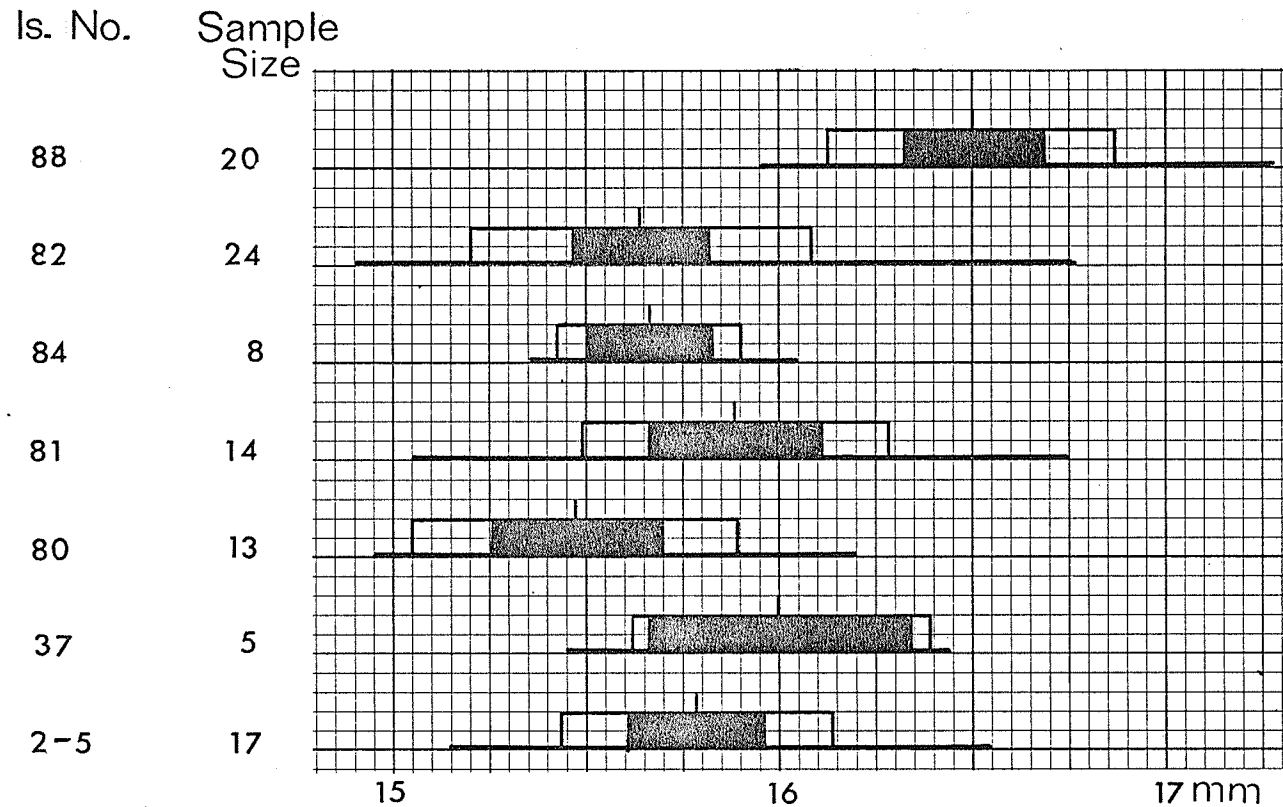


Fig. 28. Variation in zygomatic breadth of adult *Microtus pennsylvanicus* captured on various islands in Notre Dame Bay. Symbols as in Fig. 16.

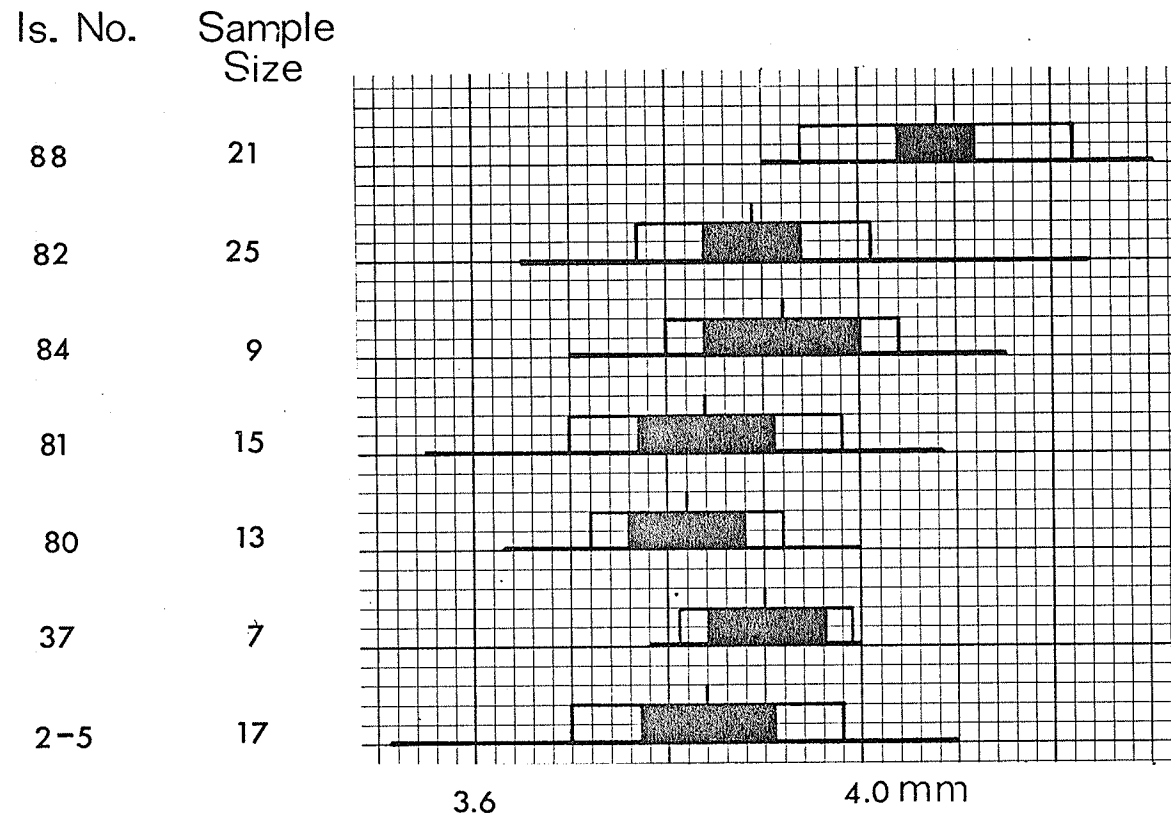


Fig. 29. Variation in interorbital breadth of adult *Microtus pennsylvanicus* captured on various islands in Notre Dame Bay. Symbols as in Fig. 16.

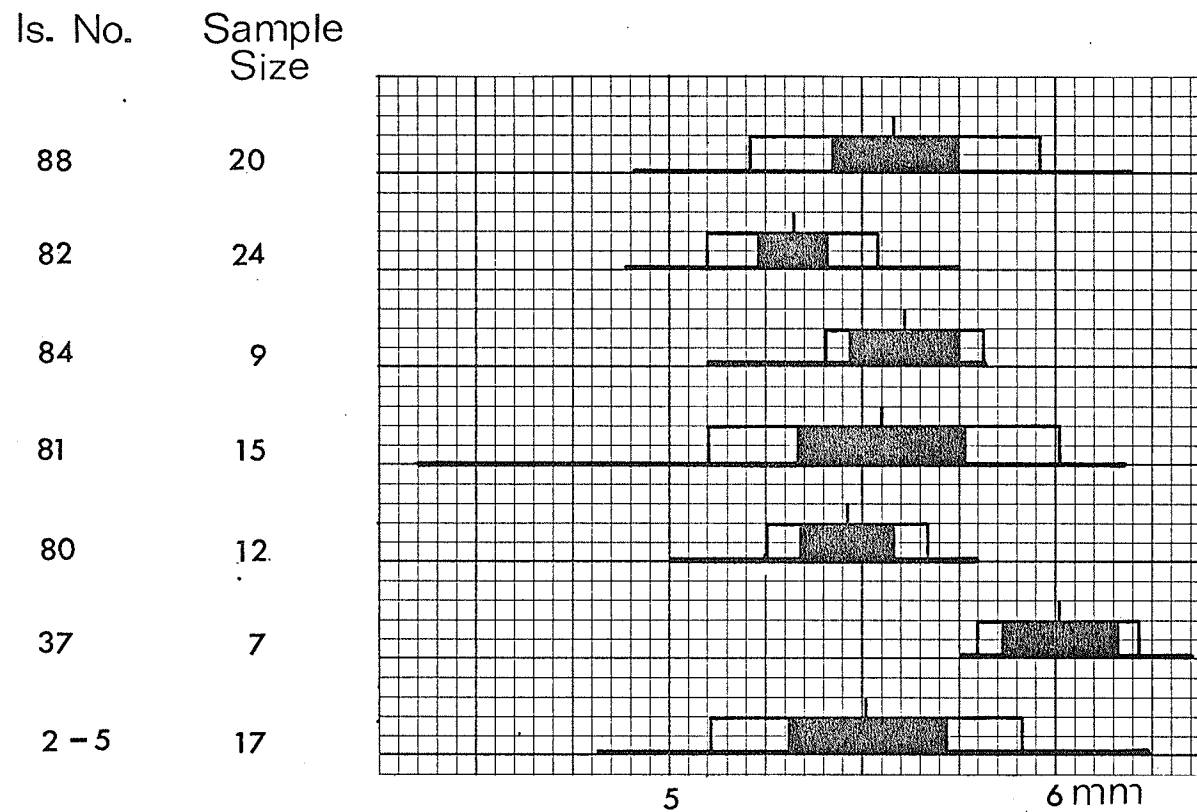


Fig. 30. Variation in rostrum length of adult *Microtus pennsylvanicus* captured on various islands in Notre Dame Bay. Symbols as in Fig. 16.

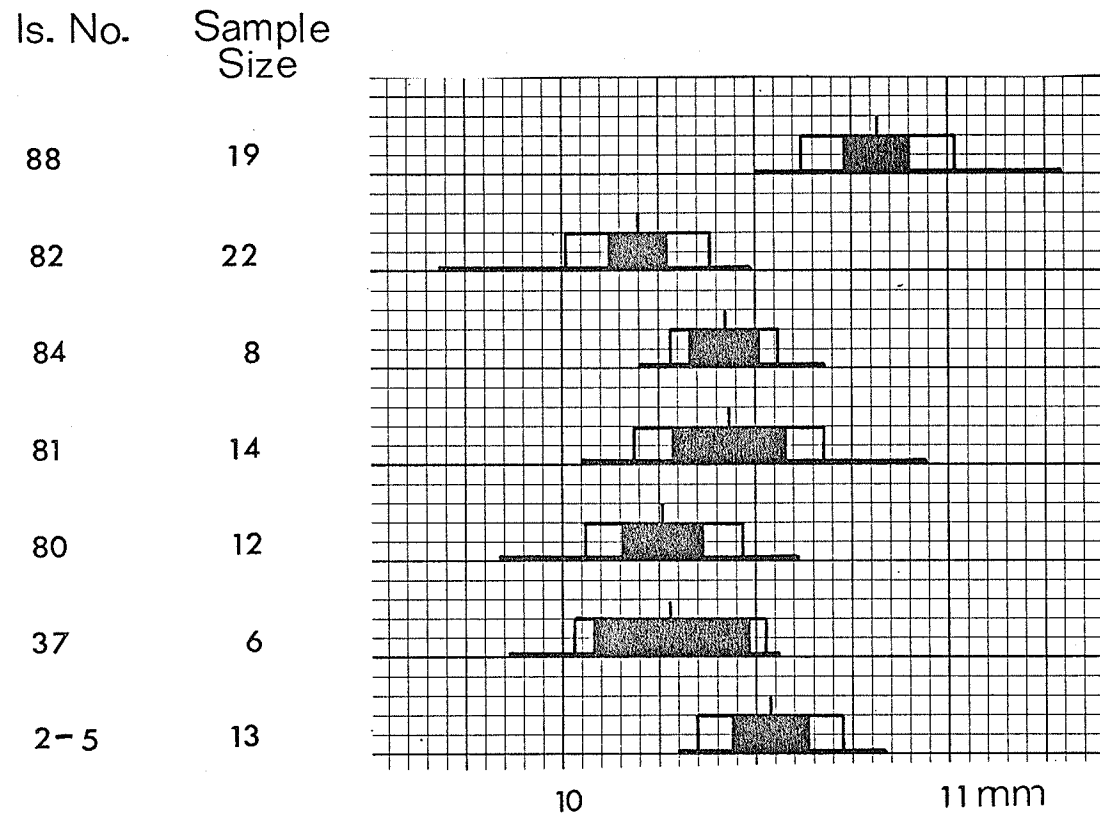


Fig. 31. Variation in cranial height of adult *Microtus pennsylvanicus* captured on various islands in Notre Dame Bay. Symbols as in Fig. 16.

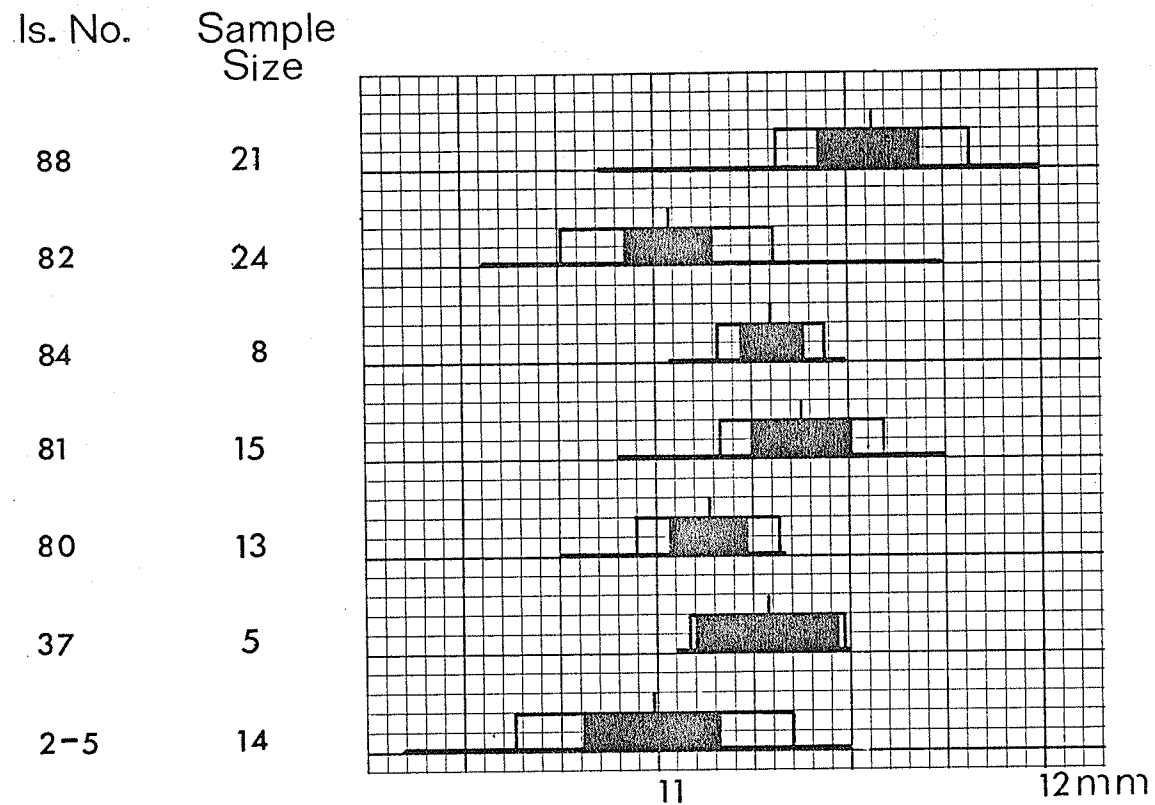


Fig. 32. Variation in cranial breadth of adult *Microtus pennsylvanicus* captured on various islands in Notre Dame Bay. Symbols as in Fig. 16.

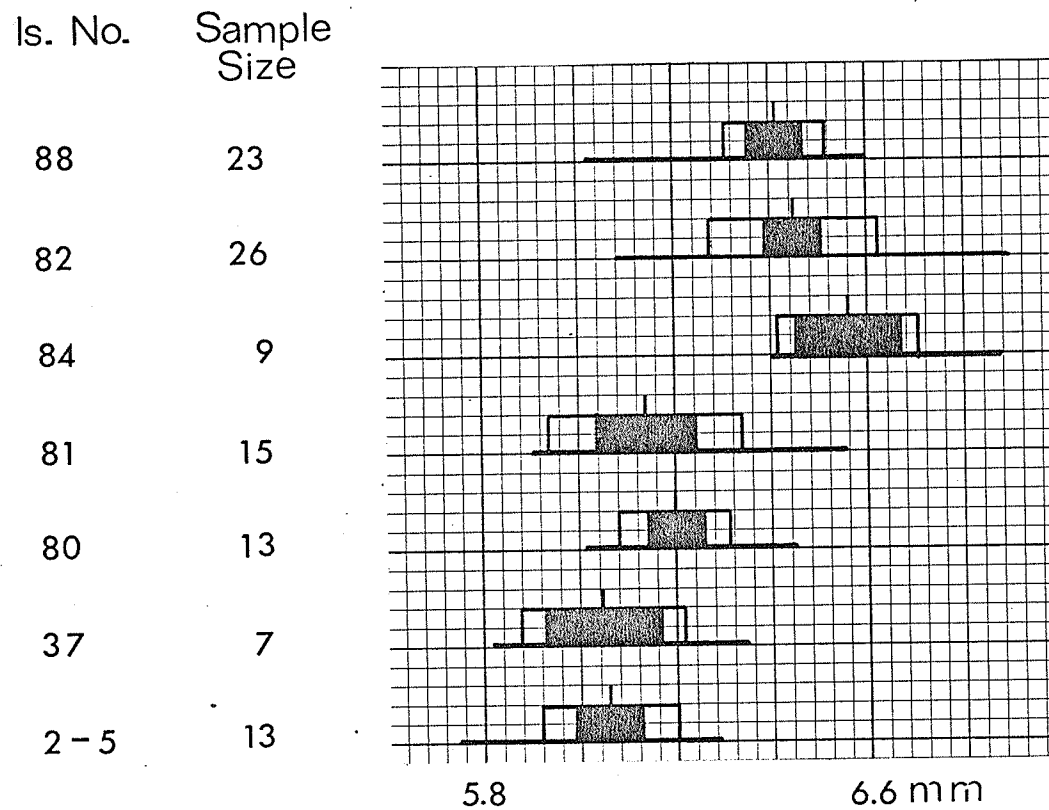


Fig. 33. Variation in mandibular alveolus length of adult *Microtus pennsylvanicus* captured on various islands in Notre Dame Bay. Symbols as in Fig. 16.

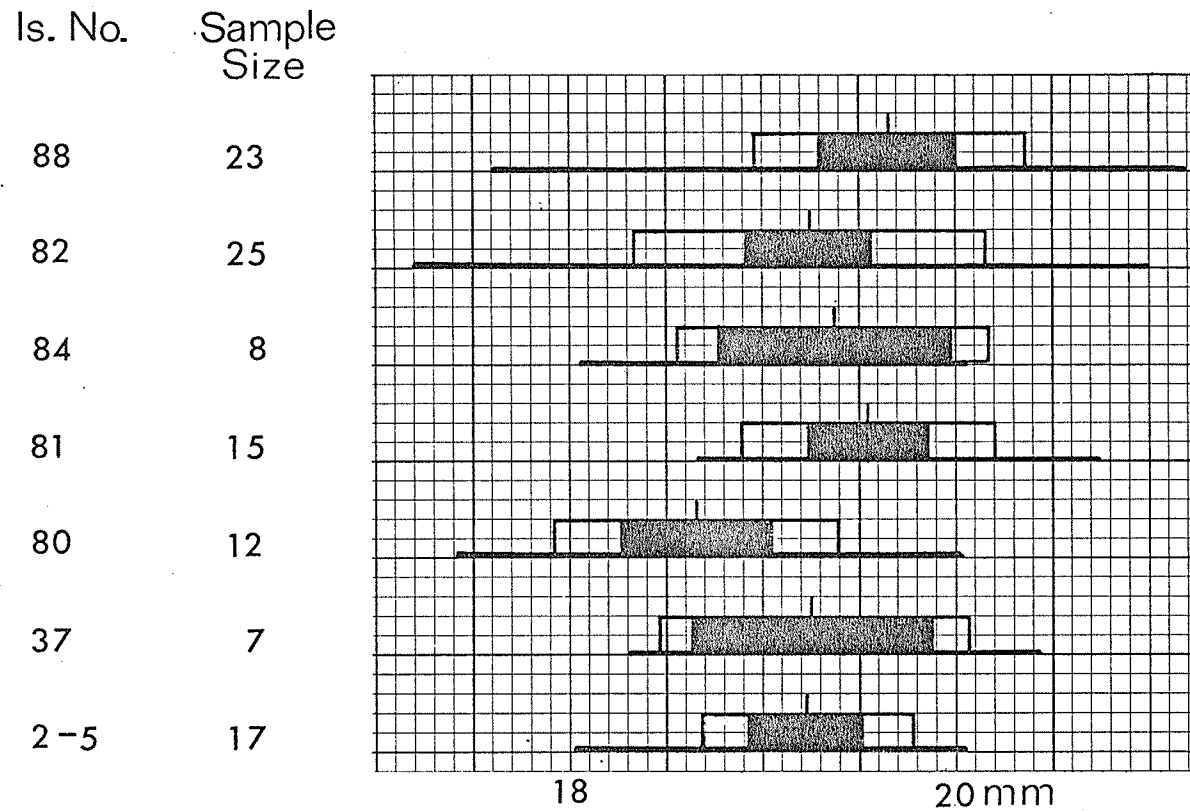


Fig. 34. Variation in femur length of adult *Microtus pennsylvanicus* captured on various islands in Notre Dame Bay. Symbols as in Fig. 16.

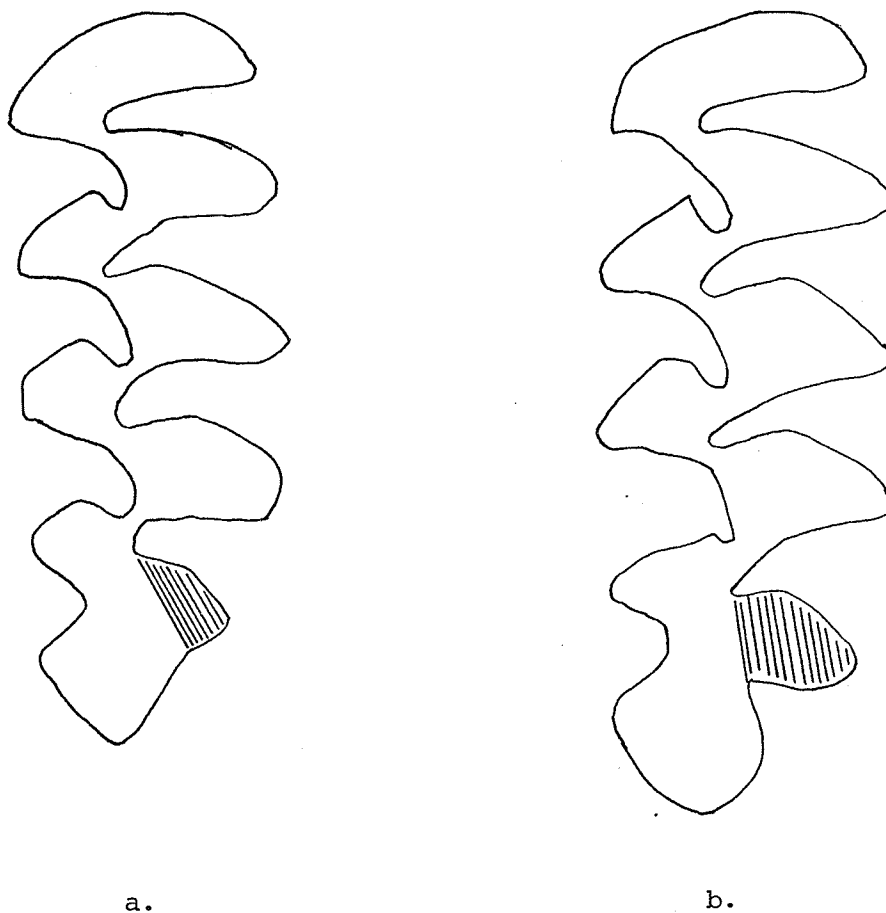


Fig. 35. Camera lucida drawings of the first lower molars of *Microtus pennsylvanicus* showing an increase in complexity of the fifth inner salient angles (shaded areas). (a.) Hummock Island (No. 5), specimen no. RRR 322. (b.) South Trump Island (No. 82), specimen no. RRR 481.

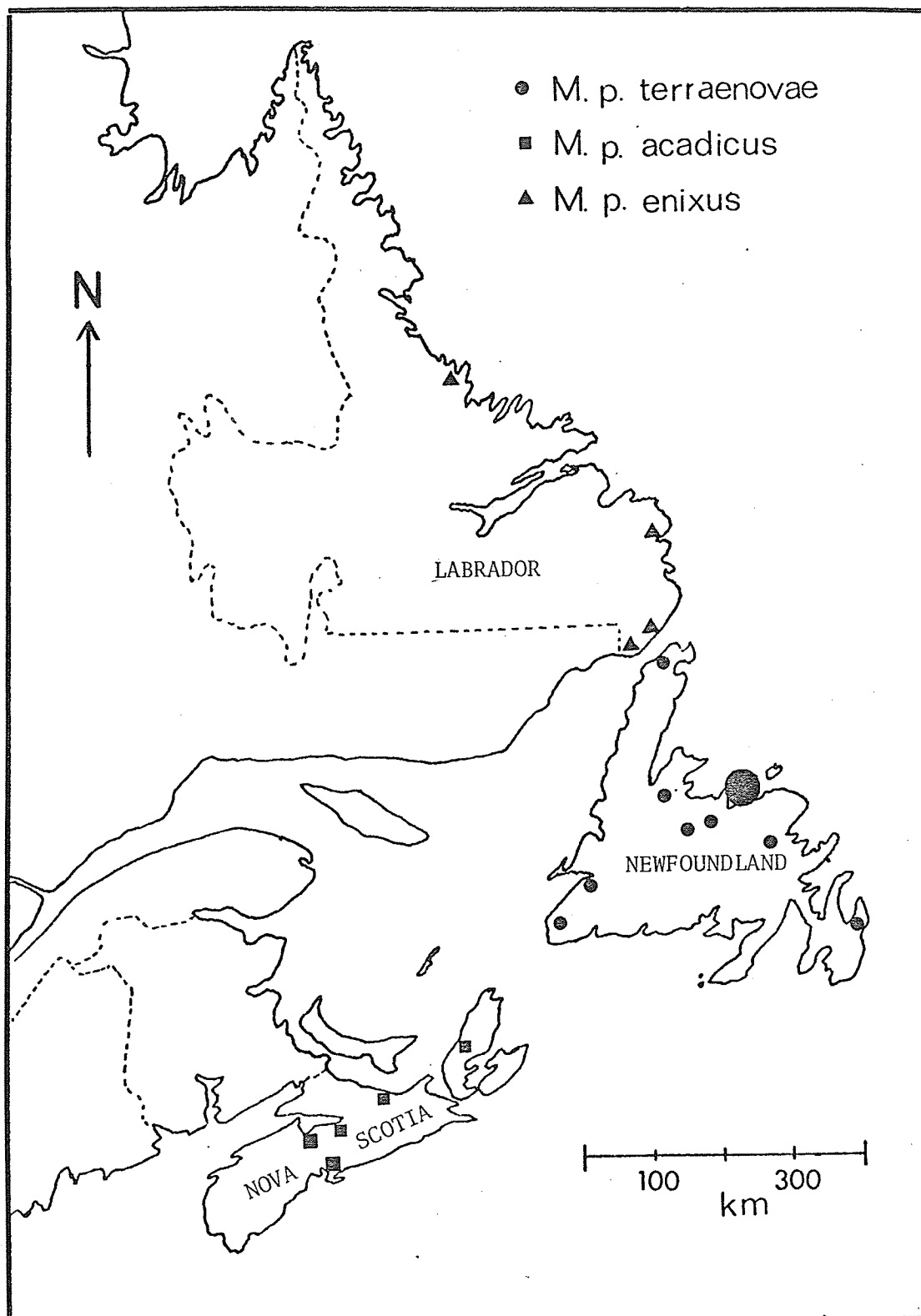


Fig. 36. Collection sites of *Microtus pennsylvanicus* examined in the study. The large black dot in Newfoundland marks the study area in Notre Dame Bay.

TABLE I

Skull measurements and "t" values for adult *Microtus pennsylvanicus*
from Newfoundland, Labrador and Nova Scotia

(1)	(2)	(3)	(4)	(5)
"t" test <i>M. p. terraenovae</i> and <i>M. p. enixus</i>	<i>M. p. enixus</i> (Labrador)	<i>M. p. terraenovae</i> (Newfoundland)	<i>M. p. acadicus</i> (Nova Scotia)	"t" test <i>M. p. terraenovae</i> and <i>M. p. acadicus</i>
t df P	N \bar{X} SD	N \bar{X} SD	N \bar{X} SD	t df P
		Basioccipital length		
0.053	9	11	9	3.581
19	6.25	6.25	5.94	19
P>0.50	0.33	0.17	0.22	0.01>P>0.001
		Palate length		
0.514	9	16	13	3.995
24	13.83	13.69	12.93	28
P>0.50	0.82	0.42	0.60	P<0.001
		Maxillary alveolus length		
1.664	10	17	15	1.374
26	6.42	6.58	6.43	31
0.20>P>0.10	0.22	0.25	0.33	0.20>P>0.10
		Condylzygomatic length		
1.197	9	12	10	2.665
20	20.28	20.72	19.70	21
0.30>P>0.20	1.09	0.55	1.18	0.02>P>0.01
		Incisive foramen length		
0.733	9	16	14	0.084
24	5.35	5.27	5.04	29
0.50>P>0.40	0.19	0.30	0.30	P>0.50
		Incisive foramen width		
1.416	9	16	13	2.817
24	1.27	1.34	1.24	28
0.20>P>0.10	0.16	0.08	0.10	0.01>P>0.001
		Diastema length		
0.754	9	16	15	6.197
24	8.43	8.30	7.56	30
0.50>P>0.40	0.65	0.20	0.43	P<0.001
		Condylbasilar length		
0.249	8	11	10	3.348
18	25.93	26.05	24.66	20
P>0.50	1.41	0.60	1.22	0.01>P>0.001
		Zygomatic breadth		
0.198	10	17	14	3.573
26	15.36	15.31	14.47	30
P>0.50	0.85	0.59	0.72	0.01>P>0.001
		Interorbital breadth		
1.133	10	16	15	4.835
25	3.77	3.84	3.57	30
0.30>P>0.20	0.14	0.15	0.15	P<0.001
		Rostrum length		
1.091	9	16	15	3.929
24	5.57	5.42	5.04	30
0.30>P>0.20	0.42	0.26	0.29	P<0.001
		Cranial height		
0.494	8	12	9	1.596
19	10.20	10.26	10.09	20
P>0.50	0.28	0.25	0.21	0.20>P>0.10
		Cranial breadth		
0.683	9	11	9	0.612
19	11.02	10.92	10.98	19
P≈0.50	0.38	0.27	0.25	P>0.50
		Mandibular alveolus length		
0.975	10	17	14	1.616
26	6.09	6.18	6.02	30
0.40>P>0.30	0.26	0.26	0.33	0.20>P>0.10

Habitat Selection

On the mainland of North America *Microtus pennsylvanicus* is largely restricted to grassy habitats (Andersen and Fleharty, 1967; Blair, 1940; Eadie, 1953; Edwards, 1963; Findley, 1951; Getz, 1961a; Grant, 1969; Gunderson, 1950; Hamilton, 1940; Lantz, 1907; Leraas, 1938; Lewin, 1968; LoBue and Darnell, 1959; Meierotto, 1967; Pearson, 1959; Root and Pearson, 1964; Thompson, 1965; Whitaker, 1967; Wirtz and Pearson, 1960; Zimmerman, 1965). However, this species has been reported occasionally in forest habitats (Beer *et al.*, 1954; Buckner, 1957; Clarke, 1940; Clough, 1964; Connor, 1960, 1966; Gabbutt, 1961; Manville, 1949; Morris, 1969; Rand, 1945; Smith and Foster, 1957; Soper, 1946, 1970; Stickel and Warbach, 1960; Whitaker, 1967).

In island situations *M. pennsylvanicus* has often been noted occupying unusual habitats such as forests (Beer *et al.*, 1954; Cameron, 1958, 1962, 1965; Dice, 1925; MacKay, 1963 as cited in Cameron, 1965; Manville, 1951; Webb, 1965; Werner, 1956) and rocky shorelines (Burt, 1958).

Cameron (1958, 1965) reported that *Microtus* on the main island of Newfoundland occurs more commonly in the forests than in the grasslands. Data collected by J. D. Folinsbee, W. O. Pruitt and P. R. Grant (personal communications), however, indicate that *M. pennsylvanicus* on the main island of Newfoundland responds to the available habitats as it does on the mainland of North America: the species occurs predominately in grassy situations and only occasionally is it captured in forest habitats.

There is a variety of habitat combinations available to the *Microtus* inhabiting Notre Dame Bay. The dominant habitat types vary with the size of the islands.

On islands of four hectares or less, tuckamoor, dwarf shrub barrens

and grassy areas are the dominant habitats. They often occur alone or in various combinations with one another. Alder patches may also occur in association with tuckamoor or barrens (Fig. 37, p. 74). To a limited extent, spruce-fir forests surrounded by belts of tuckamoor are present in the area. Naturally the shoreline habitat is common to every island, but it forms only a small percent of the total cover (except on small, exposed islands such as Nos. 18 and 40 where this habitat covers the entire area). Bogs and salt marshes are rare on the smaller islands.

On the larger islands, spruce-fir forest is by far the dominant habitat. Bogs, the next most important, often cover extensive tracts as on Coal All (No. 22), Chapel (No. 32), Farmers and New World (No. 89) islands. Tuckamoor and dwarf shrub barrens are found only on exposed sites such as along the edges of shorelines and bogs and around ridge tops (Fig. 38, p. 74). These habitats reach their maximum development on wind-swept islands in Friday Bay and Bay of Exploits where they form broad belts around the spruce-fir forests. The shoreline-ecotone is present around forested islands in Dildo Run and on protected islands in Bay of Exploits. Alder patches may cover areas as extensive as do the barrens and tuckamoor. Grassy areas are isolated and restricted in size; on many islands they are not present. As on the small islands, the shoreline habitat is omnipresent but contributes very little to the total cover, while the salt marsh is the most restricted of all habitat types.

During the field investigations I found meadow voles associated with all habitat types. Table II (p. 84) indicates the presence of *Microtus* in the eight major habitats. This information is based on 32,800 TN from 56 islands.

Not all of the habitats were systematically sampled; therefore, one must not use the data in Table II to infer anything about habitat

preference. Nonetheless, these data indicate that *M. pennsylvanicus* was captured frequently in the spruce-fir forest, tuckamoor and alder patches.

Certain of my trapping programmes, however, have revealed information on the voles' habitat preferences. I found that, during the summer, habitat selection appeared random on small grassy or barren islands and that on completely forested islands the shoreline and shoreline-ecotone or tuckamoor were preferred to the interior spruce-fir forest. On large islands where a diversity of habitats exists, tuckamoor, alder patches and berry patches were utilized throughout the year. Old-fields and bogs were utilized primarily during the summer and fall, less so during the winter and almost not at all during the spring.

During the study I captured voles on 16 islands [Nos. 2, 3, 4, Little Cranpot (No. 16), Mile (No. 19), Grassy Rock (No. 37), Sun Rock (No. 43), Nos. 53, 54, Hurts (No. 62), Nos. 65, 71, Gooseberry (No. 77), Fools Harbour (No. 80), No. 81 and Matthews (No. 88)] which are chiefly carpeted with dwarf shrub barrens and/or grassy areas. On these small islands (<0.008 to 4.07 ha) the voles utilized all available space and cover.

Pyke Island (No. 39) is mantled with a well developed spruce-fir forest (Fig. 9, p. 18) and girdled by a narrow, dense shoreline-ecotone (Fig. 8, p. 17). Between 7 June and 8 July 1967 this 11.84-ha island was live trapped with 1082 TN. Sherman traps were set in the interior of the forest (in groups of five, scattered along a trail and in a 100-m x 60-m grid) and along the ecotone. Table III (p. 85) gives the trapping results for the two habitats. The χ^2 value indicates that there is a highly significant difference between the number of captures. This demonstrates that the voles intensively utilized the shoreline-ecotone and avoided the interior spruce-fir forest.

Shellbird Island (No. 42), which is covered with a dense spruce-fir forest and surrounded by a narrow belt of tuckamoor (Fig. 7, p. 16), was trapped with 500 TN during the summer of 1967. The records indicate that 20 voles inhabited this 0.57-ha island. Well-worn runways were common beneath the tuckamoor just above the storm tide line; one such trail, extending over bare needle litter only 1.5 m from this line, was 2 cm wide and 1.5 cm deep. *Microtus* were frequently seen scurrying over the exposed intertidal zone; I caught three voles by hand and found a fourth dead in this zone. In order to determine how far voles were ranging out into the littoral zone, I placed a live trap among some rocks 41 m seaward from the high tide line and just above water at low tide. On the third day, a vole was captured at this site. In conjunction with a detailed botanical study of Shellbird Island, the dense spruce-fir forest was cut into a grid with 5-m intervals. This allowed me access to the otherwise impenetrable interior. At this time I made an exhaustive search for vole sign, but could find none in the interior. These observations suggest that the voles were utilizing the shoreline portion of the island.

A 0.44-ha island, Little Solid (No. 41), covered predominantly with tuckamoor and a small dwarf shrub barren (approximately 0.04 ha) was live trapped with 822 TN between 12 June and 29 August 1967. From the vole sign (Fig. 39, p. 75) and trapping records, it was obvious that the three resident *Microtus* occupied the entire island. Little Solid Island is so narrow, however, that a vole could never be more than 15 m from the shoreline.

In order to study the habitat preferences of *Microtus* on larger islands where a greater number of habitats are available, I began a mark-recapture programme in September 1968. An old, isolated homesite

at Sam Keefe's Cove on South Trump Island (No. 82) (Fig. 40, p. 75) was selected for the study because it possessed two desirable characteristics: a diversity of habitats in a limited area and a relatively dense vole population. According to local fishermen, Sam Keefe's Cove had been abandoned for at least 50 years. A 1.36-ha plot was laid out so as to include all available habitats (Fig. 41, p. 76).

Table IV summarizes the trapping results for the four seasons on the SKC plot. The data were transformed into an index, number of captures/100 TN, which depicts the relative number of captures in each habitat. Assuming that all *Microtus* on the plot had an equal opportunity to enter a trap and that voles of equal trappability (Andrzejewski *et al.*, 1967; Bujalska and Ryszkowski, 1964; Davis and Emlen, 1956; Kikkawa, 1964; Tanaka, 1966) were evenly distributed among the habitats, then this index denotes the relative abundance of voles in each habitat type. For each trapping period, the habitats are arranged according to the greatest number of captures/100 TN. In the fall and summer, the ranges of the number of captures/100 TN are only 6.3 and 6.5, respectively, compared to 16.9 and 18.0 for the winter and spring, respectively. This variation denotes that the voles were more concentrated in fewer habitats during winter and spring than during fall and summer. Chi-square was calculated to test the null hypothesis that the voles were evenly distributed during each of the trapping periods. The null hypothesis must be rejected for all seasons ($P < 0.005$) which suggests that the voles had strong habitat preferences during each season. From the habitat ranking in each season, it is obvious that the preferences changed during the course of the year.

The data from Table IV were broken down by habitat type in Fig. 42 (p. 77). Each habitat was tested to determine whether it was utilized

to the same extent during each of the trapping seasons. There is no statistically significant difference ($P > 0.50$) in the seasonal utilization of the tuckamoor, but there are highly significant differences in the seasonal utilization of the other habitat types. The tuckamoor was occupied at a relatively high level throughout the year (mean captures/100 TN = 16.8). The alders were likewise heavily utilized (yearly mean captures/100 TN = 13.0) but there was a drop in utilization in the spring. The berry patches were occupied throughout the study (yearly mean captures/100 TN = 12.2) with a peak during the summer. The bog was occupied at all seasons (yearly mean captures/100 TN = 9.0) but at very low levels in the winter and spring. Surprisingly, the meadow was the least utilized of all habitats (yearly mean captures/100 TN = 7.6), on a yearly basis only 45% that of the tuckamoor. Voles were scarce here in the winter and completely absent in the spring. During the summer, however, only the berry patches were more intensively utilized than were the meadows.

The habitat preferences of the voles in Notre Dame Bay were probably affected by several biotic and physical factors, such as habitat availability, food abundance, population density, predation pressure, lack of interspecific competition and microenvironmental conditions (see Bendell, 1961; Cameron, 1965; Findley, 1951; Goertz, 1964; Grant, 1969; Lewin, 1968; Linduska, 1950; Tast, 1968).

On small islands the meadow voles often had little opportunity to display habitat preferences. If only one or two habitats were available, the voles had to occupy these habitats or emigrate. Under these circumstances, the above mentioned factors often contributed to the extirpation of small insular populations (see section on Island Colonization and Inter-Island Movements, pp. 132-134).

On larger islands it was difficult to determine which of the factors were most influential in the voles' habitat utilization in the summer and fall, but for winter and spring the major factors were more apparent. At this time of the year I captured *Microtus* and noted their sign only in habitats where there was snow cover. Harsh microenvironmental conditions and predation seemed to be the two factors which kept voles out of the snow-free areas.

The Comfort Cove meteorological station recorded 79.0 cm of precipitation between 1 November 1968 and 31 May 1969; this included 37.1 cm of rain and 440.1 cm of snow (Fig. 43, p. 78). During this period there were 96 days in which the macroenvironmental temperature fluctuated across the freezing point (Fig. 44, p. 79).

During this winter and spring, the snow was unevenly distributed on the SKC plot due to high winds and frequent thaws. Throughout these seasons snow accumulated in the tuckamoor and alder patches, but was frequently absent from the meadow, bog and berry patches. For example, on 17 January 1969, I recorded a snow depth of 55 to 85 cm in the tuckamoor and alder patches, while the meadow, bog and berry patches had an uneven snow cover varying from 10 to 130 cm. Later in the winter the snow cover was even more irregular; on 11 February 1969, approximately 60% of the meadow, bog and berry patches were snow free and the remaining 40% were covered by only 1 to 25 cm of snow, while the tuckamoor and alder patches were completely covered with 30 to 90 cm of snow (Figs. 45-47, pp. 80-82).

Most of the meadows and bogs I visited during these months were either snow free or covered with dense "sigoqtoaq" (sun crust, Pruitt, 1960) or ice sheets (Fig. 48, p. 83). These dense ice sheets provided the voles with little, if any, insulation from the fluctuating temperatures

of the macroenvironment (Formozov, 1946) and made feeding extremely difficult, if not impossible.

Pruitt (1959) pointed out that snow cover is a factor of major importance in the distribution of some small mammals. He found great fluctuations in microenvironmental temperatures and humidities where there was an intermittent snow cover and winter rains, whereas a permanent winter snow cover created a stable subnivean microenvironment with relatively warm temperatures and a completely saturated atmosphere.

Formozov (1946) also stressed the importance of deep snow to the overwintering of voles and noted that voles preferred to winter beneath snow drifts and avoided snow-free areas. Morris (1969) reported that snow cover was one of the major factors regulating the winter distribution of *M. pennsylvanicus*. He found that meadow voles invaded aspen stands during the winter where there was protective snow cover despite the presence of *Clethrionomys*. Golley (1961) mentioned that a persistent snow cover lowered the mortality of *M. pennsylvanicus* during the winter by reducing predation, especially avian predation.

Throughout my study, predation pressure was not evenly exerted since some vole populations were heavily preyed upon for varying periods of time (see section on Predation, pp. 176-181). It is quite possible that the *Microtus* have adapted to this infrequent but occasionally intense predation by utilizing forest habitats (spruce-fir forests, tuckamoor, alder patches and shoreline-ecotones) which provide maximum cover throughout the year.



Fig. 37. Low alder patch on the right meets dwarf shrub barren on the left and tuckamoor in the background, Glead Island (No. 14), June 1967.



Fig. 38. Dwarf shrub barrens and tuckamoor on the exposed cliff top at the west end of Glead Island (No. 14), June 1967. Just offshore is my research vessel, the "Aivik."

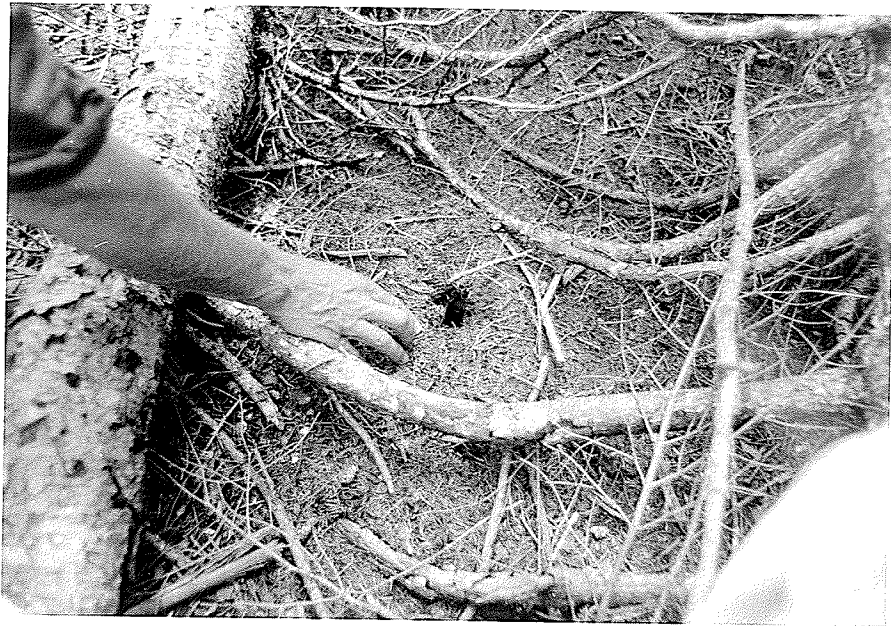


Fig. 39. Actively used burrow entrance of *Microtus* on the forest floor of Little Solid Island (No. 41), July 1967.

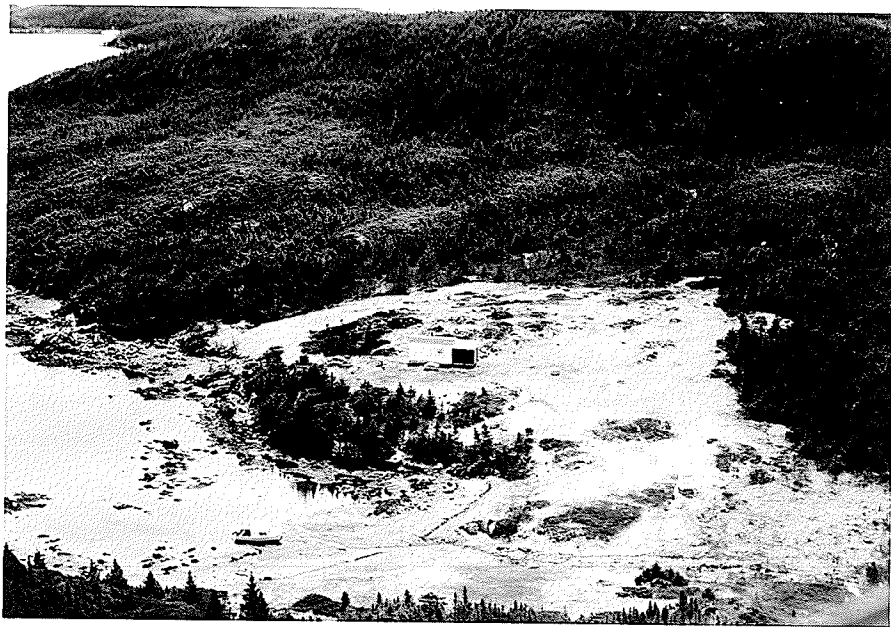


Fig. 40. Aerial view of Sam Keefe's Cove, South Trump Island (No. 82), May 1969. Note the base camp situated in the clearing. Field operations were carried out from this camp from September 1968 to August 1969.

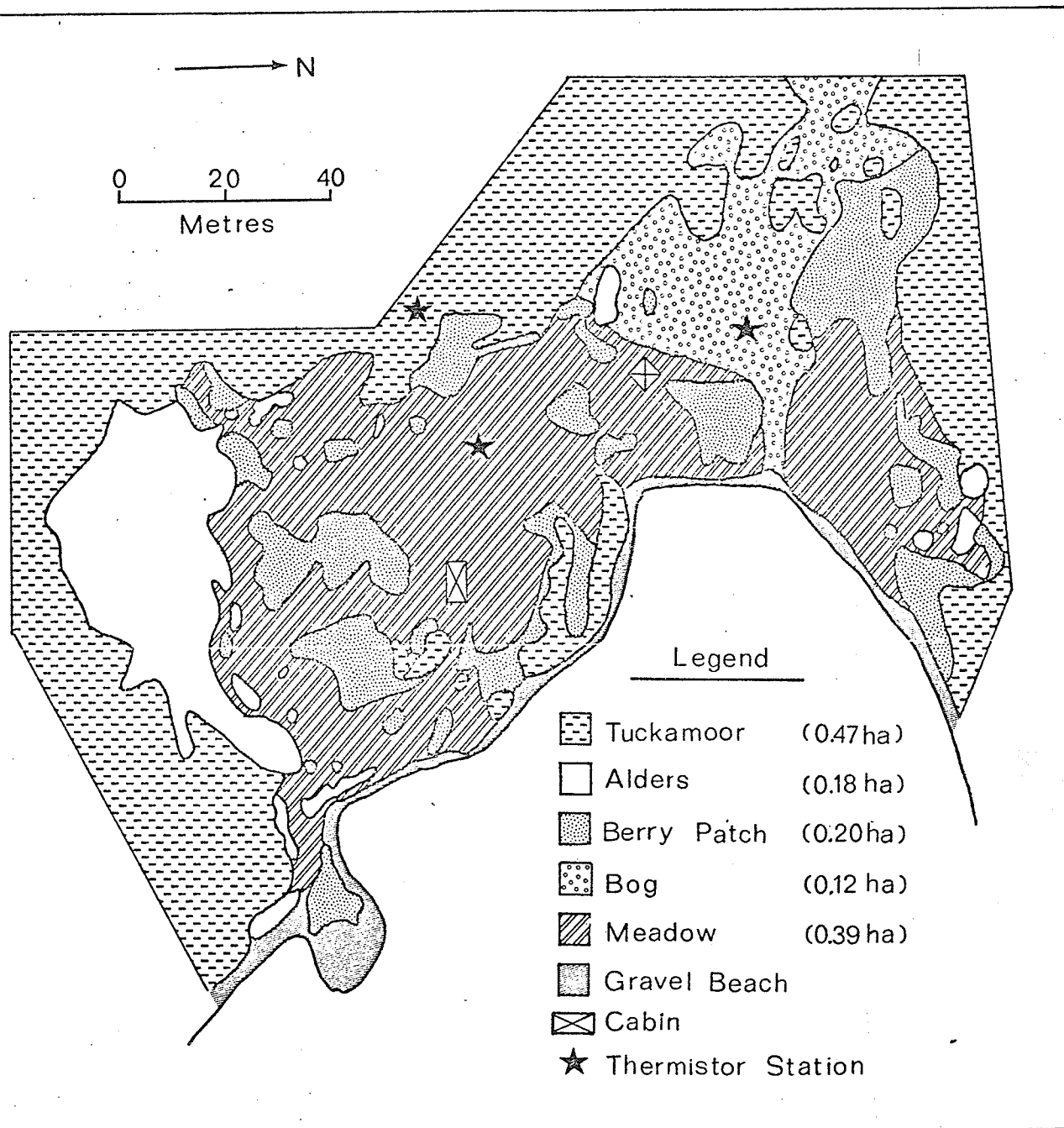


Fig. 41. Habitat map of the SKC plot, South Trump Island (No. 82), October 1968. For description of habitat types see section on Study Area (pp. 3-23).

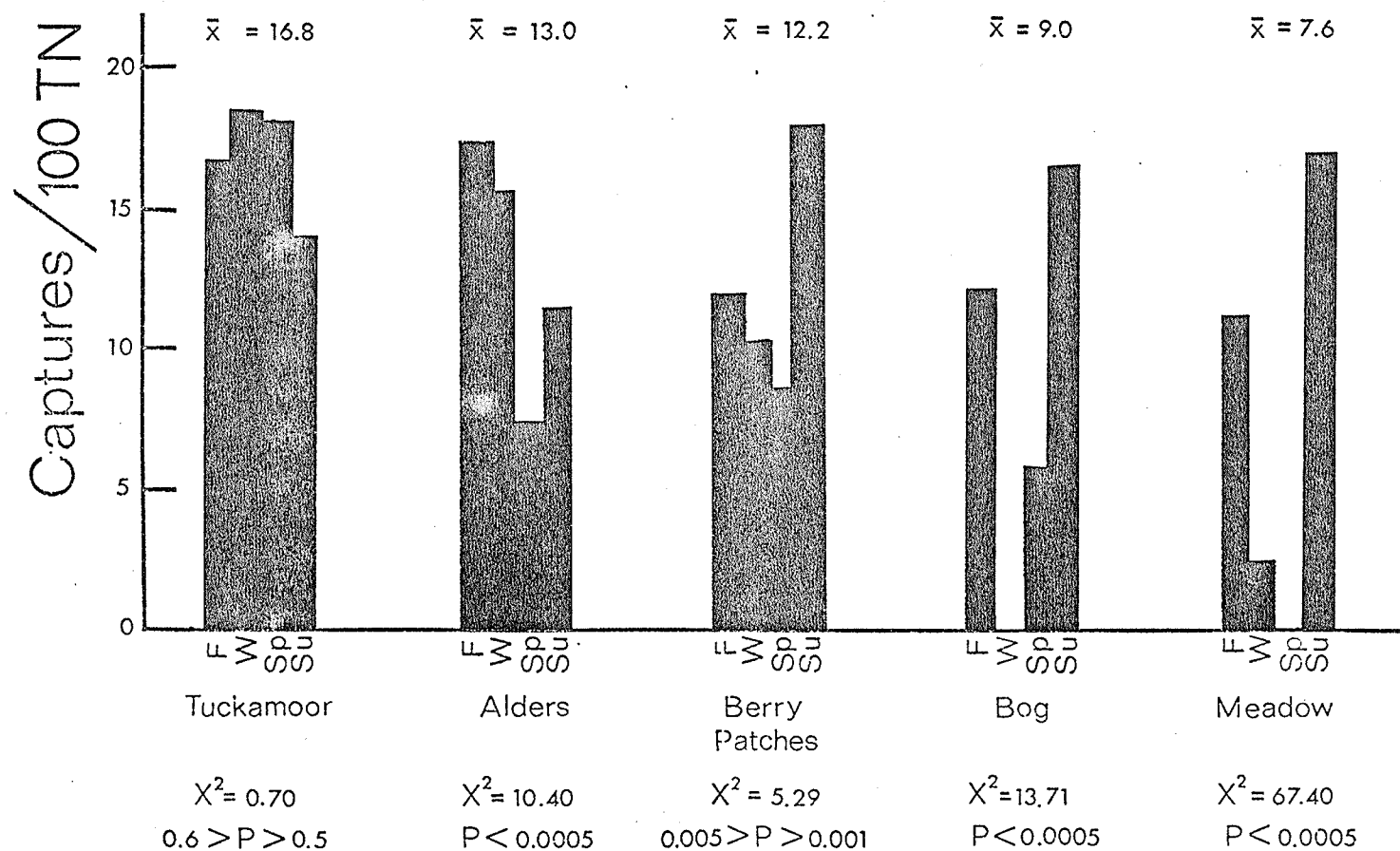


Fig. 42. Habitat selection of *Microtus* on the SKC plot, South Trump Island (No. 82) from September 1968 through August 1969. Mean number of captures/100 TN for each habitat type during the four trapping seasons (F = fall, W = winter, Sp = spring, Su = summer) is given above each histogramme.

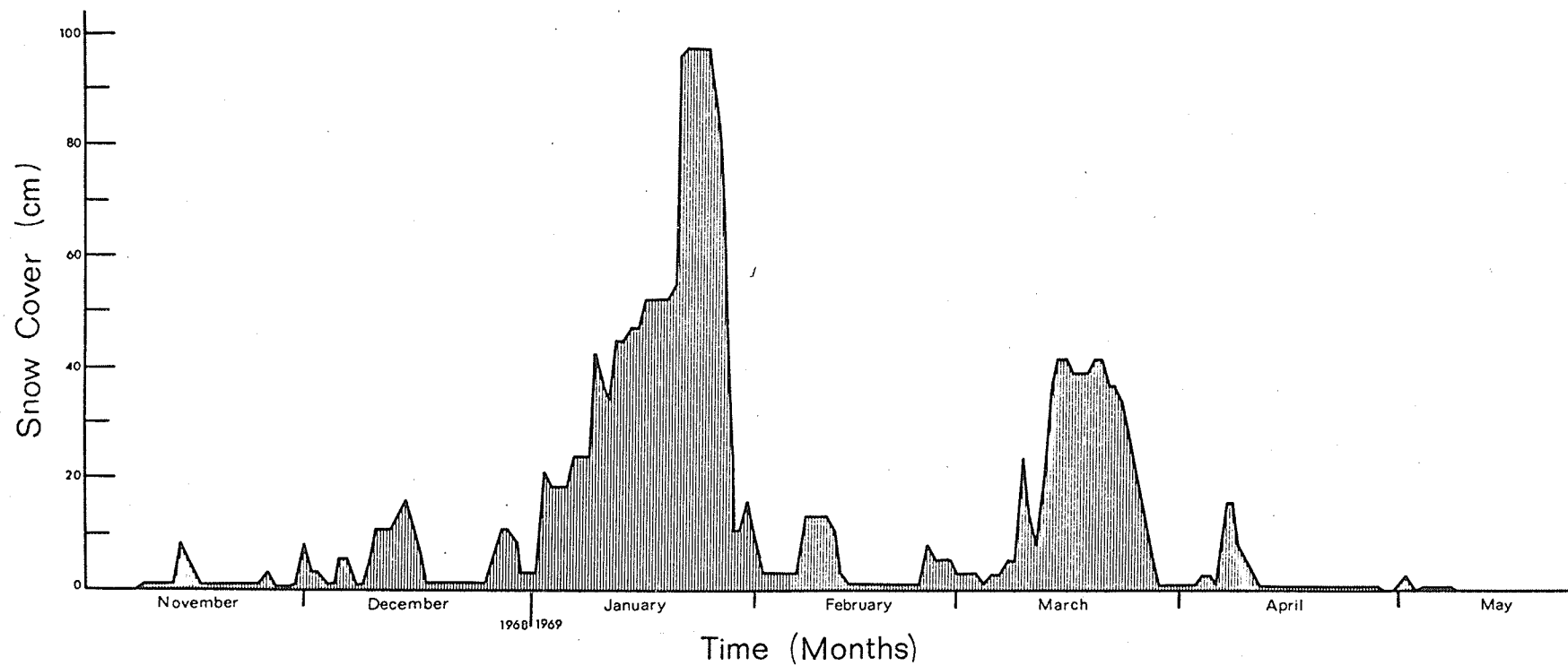


Fig. 43. Snow depth recorded by the Comfort Cove meteorological station between November 1968 and May 1969.

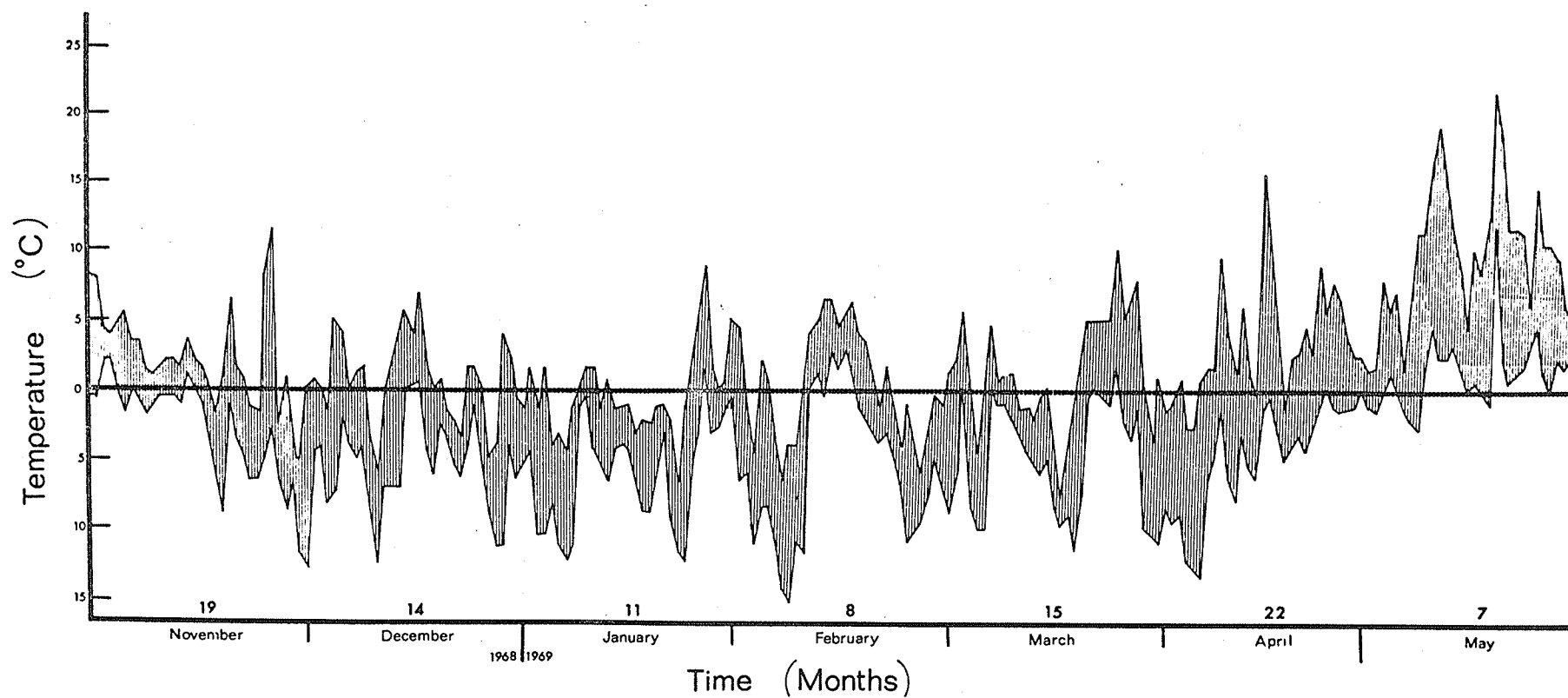


Fig. 44. Daily maximum and minimum macroenvironmental temperatures recorded by the Comfort Cove meteorological station between November 1968 and May 1969. The number of days in which the temperature fluctuated across the freezing point is given for each month.



Fig. 45. Portion of the meadow on the SKC plot, South Trump Island (No. 82), during a winter thaw, 1 March 1969. During the winter much of the meadow, bog and berry patches on the SKC plot were snow-free as a result of high winds, frequent thaws and rain. Note the abandoned *Microtus* burrows. The voles deserted the meadow during the winter and spring trapping seasons.



Fig. 46. Tuckamoor on the SKC plot, South Trump Island (No. 82), during a winter thaw, 1 March 1969. There is from 30 to 60 cm of snow present between the trees. Snow persisted in the tuckamoor throughout the winter and spring. *Microtus* utilized this habitat throughout the year.



Fig. 47. Alder patch on the SKC plot, South Trump Island (No. 82), during a winter thaw, 1 March 1969. There is between 30 and 60 cm of snow cover. Snow cover persisted in the alders throughout the winter and early spring. *Microtus* utilized this habitat throughout the year but primarily during the summer, fall and winter.



Fig. 48. Small, semi-sheltered bog on South Trump Island (No. 82) covered with dense "siqoqtoaq" (sun crust) and recently formed drifts, February 1969. During the winter of 1968-69, bogs and grassy areas were often covered with dense snow and ice which provided little insulation to *Microtus*.

TABLE II

Presence of *Microtus* in the major habitats

	Spruce-fir forest	Tuckamoor	Alder patch	Dwarf shrub barren	Grassy area	Bog	Salt marsh	Shoreline
Number of examples of each habitat trapped	14	24	7	33	22	4	1	8
Number of examples of each habitat with <i>Microtus</i>	10	16	6	21	16	3	1	5

TABLE III

Results of mark-recapture study on Pyke Island (No. 39)
between 7 June and 8 July 1967

Habitat	TN	Captures
Shoreline-ecotone	530	30
Spruce-fir forest	552	2

$$\chi^2 = 26.2, P < 0.001$$

TABLE IV

Seasonal habitat selection of *Microtus* on the SKC plot

Habitat	TN	Captures	Captures/100 TN
Fall 1968 (24 September-7 October and 14 October-2 November)			
Alder	379	66	17.4
Tuckamoor	524	88	16.8
Bog	490	59	12.1
Berry patch	889	106	11.9
Meadow	<u>368</u>	<u>41</u>	<u>11.1</u>
Total = 2650		Total = 360	$\bar{X} = 13.3$
$\chi^2 = 12.13, P < 0.0005$			
Winter 1969 (25 February-13 March)			
Tuckamoor	290	54	18.6
Alder	147	23	15.7
Berry patch	351	36	10.3
Meadow	84	2	2.4
Bog	<u>58</u>	<u>1</u>	<u>1.7</u>
Total = 930		Total = 116	$\bar{X} = 12.4$
$\chi^2 = 23.57, P < 0.0005$			
Spring 1969 (25 April-11 May)			
Tuckamoor	881	158	18.0
Berry patch	604	53	8.8
Alder	271	20	7.4
Bog	154	9	5.8
Meadow	<u>352</u>	<u>0</u>	<u>0.0</u>
Total = 2262		Total = 240	$\bar{X} = 10.6$
$\chi^2 = 89.84, P < 0.0005$			
Summer 1969 (12-21 August)			
Berry patch	212	38	17.9
Meadow	282	48	17.0
Bog	91	15	16.5
Tuckamoor	318	44	13.8
Alder	<u>131</u>	<u>15</u>	<u>11.4</u>
Total = 1034		Total = 160	$\bar{X} = 15.5$
$\chi^2 = 3.74, 0.005 > P > 0.001$			

Food Habits

Throughout their range *Microtus* are primarily grazers, feeding on the vegetative parts of grasses and forbs, although, during the winter, the bark of trees and shrubs is often included in their diets (Bailey, 1924; Godfrey, 1953; Hamilton, 1940; Jameson, 1958; Lantz, 1907; Linduska, 1942, 1950; Parker, 1941; Siegler, 1937; Summerhayes, 1941; Thompson, 1965). Occasionally seeds, nuts and berries are also consumed (Martin, 1956; Martin *et al.*, 1961; Williams, 1955). A few investigators have even reported that *Microtus* has a propensity for meat (Martin, 1956; Voge, 1950; Wellwood, 1956; Zimmerman, 1965).

The results of the cafeteria food tests conducted in the summer and winter seasons on the SKC plot, South Trump Island (No. 82), are presented in Tables V and VI (pp. 97-98), respectively. For each season I divided the plants into five categories based upon the voles' acceptance of the species. Class I includes those species readily eaten by all the voles; class IV includes those plants rejected by all the test animals. The voles displayed intermediate levels of acceptance to the plants in classes II and III. Class V is composed of those plant species which met with varying degrees of acceptance; some of the test animals rejected the species, others consumed small to moderate portions, while still others readily devoured them. The presence of Class V points out that the voles possessed highly individualistic appetites.

In Tables V and VI, the habitats on the SKC plot are listed for each plant species in the fifth column. A large number of plants characteristic of the tuckamoor, particularly the ericaceous species, are present in classes I and V for both summer and winter. The voles' preferences for these species suggest that their appetites were adjusted

to their existence in the tuckamoor (see section on Habitat Selection, pp. 66-86). The predominance of typical meadow species in class I during the summer test demonstrates that the *Microtus* had a definite preference for herbaceous vegetation and took advantage of it when it was available.

In addition to the food preference tests, I also made numerous field observations on the food habits of *Microtus* throughout the study area. Data from these observations, as well as from the food preference tests, are listed by vegetative categories in Table VII (pp. 99-101). The table should not be considered exhaustive since the grasses, sedges and rushes, and probably the lichens and mosses as well, are under-represented due to the difficulty of identifying these groups in the field.

Although the voles rejected *Cladonia rangiferina* in the feeding tests, I observed sign which suggested that lichens were utilized by voles in the study area. I discovered exposed subnivean runways which were filled with the foliose lichen, *Peltigera* sp. Although the thalli had vole tooth marks on them, there is the possibility that the lichen had only been cleared from the runways. To my knowledge, there are no reports of *Microtus* feeding on lichens, but Llano (1956) mentioned that lemmings consumed tundra lichens.

I also found piles of *Sphagnum* spp., *Brachythecium* sp., *Dicranum polysetum* and *Ceratodon purpureus* clipped into small pieces by the voles. As with the lichens, I am not positive that these piles actually represented feeding sign. The cafeteria tests, however, demonstrated that the voles definitely fed on mosses. Although researchers in North America and Britain report that bryophytes are insignificant in the diets of voles and lemmings (Grout; 1903; Martin *et al.*, 1961; Summerhayes, 1941; Thieret, 1956; Thompson, 1965), Russian biologists stress the

importance of mosses in microtine diets (Koshkina, 1961; Nasimovich *et al.*, 1948 as cited in Marsden, 1964; Shtil'mark, 1965; Vorontsev, 1961 as cited in Shtil'mark, 1965).

In view of my observations I believe that it is possible that the non-vascular plants played a significant role in the meadow voles' diets on the small, densely forested islands where this vegetation is dominant on the forest floor (Fig. 49, p. 93).

The grasses, sedges and rushes were available to the voles during the late spring, summer and fall; at these times they were heavily utilized. I also observed vole feeding sign on the apical shoots of *Scirpus cespitosus* in the winter.

Most of the forbs, like the grasses and their allies, were available primarily during the summer, but I found subnivean food caches stocked with the leaves and roots of *Leontodon autumnalis* and *Trifolium* spp. In February I discovered abundant sign of voles feeding upon the tough, bristly leaves of *Sarracenia purpurea*; one specimen had 25 of the 29 leaves eaten and half of these had been chewed to the roots.

On the small islands, the forbs along the shoreline, particularly *Plantago juncooides*, *Lathyrus japonicus*, *Ligusticum scothicum* and *Cochlearia tridactylites*, were heavily fed upon by *Microtus* (Fig. 50, p. 93). During hot, dry periods it is possible that the succulent, shoreline species, *Plantago*, *Cochlearia*, as well as *Sedum*, *Mertensia* and *Cakile*, were sources of fresh water for the voles.

Surprisingly, the voles fed upon almost as many shrubs as forbs. The dominant species of the dwarf shrub barrens were all utilized at one season or another. *Juniperus communis*, *Empetrum nigrum*, *Vaccinium angustifolium* and *V. Vitis-Idaea* were major overwintering foods.

Figs. 51 and 52 (pp. 94-95) illustrate typical overwinter damage inflicted on three of these species by the meadow voles; such sign was clearly visible for one to two years. *Kalmia angustifolia* was an important item in the voles' diets throughout the year. This is interesting, since the shrub is reputedly poisonous to sheep and cattle (Billington, 1949; Kingsbury, 1964). Thompson (1965) tested the food preferences of *Microtus pennsylvanicus* on 30 species of plants; he found that native boreal and bog plants, including ericaceous species, occupied the eight lowest levels of preference.

None of the tree species appeared to be heavily utilized, but more feeding sign was noted on *Larix laricina* and *Picea mariana* than on *Abies balsamea* and *Acer spicatum*.

One of the most noteworthy features of Table VII is the number and variety of plants. Undoubtedly I overlooked species of plants utilized by *Microtus*, particularly in the salt marsh habitat. Nonetheless, this list of 73 species includes 24.8% of all plants recorded from the study area (see Appendix B, pp. 187-193).

The habitats of the vascular plants listed in Table VII were extracted from Appendix B and are given in Table VIII (p. 102). The non-vascular plants were omitted from the data because there is no comprehensive list available. Table VIII does not take into account the abundance or the cover of the species in each habitat, nor the voles' food preferences, but it does give an indication of the number of species which could be utilized by *Microtus* in each of the habitats. The numbers suggest that the voles of Notre Dame Bay could subsist on the available plant species in most of the major habitats (see Table II, p. 84). The only possible exception is the salt marsh, but my data on this uncommon habitat are very limited.

In addition to the plants, some of the meadow voles may have included animal tissue in their diets. I base this statement on the following evidence:

1. In the early spring fishermen were often forced to temporarily remove their lobster traps from shallow waters to avoid having them crushed by arctic pack ice. At this time the traps were piled on the shore of convenient islands (Fig. 53, p. 96). Lobster bait consisting of cod heads (*Gadus*), tomcods (*Microgadus*), flounders (Bothidae) and cunners (*Tautogolabrus*) was left in the traps along with attached periwinkles (*Littorina*) and scavenging purple starfish (*Asterias vulgaris*) and green sea urchins (*Strongylocentrotus drobachiensis*). Some fishermen also stored their traps on the islands when not in use at other times of the year. While the traps were ashore, their "heads" (string netting) were frequently damaged by voles; some fishermen were of the opinion that the voles clipped the netting while feeding on the lobster bait.

2. I found the remains of crabs (*Cancer*), sea urchins, soft-shelled clams (*Mya arenaria*) and even small flounders deep in *Microtus* runways on many of the small islands. It is possible that these remains had been placed in the runways by foxes, ravens or gulls, but, since no signs of these animals were present in the immediate vicinity, it seems more likely that the voles had dragged the remains into their runways.

3. As mentioned in the section on Habitat Selection (pp. 68-69), the voles on some islands spent considerable time along the shorelines and even ventured into the intertidal zone.

It is quite possible that the meadow voles which frequented the shorelines

obtained a fair proportion of their energy requirements from the sea.

Hatt *et al.* (1948) noted that *Peromyscus maniculatus gracilis* inhabiting the islands in Lake Michigan fed on a varied diet of beach drift including the remains of birds, fish, crayfish and snails.



Fig. 49. Mosses and foliose lichens carpeting the forest floor on Shellbird Island (No. 42), July 1967.



Fig. 50. Vole feeding sign on *Ligusticum scoticum* on the rocky shore of Shellbird Island (No. 42), July 1967. Arrows indicate stems which have been clipped by voles.



Fig. 51. *Microtus* overwintering sign on *Juniperus communis* in dwarf shrub barren on Glead Island (No. 14), June 1967. Branches have been stripped of bark and needles by voles. For scale, note the Sherman live trap. Overwintering sign similar to this was found over much of Glead Island during summer 1967, but no voles were seen or captured (see section on Island Colonization and Inter-Island Movements, pp. 132-134).



Fig. 52. *Microtus* overwintering sign on *Empetrum nigrum* and *Vaccinium Vitis-Idaea*, Glead Island (No. 14), June 1967. Plants have been clipped at ground level over an area of approximately 0.8 m x 1.5 m.



Fig. 53. Lobster traps stored on the south end of Shellbird Island (No. 42), July 1967. Voles reputedly feed upon scraps of bait left in lobster traps.

TABLE VI

Results of winter food preference tests on SKC plot

Species	Number voles tested	Portion consumed by each vole*	Plant parts consumed†	Habitat ^s					
				2	3	4	5	6	8
I. Complete acceptance									
<i>Pyrus floribunda</i>	3	3D	bk, f				x		x
<i>Rosa nitida</i>	7	7D	f				x		x
<i>Ledum groenlandicum</i>	2	2D	l, f, st	x					x
<i>Kalmia angustifolia</i>	2	2D	l, f, st	x					x
<i>Vaccinium angustifolium</i>	6	1C, 5D	st, bk, bd	x		x			
<i>V. Vitis-Idaea</i>	3	3D	st, l	x		x			
<i>Lonicera villosa</i>	7	2C, 5D	bk, bd	x	x		x		x
<i>Hieracium floribundum</i>	7	7D	l				x		
II. Moderate acceptance									
<i>Betula Michauxii</i> or <i>B. pumila</i>	7	5B, 2C	r, bk, st						x
III. Poor acceptance									
<i>Abies balsamea</i>	7	6A, 1B	l	x	x				
<i>Sanguisorba canadensis</i>	7	6A, 1B	r	x	x		x		x
<i>Sarracenia purpurea</i>	2	2B	l						x
<i>Gaultheria hispidula</i>	7	1A, 6B	l	x		x			
<i>Viburnum cassinoides</i>	7	7B	bk	x			x		
<i>Achillea Millefolium</i>	3	1A, 2B	st, l, f				x		
IV. Rejection									
<i>Fucus</i> sp.	7	7A	none						x
<i>Cladonia rangiferina</i>	3	3A	none	x					x
<i>Racomitrium lanuginosum</i>	7	7A	none				x		
<i>Juncus</i> sp.	7	7A	none						x
V. Varying acceptance									
<i>Sphagnum recurvum</i>	7	5A, 2D	th						x
<i>Dicranum undulatum</i>	7	4A, 1B, 2D	th				x		x
<i>Pleurozium schreberi</i>	7	6A, 1D	th	x			x		
<i>Polytrichum</i> sp.	6	1A, 5D	th				x		x
<i>Picea mariana</i>	7	1A, 3B, 1C, 2D	l, bk	x	x				x
<i>Larix laricina</i>	6	2A, 3B, 1D	bk	x					x
<i>Juniperus communis</i>	3	1B, 2D	bk, st	x	x	x	x		
<i>Myrica Gale</i>	7	2B, 2C, 3D	bk, bd, f						x
<i>Alnus crispa</i>	2	1A, 1C	st, bk		x				
<i>Pyrus decora</i>	7	1B, 3C, 3D	bk, bd	x	x		x		
<i>Empetrum nigrum</i>	7	1A, 6D	bk	x	x	x	x		
<i>Rhododendron canadense</i>	5	2B, 1C, 2D	bk, f	x					x
<i>Andromeda glaucophylla</i>	7	1B, 1C, 5D	l, st						x
<i>Chamaedaphne calyculata</i>	6	3B, 1C, 2D	l, st						x

* Portion consumed: A = 0%; B = 1-30%; C = 31-60%; D = 61-100%.

† Plant parts: r = roots; st = stems; bd = buds; l = leaves; th = thalli; bk = bark; f = fruits, berries and seeds. Listed in descending order of utilization.

§ Habitat code: 2 = tuckamoor; 3 = alder patch; 4 = dwarf shrub barren; 5 = grassy area; 6 = bog; 8 = shoreline. There were no spruce-fir forests (habitat code no. 1) or salt marshes (habitat code no. 7) on the SKC plot.

TABLE V
Results of summer food preference tests on SKC plot

Species	Number voles tested	Portion consumed by each vole*	Plant parts consumed†	Habitat ^s					
				2	3	4	5	6	8
I. Complete acceptance									
<i>Polytrichum</i> sp.	3	3D	th				x	x	
<i>Alopecurus pratensis</i>	6	6D	1, st, f				x		
<i>Agropyron repens</i>	3	3D	1, st, f				x		
<i>Carex nigra</i>	3	3D	1, st, f				x	x	
<i>Luzula campestris</i>	3	3D	1, st, f				x	x	
<i>Atriplex patula</i>	3	3D	1, st, f				x		
<i>Ranunculus repens</i>	3	3D	1, f, st				x		
<i>Sanguisorba canadensis</i>	3	3D	1, f, fl, st	x	x		x	x	
<i>Lathyrus japonicus</i>	3	3D	1, st, f						x
<i>Epilobium angustifolium</i>	3	3D	f, l				x		
<i>Vaccinium angustifolium</i>	3	3D	1, f, st	x		x			
<i>Lonicera villosa</i>	3	3D	l	x	x		x	x	
<i>Leontodon autumnalis</i>	3	3D	1, st, f				x		
II. Moderate acceptance									
<i>Pyrus decora</i>	3	3C	1, st	x	x		x		
<i>Veronica agrestis</i>	3	2B, 1C	l				x		
<i>Aster radula</i>	3	2C, 1D	st, f				x	x	
<i>Achillea Millefolium</i>	3	1C, 2D	st, 1, f				x		
III. Poor acceptance									
<i>Myrica Gale</i>	3	2A, 1B	l					x	
<i>Rumex acetosella</i>	3	1A, 2B	f, l				x		
<i>Thalictrum polygamum</i>	3	2A, 1B	f				x		
<i>Potentilla fruticosa</i>	3	3B	l				x	x	
IV. Rejection									
<i>Cladonia rangiferina</i>	3	3A	none	x				x	
<i>Abies balsamea</i>	3	3A	none	x	x				
<i>Picea mariana</i>	3	3A	none	x				x	
<i>Juniperus communis</i>	3	3A	none	x	x	x	x		
<i>Ribes</i> sp.	3	3A	none				x		
<i>Rubus idaeus</i>	3	3A	none				x		
<i>Solidago rugosa</i>	3	3A	none				x		
V. Varying acceptance									
<i>Larix laricina</i>	3	1A, 1B, 1C	l	x				x	
<i>Iris versicolor</i>	3	1B, 2D	1, st						x
<i>Pyrus floribunda</i>	3	1A, 1B, 1D	1, f, bk				x	x	
<i>Rosa nitida</i>	3	1A, 2D	1, st, f				x	x	
<i>Empetrum nigrum</i>	3	2B, 1D	l	x	x	x	x		
<i>Ledum groenlandicum</i>	3	2A, 1D	1, b, f	x				x	
<i>Rhododendron canadense</i>	3	1A, 2D	f, l	x				x	
<i>Kalmia angustifolia</i>	3	1A, 1B, 1D	f, l	x				x	
<i>Vaccinium Vitis-Idaea</i>	3	1A, 1B, 1D	l	x		x			
<i>Plantago juncoides</i>	3	1B, 1C, 1D	l						x

* Portion consumed: A = 0%; B = 1-30%; C = 31-60%; D = 61-100%.

† Plant parts: r = roots; st = stems; bd = buds; l = leaves; th = thalli; bk = bark; f = fruits, berries and seeds; fl = flowers. Listed in descending order of utilization.

‡ Habitat code: 2 = tuckamoor; 3 = alder patch; 4 = dwarf shrub barren; 5 = grassy area; 6 = bog; 8 = shoreline. There were no spruce-fir forests (habitat code no. 1) or salt marshes (habitat code no. 7) on the SKC plot.

TABLE VII

Foods of *Microtus* in the study area

Species	Part utilized *					Season of utilization †				Type of observation	
	r	st tw bd	l th	bk	f fl	Sp	Su	F	W	Field obser- vation	Feed- ing test
Lichens and mosses											
<i>Peltigera</i> sp.			x						x	x	
<i>Sphagnum recurvum</i>			x						x		x
<i>Sphagnum</i> spp.			x						x	x	
<i>Ceratodon purpureus</i>			x						x	x	
<i>Dicranum polysetum</i>			x						x	x	
<i>D. scoparium</i>			x						x		x
<i>Brachythecium</i> sp.			x						x	x	
<i>Pleurozium schreberi</i>			x						x		x
<i>Polytrichum</i> sp.			x				x		x		x
Grasses, sedges and rushes											
<i>Alopecurus pratensis</i>		x	x		x		x	x			x
<i>Agropyron repens</i>		x	x		x		x	x			x
<i>Scirpus cespitosus</i>		x	x		x				x	x	
<i>Carex nigra</i>		x	x		x		x	x			x
<i>Carex</i> sp.		x	x		x		x	x		x	
<i>Luzula campestris</i>		x	x		x		x	x			x
Forbs											
<i>Smilacina stellata</i>		x	x				x			x	
<i>Maianthemum canadense</i>		x	x				x			x	
<i>Iris setosa</i>		x	x					x	x	x	
<i>I. versicolor</i>		x	x				x				x
<i>Rumex acetosella</i>			x		x		x				x
<i>Atriplex patula</i>		x	x		x		x			x	x
<i>Ranunculus repens</i>		x	x		x		x				x
<i>Thalictrum polygamum</i>					x						x
<i>Sanguisorba canadensis</i>	x	x	x		x		x	x		x	x
<i>Cochlearia tridactylites</i>		x	x					x		x	
<i>Cakile edentula</i>		x	x		x		x			x	
<i>Sarracenia purpurea</i>			x						x	x	x
<i>Sedum Rosea</i>		x	x				x			x	
<i>Potentilla norvegica</i>			x				x			x	
<i>Trifolium</i> spp.	x	x	x			x	x	x	x	x	
<i>Lathyrus japonicus</i>		x	x		x		x			x	x
<i>Epilobium angustifolium</i>			x		x		x				x
<i>Cornus canadensis</i>			x				x			x	
<i>Ligusticum scothicum</i>		x	x				x	x		x	
<i>Conioselinum chinense</i>		x	x				x			x	

TABLE VII (continued)

Species	Part utilized *					Season of utilization †				Type of observation	
	r	st tw bd	l th	bk	f fl	Sp	Su	F	W	Field obser- vation	Feed- ing test
<i>Mertensia maritima</i>		x	x				x			x	
<i>Veronica agrestis</i>			x				x				x
<i>Plantago juncooides</i>		x	x		x		x			x	x
<i>Galium palustre</i> or <i>G.</i> <i>triflorum</i>		x	x				x			x	
<i>Lonicera villosa</i>		x	x	x		x	x	x	x	x	x
<i>Viburnum cassinoides</i>				x	x				x	x	x
<i>Solidago sempervirens</i>			x				x			x	x
<i>Aster radula</i>		x	x		x		x				x
<i>Aster</i> spp.		x	x				x			x	
<i>Achillea Millefolium</i>		x	x		x		x				x
<i>Leontodon autumnalis</i>	x	x	x		x	x	x	x	x	x	x
<i>Taraxacum officinale</i>			x				x			x	
<i>Hieracium floribundum</i>			x						x		x
Shrubs											
<i>Taxus canadensis</i>				x					x	x	
<i>Juniperus communis</i>		x	x	x	x			x	x	x	x
<i>J. horizontalis</i>			x	x		x	x	x	x	x	
<i>Myrica Gale</i>		x	x	x	x	x	x	x	x	x	x
<i>Betula Michauxii</i> or <i>B.</i> <i>pumila</i>	x	x		x					x		x
<i>Alnus crispa</i>				x	x			x	x	x	x
<i>Pyrus decora</i>			x	x	x	x	x	x	x	x	x
<i>P. floribunda</i>			x	x	x	x	x	x	x	x	x
<i>Potentilla fruticosa</i>			x				x				x
<i>Rubus idaeus</i>		x	x					x		x	x
<i>Rosa nitida</i>		x	x	x	x	x	x	x	x		x
<i>Empetrum nigrum</i>			x	x		x	x	x	x	x	x
<i>Nemopanthus mucronata</i>				x	x				x	x	
<i>Ledum groenlandicum</i>		x	x	x	x	x	x	x	x	x	x
<i>Rhododendron canadense</i>			x	x	x	x	x	x	x		x
<i>Kalmia angustifolia</i>		x	x	x	x	x	x	x	x	x	x
<i>Andromeda glaucophylla</i>		x	x	x					x	x	x
<i>Chamaedaphne calyculata</i>		x	x	x					x	x	x
<i>Gaultheria hispidula</i>			x						x		x
<i>Vaccinium angustifolium</i>		x	x	x	x	x	x	x	x	x	x
<i>V. Oxycoccus</i>		x	x		x			x		x	
<i>V. uliginosum</i>		x	x						x	x	
<i>V. Vitis-Idaea</i>		x	x			x	x	x	x	x	x

TABLE VII (continued)

	Part utilized *					Season of utilization †				Type of observation	
	r	st tw bd	l th	bk	f fl	Sp	Su	F	W	Field obser- vation	Feed- ing test
Trees											
<i>Abies balsamea</i>			x						x		x
<i>Picea mariana</i>		x	x	x					x	x	x
<i>Larix laricina</i>			x	x		x	x	x	x	x	x
<i>Acer spicatum</i>				x					x		x
Total: 73	4	42	68	22	31	15	46	28	41	51	48

* Part utilized: r = roots; st = stems; tw = twigs; bd = buds; l = leaves; th = thalli; bk = bark; f = fruits, berries and seeds; fl = flowers.

† Season of utilization: Sp = spring; Su = summer; F = fall; W = winter.

TABLE VIII

Number of vascular plant species utilized by *Microtus*
in the major habitats

	Spruce-fir forest	Tuckamoor	Alder patch	Dwarf shrub barren	Grassy area	Bog	Salt marsh	Shoreline
Number of vascular plant species fed upon by <i>Microtus</i>	11	17	14	14	29	27	0	10
Number of vascular plant species recorded	41	30	18	20	90	67	23	29

Home Range

It is a well established fact that meadow voles possess small home ranges. In 1909 Seton mentioned that *Microtus drummondii* (later reclassified *M. pennsylvanicus drummondii*) had home ranges which were probably less than 50 feet (15.3 m) in diameter. Since Seton's time, many researchers have attempted to determine the size of the meadow voles' home ranges. Several techniques have been used to calculate home range size. The average home range of *M. pennsylvanicus*, as determined by the minimum area, inclusive boundary strip and exclusive boundary strip methods (for explanation of these techniques, see Van Vleck, 1969), varies from 0.029 to 0.95 acres (0.012 to 0.384 ha) (Blair, 1940; Getz, 1961b; Gunderson, 1950; Hamilton, 1937a; Hayne, 1950; Manville, 1951; Robinson and Falls, 1965; Van Vleck, 1969).

Between 1967 and 1969 I delimited the home ranges of the *M. pennsylvanicus* residing on the SKC plot [South Trump Island (No. 82)], Pyke Island (No. 39), Shellbird Island (No. 42) and Little Solid Island (No. 41) with a total of 11,272 TN. I calculated the home ranges using the minimum area method as proposed by Hayne (1950) and the greatest diameter technique as applied by Stickel (1960) and Beer (1961). The former gives an area which is bound by the line connecting the outermost points of capture. The latter is the straight-line distance between the two furthest capture sites within the home range. For both measurements I used only the records from voles captured at three or more trap sites.

Admittedly, the minimum area is an unrealistic measure of the area actually utilized by a meadow vole, because in the calculated home range there may be extensive areas which are never visited. However, since the technique is widely used (Beer, 1961; Godfrey, 1954; Hayne, 1950;

Sheppe, 1966), I calculated the home ranges as minimum areas to allow comparison with other studies.

Tables IX-XII (pp. 123-126) present home range data for the *Microtus* captured during the fall, winter, spring and summer seasons, respectively, on the 1.36-ha SKC plot. The results were broken down by sex for each season. In the winter and summer too few individuals were captured at three or more sites to give an adequate estimate of the home ranges of the voles inhabiting the plot. Nonetheless, the data were included to supplement the fall and spring records.

Stickel (1960) pointed out that, if a plot is too small, the calculated home ranges will be smaller than the actual home ranges as evidenced by the fact that most of the animals will be captured at least once on the outer edge of the plot. During my fall trapping season (Fig. 54, pp. 112-113) only 38% of the home ranges included one or more capture sites on the edge of the plot, indicating that it was large enough to give a valid estimate of home range size. In the spring, however, 86% of the home ranges bordered on the edge (Fig. 55, pp. 114-115), suggesting that the plot was too small during this season; the home ranges in Table XI are therefore probably underestimated. The few home ranges determined in the winter and summer on the SKC plot suggest that the plot was sufficiently large during these seasons.

The following are salient facts regarding the seasonal changes in the home ranges of the voles on the SKC plot.

1. The majority of the voles possessed small home ranges during the fall (Table IX and Fig. 54). I found no difference in home range size associated with age or sex; the differences between the male and female home ranges noted in Table IX are not statistically significant.

The small amount of overlap between the home ranges in Fig. 54 suggests that the voles were territorial and that they excluded members of their own sex more than members of the opposite sex: 29% of the male home ranges overlap, 24% of the female home ranges overlap, and, if Figs. 54a and 54b were to be superimposed, 41% of the male and female home ranges would overlap. There were, however, 38 other voles on the plot during the fall which were captured at fewer than three trap sites; it was impossible to ascertain whether these animals were trap-shy residents with home ranges on the plot or only transients passing through the plot. There could have been, therefore, more home range overlap than shown in Fig. 54. The small size of the fall home ranges and the apparent territoriality appeared to be associated with an abundance of food and cover in all habitats, a lack of sexual activity (see section on Reproduction, pp. 164-171) and a high population density.

2. Comparison between Tables IX and X indicates that the home ranges were about the same size in the winter as in the fall, but the scanty winter data are inconclusive.

3. By spring the voles had more than doubled the sizes of their home ranges (Table XI and Fig. 55), especially if the spring home ranges were underestimated due to the size of the plot. The calculations in Table XIII (p. 127) demonstrate that the males were the cause of the increase in the average home range size. As the home ranges increased, the apparent territoriality decreased: 64% of the male home ranges overlap in Fig. 55a, 40% of the female home ranges overlap in Fig. 55b, and 69% of the male and female home ranges overlap. These changes in home range size and overlap could have been associated with the voles' increased sexual activities: they were reaching their sexual peak for the year. The changes may also have been due to a decline in habitat quality

and/or a decrease in population density.

4. The summer home ranges (Table XII) were about the same size as those delimited in the previous fall. The factors responsible for the maintenance of small home ranges throughout the summer appeared to be the same as those operating in the fall: cessation of sexual activity, high population density and abundance of food and cover.

In addition to the foregoing seasonal changes in average home range size on the SKC plot there was great variation between the minimum and maximum home range sizes for each season (Table IX-XII), especially during the fall. An example of this variation is provided by the records of two juvenile females:

1. Female 0240 was captured six times between 17 October and 1 November 1968 within an area of 21 m^2 . During the winter, spring and summer trapping seasons, she was captured an additional nine times within an area of only 136 m^2 . Her home range in the centre of the plot was carefully delimited by frequent shifting of the trap sites.

2. Female 2100 was first captured on the SKC plot on 25 September 1968 and recaptured three more times between 26 September and 4 October. Between 3-7 October I happened to have 42 live traps set in a bog south of the study plot. On 5 and 6 October female 2100 was recaptured in this bog, more than 160 m from her last capture site. Within eight days she had returned to the plot and was recaptured 12 more times between 14 October and 2 November. She was not recaptured, however, during the subsequent trapping seasons. If her range is calculated only from the capture sites on the SKC plot, it is 2750 m^2 ; if calculated from all

capture sites, it is $10,600 \text{ m}^2$ which is 72.5 times larger than the average fall home range on the plot.

In order to keep the results of this study comparable with those of other investigators, I omitted the records of female 2100 from all calculations.

Between 7 June and 29 August 1967 Pyke Island was live trapped with 3074 TN. Prior to 8 July, the traps were evenly distributed between the interior spruce-fir forest and the shoreline-ecotone (Table III, p. 85); after that date they were employed only along the ecotone. During the summer a total of 19 voles was captured on the island; six of these voles were removed to other islands (see section on Island Colonization and Inter-Island Movements, pp. 136-138).

Table XIV (p. 128) presents the home range data for the remaining Pyke Island voles which were captured at three or more trap sites.

In the section on Habitat Selection (p. 68) I mentioned that the Pyke Island voles utilized only the shoreline-ecotone and avoided the interior forest during the first half of summer 1967. Had this been the case throughout the entire summer, then the minimum area method would vastly overestimate the size of the actual home ranges. For this reason, I also expressed the voles' ranges as shoreline home ranges in Table XIV. These were calculated as narrow bands the width of the shoreline-ecotone (5 m) extending as far around the periphery of Pyke Island as needed to include all capture sites. Although these shoreline home ranges are smaller than the minimum area home ranges on Pyke Island, they are still ten times larger than the largest SKC home ranges (spring ranges)

which were calculated as minimum areas.

During summer 1967 I observed several major home range shifts involving inter-island movements (see section on Island Colonization and Inter-Island Movements, pp. 134-137), but I omitted them from the figures and calculations. The large home ranges on Pyke Island did not consist of several small home ranges lumped into a single huge one; they were simply the result of long, rapid and frequent movements.

It is convenient to express these movements as movement indices, which were calculated by dividing the sum of the distances between successive capture sites by the total number of days between the first and last captures. Figs. 56-59 (pp. 116-119) depict the variation in movement recorded for the Pyke Island voles:

1. Female 0012 had the smallest movement index of any Pyke Island vole (Fig. 56). In 45 days she was captured 13 times and moved only 10 m/day within a home range whose greatest diameter was 107 m.

2. The female with the largest index was no. 1010 (Fig. 57). With 16 captures in 21 days she covered an average 47.7 m/day within a greatest diameter of 113 m.

3. The movement indices of the females were considerably smaller than those of the males. Male 0033 was captured 11 times in 14 days within a greatest diameter of 223 m (Fig. 58). His index, 64.5 m/day, is the smallest of the male indices yet it is almost a third larger than the preceeding female's index.

4. Over a 49-day period male 0004 had a fantastic movement index of 104 m/day within a greatest diameter of 259 m (Fig. 59). He crossed from one side of his range to the other with considerable

speed; for example, he traversed a distance of 213 m (point A to B in Fig. 59) in less than 8.5 hours. If he had confined his activities to the shoreline-ecotone during this period, he would have had to cover at least 517 m.

In addition to the large size of the Pyke Island male and female home ranges, there was a difference in the distribution of the home ranges about the island. The female home ranges were scattered around the periphery of the island with relatively little overlap (Figs. 60a, p. 120), whereas the male home ranges encompassed the greater portion of the island and showed extensive overlap (Fig. 60b, p. 121). Since the male home ranges were so huge, the extensive overlap does not necessarily indicate that there was considerable contact between the seven male voles.

The voles inhabiting smaller forested islands in the immediate vicinity of Pyke Island also possessed large home ranges.

Twenty voles inhabited Shellbird Island during summer 1967; of these, only two were adult females and the rest were juveniles born that summer. Statistical information on the home ranges of 15 voles is presented in Table XV (p. 129). Although only the shoreline-ecotone appeared to be utilized on Shellbird Island (see section on Habitat Selection, p. 69), I did not calculate the home ranges as shoreline home ranges as was done with the Pyke Island ranges; since Shellbird Island is only 0.57 ha, the shoreline home ranges are quite similar to the minimum area home ranges given in Table XV. There is no statistical difference between the size of the male and female home ranges, and there appeared to be no territoriality. This was probably due to the age of the juveniles and the absence of sexually mature males.

Four voles inhabited Little Solid Island during the summer of 1967. Data on their home ranges are presented in Table XVI (p. 130). One vole was an adult male which was captured six times between 13-17 June; during the latter half of June he emigrated to Pyke Island (Fig. 62, p. 144). The other three voles were young of the year. They were recaptured from 17-45 times between 24 July and 29 August. All four voles ranged over the entire island.

It is generally believed that home range size is related to the size and food habits of an animal (McNab, 1963), but it is realized that, within limits, the home range of a species may vary considerably in size. Several studies on small rodents have shown that home range size is inversely affected by habitat quality (Beer, 1961; Blair, 1951; Layne, 1954; Linduska, 1942; Quimby, 1951; Stickel, 1948; Townsend, 1935; Yerger, 1953) and population density (Bendell, 1959; Blair, 1940; Getz, 1961b; Linduska, 1942; Quimby, 1951; Sheppe, 1966; Stickel, 1960). It has also been mentioned that age affects home range size (Burt, 1943) and that male rodents often possess larger home ranges than females, particularly during the breeding season (Bergstedt, 1966; Blair, 1940; Brown, 1962; Getz, 1961b; Hamilton, 1937a; Hayne, 1950; Howell, 1954; Manville, 1951; Townsend, 1935; Van Vleck, 1969). For island situations it has been shown by Ozoga and Phillips (1964) that intraspecific competition limits an individual's home range to a greater extent than does interspecific competition.

Sexual activity, population density, habitat diversity and island size appeared to be the major factors affecting the size of the *Microtus* home ranges on the SKC plot, Pyke Island, Shellbird Island and Little Solid Island (Table XVII, p. 131 and Fig. 61, p. 122). An increase in

population density or habitat diversity had a negative affect on home range size, whereas an increase in sexual activity had a positive affect, particularly on the male home ranges. Island size was also a limiting factor on the smaller islands. Seasonal changes in habitat quality likewise affected the size of the voles' home ranges: during early spring when herbaceous cover was scarce, the home ranges were larger than in summer and fall when herbaceous food and shelter were abundant. All these factors were inextricably related.

The size of a mammal's home range is governed by the various biotic and physical factors listed above, but, unfortunately, it can also be influenced by the technique employed in determining it. Hayne (1950) and Robinson and Falls (1965) have demonstrated that the greater the distance between traps, the larger the home ranges of rodents appear. When a small plot is intensively trapped it is possible that the traps are so effective that they do not allow individuals to utilize their entire home ranges (D. L. Pattie, personal communication). Thus, had I used the same trapping techniques on the SKC plot as were used on Pyke, Little Solid and Shellbird islands, I might have found that the home ranges of the SKC voles were somewhat larger than given in Tables IX-XIII, as is suggested by the trap records of female 2100 (pp. 123-127).

Based on my experience with the Newfoundland vole, I suggest that future studies concerned with the home ranges of small mammals give more attention to individuals with unusually large home ranges, to determine their relative abundance in the population and to evaluate their importance to the dispersal of the species. In order to accomplish this, it will be necessary to shift the emphasis from live trapping to some other technique with fewer inherent biases, such as radio tagging.

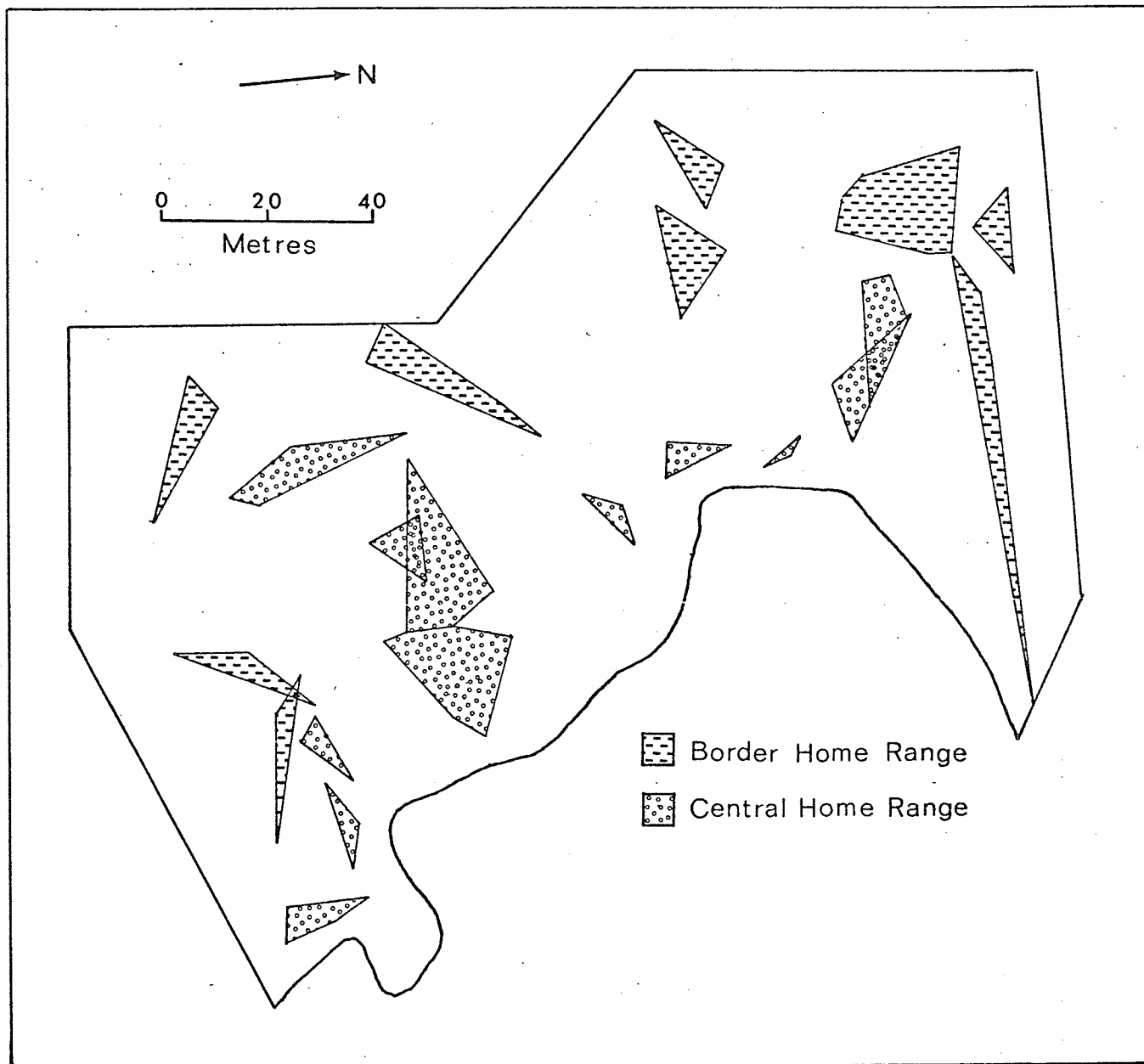


Fig. 54a. Home ranges of male *Microtus* captured at three or more sites during the fall trapping period (24 September-7 October and 14 October-2 November 1968) on the SKC plot, South Trump Island (No. 82). See Table IX (p. 123) for data on these home ranges. Home ranges delimited for voles captured at one or more trap sites on the edge of the plot are referred to as border home ranges. Home ranges delimited for voles not captured at trap sites on the edge of the plot are referred to as central home ranges.

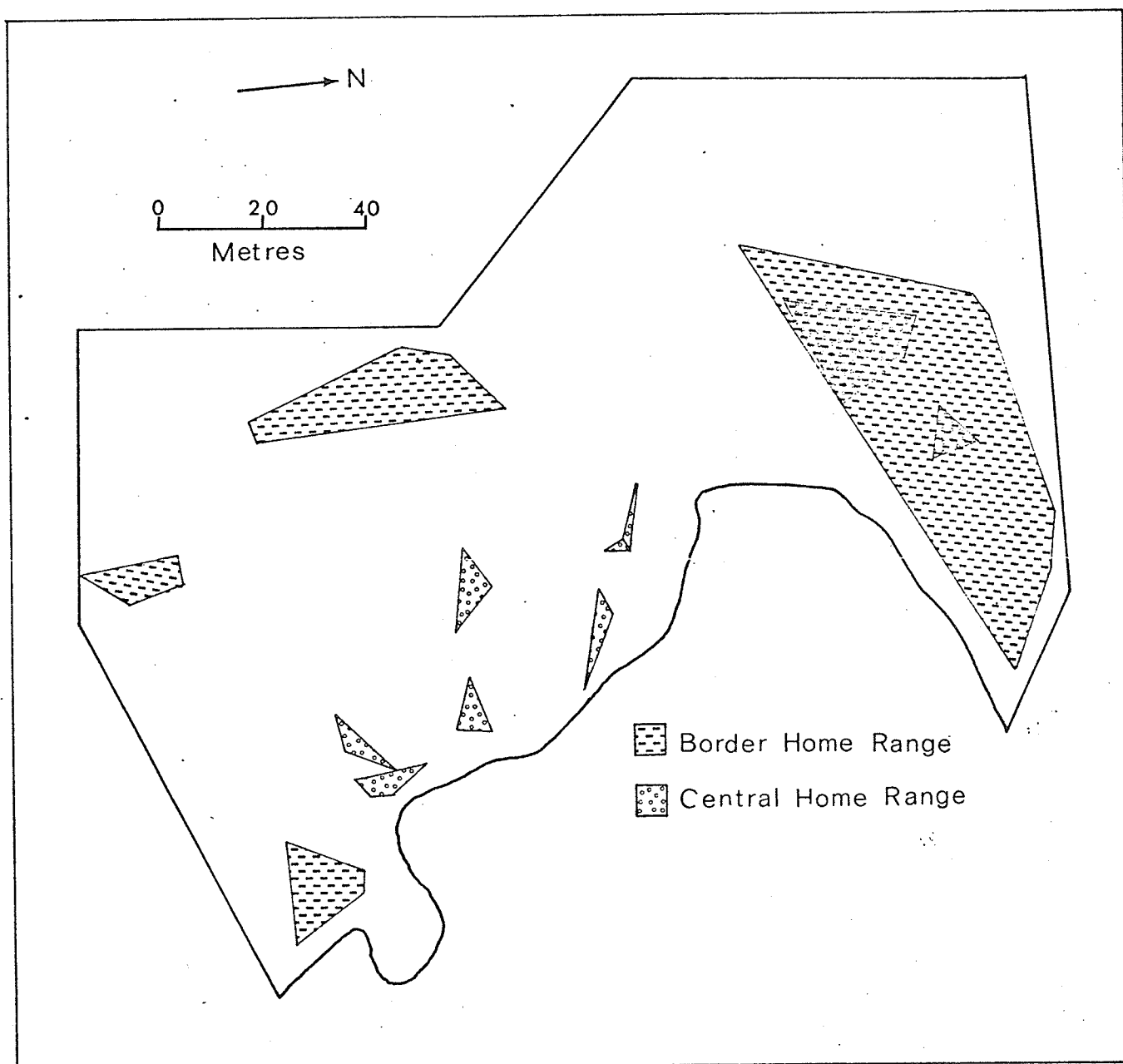


Fig. 54b. Home ranges of female *Microtus* captured at three or more sites during the fall trapping period (24 September-7 October and 14 October-2 November 1968) on the SKC plot, South Trump Island (No. 82). See Table IX (p. 123) for data on these home ranges and Fig. 54a for explanation of symbols.

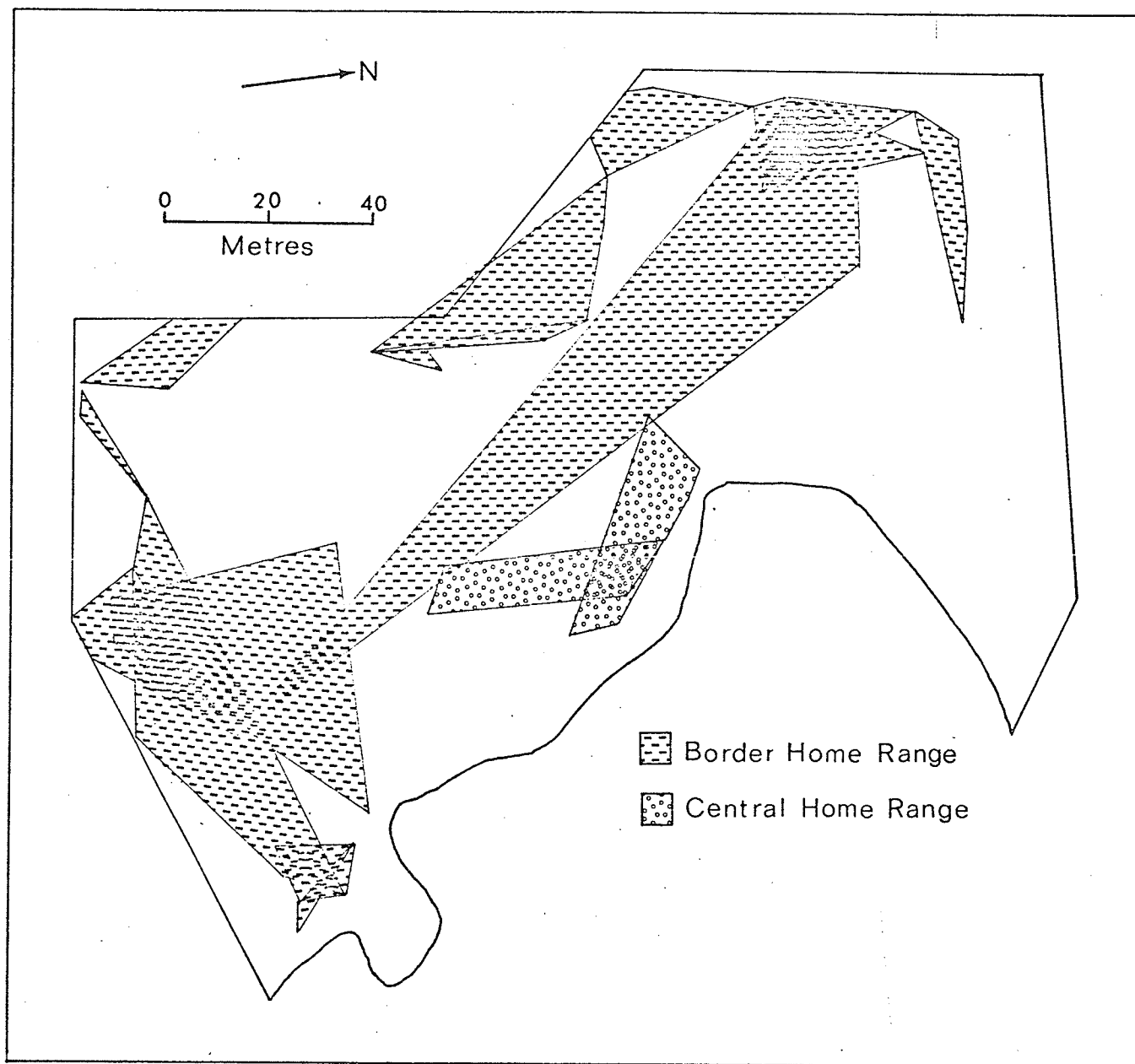


Fig. 55a. Home ranges of male *Microtus* captured at three or more sites during the spring trapping period (25 April–11 May 1969) on the SKC plot, South Trump Island (No. 82). See Table XI (p. 125) for data on these home ranges and Fig. 54a for explanation of symbols.

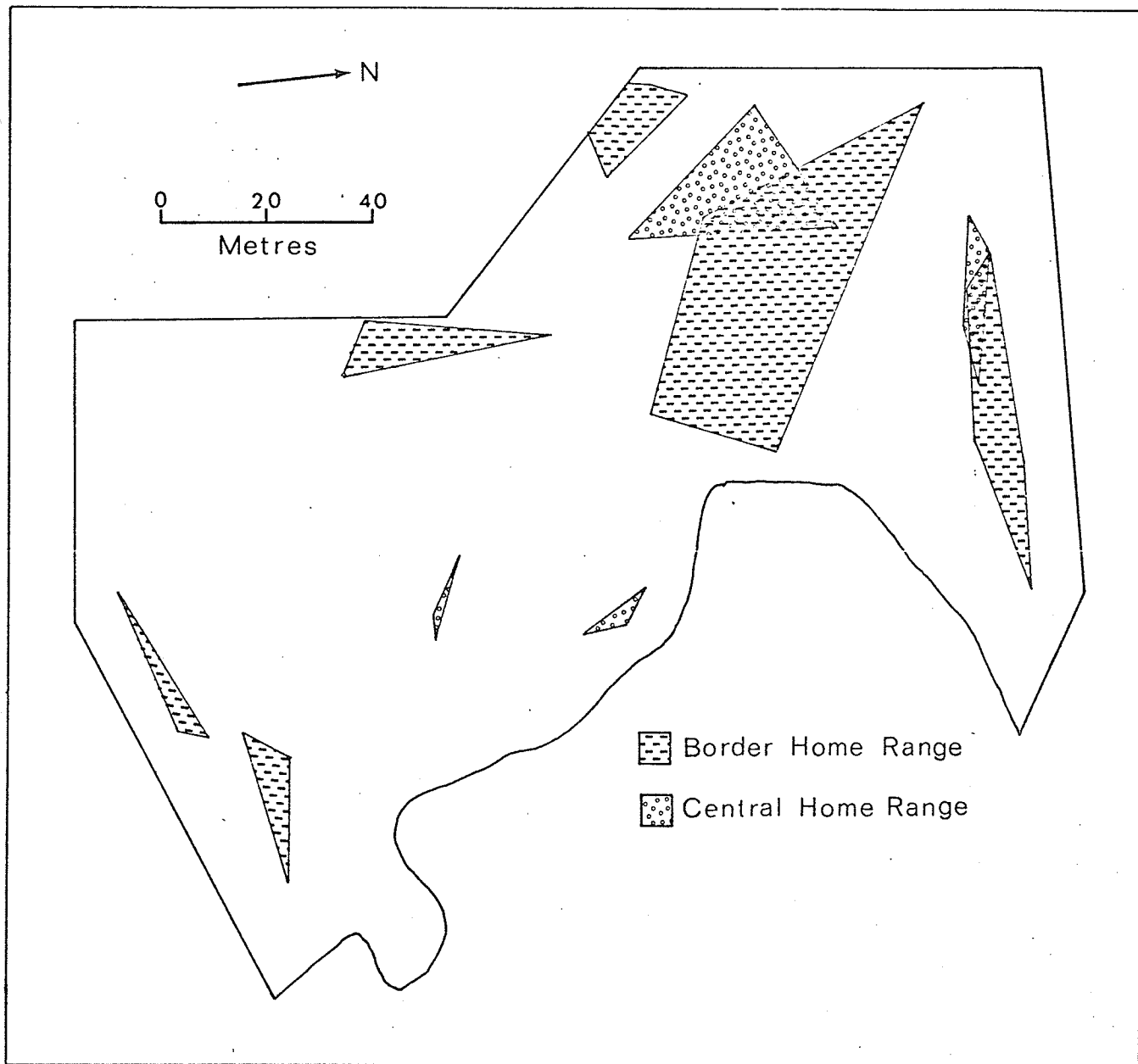


Fig. 55b. Home ranges of female *Microtus* captured at three or more sites during the spring trapping period (25 April-11 May 1969) on the SKC plot, South Trump Island (No. 82). See Table XI (p. 125) for data on these home ranges and Fig. 54a for explanation of symbols.

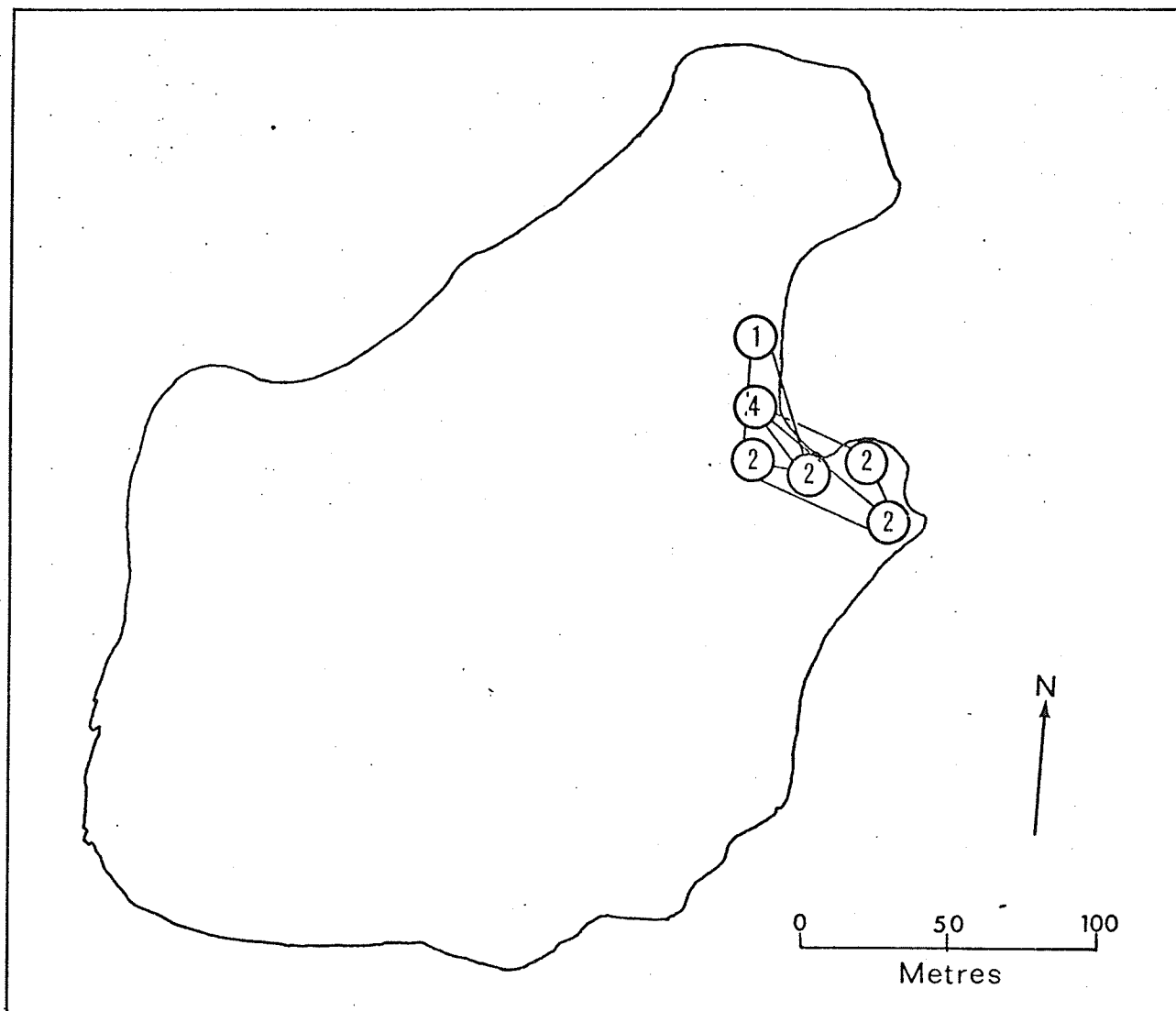


Fig. 56. Home range of female *Microtus* 0012 on Pyke Island (No. 39) for the period 11 July-26 August 1967. This home range calculated as a minimum area is 0.17 ha and calculated as a shoreline range is 0.09 ha. The movement index for this period is 10 m/day within a greatest diameter of 107 m. Circles represent capture sites, and numbers in circles refer to number of captures. Straight lines join successive capture sites.

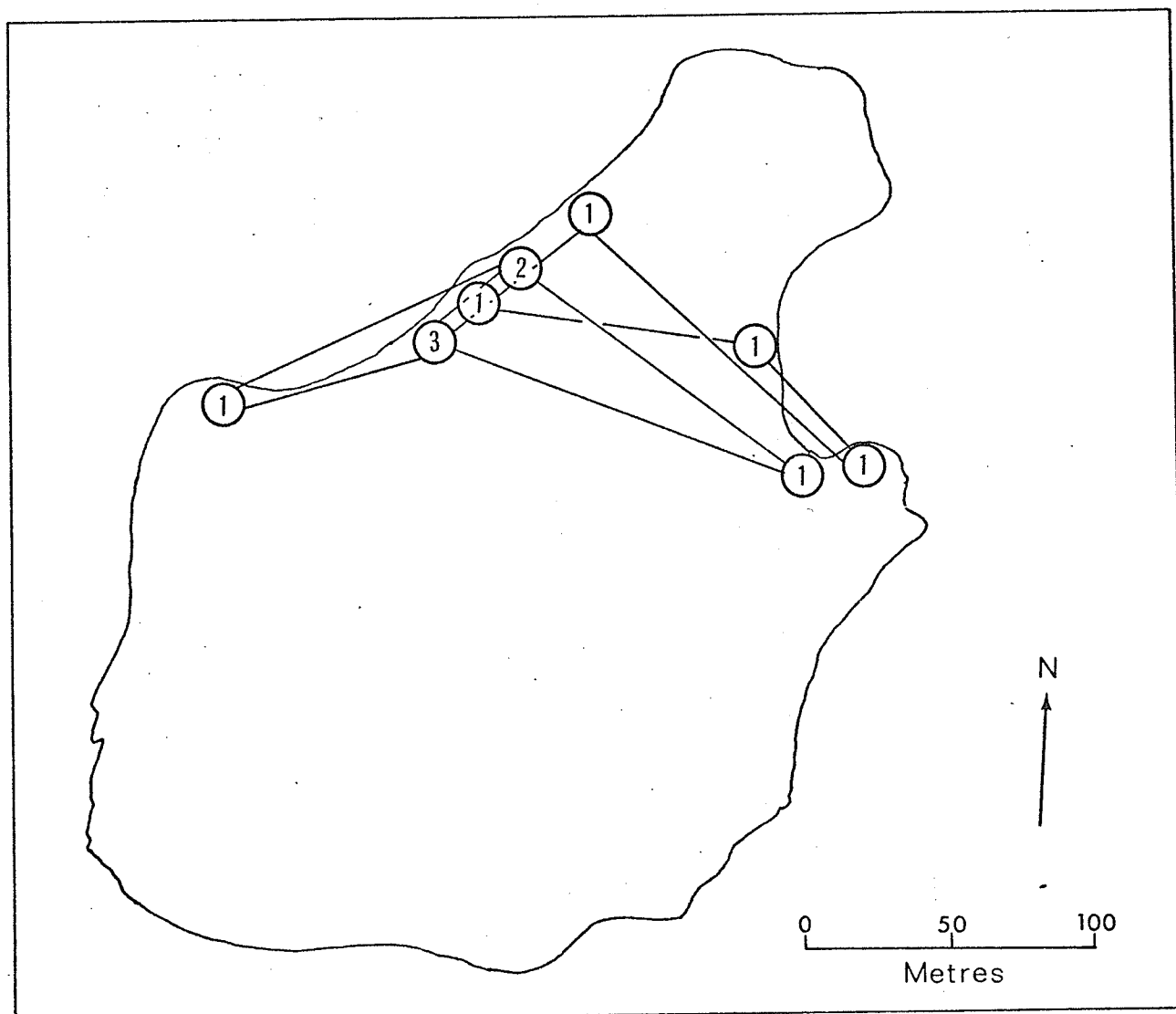


Fig. 58. Home range of male *Microtus* 0033 on Pyke Island (No. 39) for the period 18 July-1 August 1967. This home range calculated as a minimum area is 1.83 ha and calculated as a shoreline range is 0.35 ha. The movement index for this period is 64.5 m/day within a greatest diameter of 223 m. Symbols as in Fig. 56.

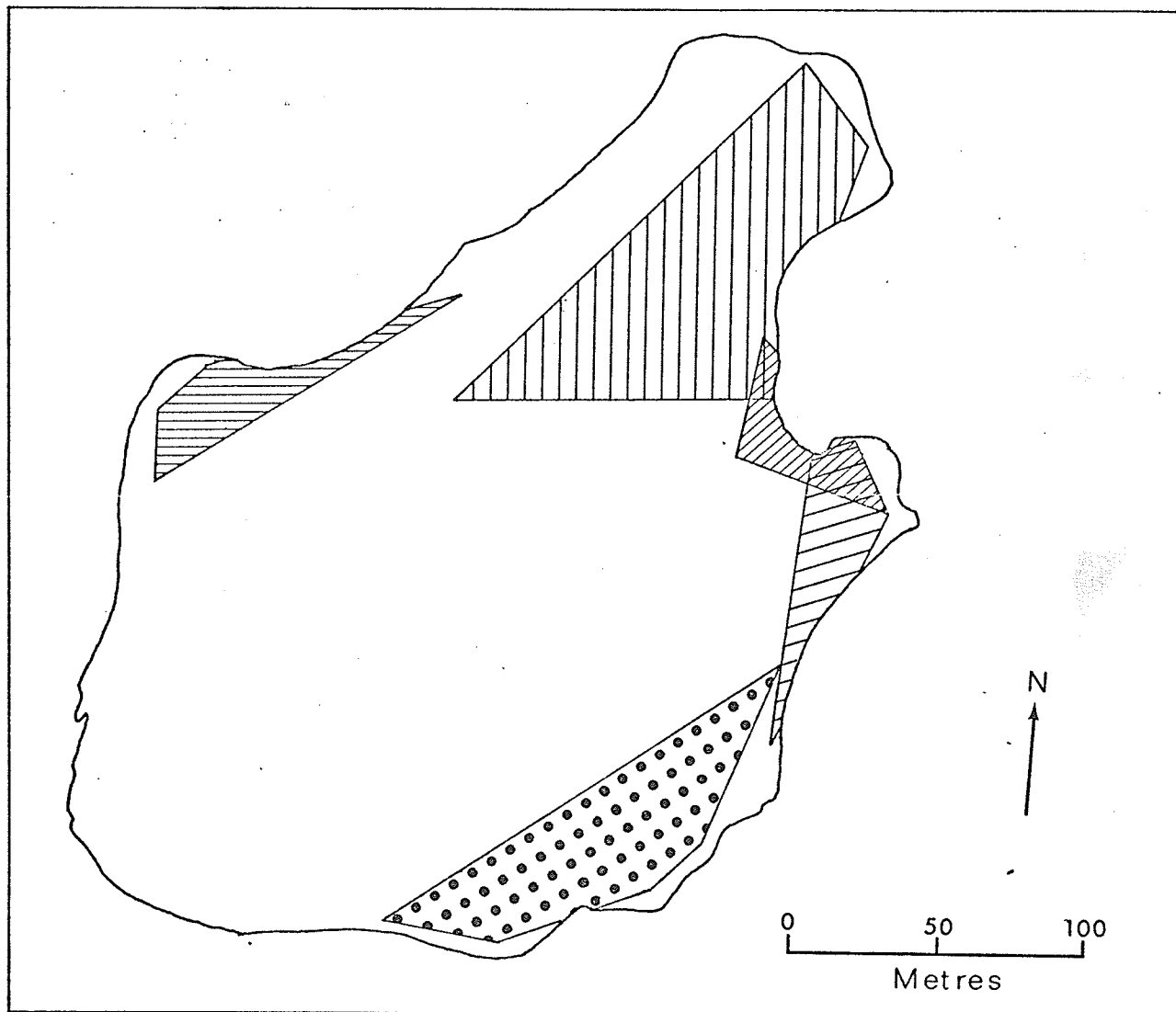


Fig. 60a. Home ranges of female *Microtus* captured at three or more sites during summer 1967 (7 June-29 August) on Pyke Island (No. 39). See Table XIV (p. 128) for data on these home ranges.

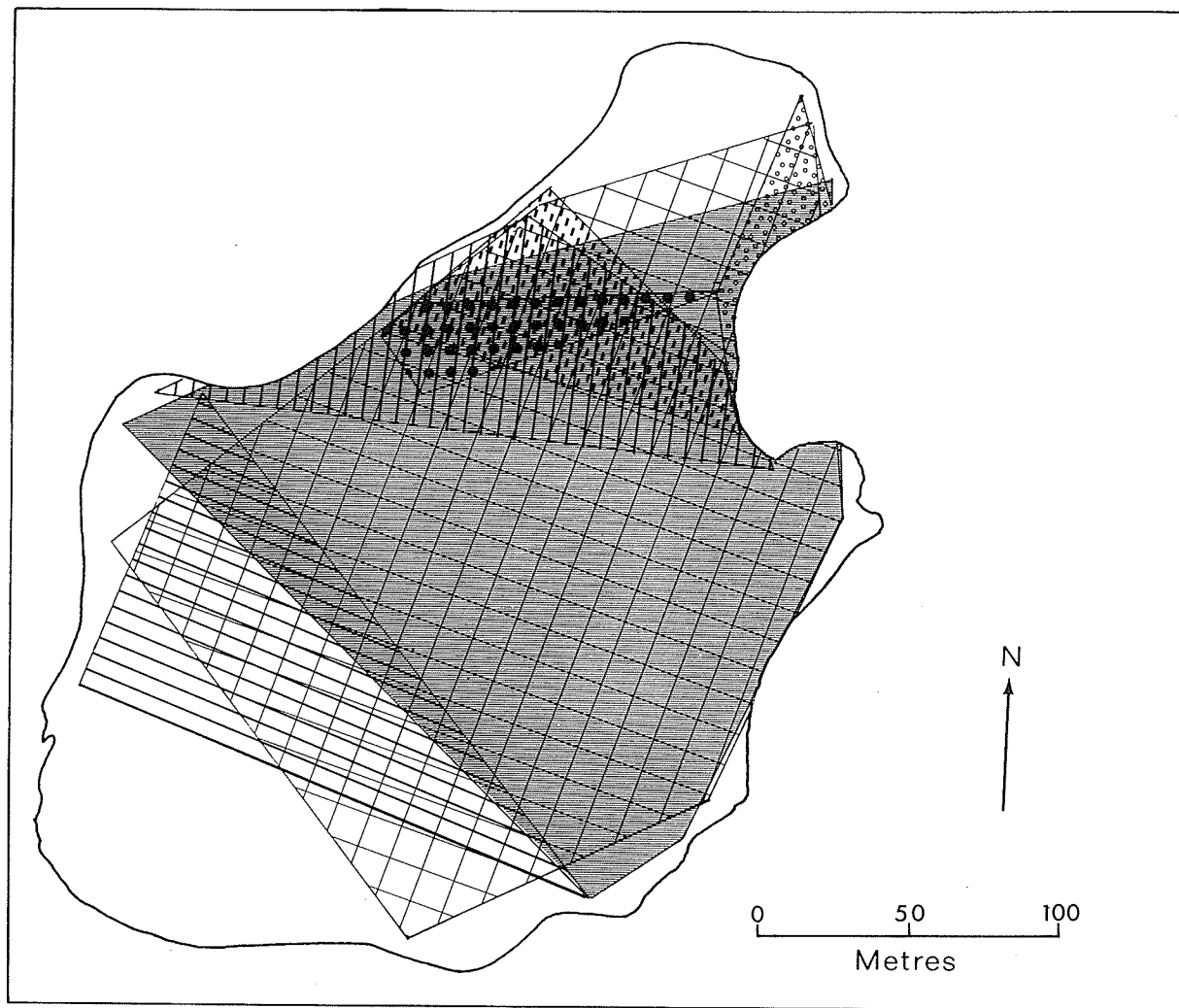


Fig. 60b. Home ranges of male *Microtus* captured at three or more sites during summer 1967 (7 June-29 August) on Pyke Island (No. 39). See Table XIV (p. 128) for data on these home ranges.

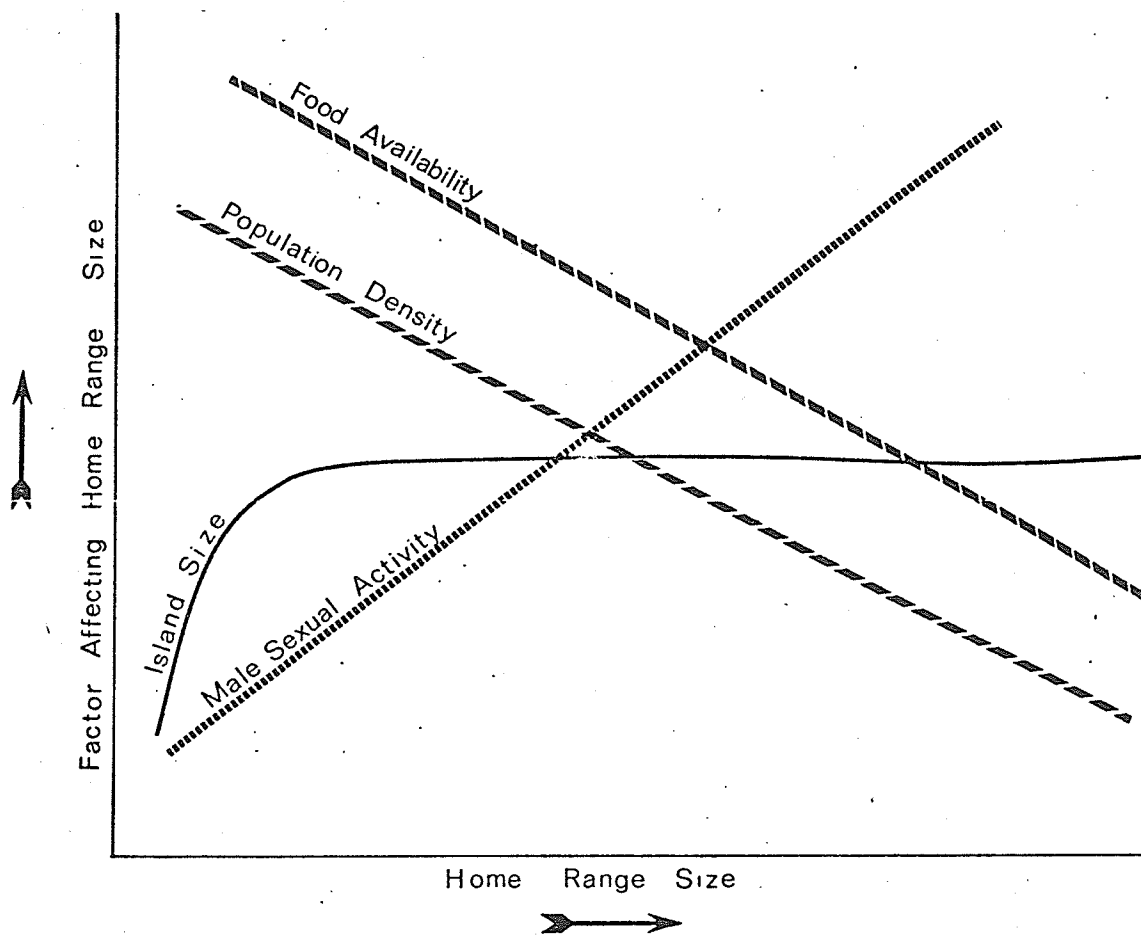


Fig. 61. Diagrammatic representation of factors affecting home range size of *Microtus* inhabiting islands in Notre Dame Bay. For explanation refer to text (pp.-110-111).

TABLE IX

Data on home ranges of *Microtus* on the SKC plot during fall 1968
(24 September-7 October and 14 October-2 November)

	N	Maximum	Minimum	\bar{X}	SD	SE
Males						
Minimum area (ha)	21	0.0272	0.0008	0.0105	0.0078	0.0017
Greatest diameter (m)	21	90.51	7.32	24.90	16.88	3.68
Captures	21	24	3	7.4	4.6	1.1
Females						
Minimum area (ha)	13	0.1688	0.0004	0.0212	0.0456	0.0127
Greatest diameter (m)	13	93.25	3.84	23.14	23.45	6.51
Captures	13	31	3	10.3	8.2	2.3
Males and females						
Minimum area (ha)	34	0.1688	0.0004	0.0146	0.0287	0.0049
Greatest diameter (m)	34	93.25	3.84	24.22	19.35	3.32
Captures	34	31	3	8.5	6.3	1.1

Tests for significant differences between males and females:

	t	df	P
Minimum area (ha)	1.059	33	0.20>P>0.10
Greatest diameter (m)	0.249	33	P>0.40
Captures	1.337	33	0.10>P>0.05

TABLE X

Data on home ranges of *Microtus* on the SKC plot during winter 1969
(25 February-13 March)

	N	Maximum	Minimum	\bar{X}	SD	SE
Males						
Minimum area (ha)	2	0.0314	0.0152	0.0231	0.0096	0.0068
Greatest diameter (m)	2	30.48	20.30	25.40	7.21	5.10
Captures	2	12	11	11.5	0.7	0.5
Females						
Minimum area (ha)	2	0.0139	0.0036	0.0080	0.0113	0.0080
Greatest diameter (m)	2	18.60	13.41	16.00	3.68	2.60
Captures	2	6	5	5.5	0.7	0.5
Males and females						
Minimum area (ha)	4	0.0314	0.0036	0.0160	0.0115	0.0057
Greatest diameter (m)	4	30.48	13.41	20.71	7.15	3.57
Captures	4	12	5	8.5	3.5	1.7

Tests for significant differences between males and females:

	t	df	P
Minimum area (ha)	1.518	3	0.10>P>0.20
Greatest diameter (m)	1.642	3	0.05>P>0.10
Captures	8.485	3	0.01>P>0.005

TABLE XI

Data on home ranges of *Microtus* on the SKC plot during spring 1969
(25 April-11 May)

	N	Maximum	Minimum	\bar{X}	SD	SE
Males						
Minimum area (ha)	19	0.2200	0.0013	0.0449	0.0575	0.0129
Greatest diameter (m)	19	156.61	12.64	41.48	32.95	7.59
Captures	19	11	3	6.4	2.7	0.6
Females						
Minimum area (ha)	10	0.1422	0.0006	0.0267	0.0426	0.0135
Greatest diameter (m)	10	74.71	11.42	33.50	19.95	6.30
Captures	10	10	4	6.1	2.4	0.8
Males and females						
Minimum area (ha)	29	0.2200	0.0006	0.0388	0.0530	0.0097
Greatest diameter (m)	29	156.61	11.42	39.06	29.01	5.39
Captures	29	11	3	6.1	2.3	0.4

Tests for significant differences between males and females:

	t	df	P
Minimum area (ha)	0.877	28	0.10>P>0.20
Greatest diameter (m)	0.612	28	0.20>P>0.30
Captures	0.267	28	0.30>P>0.40

TABLE XII

Data on home ranges of *Microtus* on the SKC plot during summer 1969
(12-21 August)

	N	Maximum	Minimum	\bar{X}	SD	SE
Males						
Minimum area (ha)	4	0.0170	0.0019	0.0093	0.0057	0.0028
Greatest diameter (m)	4	38.28	17.62	25.09	9.19	4.59
Captures	4	4	3	3.5	0.6	0.3
Females						
Minimum area (ha)	4	0.0363	0.0006	0.0117	0.0162	0.0081
Greatest diameter (m)	4	41.57	13.50	27.70	14.26	7.13
Captures	4	4	3	4.0	0.5	0.3
Males and females						
Minimum area (ha)	8	0.0363	0.0006	0.0105	0.0117	0.0042
Greatest diameter (m)	8	41.57	13.50	26.40	11.19	3.96
Captures	8	4	3	3.4	0.5	0.2

Tests for significant differences between males and females:

	t	df	P
Minimum area (ha)	0.269	7	P>0.40
Greatest diameter (m)	0.307	7	0.40>P>0.30
Captures	0.655	7	0.30>P>0.20

TABLE XIII

Values of "t" for fall and spring home ranges of *Microtus*
on the SKC plot

"t" test	Fall ranges	Spring ranges
\bar{X} minimum area (ha)		
t = 2.714 df = 39 P < 0.005	Males 0.0105	Males 0.0449
t = 0.294 df = 22 0.40 > P > 0.30	Females 0.0212	Females 0.0267
t = 2.715 df = 62 P < 0.005	Males and females 0.0146	Males and females 0.0388
\bar{X} greatest diameter (m)		
t = 2.030 df = 39 P ≈ 0.025	Males 24.90	Males 41.48
t = 1.220 df = 22 0.20 > P > 0.10	Females 23.14	Females 33.50
t = 2.422 df = 62 0.01 > P > 0.005	Males and females 24.22	Males and females 39.06

TABLE XIV

Data on home ranges of *Microtus* on Pyke Island (No. 39) during summer 1967
(7 June-29 August)

	N	Maximum	Minimum	\bar{X}	SD	SE
Males						
Minimum area (ha)	7	8.6601	0.2562	3.0262	3.3410	1.2626
Greatest diameter (m)	7	465.73	144.17	292.19	116.25	44.68
Shoreline range (ha)	7	0.560	0.092	0.327	0.161	0.061
Captures	7	31	4	12.5	10.2	3.9
Females						
Minimum area (ha)	5	1.5621	0.1692	0.6697	0.5787	0.2590
Greatest diameter (m)	5	249.77	110.57	189.89	59.38	26.56
Shoreline range (ha)	5	0.175	0.090	0.120	0.036	0.016
Captures	5	26	8	16.2	6.6	3.0
Males and females						
Minimum area (ha)	12	8.6601	0.1692	2.0436	2.7721	0.8010
Greatest diameter (m)	12	465.73	110.57	249.41	106.80	30.83
Shoreline range (ha)	12	0.560	0.090	0.241	0.161	0.047
Captures	12	31	4	14.1	8.7	2.5

Tests for significant differences between males and females:

	t	df	P
Minimum area (ha)	1.540	11	0.10>P>0.05
Greatest diameter (m)	1.788	11	0.10>P>0.05
Shoreline range (ha)	2.807	11	0.01>P>0.005
Captures	0.692	11	0.30>P>0.20

TABLE XV

Data on home ranges of *Microtus* on Shellbird Island (No. 42) during summer 1967
(17 July-29 August)

	N	Maximum	Minimum	\bar{X}	SD	SE
Males						
Minimum area (ha)	5	0.4282	0.0142	0.1706	0.1649	0.0737
Greatest diameter (m)	5	129.54	48.73	97.72	37.88	16.95
Captures	5	36	3	17.2	14.0	6.3
Females						
Minimum area (ha)	10	0.2148	0.0105	0.1018	0.0584	0.0185
Greatest diameter (m)	10	134.63	57.26	88.88	31.59	9.99
Captures	10	21	8	11.6	4.3	1.4
Males and females						
Minimum area (ha)	15	0.4282	0.0105	0.1261	0.1070	0.0276
Greatest diameter (m)	15	134.63	48.73	91.81	32.70	8.44
Captures	15	36	3	13.4	8.7	2.2

Tests for significant differences between males and females:

	t	df	P
Minimum area (ha)	1.154	14	0.20>P>0.10
Greatest diameter (m)	0.476	14	0.40>P>0.30
Captures	1.194	14	0.20>P>0.10

TABLE XVI

Data on home ranges of *Microtus* on Little Solid Island (No. 41) during summer 1967
(12 June-29 August)

	N	Maximum	Minimum	\bar{X}	SD	SE
Males						
Minimum area (ha)	2	0.2490	0.1048	0.1770	0.1018	0.0720
Greatest diameter (m)	2	148.43	98.45	123.40	35.36	25.00
Captures	2	46	6	26.0	28.3	20.0
Females						
Minimum area (ha)	2	0.2050	0.1990	0.2020	0.0042	0.0030
Greatest diameter (m)	2	120.00	113.40	116.70	4.67	3.30
Captures	2	25	18	21.5	5.0	3.5
Males and females						
Minimum area (ha)	4	0.2490	0.1048	0.1894	0.0605	0.0303
Greatest diameter (m)	4	148.43	98.45	120.09	20.95	10.47
Captures	4	46	6	23.8	16.8	8.4

Tests for significant differences between males and females:

	t	df	P
Minimum area (ha)	0.347	3	0.30 < P < 0.40
Greatest diameter (m)	0.266	3	P > 0.40
Captures	0.222	3	P > 0.40

TABLE XVII

Comparison of *Microtus* home ranges under various population and environmental conditions

Study area	Study area size (ha)	Habitat [*]							Season and year	Population density (voles/ha)	Sexual activity	\bar{X}	\bar{X}
		1	2	3	4	5	6	8				minimum area (ha)	greatest diameter (m)
SKC plot (No. 82)	1.36		x	x	x	x	x	x	Fall 1968	53.0	inactive	0.0146	24.22
SKC plot (No. 82)	1.36		x	x	x	x	x	x	Spring 1969	42.6	active	0.0388	39.06
Shellbird Is. (No. 42)	0.57	x	x					x	Summer 1967	35.1	active	0.1261	91.81
Little Solid Is. (No. 41)	0.44		x		x			x	Summer 1967	6.8	active	0.1894	120.09
Pyke Is. (No. 39)	11.84	x	x					x	Summer 1967	1.1	active	2.0436	249.41

* Habitat code: 1 = spruce-fir forest; 2 = tuckamoor; 3 = alder patch; 4 = dwarf shrub barren; 5 = grassy area; 6 = bog; 8 = shoreline. There were no salt marshes (habitat no. 7) on these study areas.

Island Colonization and Inter-Island Movements

Not all of the islands in Notre Dame Bay simultaneously possessed *Microtus* populations. This was due to a high rate of extirpation among the insular populations. Table XVIII (pp. 148-150) lists the islands investigated and the status of *Microtus* on them. These data show that, between 1966 and 1969, the percent of recent extirpation on islands I visited varied from 7.7 to 23.5%.

The following are three examples of extirpated populations:

1. Fishermen from Summerford reported that voles were extremely abundant on Glead Island (No. 14) during July and August 1966; according to them, voles ran in every direction when rocks were overturned. The fishermen said that the voles were still common in the spring of 1967, especially beneath their stored lobster traps. In June and August 1967 I trapped Glead Island with 622 TN and spent seven days searching this 44.8-ha island for vole sign. During this time I found extensive overwintering sign consisting of runway systems, fecal piles and severely damaged shrubs (Figs. 51-52, pp. 94-95), but no voles were seen or captured nor was any fresh sign observed. The voles had definitely been as numerous as the fishermen had reported, but the population had been extirpated some time during late spring 1967.

2. Local men reported that voles were numerous in the meadows and hay barns on Black Island (No. 78) during the haying season in the summer of 1968. I had the opportunity to investigate this 66.4-ha island during a thaw in February 1969. Only a single subnivean runway was located in a small meadow; no other vole sign was found in the tuckamoor, bogs, dwarf shrub barrens or hay barns.

A few house mouse (*Mus musculus*) tracks were seen in the snow as well as abundant weasel (*Mustela erminea*) sign. The *Microtus* population had evidently vanished during the fall or winter of 1968.

3. In the summer of 1966 Pruitt and Forsey collected 15 voles from Grassy Rock (No. 37), four from Pyke Island (No. 39), one from Little Solid Island (No. 41) and noted fresh sign on Shellbird Island (No. 42). During the summer of 1967 I live trapped a total of 40 voles on these four islands. By the summer of 1968 the voles had disappeared from both Pyke and Little Solid islands, while on Grassy Rock there was only a single unmarked adult female and on Shellbird Island there was one marked adult female and her litter of three. In 1969 voles appeared to be absent from all of these islands.

There are several possible factors which may have been responsible for the extirpation of insular populations of *Microtus* in Notre Dame Bay. The various forces which are reputed to influence the cyclic fluctuations of small mammals on the continents (for reviews see Elton, 1942; Krebs, 1964b; Lack, 1954) can affect insular populations as well. Due to the isolated nature of island populations they are usually more vulnerable to extirpation than are mainland populations. Intense predation (see section on Predation, pp. 176-181), adverse weather conditions (Asahi, 1962 as cited in Grant, 1966; Berry, 1968; Negus *et al.*, 1961), food shortages (Berry, 1968; Sheppe, 1965b; Christian *et al.*, 1960), emigration (Sheppe, 1965b), social stress (Christian *et al.*, 1960), genetic drift (Anderson, 1960; Foster, 1965) and the ecological incompatibility of similar species (Grant, 1966) have all been cited as influencing the destinies of insular populations. It is quite likely that more than one

factor was responsible for the elimination of any of the island vole populations in Notre Dame Bay.

It has been pointed out that the size of an island is also a major factor in the longevity of an insular population (Beer *et al.*, 1954; Sheppe, 1965b; Webb, 1965). In Notre Dame Bay a vole population on an island of a few hectares or so is highly ephemeral; any one of a multitude of physical and biotic forces such as drought, poor snow conditions or concentrated predation could easily extirpate such a population. Only by repeated recolonization can a population be perpetuated on a small island for several years. An island of 100 ha or so can support a population for several years without recolonization, because there are fewer forces which could decimate the population; a complete and intense forest fire may be such a force. A population inhabiting an island the size of Newfoundland would seem to be just about immune to extirpation; only a devastating force equivalent to complete glaciation could eliminate *Microtus*.

More important than the number of insular populations which had been extirpated in Notre Dame Bay is the number of islands which did possess vole populations. The mere presence of *Microtus* on the islands, particularly the isolated islands such as Matthews (No. 88), Mouse (No. 87), the Cranpots (Nos. 15 and 16), Yellow Fox (No. 12) and the Hummock islands (Nos. 1-5), demonstrates that the voles' abilities to colonize the islands were greater than the effects of the various factors responsible for extirpation.

During the summer of 1967 I recorded 16 inter-island movements made by marked voles (Figs. 62-63, pp. 144-145); in 1968 two more inter-island movements were noted. The difference in the number of movements

observed in 1967 and 1968 was most likely due to different trapping methods and to a change in the weather. In 1967 I simultaneously live trapped a cluster of small islands while in 1968 no such trapping programme was conducted. The weather was generally hot, dry and calm during summer 1967 whereas it was generally cool, wet and windy in summer 1968.

These inter-island crossings were not confined to a specific age or sex group; movements were made by adults and juveniles and by males and females alike. These travels appeared to represent both dispersal and homing movements.

Four juvenile voles emigrated from Shellbird Island and established new home ranges on Pyke Island and Grassy Rock (Fig. 62). The three juvenile females which emigrated all utilized islands as stepping-stones. Females 0042 and 0035 both stopped on Little Solid Island long enough to be trapped once each and then proceeded on to Pyke Island where they established new home ranges. The third female, no. 0025, made the longest inter-island movement recorded. She was captured on Shellbird Island seven times from 17-25 July; at this time she was a virgin. On 1 August she was recaptured on Cave Island (No. 38), 1130 m to the southwest. After six recaptures I closed the traps on Cave Island because she appeared to be the only vole on the island. Twenty days later I set traps on Grassy Rock (Fig. 12, p. 21); female 0025 was recaptured there in a pregnant condition. When she arrived at Grassy Rock the only other vole on the island was an adult male. It is interesting to note that this male vole had also immigrated to Grassy Rock sometime after May 1966 when Pruitt and Forsey removed the entire vole population. The fourth juvenile vole to emigrate from Shellbird Island, male 0034, made the fastest inter-island movement recorded: in less than 16 hours he

traversed a straight-line distance of 610 m. The dispersal movements of these four juveniles may have been prompted by intraspecific competition possibly for food or shelter on Shellbird Island or possibly just by innate dispersal drives (Howard, 1960). In any case, the records clearly indicate the ease with which *Microtus* colonized the islands in the study area.

The inter-island crossings of male 2000 from Little Cranpot Island (No. 16) to Big Cranpot Island (No. 15) in 1967 also may have represented dispersal movements (Fig. 63). From 7-10 June this male was captured five times on Little Cranpot Island in an area less than 25 m x 10 m; he was the only vole captured in 191 TN. On 27 June, Big Cranpot Island was live trapped, and male 2000 was recaptured there. I transported the vole back to his original home site on Little Cranpot Island, a distance of 270 m. Two days later he was again recaptured on Big Cranpot Island, and, for a second time, I returned him to Little Cranpot Island. On 3 July he appeared on Big Cranpot Island for the third time. These records of male 2000 suggest that he was attempting to leave Little Cranpot Island with its grassy areas and dwarf shrub barrens and to establish a new home range on the forested Big Cranpot Island. It is quite possible, however, that he was not shifting his home range, but, rather, that the two islands were both included within his home range.

Five of the inter-island crossings were made by three *Microtus* while homing:

1. On 25 June 1967 I captured a pregnant female, no. 0400, on Pyke Island. In the hopes of starting a new colony, I released her on Little Solid Island that same day (Fig. 64, p. 146). On 17 July 1967 she was recaptured on the north end of Pyke Island. She had delivered and weaned her litter on Little Solid Island

before returning to Pyke Island [the three juveniles on Little Solid Island referred to in the section on Home Range (p. 110) were probably her offspring]. Female 0400 wandered about Pyke Island and finally set up a home range along the northwest shore. She became pregnant in August. On 13 August I transported her to Stearn Rock (No. 40), 70 m east of Pyke Island; I wanted to determine whether she would attempt the water crossing while pregnant or if she would remain on the rock and try to subsist on its scant vegetation. After two weeks she was recaptured in her old home range on the northwest shore of Pyke Island, and, at this time, she was very close to parturition.

2. Adult male 0050 was captured on Pyke Island on 4 July 1967. As was the case with female 0400, I transported male 0050 to Little Solid Island. Two days later he returned to Pyke Island where he was recaptured an additional ten times.

3. In the summer of 1968 the third case of homing across water was observed. Adult male 1154 was first captured on a small rock 75 m south of Camel Island (No. 8) on 16 August. He was released that same day on the shore of Camel Island opposite the rock. On 25 August he was recaptured on the rock and again transported to Camel Island. Three days later he was recaptured for the third time on the small rock.

The inter-island crossings made by voles 0400, 0050 and 1154 can be considered homing movements only if it is assumed that these voles had had no past experience on the islands upon which they were released. I cannot prove that these voles lacked such experience, but it is unlikely, particularly for female 0400 on Stearn Rock.

Not all transplanted voles returned to Pyke Island after being released on other islands. On 12 June 1967 I released three male and two female Pyke Island voles on Sun Rock (No. 43), 1000 m from Pyke Island. On 25 June 1967 I released a single female on island No. 54, 2375 m from Pyke Island, and on 2 July 1967 another female was transported to island No. 44, 1275 m from Pyke Island. Sun Rock and island Nos. 44 and 54 are small grassy islands uninhabited by other *Microtus* prior to these introductions. None of the transplanted voles were recaptured on Pyke Island. The two females and two of the males remained on Sun Rock and established a colony; the third male disappeared from the island shortly after the introduction and was never recaptured. The two females introduced to island Nos. 44 and 54 were likewise never recaptured after being released on these islands.

In order to get additional information on the voles' homing abilities across open sea, I transplanted the entire Mile Island (No. 19) vole population of 15 animals to Mile Island Rock (No. 18) during August 1968. These two islands are separated by 635 m of open sea, and the nearest island to either is 850 m southeast of Mile Island Rock. None of the transplanted voles had traversed the long stretch of sea back to Mile Island by 19 November 1968, but there was fresh sign on Mile Island Rock indicating that there were at least some voles occupying the rock. It is possible that these voles did not return to Mile Island because the island was barely visible from the rock; Mile Island subtended an angle of only 1° above the horizon when viewed from sea level on the shore of Mile Island Rock.

Since none of the Mile Island voles successfully homed across the long stretch of open sea, I decided to test the homing abilities of

Microtus under completely terrestrial conditions. On 16 August 1969 I transported three adult and five juvenile voles from the SKC plot, where they had resided, to a bog south of the plot. These voles were released 275 to 335 m beyond their trap-determined home ranges. Two adults and two juveniles successfully homed within one to three nights. The fastest homing time was recorded for an adult male who traversed a distance of 315 m in less than 28 hours. It is possible that the other four voles later returned to the plot since I was only able to trap until 21 August. However, the records of the four voles which were recaptured further substantiate the homing abilities of the insular voles.

Terrestrial homing movements of this magnitude have been reported for *M. pennsylvanicus* by Robinson and Falls (1965), but to my knowledge there is no previous record indicating that small terrestrial rodents have the ability to home across open water.

Several authors have noted *M. pennsylvanicus* swimming (Bailey, 1924; Baker, 1951; Blair, 1939; Clough, 1965; Connor, 1966; Edwards, 1963; Getz, 1967; Harris, 1953; Peterson, 1947; Smyth, 1948), yet this species, along with most other small rodents, is rarely credited with the ability to swim to isolated islands. Instead it is generally held that small mammals have colonized islands by crossing ice bridges, or by being passively transported by rafts or man (Banfield, 1961; Beer *et al.*, 1954; Cameron, 1958, 1962; Corbet, 1964; Fall *et al.*, 1968; Foster, 1965; Hatt *et al.*, 1948; Jackson, 1920; Manville, 1949, 1951; McCabe and Cowan, 1945; Ozoga and Phillips, 1964; Werner, 1956; Wheeler, 1956). While discussing the colonization of islands in the Gulf of St. Lawrence by mammals, Denman (1965) went as far as saying, "A few inches depth of water a few feet wide would be an almost insurmountable barrier

to most small mammals, particularly as they would have no knowledge of their danger."

All of the rapid inter-island movements noted during the summers of 1967 and 1968 strongly suggested that the voles were not passively rafted about on floating debris, but, rather, that they actively swam from island to island. However, I never saw a vole swimming among the islands nor had any of the local fishermen with whom I discussed the matter. For this reason I conducted swimming tests on *Microtus* during the late summer and fall of 1968. A total of eight tests was conducted on three occasions under different environmental conditions. The environmental conditions and the results of the tests are presented in Table XIX (p. 151).

In seven of the eight trials the voles oriented to the object which subtended the greatest angle above the horizon (Fig. 65, p. 147). The smallest object to which a vole oriented subtended an angle of $2^{\circ}35'$ (trial 3). Four voles (trials 1, 3, 4 and 5) initially oriented to the boat despite the disturbance created by persons in it; the boat subtended an angle of approximately 38° in all tests. Sheppe (1965c) also noted that *Peromyscus leucopus* which had been released from a boat often swam back to it. In my study, trial 8 especially demonstrated that the voles were orienting to the tallest silhouette on the horizon. At 6:12 pm the vole was released 156 m from the nearest island; this island subtended an angle of $5^{\circ}20'$ to the southeast of the release site. At this time the setting sun looked as if it were perched on top of a hill 530 m to the southwest of the release site; this hill subtended an angle of only 4° , but the sun on top of the hill subtended an angle of 8° . The vole swam hesitantly toward the setting

sun for 32 minutes; he drowned shortly after the sun set below the horizon.

Sheppe (1965c) found that swimming *Peromyscus* oriented to the shoreline. Likewise, Aho and Kalela (1966) and Myllymaki *et al.* (1962) determined that *Lemmus lemmus* oriented to dark silhouettes on the shore.

In my study it appeared that wave action of 8 cm or more in height adversely affected the voles' orienting abilities (trials 1 and 5). Female 4150 swam for the most prominent land due north, but the waves created by the wind from the northeast blew her off course. Female 1241 swam in circles near the release site, apparently unable to orient in the 10-cm high waves. Relatively strong surface currents likewise adversely affected the navigational abilities of the voles (trials 1 and 3), but weak surface currents apparently had little affect upon them (trials 4, 6, 7 and 8). Fog and overcast skies did not affect the voles' abilities to orient (trials 1 and 4).

Sheppe (1965c) mentioned that fish (*Micropterus salmoides*, *Esox lucius* and *Lepomis*), water snakes (*Natrix sipedon*), turtles (*Chelydra serpentina*) and gulls were potential predators of swimming *Peromyscus*. I often saw terns (*Sterna*) and gulls (*Larus*) diving for fish on the surface of the sea when they were within 50 m of the boat. During several swimming tests I observed one gull and several terns flying over the voles. The gull glanced down at the test vole but did not attack. Only one tern paid any attention to the test vole; it dived within 6 m of the vole and then flew off. Cunnners (*Tautogolabrus*) often attacked small wounded animals that accidentally entered the subtidal or intertidal zones; however, to my surprise, they did not attack the swimming voles.

The voles were never observed to dive below the surface. Two of the voles which swam for five and seven minutes got only the fur on their

legs and a few hairs on their abdomens wet (trials 6 and 7). The fur was completely saturated ventral to the mid-lateral lines on the two voles which drowned (trials 1 and 8). Only one vole was wet on the dorsum as well as the venter. I accidentally submerged this vole at the onset of the trial (trial 3). Nonetheless, he managed to swim for 16 minutes against a current.

The voles kept their tails in the water and undulated them sideways in a sculling-like fashion. When they began to drown, the last few centimetres of the tail were turned up out of the water perpendicular to the body axis.

Average swimming speeds of 29.5 to 45.2 cm/sec. were recorded across distances of 45 to 111 m (trials 2, 3, 6 and 7). Female 4130 (trial 7) was clocked at a speed of 60 cm/sec. for a distance of 12 m.

Getz (1967) reported maximum swimming times of only 1.43 to 4.61 minutes for *M. pennsylvanicus* placed in an aquarium with 15°C water. Clough (1965) recorded survival times ranging from 221 to 727 seconds (3.68 to 12.10 minutes) for wild-caught *M. pennsylvanicus* in glass battery jars with water at 9.5°C. Perhaps Getz's and Clough's voles survived for shorter periods than did my voles (Table XIX) because their animals were subjected to highly unnatural conditions and were given no opportunity to swim toward a goal. Sheppe (1965c) noted that *Peromyscus* will not begin to swim if there is no land in sight. There is also the possibility that my voles swam for longer periods because they were larger. Getz (1967), Starrett and Fisler (1970) and Wilber (1958) have found that there is a direct relationship between body size and swimming ability in rodents. It is also possible that natural selection has equipped the insular voles with greater swimming abilities than their

mainland relatives. The Notre Dame Bay voles apparently are as adept at swimming as are *Peromyscus leucopus* (Sheppe, 1965c) and *Lemmus lemmus* (Myllymaki *et al.*, 1962).

From my tests it is apparent that, given the proper weather conditions, meadow voles were capable of colonizing most of the islands in the study area by swimming. It appears that water crossings could be made at any time of day or night as long as the sea was relatively calm. A prolonged period of dead calm weather, such as occurred in the summer 1967, was probably a time of maximum island colonization.

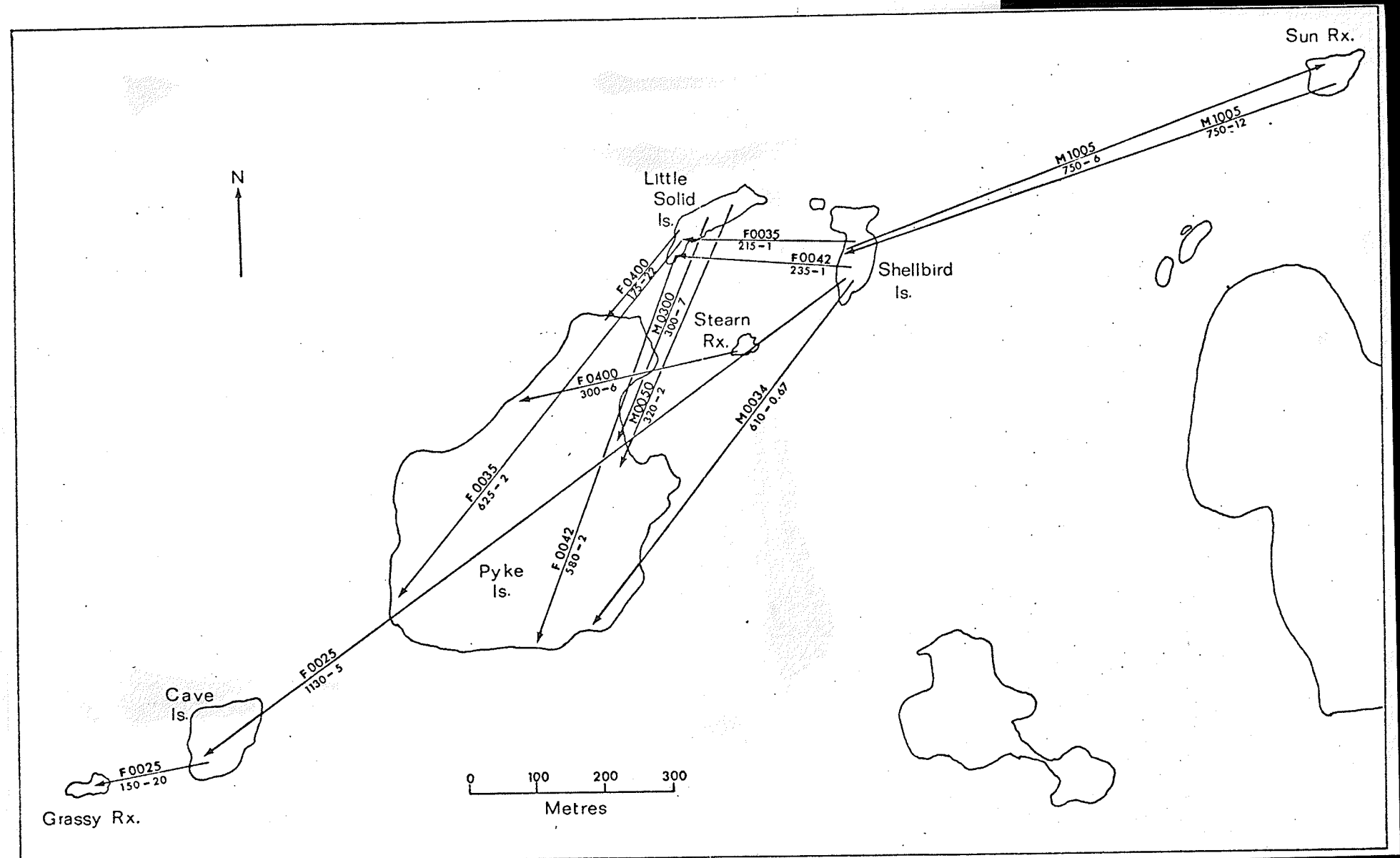


Fig. 62. Thirteen inter-island movements recorded for marked *Microtus* in summer 1967 among seven islands [Grassy Rock (No. 37), Cave (No. 38), Pyke (No. 39), Stearn Rock (No. 40), Little Solid (No. 41), Shellbird (No. 42) and Sun Rock (No. 43)]. Each arrow represents one movement and extends from the last capture site on an island to the first capture site on another island. Sex (M = male and F = female) and vole identification number are given above the lines; map distances in metres and numbers of days between captures are given below the lines.

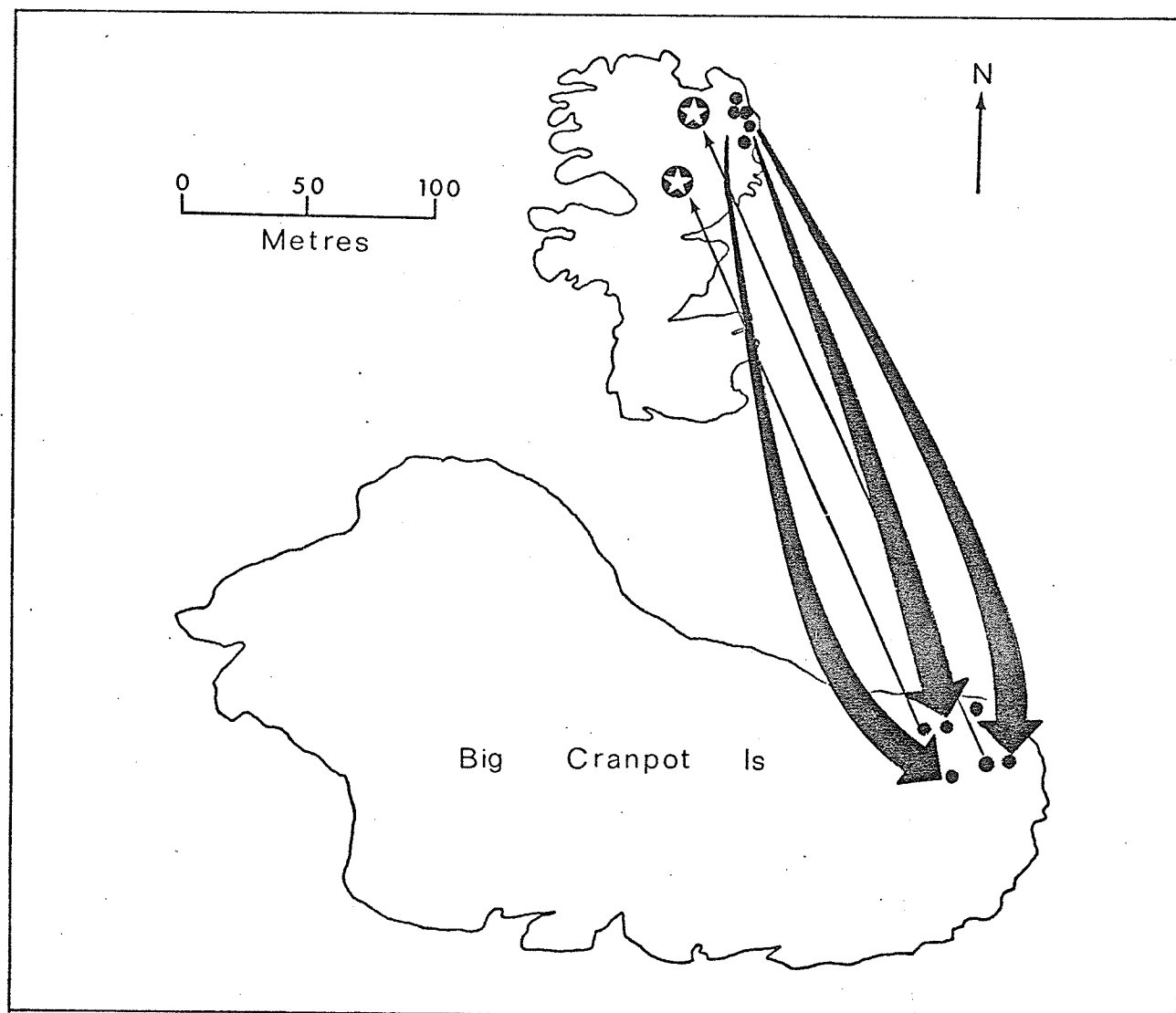


Fig. 63. Three inter-island movements recorded for male *Microtus* 2000 between Little Cranpot Island (No. 16) and Big Cranpot Island (No. 15) during the period 7 June to 3 July 1967. Wide arrows represent movements made by the vole from the last capture site on Little Cranpot Island to the first capture site on Big Cranpot Island. Thin arrows represent transportations of the vole from Big Cranpot Island to Little Cranpot Island. Stars indicate sites on Little Cranpot Island where the vole was released. Dark circles indicate capture sites.

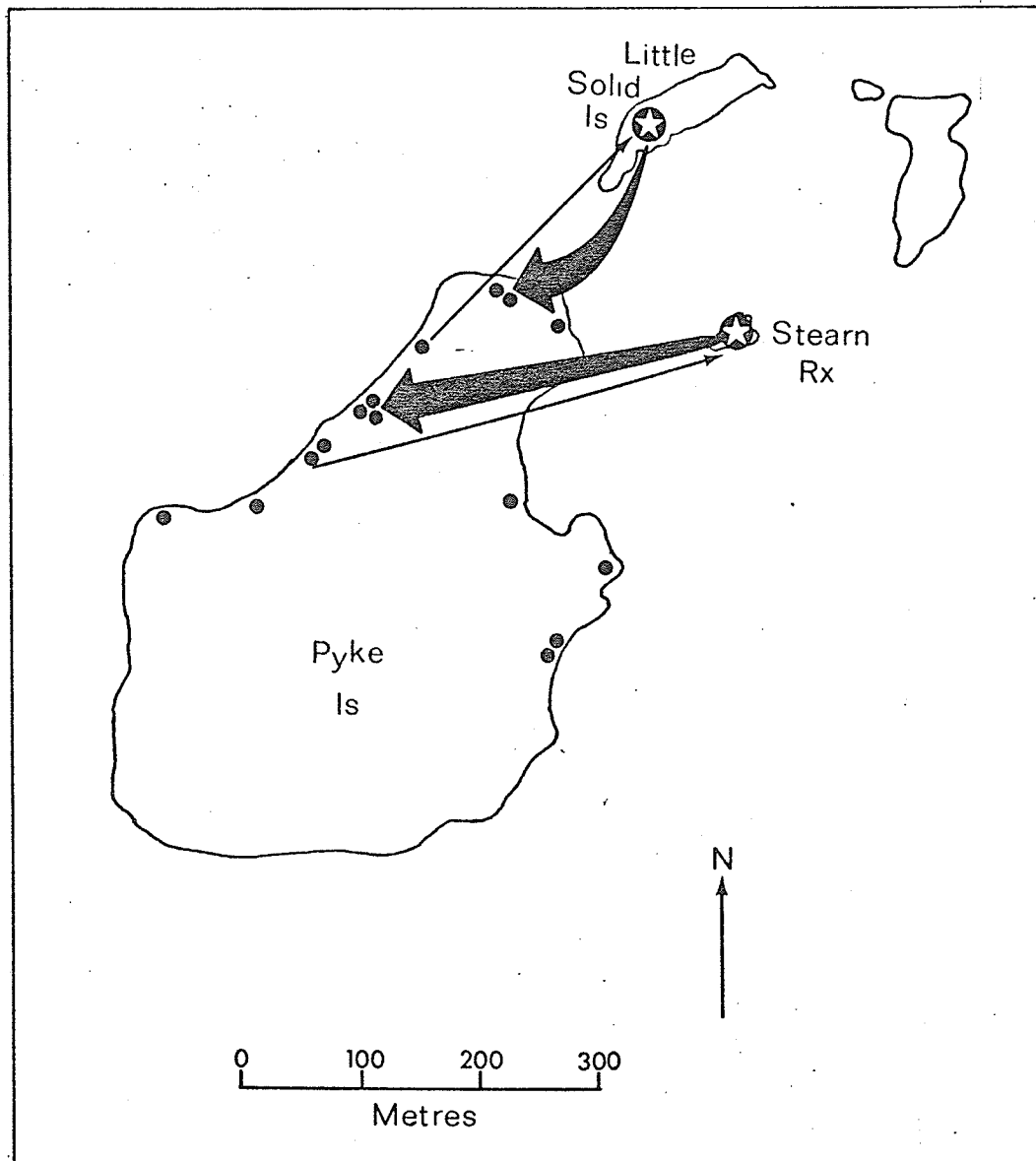


Fig. 64. Two inter-island homing movements recorded for female *Microtus* 0400 during the period 25 June to 28 August 1967. Thin arrows represent transportations of the vole from Pyke Island (No. 39) to two small neighboring islands [Stearn Rock (No. 40) and Little Solid (No. 41)]. Wide arrows represent movements made by the vole from a release site to the first capture site on Pyke Island. Stars indicate release sites on the small islands. Dark circles indicate capture sites.

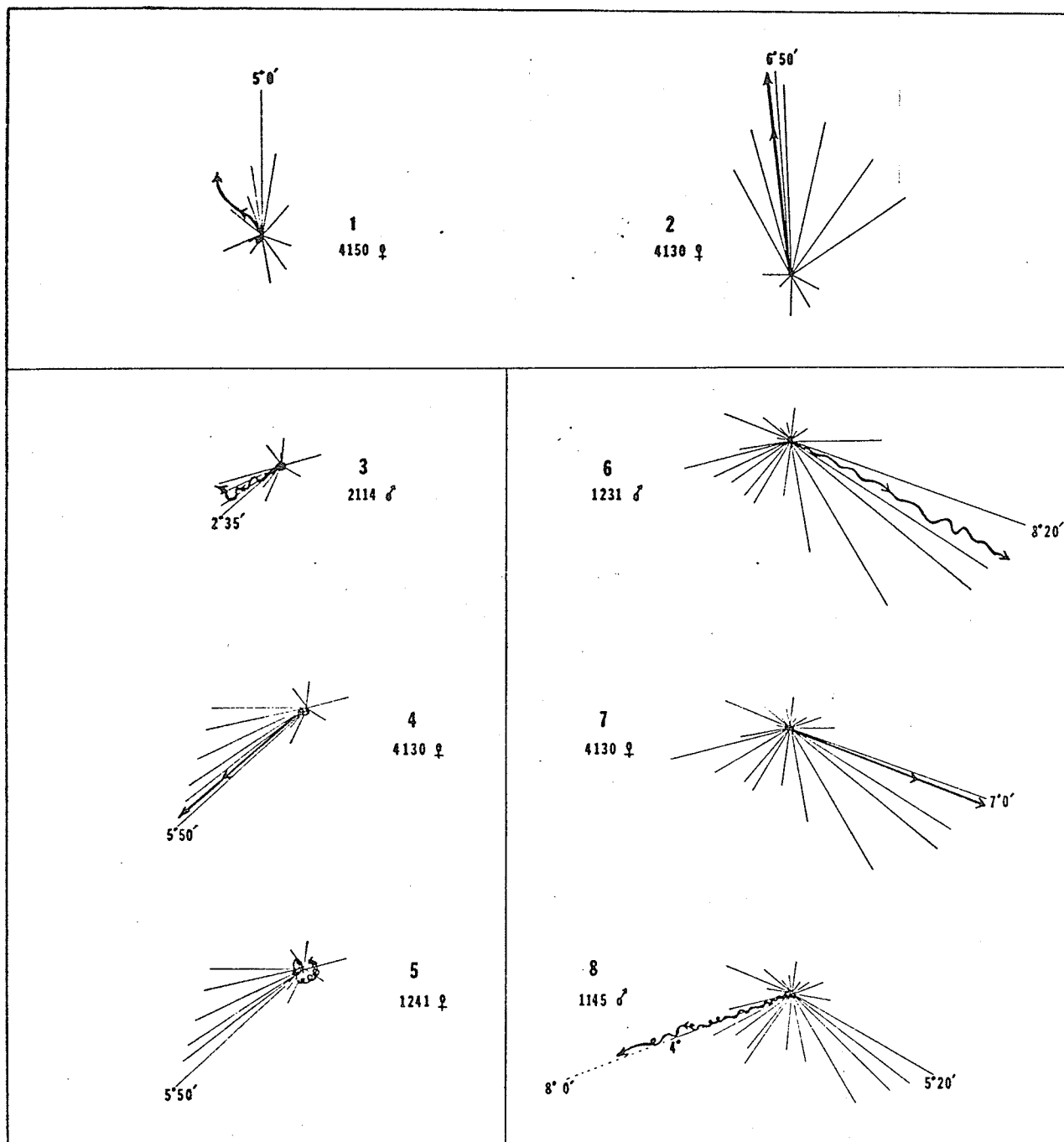


Fig. 65. Schematic representation of eight swimming trials conducted on *Microtus* in Notre Dame Bay. Centre of each sunburst represents a release site. Each line extending out from the release site represents an angle subtended by an object on the horizon: the longer the line, the higher the object appeared on the horizon from the release site. Greatest angle subtended by an object on the horizon is given in degrees and minutes for each trial. Arrow extending out from each release site represents the path taken by the released vole.

TABLE XVIII

Occurrence of *Microtus* on the islands in Notre Dame Bay

Island number	Census technique*	Annual record ^s			
		1966	1967	1968	1969
1	fo				+
2	r				+
3	r				+
4	r				+
5	r				+
6	fo		+		
7	fo			0	
8	r, mr, fo	+	+	+	+
9	fo		0		
10	fo		+		
11	fo		0		
12	mr, fo			+	+
13	fo		0		
14	r, fo, il	+	†	0	
15	mr		+	0	
16	r, mr, fo	+	+	0	
17	fo			0	
18	fo			0	
19	r, mr, fo	+	+	+	0
20	r			0	
21	r			0	
22	fo			0	
23	r			†	
24	r			0	
25	fo			†	
26	fo			0	
27	r			0?	
28	fo			0	
29	fo			†	
30	fo			†	
31	fo			†	
32	r, fo	+	0?		
33	r			0	
34	r			†	
35	fo			0	
36	r, fo	+	0	0	0
37	r, mr	+	+	+	0
38	mr		+		
39	r, mr, fo	+	+	0	0?
40	r, mr		0		
41	r, mr, fo	+	+	0	0
42	r, mr, fo	+	+	+	0
43	r, mr, fo	+	0	+	0
44	r, fo	0	0		

TABLE XVIII (continued)

Island number	Census technique *	Annual record ^s			
		1966	1967	1968	1969
45	fo			0	
46	fo		†?		
47	fo	†			
48	fo	†			
49	fo		†		
50	mr		0		
51	r			0	
52	r, mr		0	0	
53	r			0	
54	r, mr	+	+		
55	r		0		
56	r		†		
57	fo		†		
58	r		0		
59	fo		0		
60	fo		0		
61	fo		†		
62	r	+	†	0	
63	fo		†		
64	fo	0			
65	r, fo			+	
66	r, fo			0	
67	r, fo			+	
68	r			+	
69	r, fo			+	
70	r, fo			+	
71	r, fo			+	
72	r, fo			+	
73	r			+	
74	fo			†	
75	r			+	
76	fo				0
77	r			+	0
78	r, il			+	†
79	fo, il			+	0?
80	r				+
81	r, mr			+	+
82	r, mr, fo			+	+
83	fo			0	
84	r, fo			+	+
85	r, fo			+	+
86	r, fo			+	+
87	r				†

TABLE XVIII (continued)

Island number	Census technique [*]	Annual record [§]			
		1966	1967	1968	1969
88	r				+
89	r, fo, il			+	
<hr/>					
No. of islands investigated:		17	34	56	26
No. of islands with voles:		13	12	24	14
No. of islands with old sign:		2	8	7	2
Percent of islands with voles:		76.5	35.3	42.8	53.5
Percent of islands with population recently extirpated:		11.8	23.5	12.5	7.7

* Census technique: r = removal trapping; mr = mark-recapture trapping
fo = field observation; il = information from local residents.

§ Annual record: + = voles present (islands to which voles were
artificially introduced are not included); 0 = voles absent; † = old sign,
but voles no longer present (islands from which vole populations were
extirpated by trapping are not included); ? = entire island not explored.

TABLE XIX

Swimming tests conducted on *Microtus* in the study area

Trial number	Vole number and sex	Starting time and date	Weather conditions	Sea conditions	Distance from nearest island (m)	Time in sea (min.)	Swimming speeds (cm/sec.)	Comments
1	4150 +	17-viii-68 6:25 pm	Overcast skies; NE wind \approx 310 cm/sec.; air temp. 14°C	Waves 5-8 cm high; current relatively strong flowing SW; surface water temp. 11°C	152	11		Swam around boat, then against current for 120 m, circling and zigzagging. Retrieved from water when she began to drown.
2	4130 +	17-viii-68 6:42 pm	Overcast skies; NE wind \approx 310 cm/sec. but release site sheltered by island; air temp. 14°C	Sea calm; no current; surface water temp. 11°C	76	3.5	$\bar{X}=44.7$	Swam directly to nearest headland.
3	2114 o→	28-viii-68 4:57 pm	Heavy fog and hard rain; calm; air temp. 16.5°C	Sea calm; current rela- tively strong flowing W; surface water temp. 12°C	90	16		Swam around boat for 2 min., then headed for rock but could not land due to sweeping current alongside island.
4	4130 +	28-viii-68 6:02 pm	Fog; NW wind \approx 135 cm/sec.; air temp. 5.5°C	Sea calm; current weak flowing ESE; surface water temp. 12°C	45	4	$\bar{X}=45.2$	Swam to boat and then directly to island.
5	1241 +	28-viii-68 6:12 pm	Fog lifting; NW wind \approx 225 cm/sec.; air temp. 5.5°C	Waves \approx 10 cm high; current weak flowing ESE; surface water temp. 12°C	47	8		Swam in circles near boat. Removed from sea after 8 min.--vole in good physical condition.
6	1231 o→	4-x-68 5:53 pm	Clear skies; calm; air temp. 19°C	Sea calm; current weak flowing S; surface water temp. 12°C	78	5	$\bar{X}=29.5$	Swam immediately away from boat toward island in zigzag course.
7	4130 +	4-x-68 6:03 pm	Clear skies; calm; air temp. 19°C	Sea calm; current weak flowing S; surface water temp. 12°C	111	7	$\bar{X}=31.3$, Exact=60.0	Swam immediately away from boat toward island in straight course.
8	1145 o→	4-x-68 6:12 pm	Clear skies; calm; air temp. 13°C	Sea calm; current weak flowing NE; surface water temp. 11°C	156	32		Swam toward setting sun. Drowned shortly after sun set below horizon.

Age Determination and Longevity

During my field study I found no evidence of winter breeding in *Microtus*. Between September 1968 and August 1969 all young were born within a ten-week period extending from the first week of May until the third week of July (see section on Reproduction, pp. 164-171). Based on this information I constructed the age classification presented in Table XX (p. 163).

The age classification consists of three basic groups: young of the year or juveniles (class I), animals born in the previous breeding season (class II) and animals born during the breeding season two years prior to trapping (class III). Classes I and II were subdivided according to the age of the voles and the time of year. Juveniles less than six months of age present in the population between May and October were assigned to class Ia. Voles from 4 to 11 months of age overwintering (November to April) for the first time were placed in class Ib. Animals 9 to 18 months of age which had overwintered once and were captured between May and October were placed in class IIa. Voles 16 to 23 months of age overwintering for the second time were included in class IIb.

Moult pattern (Appendix D, pp. 195-197) and femur length were the primary criteria used to distinguish the various age classes; pelvis length, sacrum width, body weight, skull angularity (Gebczynska, 1964) and the development of certain skull crests and processes (Snyder, 1954) were also taken into consideration and used as checks.

Several investigators have found that moult patterns are useful in determining the age of microtines (Ecke and Kinney, 1956; Hamilton, 1938; Kellogg, 1946; Koponen, 1970; Shanks, 1948). For voles captured between May and October I used moult pattern to distinguish members of class Ia

from members of classes IIa and III. By November all young voles had passed through the juvenal and post-juvenal moults; therefore, moult pattern could not be used to distinguish between overwintering individuals (classes Ib and IIb).

When working with Alaskan microtines Pruitt (1966) found that ratios which included femur length as one term were particularly useful in segregating age groups. I found femur length to be a reliable aging criterion throughout the year and therefore utilized it to distinguish between overwintering voles (classes Ib and IIb) as well as between overwintered voles (classes IIa and III). Fig. 66 (p. 158) is a diagrammatic representation of femur growth based on 371 specimens collected between September 1968 and August 1969. When the young (class Ia) left the nests their femora were about 8 mm long. From May through August the femora of members of class Ia grew rapidly until they reached a length of approximately 15.5 to 17.5 mm. Growth ceased in the fall, and the femora remained at this size from October through February (class Ib). At the beginning of the breeding season the femora rapidly increased to the adult size of approximately 18 to 20 mm (class IIa); they remained at this size throughout the following summer and fall. The femora of the few animals which survived into their third summer increased to a maximum of about 21 mm.

Pelvis length proved to be almost as useful as femur length in segregating the specimens into age classes. In Table XX there is some overlap in pelvis length between classes Ia and IIa; this was caused by a few juveniles which bred in their first summer (see section on Reproduction, pp. 165-166). There was, however, no overlap of pelvis length between classes Ib and IIb or between IIa and III.

As described by Guilday (1951) and Dunmire (1955), the shape of the innominate can be used to segregate sexually mature males from sexually mature females. In addition, I found that it was possible to separate, by the development of the innominate bone, those individuals which had never bred from those which had bred at least once (Fig. 67, p. 159). It was also possible to distinguish primiparous females from multiparous females during the first half of their pregnancies. For the first half of pregnancy the innominate bones of primiparous juveniles were similar in shape to those of nonparous juveniles (Fig. 67d). During the second half of pregnancy the pubic and ischial arms of the innominate bones elongated and took on the appearance of adult parous innominate bones (Fig. 67c). At this time the pubic symphysis opened up to a width of 2 to 7 mm and permanently remained in this condition after parturition.

Sacrum width was likewise helpful in dividing sexually mature from sexually immature voles. The sacra of sexually immature voles were less than 6 mm in width whereas those of voles which were sexually active were greater than 6 mm. In the spring when the overwintered juveniles (class Ib) were becoming sexually active (males: enlarged abdominal testes; females: perforate vaginae but not noticeably pregnant), the sacra widths were 5.5 mm or greater.

Body weight has been utilized by many investigators as the major criterion for aging small mammals (Chitty, 1952; Hamilton, 1937b; Hoffmann, 1958; Krebs, 1964b, 1966; Lecyk, 1962; Negus *et al.*, 1961). I found, however, that body weight was a poor criterion to use to age voles over 35 gm (Fig. 68, p. 160). During the spring and summer most of the members of classes Ia and IIa could be distinguished from one another by body weight alone. During the winter, however, the

body weights of classes Ib and IIb overlapped considerably, making it difficult to age certain individuals. Likewise, it was virtually impossible to separate class IIa from class III by body weight due to the complete overlap in these classes. Whitmoyer (1956) also stressed the lack of reliability in age estimates of *M. pennsylvanicus* based only on body weights.

In Notre Dame Bay the voles gained and lost weight during various seasons as follows (Fig. 68). Body weight increased rapidly from birth until autumn when growth ceased. During the first winter body weight decreased as much as 10 gm. In the following spring there was a rapid increase in weight, but, after the reproductive season, body weight decreased to a winter low. Individuals which survived through their second winter (class III) likewise displayed this fluctuation in body weight during the following spring, summer and fall seasons. This seasonal fluctuation in body weight has been noted for several microtines (Barbehenn, 1955; Chitty, 1952; Fuller, 1969; Pokrovski and Bolshakov, 1969).

I included both Snyder's and Gebczynska's age classifications in Table XX to allow persons using these classifications to relate their material to my collection. I found, however, that both aging methods were of limited value in my study. Snyder's classification, based on development of the lamboidal crest, mastoid-exoccipital crest and paroccipital process, is too subjective. Even after examining my entire series of 470 specimens I did not feel confident in the placing of them into Snyder's nine classes. Gebczynska's age classification, based on angularity of the skull, is more refined than my classification for aging juvenile voles. However, her classification lumps the older

animals into a single age class, thereby masking the actual age structure of the population.

Members of my age class III were not common and could have been easily overlooked when a small sample was taken. The following live-trapping records further substantiate the existence of the old age class. In September 1968 I live trapped one male and four females which, from all external signs (body weights over 45 gm, vaginae closed or testes adult size, scars on bodies), had overwintered and had bred in the past breeding season and thus belonged to age class IIa. These voles were captured from 5 to 20 times (average 12.7) during the following year. The male was last captured on 7 May 1969; the females were all snap trapped during August 1969.

I plotted the relative abundance of the five age classes in the Notre Dame Bay vole population for the period of September 1968 through August 1969 in Fig. 69 (p. 161). Using the data from this figure, I schematically represented the cohorts as they might have existed in the population over a period of 30 months (Fig. 70, p. 162). In Fig. 69 age class IIb was probably underestimated in December and January due to the small samples which I examined. For this reason I smoothed the curves in Fig. 70 in order to give a more realistic picture of the population structure.

The life span of most microtines is usually recorded as being less than one year (Fisher, 1945; Gebczynska, 1964; Hamilton, 1937b; Jackson, 1961; Leslie and Ranson, 1940; Manning, 1956; Martin, 1956; Miller and Getz, 1969; Schwarz *et al.*, 1964; Wasilewski, 1956 as cited in Gebczynska, 1964), but occasionally voles are noted to live more than three years (Gebczynska, 1964). Blair (1948) calculated that the average

life span of the meadow vole was 4.23 ± 0.22 months while Beer and MacLeod (1961) found that relatively few *M. pennsylvanicus* reached an age of more than two or three months. Getz (1960) reported that *M. pennsylvanicus* had an average life span of only 0.7 months.

Hamilton (1937b) listed three factors which appeared to be responsible for the short life span of *Microtus*: attainment of sexual maturity at an uncommonly early age, extreme prolificness and little cessation of activity in search of food. From my data it is apparent that many of the voles in Notre Dame Bay lived beyond the age of one year. This increase in longevity seemed to be related to a delay in sexual maturity and to a reduction in prolificness (see section on Reproduction, pp. 165-166).

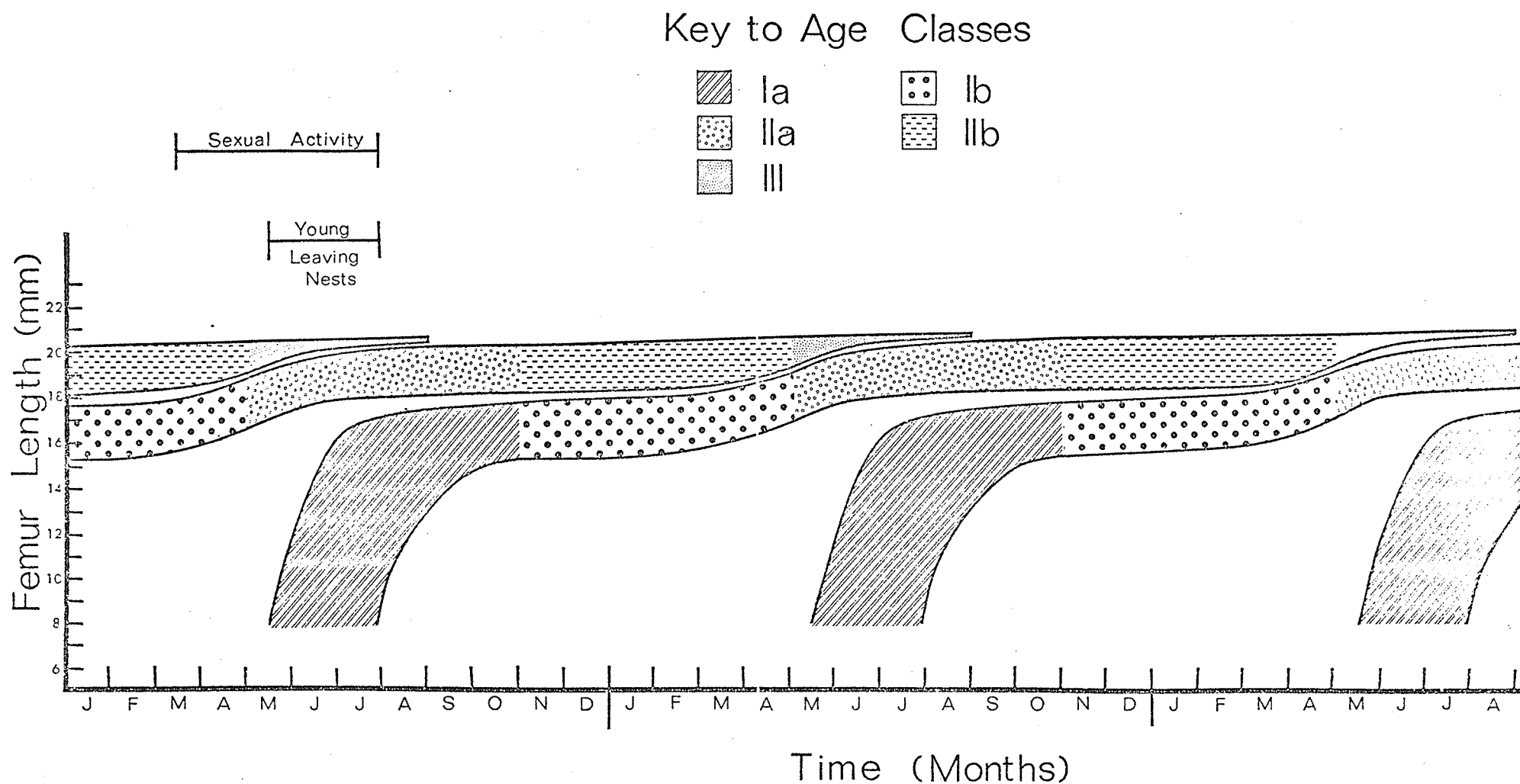


Fig. 66. Diagrammatic representation of femur growth in cohorts of *Microtus* over a theoretical 32-month period. Each cohort is broken into the five age classes presented in Table XX (p. 163). Femur data were collected from 371 specimens taken between September 1968 and August 1969 in Notre Dame Bay.

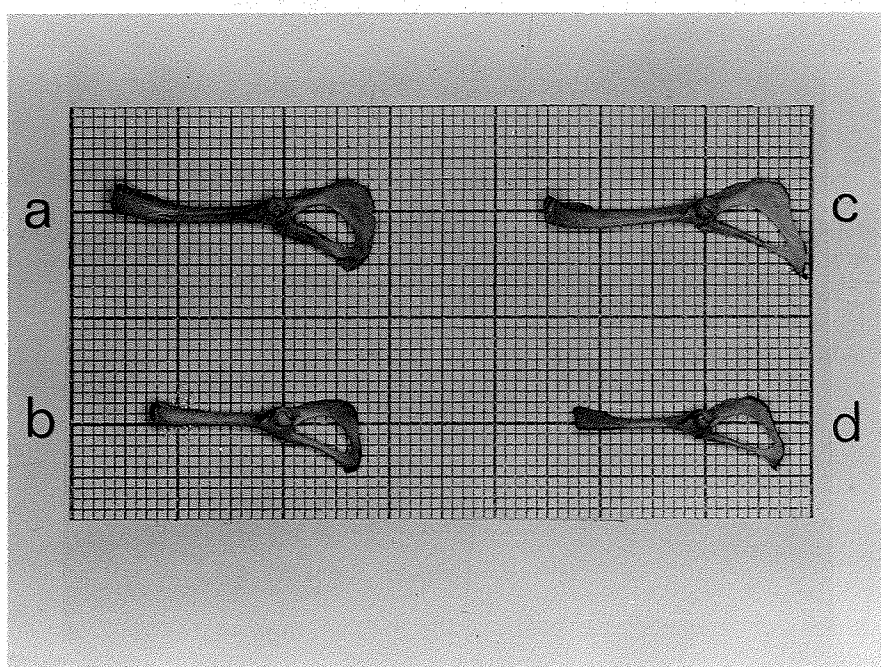


Fig. 67. Innominate bones of male and female *Microtus pennsylvanicus*.
(a) Adult male, specimen no. RRR 393. (b) Juvenile male, specimen no. RRR 443. (c) Adult female (multiparous), specimen no. RRR 334. (d) Juvenile female (nonparous), specimen no. RRR 495. Scale in millimetres.

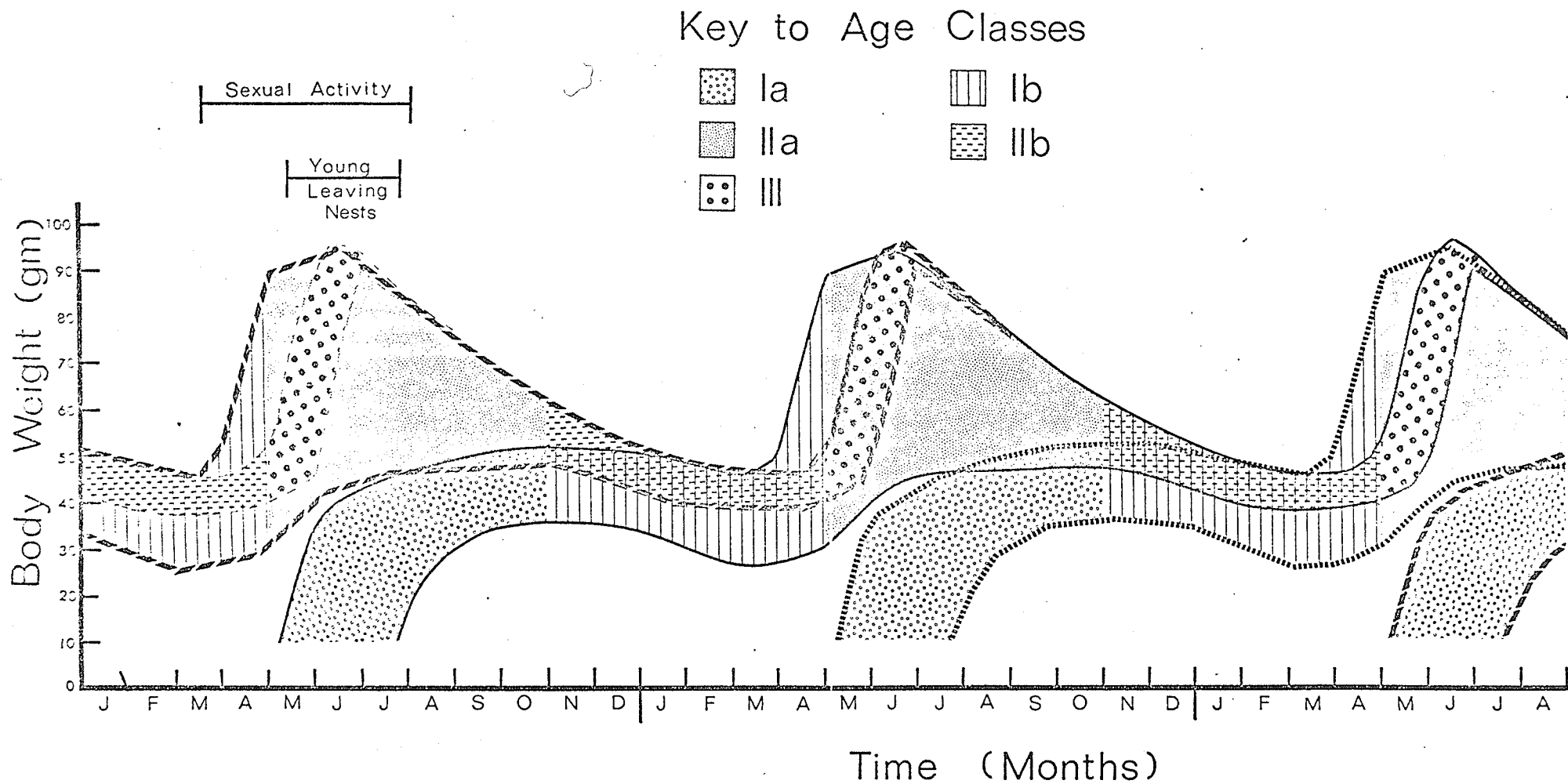


Fig. 68. Diagrammatic representation of body weight fluctuations in cohorts of *Microtus* over a theoretical 32-month period. Each cohort is broken into the five age classes presented in Table XX (p. 163). Body weight data were obtained from 458 snap-trapped specimens and 397 records of live-trapped voles captured between September 1968 and August 1969 in Notre Dame Bay.

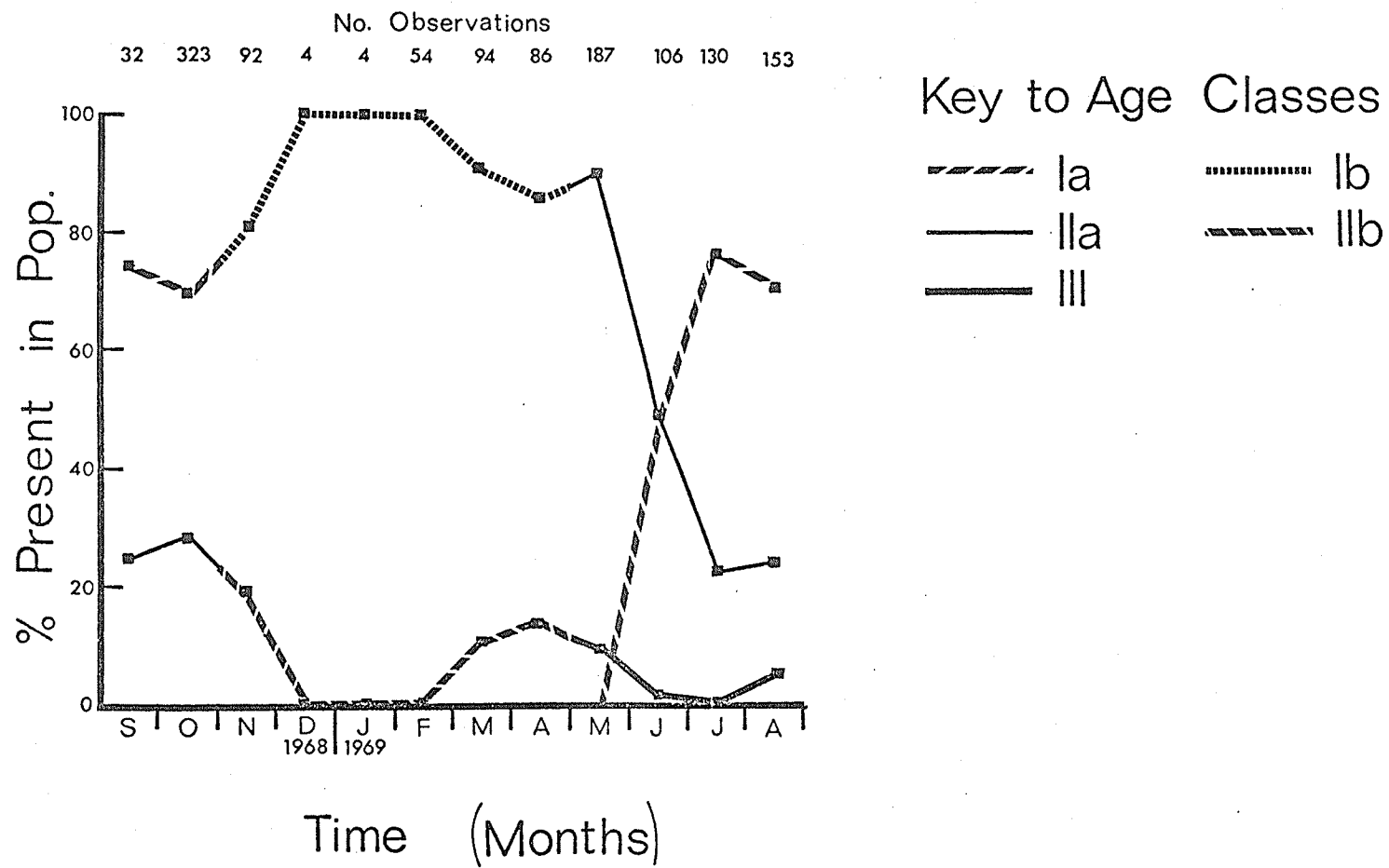


Fig. 69. Percent of each age class present in the Notre Dame Bay *Microtus* population for the period September 1968 through August 1969. These data were obtained from 470 snap-trapped voles and 795 observations on live-trapped voles.

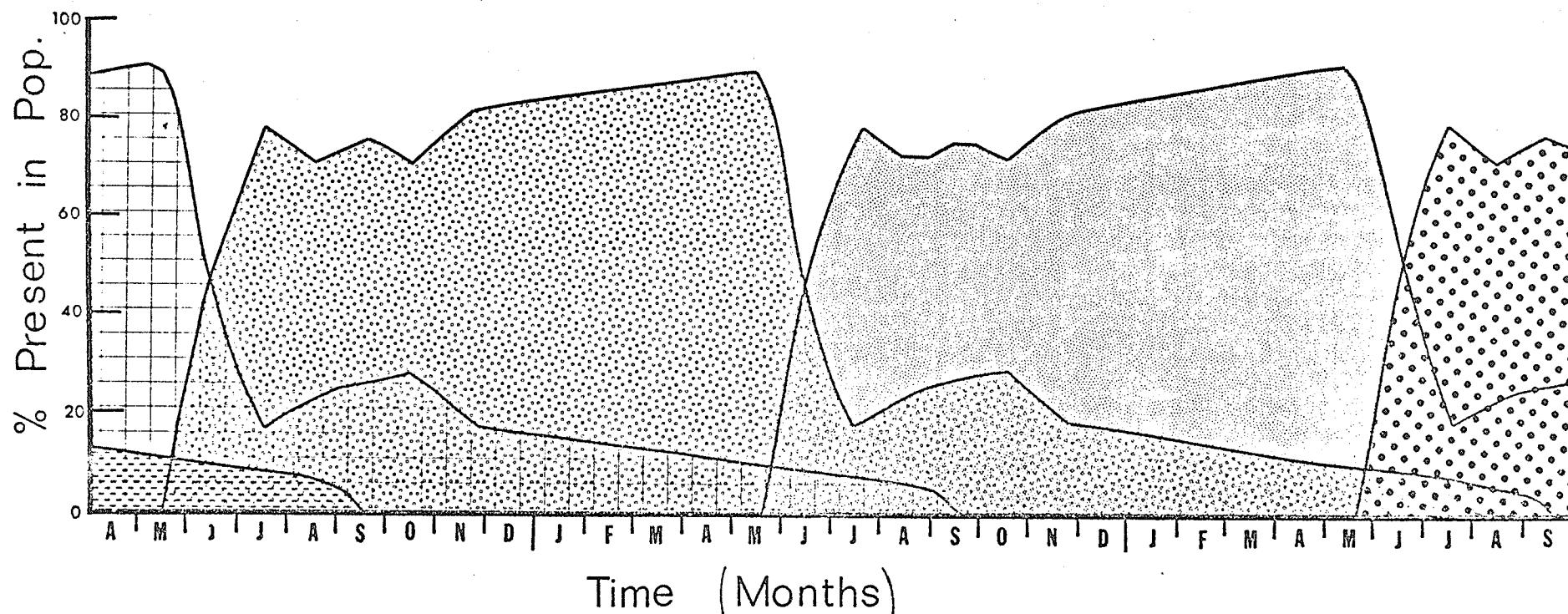


Fig. 70. Diagrammatic representation of *Microtus* cohorts during a theoretical 30-month period. Each cohort is represented by a type of shading. Data were taken from Fig. 63 but were modified for the months of December, January, February, June and July to give a more realistic picture of the population structure. Cohorts were not divided into age classes.

TABLE XX

Age classes of *Microtus* based on 470 specimens
captured between September 1968 and August 1969

Age class	Name	Season	Age (months)	Moult pattern	Femur length (mm)	Pelvis length (mm)	Sacrum width (mm)	Body weight (gm)	Snyder's age classification	Gebczynska's age classification
Ia	Juvenile	May-Oct.	<6	Regular or prime	7.6-17.7	9.8-20.9	2.9-6.2	10-50	4-9	I, II, III
Ib	Overwintering juvenile	Nov.-Ap.	4-11	Irregular or prime	15.1-18.0	18.5-21.9	4.6-6.4	25-50	7-9	III
IIa	Adult	May-Oct.	9-18	Irregular or prime	16.0-20.5	19.3-25.1	4.8-7.5	29-90	10-12	IV
IIb	Overwintering adult	Nov.-Ap.	16-23	Irregular or prime	18.0-20.5	23.1-25.4	6.3-8.2	38-62	11-12	IV
III	Old age	May-Aug.	21-27	Irregular or prime	21.0-21.2	25.4-26.4	7.6-8.2	38-95	12	IV

Reproduction

During this study I used the presence of scrotal testes as the criterion delimiting the period of male sexual activity for both live-trapped and snap-trapped male voles. Because scrotal testes do not always produce sperm (Beer and MacLeod, 1961), this period encompasses the seasons of sexual maturation and sexual regression as well as the season of fecundity.

I considered snap-trapped females to be sexually active if they had recently copulated (mucus plug present in vagina), were visibly pregnant (embryos and/or swollen uterus present), were postpartum (flaccid uterus and large placental scars present) or were lactating. Live-trapped females were considered sexually active if they had recently copulated, were obviously pregnant (determined by palpating the abdomen) or were lactating.

Sexual activity was confined to the spring and summer seasons and to a limited extent to early autumn; I found no evidence of winter breeding.

Between 27-30 May 1966 Pruitt captured nine voles weighing from 11 to 12 gm. The presence of these young animals indicates that in 1966 the duration of pregnancies (period in which the population contained pregnant females: date of earliest conception to date of last parturition) had begun by at least 27 April. This date is based on the assumptions that *M. pennsylvanicus* has a gestation period of 21 days and that three or four days after birth a juvenile gains approximately one gramme per day until one month of age (Bailey, 1924; Hamilton, 1937b). Due to the limited trapping data for 1966 I have no information on the last parturition of the year.

In 1967 the duration of pregnancies extended from about the first

week in May to at least the first week in September. This information is based on live-trap records of newly weaned juveniles in the spring and obviously pregnant females in the autumn.

The period of sexual activity appeared to be shorter during 1968 than in 1967. The duration of pregnancies in 1968 extended from about 29 May to 18 August. These estimates are founded on captures of juveniles in the spring and on known parturition dates of females captured in August.

I have more data regarding the breeding season in 1969 than for the previous years due to the large number of snap-trapped specimens taken in that year (Fig. 71, p. 169). In 1969 all sexual activity was confined to the months of March to August. The production of young was restricted to a shorter period; from data on embryos and newly weaned juveniles I calculated that the duration of pregnancies extended from 15 April to 26 July.

Several authors have reported *M. pennsylvanicus* breeding throughout the year (Beer and MacLeod, 1961; Connor, 1960; Corthum, 1967; Linduska, 1950; Keller, 1968). Others have reported that breeding ceased during midwinter (Golley, 1961; Hamilton, 1941), and still others have noted that breeding was confined to the spring and fall (Getz, 1960; Gunderson, 1950). The length of the breeding season for *M. pennsylvanicus* seems to vary from area to area depending upon the local physical and biotic factors.

In Notre Dame Bay juveniles (age class Ia) formed only a small portion of the breeding population. Of 334 juveniles examined during the study only 16 (4.8%) were sexually active (Fig. 71).

The data from these 16 individuals suggested that juveniles became

sexually active more readily when the population levels were low than when they were high. During the breeding seasons of 1967 and 1968 I worked with relatively low vole populations; with 13,701 TN I captured 115 juveniles of which 9 (7.8%) were sexually active. In the 1969 breeding season I worked on islands which possessed higher vole populations. In 8090 TN I captured 219 juveniles of which only 7 (3.2%) were sexually active. The difference between the number of breeding juveniles in these two periods is statistically significant ($\chi^2 = 3.90$, $0.05 > P > 0.02$).

More juvenal females bred in their first summer than did juvenal males: 6.9% of the females bred versus 2.9% of the males (Table XXI, p. 170).

From my live-trapping records I estimated that the youngest sexually active males and females were between five and six weeks of age.

It is unusual to find that breeding juveniles are scarce in a population of *M. pennsylvanicus*. Many investigators (e.g., Bailey, 1924; Beer and MacLeod, 1961; Hamilton, 1941; Keller, 1968; Koplin, 1962) have noted that members of this species commonly breed as juveniles. Bailey stated that females in captivity may mate when only 25 days old and males may mate when only 45 days old.

In this study 525 voles were autopsied between 1966 and 1969, and, of these, only 29 were pregnant females. These females carried a total of 168 viable embryos, the number/female ranging from 1 to 9 with an average of 5.79 (Table XXII, p. 171). In 7 females there was a total of 11 resorbed embryos which is a resorption rate of 6.2%. My data are comparable to the figures reported for *M. pennsylvanicus* in other parts of its range: mean litter size from 3.0 to 6.3 with most

common mean about 5 (Bailey, 1924; Beer and MacLeod, 1961; Connor, 1966; Corthum, 1967; DeCoursey, 1957; Goin, 1943; Hamilton, 1941; Harris, 1953; Keller, 1968; Poiley, 1949; Storm and Sanderson, 1968; Townsend, 1935).

In 38 postpartum females I found 280 placental scars. The number of scars/female ranged from 3 to 15, with a mean of 7.34. These figures do not agree with the embryo counts because of the following complications:

1. Placental scars in *M. pennsylvanicus* are visible in the uterine horns for 45 to 49 days after parturition (Corthum, 1967). During the period in which the scars are disappearing, it is easy to miscount.
2. Placental scars in multiparous rodents often represent two successive litters (Tupikova, 1964).
3. Scars from different litters may fuse into one another (Tupikova, 1964).
4. After parturition it is difficult to distinguish between scars left by healthy fetuses and resorbed embryos (Tupikova, 1964).

I found that some females produced at least two litters during a single breeding season. The live-trapping records indicate that three females in 1967 and one in 1968 had given birth to two litters each. In 1969 I examined eight females which possessed from 10 to 15 placental scars. Since I never observed any female with this number of embryos (including resorbed embryos), the scars probably represented two consecutive litters; there is a slight possibility that the scars represented three litters.

In contrast to my findings, Bailey (1924) reported that one

M. pennsylvanicus kept in captivity produced 17 litters in a single year. Hamilton (1941) stated that female *Microtus* may produce eight to ten litters/year during a "mouse year" but no more than five or six litters in years of scarcity. Beer and MacLeod (1961), Storm and Sanderson (1968) and others have likewise found that meadow voles are capable of producing eight to ten litters/female/year.

The shortness of the breeding season, the scarcity of sexually mature juveniles and the small number of litters/female/year have resulted in a low reproductive rate for insular *Microtus* in Notre Dame Bay. This is in agreement with the findings of other researchers working with island populations of rodents. Jewell (1966) found that insular populations of both *Clethrionomys glareolus* and *Apodemus sylvaticus* had shorter breeding seasons and fewer young breeding in their first summer of life than do mainland populations. Berry (1968) likewise reported shorter breeding seasons for an island population of *Mus musculus*.

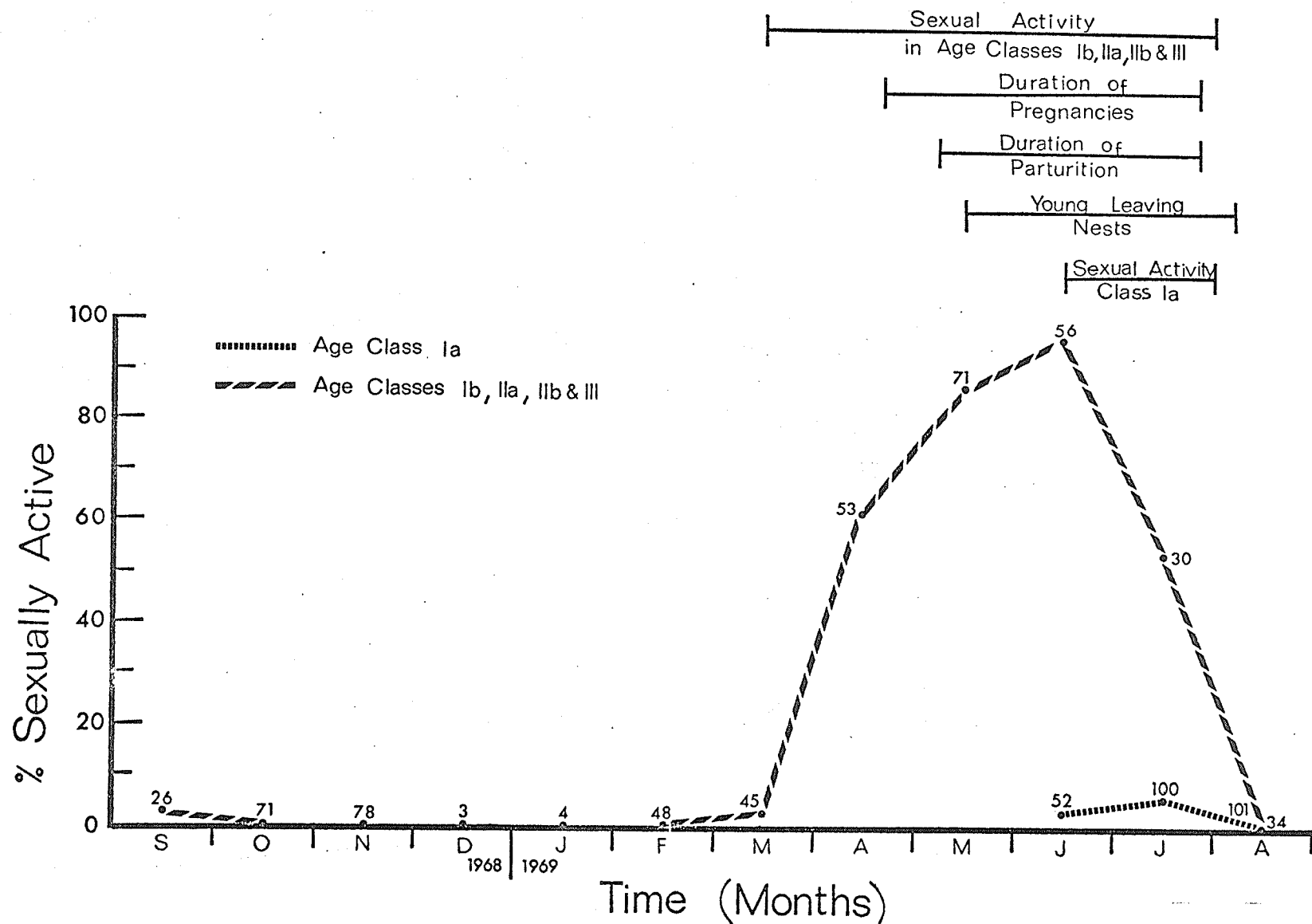


Fig. 71. Period of sexual activity in *Microtus* in Notre Dame Bay. The number of observations is given for each month. Information on sexual activity was gathered from 470 snap-trapped voles and 302 records of live-trapped voles captured between September 1968 and August 1969.

TABLE XXI

Participation in breeding by male and female juveniles (class Ia)
during the summers of 1967, 1968 and 1969

	Number captured	Number breeding	Percent breeding
Male juveniles	175	5	2.9
Female juveniles	159	11	6.9

$$\chi^2 = 2.84, 0.10 > P > 0.05$$

TABLE XXII

Embryo counts from *Microtus* captured in the study area

Date	Capture site (island no.)	Number viable embryos	Average crown-rump length (mm)	Number resorbed embryos
27-v-66	37	7	24.0	0
28-v-66	37	9	6.0	0
28-v-66	37	7	8.0	0
29-v-66	37	8	8.0	0
6-v-69	82	7	6.5	0
27-v-69	81	6	minute swellings	0
28-v-69	81	4	18.0	1
28-v-69	81	6	23.5	2
29-v-69	81	4	9.0	1
29-v-69	81	8	5.0	0
30-v-69	81	8	7.8	0
12-vi-69	88	7	25.3	1
12-vi-69	88	3	9.3	2
12-vi-69	88	4	3.8	0
13-vi-69	88	8	5.0	0
14-vi-69	88	3	28.7	0
14-vi-69	88	5	26.3	1
15-vi-69	88	1	10.6	3
16-vi-69	88	5	14.3	0
16-vi-69	88	7	27.0	0
17-vi-69	88	8	16.0	0
24-vi-69	80	7	11.5	0
25-vi-69	80	7	minute swellings	0
25-vi-69	80	5	<3.0	0
27-vi-69	82	5	5.0	0
4-vii-69	84	5	3.0	0
4-vii-69	84	3	5.1	0
4-vii-69	84	7	6.3	0
5-vii-69	84	5	8.0	0

 $\bar{X} = 5.79$

SD = 3.46

SE = 0.345

Parasites

To date, Dr. C. Hopla has examined the Siphonaptera material collected from the meadow voles in Notre Dame Bay. A total of 197 specimens were identified belonging to three species: *Megabothris asio* Baker, 1904, *Epitedia wenmanni* Rothschild, 1904 and *Atyphloceras bishopi* Jordan, 1933 (Table XXIII, p. 174).

According to Hopla (personal communication), *Megabothris asio asio* is typically the flea most closely associated with *Microtus pennsylvanicus* in the region that includes Newfoundland. Sixty-seven specimens of this flea were collected from 15 islands in Dildo Run, Friday Bay and Bay of Exploits.

Epitedia wenmanni is normally associated with the cricetid rodents *Peromyscus* and *Neotoma* further south, but in the more northerly regions of North America this flea has adapted to microtine rodents (Hopla, personal communication). The majority of the fleas in my collection, 98, belong to this species, but they were collected from only eight islands in Friday Bay and Dildo Run. Four specimens were also collected from two *Mustela erminea* on Black Island (No. 78). Hubbard (1947) suggested that adults of this species are taken most commonly in the winter months whereas Benton (1955) noted that this species was found mostly in the spring and fall with smaller numbers in winter and summer. My collection includes specimens taken from November through June.

Atyphloceras bishopi is an uncommon flea and is rarely taken in large numbers (Hopla, personal communication). Despite intensive collecting, Holland (1949) reported only three specimens taken from Canada. According to Holland and Benton (1968) this species is a winter flea; in their work in Pennsylvania all specimens were collected between

September and May and most of these were taken between November and March. I collected 28 specimens from four islands in Friday Bay during the months of November through April. Since I was working only in Friday Bay during this time it is quite probable that this species had a wider distribution in Notre Dame Bay than my data indicate.

Up to this time, Mr. F. Smith has examined the helminths from 37 *Microtus*. So far he has discovered two species of nematodes, *Trichuris opaca* Barker and Noyes, 1915 and *Protospirura muris* (Gmelin, 1790) Seurat, 1915 and two or possibly three species of cestodes, *Monoecocestus* sp. Beddard, 1914, *Paranoplocephala troeschi* Rausch, 1946 and perhaps *Paranoplocephala* sp. Luhe, 1910 (Table XXIV, p. 175).

Unfortunately, the blood slides have not yet been examined.

Wodzicki (1965) mentioned that one of the factors enhancing the success of the rabbit as a colonizing species in New Zealand is its reduced parasitic fauna. It would be interesting to determine if a reduction in the parasitic fauna of *M. p. terraenovae* has likewise been a factor responsible for its success as a colonizer.

TABLE XXIII

Siphonaptera collected from 112 *Microtus* in the study area

Collection site (island no.)	<i>Megabothris asio asio</i>		<i>Epitedia wenmanni</i>		<i>Atyphloceras bishopi</i>	
	♂	♀	♂	♀	♂	♀
2-5	1	2				
15	4	3				
16	5	3				
19	1	2				
39	1	7				
41		1				
42	4	4	3	2		
43	2	3				
54	1					
77			1	9	1	
80	1	3	11	15	4	5
81	1	3	2	4		
82	1	6	1	15		2
84	2	2	13	20	8	8
85		3				
88		1	1	1		
Total:	24	43	32	66	13	15
	67		98		28	

TABLE XXIV

Helminths collected from 37 *Microtus* in the study area

Collection site (island no.)	<i>Protospirura muris</i>	<i>Trichuris opaca</i>	<i>Monoecocestus sp.</i>	<i>Paranoplocephala troeschi</i>	<i>Paranoplocephala troeschi</i> or <i>P. sp.</i>
42		1			
43		1			
65		2			
77			1+	19	1
80	3	2	1+	1	1
82	9			1	
84	7	7	2+		4+
86					1
89		4			
Total:	19	17	4+	21	7+

Predation

In Notre Dame Bay there were only three predators which regularly fed upon *Microtus*: coloured fox (*Vulpes fulva*), short-tailed weasel (*Mustela erminea*) and rough-legged hawk (*Buteo lagopus*).

Fox sign was observed on Upper Black, Shag Cliff (No. 6), The Sugar Loaf (No. 7), Yellow Fox (No. 12), Glead (No. 14), Mile (No. 19), Coal All (No. 27), Chapel (No. 32), Inspector (No. 36), Grassy Rock (No. 37), Pyke (No. 39), Sun Rock (No. 43), Nos. 52 and 74, Gooseberry (No. 77), Black (No. 78), North and South Trump (Nos. 86 and 82) and New World (No. 89) islands. According to local residents there was a huge fox population in the region during the winter of 1966-67 when foxes were commonly seen scavenging about the villages and along the shorelines.

The fishermen reported that foxes wandered from island to island when the sea was frozen. If the winter was mild and the sea did not freeze, then the foxes were confined to those islands on which they had spent the previous summer. In August 1968 I noted fox sign in the meadows and bogs of North and South Trump islands. The following winter was mild, and, consequently, the foxes were restricted for the entire winter to North and South Trump islands which at low tide are separated by only a shallow channel ("tickle") approximately 1.5 m wide. When tracking snow fell, I was able to gain information on the number of foxes present on the two islands. With the assistance of the local fox trapper from Virgin Arm, Carl Ings, who is familiar with the area, I estimated that there were between 5 and 13 foxes overwintering on North and South Trump islands. The two islands have a total area of 2.97 km^2 and there were, therefore, from 1.7 to 4.4 foxes/km^2 on the islands. Carl Ings estimated that there had been 30 foxes on these two islands

during the winter of 1966-67.

In the winter of 1968-69 I spent considerable time following fox trails on the Trump islands, and during this time I collected 176 fox scats. The results of the scat analysis are presented in Fig. 72 (p. 180).

Microtus and berries were the only food items obtained from the interior of the islands. The foxes usually ate entire voles, but on seven occasions I noted a most peculiar feeding habit: the fox had skinned and eviscerated a vole before consuming its carcass and had left the skin and viscera lying on the snow. Berries, mainly *Vaccinium angustifolium*, were a staple food item during the autumn.

The remaining items in the fox diets were secured from the sea. Many sea birds (Appendix E, pp. 198-202), primarily gulls (*Larus* spp.) and alcids, which had been crippled by hunters, formed a large portion of their diets. At low tide the foxes often searched for sea urchins (*Strongylocentrotus drobachiensis*) along the littoral zone and, upon finding one, would take it ashore, break it open and devour the soft internal organs as well as test fragments and spines. The moose (*Alces alces*) remains in the fox scats were simply derived from one or two discarded skins which had washed ashore on Trump Island from one of the nearby settlements. The seal (*Phoca* sp.) remains were likewise scavenged from the shore. The foxes occasionally fed upon beach fleas (Talitridae) which were numerous beneath the flotsam, and several scats were composed primarily of these amphipods.

Ermine sign was noted only on Upper Black, Chapel, New World and Black islands. In February and March 1969 I collected 88 scats, the hind leg of a snowshoe hare (*Lepus americanus*), two murre (*Uria aalge*) wings and the wing of an unidentified sea duck from three weasel nests

on Black Island. The scat analysis (Fig. 73, p. 181) indicated that the weasels preyed primarily upon *Microtus* and small Passeriformes and scavenged on the remains of sea birds; the other items in their diets were only occasionally eaten.

Rough-legged hawks were common in the area during their spring and fall migrations. Several were seen hunting over the meadows and bogs of South Trump Island during September and October 1968 and again from 7-15 May 1969. During these periods the hawks, as evidenced by their pellets, consumed a considerable number of voles; one particular pellet contained the remains of at least five voles.

In addition to the three major predators mentioned above, there were several other birds (goshawk, pigeon hawk, glaucous gull, Iceland gull, great black-backed gull, herring gull, boreal owl, gray jay, raven, crow and northern shrike) and mammals (rat, dog, arctic fox, black bear, mink, otter and cat) which may have occasionally preyed on the meadow voles (see Appendices E and F, pp. 198-209, for the status of these animals in the study area).

I could find no discernible pattern to the predation pressure applied to the *Microtus* on the islands in the study area. Some insular population were heavily preyed upon for a matter of a few hours to several months or years, while other populations appeared to be relatively free from predation for varying periods of time.

The large islands such as Coal All (900 ha), Chapel (4700 ha) and New World (18,100 ha) probably supported foxes and weasels at all times. On the smaller islands these carnivores were usually only transient unless they became trapped when the sea ice broke up in spring; at these times the carnivores could have exerted severe pressure on the

isolated vole populations.

According to Pearson (1966) carnivores can subsist on alternate prey species while reducing their primary prey to extremely low densities. On the islands in Notre Dame Bay *Microtus* is one of the major prey species of both foxes and weasels. As I indicated earlier, foxes and weasels could subsist by scavenging along the sea. Thus it would have been possible for them to remain at relatively high numbers even though they were rapidly extirpating their primary prey, *Microtus*. Many of the insular vole populations including those on islands as large as Glead (44.8 ha) and Black (64.5 ha) may have been extirpated by foxes and/or weasels when these carnivores were unable to emigrate to other islands.

Since rough-legged hawks are highly mobile, they could not be trapped by open water on an island as was often the case with foxes and weasels. Therefore, they probably never had such deleterious effects upon a low density *Microtus* population inhabiting a relatively large island. Conceivably though, rough-legged hawks, as well as any other predator, could have easily eliminated *Microtus* from a small island in a short time if only a few voles were present.

Maher (1965), Schnell (1964) and Sheppe (1965b) have also reported that predators are capable of extirpating insular populations of rodents.

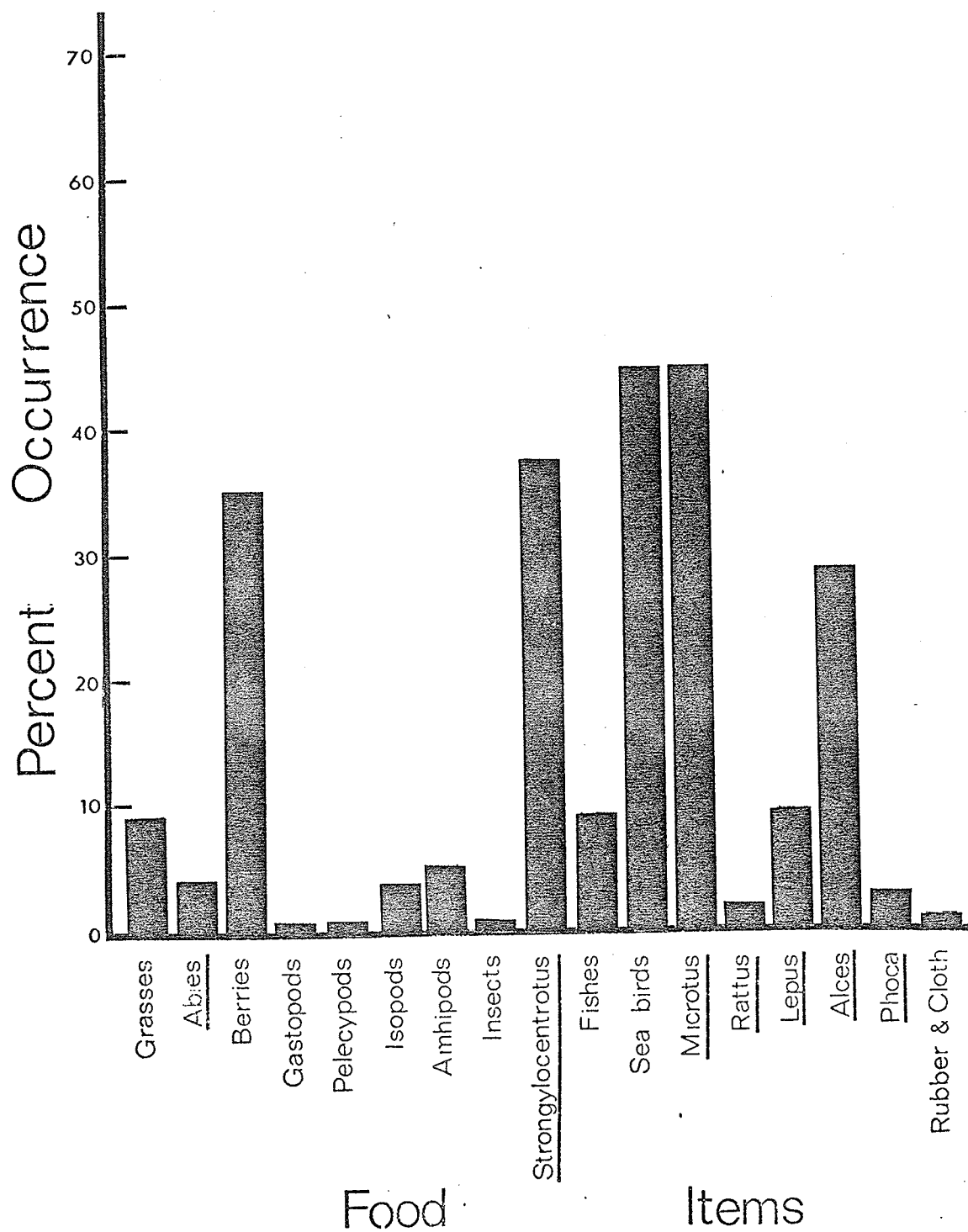


Fig. 72. Food items recorded in 176 fox (*Vulpes fulva*) scats from North and South Trump islands (Nos. 86 and 82).

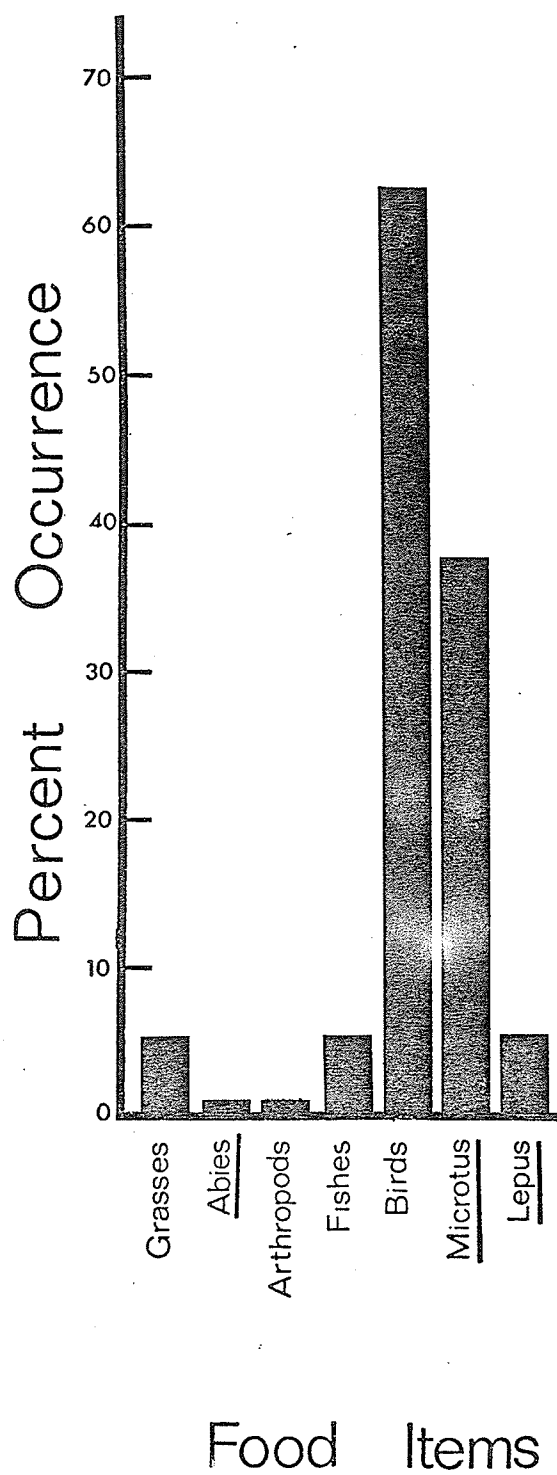


Fig. 73. Food items recorded in 88 weasel (*Mustela erminea*) scats from Black Island (No. 78).

SUMMARY AND CONCLUSIONS

In terms of abundance and ability to colonize, the meadow vole, *Microtus pennsylvanicus terraenovae*, is the most successful terrestrial mammal inhabiting the islands of Notre Dame Bay, Newfoundland. This is quite unusual since these islands are primarily forested and do not provide typical habitat. The voles have adjusted by modifying their habitat selection, food habits, home ranges, dispersal abilities and fecundity.

On small islands where only one or two habitats are present, the voles are forced to utilize these habitats or emigrate. On larger islands with a wider variety of habitats, the voles utilize the forest habitats throughout the year and the grassy habitats during summer and fall. The voles' habitat selection appears to be in response to the scarcity of grassy areas and to the harsh winter microenvironment in the snow-free grassy areas. Predation can occasionally be intense, and this may be another factor forcing the voles to utilize the forest habitats which provide maximum shelter throughout the year.

A total of 64 vascular and 9 non-vascular plant species was recorded in the voles' diets; this includes almost 25% of the total number of species recorded for the study area. The large number of forest species in the voles' diets indicate that they are well adjusted to their forest existence. Some voles probably scavenge upon animal remains in the intertidal zone.

The voles' home ranges are affected by the habitat quality: the largest home ranges (mean minimum area = 2.0436 ha) were recorded in

spruce-fir forest on Pyke Island while the smallest ranges (mean minimum area = 0.0146 ha) were recorded on the SKC plot where a variety of forest and grassy habitats occur. Population density, season of the year, sex, sexual activity and island size also influence home range size. Four inter-island home range shifts were recorded in 1967. The meadow voles can home equally as well across open water as across land; five inter-island movements were made by homing voles in 1967.

The voles possess great powers of dispersal which enable them to colonize the islands. Several of the 18 inter-island movements recorded in 1967 and 1968 appeared to be made by dispersing voles; the longest dispersal movement was 1130 m and the fastest dispersal movement was 610 m in less than 16 hours. These inter-island movements were accomplished by swimming. During tests, the voles swam for periods of up to 32 minutes at speeds of up to 60 cm/sec. Swimming voles oriented to objects on the horizon; the smallest object to which a vole oriented subtended an angle of $2^{\circ}35'$. Under ideal weather conditions, the voles could probably colonize almost any island in the study area by swimming.

Due to a short breeding season (confined to spring and summer), a scarcity of breeding juveniles (only 4.8% of 334 juveniles examined were sexually active) and a small number of litters/female/year (maximum recorded number of 2 or possibly 3), the meadow voles have a low reproductive rate. This control of the population may be a factor which reduces the possibility of extirpation by over-exploitation of a marginal habitat.

Even with these ecological modifications, insular populations of *Microtus* are often extirpated. Nineteen of the 89 islands investigated had recently had their vole populations extirpated. Small islands can

support vole populations for only a short time (possibly only a few years maximum) without recolonization. Larger islands can sustain vole populations for longer periods because there are fewer factors which can eliminate larger colonies. There are several biotic and physical forces which are capable of eliminating insular populations; the two most apparent forces were adverse weather conditions and intense predation.

Since colonization and extirpation are so fortuitous, the populations on the various islands do not fluctuate in synchrony.

Several morphological variations, including differences in pelage colouration, skeletal measurements and molar tooth patterns, were recorded among the insular vole populations. These variations were not related to the degree of isolation, to island size or to habitat type. Since the insular populations were often short-lived, the anatomical variations can not be considered to be of taxonomic importance. These variations are probably the result of genetic drift.

APPENDICES

10	Knights	Knights	Knights	166.50	1, 7, 8
11	--	Dallies	Dallies	1.29	2, 5, 8
12	Yellow Fox	Fish	Yellow Fox	56.60	1, 2, 3, 4, 8
13	Mann Rxs.	Mann Rxs.	Mann Rxs.	0.89	5, 8
14	Gleed	Gleeds	Gleed	44.80	1, 2, 3, 4, 6, 8
15	Cranpot	Big Cranpot	Big Cranpot	3.03	1, 2, 4, 8
16	--	Little Cranpot	Little Cranpot	0.69	3, 4, 8
17	Comfort	Comfort Gull	Comfort	13.30	1, 2, 4, 8
18	--	--	Mile Is. Rx.	<0.08	8
19	--	Nannyback or Mile	Mile	0.81	3, 4, 5, 8
20	--	--	Grabs	0.16	4, 5, 8
21	--	--	No. 34	0.28	5, 8
22	--	--	No. 21	0.12	2, 4, 8
23	--	Shellbird	No. 20	1.20	2, 4, 8
24	--	Shellbird	No. 33	0.44	4, 8
25	--	Shellbird	No. 22	0.44	4, 5, 8
26	--	--	No. 23	0.12	8
27	Coal All	Coal All	Coal All	900.00	1, 2, 6, 8
28	Green	Green	Green	0.65	5, 8
29	--	Dog Is. West	Dog Is. West	0.36	2, 4, 8
30	--	--	No. 17	0.16	4, 8
31	--	--	No. 18	0.08	4, 8
32	Chapel	Chapels	Chapel	4700.00	1, 2, 3, 4, 5, 6, 7, 8
33	--	--	Pimple	0.40	4, 5, 8
34	--	--	Gabbro	0.32	1, 4, 8
35	--	Powder House	Powder House	0.20	4, 8
36	Inspector	Mint	Inspector	72.60	1, 2, 3, 5, 7, 8
37	--	Grassy Rx.	No. 1	0.28	5, 8
38	--	Cave	Cave	0.77	1, 2, 8
39	Pyke	Solid	Pyke	11.84	1, 2, 8
40	--	--	Stearn Rx.	<0.08	8
41	--	Little Solid	No. 6	0.44	2, 4, 8
42	--	Shellbird	Little Solid	0.57	1, 8
43	--	Sun Rx.	No. 5	0.36	5, 8
44	--	Butterfly Rx.	Crow Rx.	0.08	4, 8
45	--	Crow Is. Rx.	Crow Is. Rx.	0.12	4, 8
46	Coffin	Horse	Coffin	21.40	1, 2, 8
47	--	--	No. 35	0.61	2, 8
48	--	--	No. 36	0.04	5, 8
49	--	--	No. 13	0.61	5, 8
50	--	Little Walls	East Walls	1.25	1, 2, 8
51	--	--	No. 7 East	0.57	2, 8
52	--	--	No. 7 West	2.00	2, 8
53	--	--	No. 11	0.93	5, 8
54	--	--	No. 4	0.40	5, 8
55	--	--	Variety	0.20	2, 8
56	--	--	<i>Empetrum</i>	0.16	4, 8
57	--	--	Rx. east of <i>Empetrum</i>	<0.08	4, 8
58	--	--	Mijum <i>Empetrum</i>	<0.08	4, 8
59	--	--	No. 38	<0.08	3, 4, 8
60	--	--	No. 39	<0.08	2, 4, 8
61	--	--	No. 40	<0.08	2, 3, 4, 8
62	--	Hurts	No. 10	0.92	4, 5, 8
63	--	--	No. 12	0.36	2, 4, 8
64	--	--	No. 37	0.20	5, 8
65	--	--	No. 27	0.20	4, 5, 8
66	--	--	No. 28	0.24	2, 8
67	--	--	No. 26	<0.08	4, 8
68	--	--	No. 32	2.30	2, 7, 8
69	--	--	No. 24	<0.08	4, 5, 8
70	--	--	No. 25	<0.08	4, 5, 8
71	--	--	No. 31	<0.08	4, 8
72	--	--	No. 30	<0.08	4, 8
73	--	Coaker	Coaker	312.00	1, 5, 8
74	--	--	No. 29	<0.08	5, 8
75	Dunnage	Dunnage	Dunnage	1054.00	1, 4, 6, 8
76	Crow Head	Crow Head	Crow Head	6.83	1, 2, 4, 8
77	Gooseberry	Gooseberry	Gooseberry	0.49	4, 5, 8
78	Black	Black	Black	64.51	2, 4, 5, 8
79	Duck	Duck	Duck (Friday Bay)	7.42	2, 4, 8
80	Fools Harbour	Fools Harbour	Fools Harbour North	3.07	2, 3, 4, 8
81	--	Rat	Fools Harbour West	0.53	5, 8
82	South Trump	South Trump	South Trump	172.20	1, 2, 3, 4, 5, 6, 8
83	--	Little Berry	Little Berry	0.29	2, 4, 8
84	South Berry	South Berry	South Berry	8.52	2, 4, 8
85	--	White	White	1.29	2, 4, 8
86	North Trump	North Trump	North Trump	125.00	1, 2, 3, 4, 5, 6, 8
87	Mouse	Mouse	Mouse	2.78	4, 5, 8
88	Matthews	Matthews	Matthews	4.07	4, 5, 8
89	New World	New World	New World	18,100.00	1, 2, 3, 4, 5, 6, 7, 8

Note: Many of the islands in the study area are unnamed on the National Topographic Series maps. For this reason I include a list of local names to assist interested persons in locating particular islands. My own field names and numbers are also given to assist anyone referring to my field journals or using my specimen collections.

In the thesis I use the official map name and/or island number given in the first column; if no official name exists I use the local name and/or island number from the first column.

*Habitat code: 1 = spruce-fir forest, 2 = tuckamoor, 3 = alder patch, 4 = dwarf shrub barren, 5 = grassy area, 6 = bog, 7 = salt marsh, 8 = shoreline.

APPENDIX A

Islands in Notre Dame Bay investigated for *Microtus*

Island number	Official map name	Local name	Field name	Size (ha)	Habitat*
1	Hummock	Hummock	Hummock	72.00	1, 2, 8
2	--	--	Hummock No. 4	0.53	2, 4, 8
3	--	--	Hummock No. 3	1.90	3, 4, 8
4	--	--	Hummock No. 2	0.89	4, 5, 8
5	--	--	Hummock No. 1	1.09	1, 2, 4, 8
6	Shag Cliff	Shag Cliff	Shag Cliff	34.30	1, 4, 8
7	The Sugar Loaf	Sugar Loaf	Sugar Loaf	2.54	1, 2, 8
8	Camel	Hummocky	Camel	61.40	1, 2, 3, 4, 6, 8
9	Duck	Stearn	Duck (Exploits)	0.81	5, 8
10	Knights	Knights	Knights	166.50	1, 7, 8
11	--	Dallies	Dallies	1.29	2, 5, 8
12	Yellow Fox	Fish	Yellow Fox	56.60	1, 2, 3, 4, 8
13	Mann Rxs.	Mann Rxs.	Mann Rxs.	0.89	5, 8
14	Gleed	Gleeds	Gleed	44.80	1, 2, 3, 4, 6, 8
15	Cranpot	Big Cranpot	Big Cranpot	3.03	1, 2, 4, 8
16	--	Little Cranpot	Little Cranpot	0.69	3, 4, 8
17	Comfort	Comfort Gull	Comfort	13.30	1, 2, 4, 8
18	--	--	Mile Is. Rx.	<0.08	8
19	--	Nannyback or Mile	Mile	0.81	3, 4, 5, 8
20	--	--	Grabs	0.16	4, 5, 8
21	--	--	No. 34	0.28	5, 8
22	--	--	No. 21	0.12	2, 4, 8
23	--	Shellbird	No. 20	1.20	2, 4, 8
24	--	Shellbird	No. 33	0.44	4, 8
25	--	Shellbird	No. 22	0.44	4, 5, 8
26	--	--	No. 23	0.12	8
27	Coal All	Coal All	Coal All	900.00	1, 2, 6, 8
28	Green	Green	Green	0.65	5, 8
29	--	Dog Is. West	Dog Is. West	0.36	2, 4, 8
30	--	--	No. 17	0.16	4, 8
31	--	--	No. 18	0.08	4, 8
32	Chapel	Chapels	Chapel	4700.00	1, 2, 3, 4, 5, 6, 7, 8
33	--	--	Pimple	0.40	4, 5, 8
34	--	--	Gabbro	0.32	1, 4, 8
35	--	Powder House	Powder House	0.20	4, 8
36	Inspector	Mint	Inspector	72.60	1, 2, 3, 5, 7, 8
37	--	Grassy Rx.	No. 1	0.28	5, 8

APPENDIX B

Plants recorded in the study area

Species	Habitat [*]							
	1	2	3	4	5	6	7	8
Lichens								
<i>Sphaerophorus fragilis</i> (L.) Pers.								x
<i>Nephroma arcticum</i> (L.) Torss.	x							
<i>Peltigera aphthosa</i> (L.) Willd.	x							
<i>P. canina</i> (L.) Willd. var. <i>rufescens</i> (Weiss)	x							
Mudd								
<i>Peltigera</i> sp.		x			x			
<i>Cladonia chlorophaea</i> (Flörke in Somm.) Spreng. sens. lat.	x							
<i>C. cristatella</i> Tuck.		x						
<i>C. fimbriata</i> (L.) Fr.		x						
<i>C. gracilis</i> (L.) Willd.		x						
<i>C. phyllophora</i> Hoffm.		x						
<i>C. pyxidata</i> (L.) Hoffm.		x						
<i>C. cfr. rangiferina</i> (L.) Web. in Wig.	x							
<i>C. scabriuscula</i> (Del. in Duby) Nyl.	x							
<i>Pycnothelia papillaria</i> (Ehrh.) Duf.		x						
<i>Parmelia saxatilis</i> (L.) Ach.								x
<i>P. sulcata</i> Tayl.	x							x
<i>Xanthoria elegans</i> (Link.) Th. Fr.								x
<i>Alectoria sarmentosa</i> (Ach.) Ach.	x							
<i>Caloplaca</i> sp.		x		x	x			x
<i>Rhizocarpon distinctum</i> Th. Fr.		x						
Mosses and liverworts								
<i>Sphagnum recurvum</i> P. de Beauv.	x					x		
<i>Sphagnum series subsecunda</i>	x					x		
<i>Ceratodon purpureus</i> (Hedw.) Brid.		x						x
<i>Dicranum polysetum</i> Sw.	x							
<i>D. scoparium</i> Hedw.					x			
<i>Dicranum</i> sp.	x	x	x					
<i>Rhacomitrium lanuginosum</i> (Hedw.) Brid.					x			
<i>Pohlia nutans</i> (Hedw.) Lindb.	x	x						
<i>Bryum</i> sp.	x	x						
<i>Aulacomnium palustre</i> (Hedw.) Schwaegr.	x							
<i>Calliergon stramineum</i> (Brid.) Kindb.		x						
<i>Brachythecium</i> sp.					x			
<i>Pleurozium schreberi</i> (Brid.) Mitt.	x	x			x			
<i>Hylocomium splendens</i> (Hedw.) B. S. G.	x							
<i>Polytrichum juniperium</i> Hedw.	x	x						
<i>Polytrichum</i> sp.					x	x		
<i>Rhytidiadelphus loreus</i> (Hedw.) Warnst.	x							

APPENDIX B (continued)

Species	Habitat*							
	1	2	3	4	5	6	7	8
Vascular plants								
<i>Equisetum arvense</i> L.					x	x		
<i>E. fluviatile</i> L.	x							
<i>E. sylvaticum</i> L.	x	x						
<i>Osmunda cinnamomea</i> L.			x					
<i>Dryopteris disjuncta</i> (Ledeb.) Morton	x							
<i>D. spinulosa</i> (O. F. Muell.) Watt	x							
<i>Onoclea sensibilis</i> L.	x							
<i>Taxus canadensis</i> Marsh.	x	x						
<i>Abies balsamea</i> (L.) Mill.	x	x	x					
<i>Larix laricina</i> (DuRoi) K. Koch						x		
<i>Picea glauca</i> (Moench) Voss	x							
<i>P. mariana</i> (Mill.) B. S. P.	x	x	x			x		
<i>Juniperus communis</i> L.			x	x	x			
<i>J. horizontalis</i> Moench				x	x			
<i>Sparganium chlorocarpum</i> Rydb.						x		
<i>Potamogeton epihydrus</i> Raf.						x		
<i>Potamogeton</i> sp.						x		
<i>Ruppia maritima</i> L.							x	
<i>Zostera marina</i> L.								x
<i>Scheuchzeria palustris</i> L.						x		
<i>Triglochin maritima</i> L.							x	
<i>T. palustris</i> L.							x	
<i>Agropyron repens</i> (L.) Beauv.					x			
<i>Agrostis alba</i> L.							x	
<i>A. geminata</i> Trin.					x			
<i>A. scabra</i> Willd.					x			
<i>Alopecurus pratensis</i> L.					x			
<i>Anthoxanthum odoratum</i> L.					x			
<i>Calamagrostis canadensis</i> (Michx.) Nutt.					x			
<i>Deschampsia flexuosa</i> (L.) Trin.					x			
<i>Elymus arenarius</i> L.								x
<i>Festuca rubra</i> L.					x			
<i>Glyceria borealis</i> (Nash) Batchelder					x			
<i>Hierochloa odorata</i> (L.) Beauv.							x	
<i>Phleum pratense</i> L.					x			
<i>Poa palustris</i> L.					x			
<i>P. pratensis</i> L.					x			
<i>Spartina alterniflora</i> Loisel.							x	
<i>S. patens</i> (Ait.) Muhl.							x	
<i>S. pectinata</i> Link							x	
<i>Carex aenea</i> Fern.							x	
<i>C. canescens</i> L.							x	
<i>C. crinita</i> Lam.							x	
<i>C. flava</i> L.					x			
<i>C. interior</i> Bailey					x			

APPENDIX B (continued)

Species	Habitat [*]							
	1	2	3	4	5	6	7	8
<i>Carex lasiocarpa</i> Ehrh.					x			
<i>C. Michauxiana</i> Boeckl.						x		
<i>C. nigra</i> (L.) Reichard						x		x
<i>C. oligosperma</i> Michx.						x		
<i>C. paleacea</i> Wahlenb.							x	
<i>C. pauciflora</i> Lightf.						x		
<i>C. rostrata</i> Stokes							x	
<i>C. stipata</i> Muhl.					x			
<i>C. straminea</i> Willd.							x	
<i>C. trisperma</i> Dewey						x		
<i>C. viridula</i> Michx.					x			
<i>Dulichium arundinaceum</i> (L.) Britton						x		
<i>Eleocharis halophila</i> Fern. & Brack.							x	
<i>Eriophorum angustifolium</i> Honckeney						x		
<i>E. virginicum</i> L.						x		
<i>Rhynchospora alba</i> (L.) Vahl					x			
<i>R. fusca</i> (L.) Ait. f.						x		
<i>Scirpus atrocinctus</i> Fern.							x	
<i>S. cespitosus</i> L.						x		
<i>S. cyperinus</i> (L.) Kunth					x			
<i>S. maritimus</i> L.							x	
<i>Juncus acuminatus</i> Michx.						x		
<i>J. articulatus</i> L.	x							
<i>J. compressus</i> Jacq.	x							
<i>J. effusus</i> L.						x		
<i>J. validus</i> Coville							x	
<i>Luzula campestris</i> (L.) DC.						x		
<i>Clintonia borealis</i> (Ait.) Raf.	x							
<i>Maianthemum canadense</i> Desf.				x				
<i>Smilacina stellata</i> (L.) Desf.				x	x			
<i>S. trifolia</i> (L.) Desf.						x		
<i>Streptopus amplexifolius</i> (L.) DC.	x							
<i>Iris Hookeri</i> Penny					x			x
<i>I. versicolor</i> L.					x			
<i>Sisyrinchium angustifolium</i> Mill.					x			
<i>Arethusa bulbosa</i> L.						x		
<i>Calopogon pulchellus</i> (Salisb.) R. Br.						x		
<i>Corallorhiza maculata</i> Raf.	x							
<i>Goodyera repens</i> (L.) R. Br.	x							
<i>G. tessellata</i> Lodd.	x							
<i>Habenaria blephariglottis</i> (Willd.) Hook.						x		
<i>H. clavellata</i> (Michx.) Spreng.						x		
<i>H. dilatata</i> (Pursh) Hook.						x		
<i>H. obtusata</i> (Pursh) Richards.						x		
<i>Listera cordata</i> (L.) R. Br.	x							
<i>Malaxis unifolia</i> Michx.						x		

APPENDIX B (continued)

Species	Habitat*							
	1	2	3	4	5	6	7	8
<i>Pogonia ophioglossoides</i> (L.) Ker.						x		
<i>Spiranthes Romanzoffiana</i> Cham.						x		
<i>Salix Bebbiana</i> Sarg.						x		
<i>Myrica Gale</i> L.						x		
<i>Alnus crispa</i> (Ait.) Pursh		x	x	x	x			
<i>Betula Michauxii</i> Spach						x		
<i>B. papyrifera</i> Marsh.	x	x						
<i>B. pumila</i> L.						x		
<i>Geocaulon lividum</i> (Richards.) Fern.	x							
<i>Polygonum aviculare</i> L.				x				
<i>P. viviparum</i> L.		x						
<i>Rumex Acetosa</i> L.					x			
<i>R. Acetosella</i> L.					x			
<i>R. crispus</i> L.					x			
<i>Atriplex patula</i> L.					x			
<i>Salicornia europaea</i> L.							x	
<i>Arenaria dawsonensis</i> Britton		x						
<i>A. lateriflora</i> L.								x
<i>Cerastium arvense</i> L.					x			
<i>C. viscosum</i> L.					x			
<i>Sagina nodosa</i> (L.) Fenzl					x			x
<i>S. procumbens</i> L.					x			
<i>Spergularia canadensis</i> (Pers.) Don							x	
<i>Spergularia</i> sp.							x	
<i>Stellaria calycantha</i> (Ledeb.) Bong.					x			
<i>S. humifusa</i> Rottb.							x	
<i>Stellaria</i> sp.					x			
<i>Nuphar variegatum</i> Engelm.						x		
<i>Nymphaea odorata</i> Ait.						x		
<i>Actaea rubra</i> (Ait.) Willd.						x		
<i>Coptis groenlandica</i> (Oeder) Fernald	x							
<i>Ranunculus abortivus</i> L.					x			
<i>R. acris</i> L.					x			
<i>R. Cymbalaria</i> Pursh			x					
<i>R. pensylvanicus</i> L. f.					x			
<i>R. repens</i> L.					x			
<i>Thalictrum polygamum</i> Muhl.			x		x	x		
<i>Cakile edentula</i> (Bigel.) Hook.								x
<i>Camelina</i> sp.		x						
<i>Capsella Bursa-pastoris</i> (L.) Medic.					x			
<i>Cochlearia tridactylites</i> Banks								x
<i>Draba arabisans</i> Michx.		x						x
<i>D. glabella</i> Pursh		x						
<i>D. minganensis</i> (Vict.) Fern.		x						
<i>Lepidium ruderales</i> L.								x
<i>L. virginicum</i> L.					x			

APPENDIX B (continued)

Species	Habitat *							
	1	2	3	4	5	6	7	8
<i>Sarracenia purpurea</i> L.						x		
<i>Drosera rotundifolia</i> L.						x		
<i>Sedum Rosea</i> (L.) Scop.								x
<i>Ribes hirtellum</i> Michx.	x							
<i>R. lacustre</i> (Pers.) Poir	x							
<i>Saxifraga aizoon</i> Jacq.		x						
<i>Potentilla Anserina</i> L.								x
<i>P. fruticosa</i> L.			x			x		
<i>P. norvegica</i> L.					x			
<i>P. tridentata</i> Ait.				x				
<i>Pyrus decora</i> (Sarg.) Hyland		x	x		x			
<i>P. floribunda</i> Lindl.		x				x		
<i>Rosa nitida</i> Willd.					x	x		
<i>Rubus Chamaemorus</i> L.						x		
<i>R. hispidus</i> L.					x			
<i>R. idaeus</i> L.					x			
<i>R. pubescens</i> Raf.		x						x
<i>Sanguisorba canadensis</i> L.			x		x	x		
<i>Spiraea latifolia</i> (Ait.) Borkh.						x		
<i>Astragalus alpinus</i> L.				x				
<i>Lathyrus japonicus</i> Willd.					x			x
<i>L. palustris</i> L.					x			
<i>Trifolium pratense</i> L.					x			
<i>T. procumbens</i> L.					x			
<i>T. repens</i> L.					x			
<i>Vicia Cracca</i> L.					x			
<i>Nemophanthus mucronatus</i> (L.) Trel.	x	x				x		
<i>Acer spicatum</i> Lam.	x	x						
<i>Impatiens capensis</i> Meerb.	x							
<i>Hypericum canadense</i> L.						x		
<i>Viola cucullata</i> Ait.					x			
<i>V. pallens</i> (Banks) Brainerd					x			
<i>Shepherdia canadensis</i> (L.) Nutt.				x				
<i>Circaea alpina</i> L.			x					
<i>Epilobium angustifolium</i> L.					x			
<i>E. glandulosum</i> Lehm					x			
<i>Oenothera perennis</i> L.								x
<i>Cornus canadensis</i> L.	x	x	x	x	x	x		
<i>C. stolonifera</i> Michx.		x						
<i>C. suecica</i> L.				x				
<i>Aralia hispida</i> Vent.	x							
<i>A. nudicaulis</i> L.	x							
<i>Angelica laurentiana</i> Fern.								x
<i>Conioselinum chinense</i> (L.) B. S. P.								x
<i>Heracleum maximum</i> Bartram			x					
<i>Ligusticum scoticum</i> L.								x

APPENDIX B (continued)

Species	Habitat*							
	1	2	3	4	5	6	7	8
<i>Monotropa Hypopithys</i> L.	x							
<i>M. uniflora</i> L.	x							
<i>Pyrola elliptica</i> Nutt.						x		
<i>P. rotundifolia</i> L.	x							
<i>P. secunda</i> L.	x							
<i>Andromeda glaucophylla</i> Link						x		
<i>Arctostaphylos Uva-ursi</i> (L.) Spreng.				x				
<i>Chamaedaphne calyculata</i> (L.) Moench						x		
<i>Gaultheria hispidula</i> (L.) Bigel.	x	x						
<i>Kalmia angustifolia</i> L.	x	x		x		x		
<i>K. polifolia</i> Wang.						x		
<i>Ledum groenlandicum</i> Retz.		x		x		x		
<i>Rhododendron canadense</i> (L.) Torr.		x		x		x		
<i>Vaccinium angustifolium</i> Ait.		x		x		x		
<i>V. macrocarpon</i> Ait.						x		
<i>V. Oxycoccus</i> L.						x		
<i>V. uliginosum</i> L.				x				
<i>V. Vitis-Idaea</i> L.	x	x	x	x		x		
<i>Empetrum nigrum</i> L.		x	x	x				
<i>Glaux maritima</i> L.								x
<i>Primula laurentiana</i> Fern.		x						
<i>Trientalis borealis</i> Raf.	x							
<i>Limonium Nashii</i> Small							x	x
<i>Halenia deflexa</i> (Sm.) Griseb.								x
<i>Menyanthes trifoliata</i> L.						x		
<i>Convolvulus sepium</i> L.								x
<i>Mertensia maritima</i> (L.) S. F. Gray								x
<i>Myosotis scorpioides</i> L.					x			
<i>Galeopsis</i> sp.					x			
<i>Lycopus uniflorus</i> Michx.							x	
<i>Mentha arvensis</i> L.					x			
<i>Prunella vulgaris</i> L.					x			
<i>Scutellaria lateriflora</i> L.					x			
<i>Digitalis purpurea</i> L.					x			
<i>Euphrasia Randii</i> Robinson					x			
<i>E. rigidula</i> Jordan					x			
<i>Rhinanthus</i> sp.					x			
<i>Veronica agrestis</i> L.					x			
<i>Utricularia cornuta</i> Michx.						x		
<i>U. geminiscapa</i> Benj.						x		
<i>Plantago juncooides</i> Lam.								x
<i>Galium palustre</i> L.	x							
<i>G. triflorum</i> Michx.	x							
<i>Linnaea borealis</i> L.								x
<i>Lonicera villosa</i> (Michx.) R. & S.		x	x			x		
<i>Sambucus pubens</i> Michx.					x			

APPENDIX B (continued)

Species	Habitat*							
	1	2	3	4	5	6	7	8
<i>Viburnum cassinoides</i> L.		x	x		x			
<i>V. edule</i> (Michx.) Raf.								x
<i>Campanula rotundifolia</i> L.					x			
<i>Achillea Millefolium</i> L.					x			
<i>Anaphalis margaritacea</i> (L.) Gray					x			
<i>Antennaria neglecta</i> Greene					x			
<i>Aster foliaceus</i> Lindl.	x							
<i>A. nemoralis</i> Ait.						x		
<i>A. puniceus</i> L.	x							
<i>A. radula</i> Ait.					x	x		
<i>Chrysanthemum Leucanthemum</i> L.					x			
<i>Cirsium arvense</i> (L.) Scop.					x			
<i>C. muticum</i> Michx.					x			
<i>C. vulgare</i> (Savi) Tenore					x			
<i>Hieracium canadense</i> Michx.					x			
<i>H. floribundum</i> Wimm. & Grab.					x			
<i>Lactuca</i> sp.					x			
<i>Leontodon autumnalis</i> L.					x			
<i>Prenanthes trifoliolata</i> (Cass.) Fern.								x
<i>Senecio Pseudo-Arnica</i> Less.								x
<i>S. vulgaris</i> L.					x			
<i>Solidago hispida</i> Muhl.								x
<i>S. rugosa</i> Ait.			x		x			
<i>S. sempervirens</i> L.				x				
<i>S. uliginosa</i> Nutt.						x		
<i>Sonchus arvensis</i> L.	x							
<i>Taraxacum officinale</i> Weber					x			

Note: The list of non-vascular plants includes only those species which I collected during the field study; it is by no means an exhaustive list. The list of vascular plants is a comprehensive list compiled by O. Forsey who conducted a botanical investigation in the study area during the summers of 1966, 1967 and 1968.

* Habitat code: 1 = spruce-fir forest, 2 = tuckamoor, 3 = alder patch, 4 = dwarf shrub barren, 5 = grassy area, 6 = bog, 7 = salt marsh, 8 = shoreline.

APPENDIX C

Thermistor stations

Station number, location & date	Thermistor number & location
I. Meadow station: centre of abandoned pasture (27 m x 36 m) on Inspector Island (No. 36), 25 June to 28 August 1968	1. 23 cm below soil surface 2. 6 cm below soil surface 3. At soil surface 4. 5 cm above soil surface 5. 15 cm above soil surface 6. 30 cm above soil surface
II. Shoreline station: 2 m above high tide line beneath 2 large spruce trees on Inspector Island (No. 36), 25 June to 28 August 1968	7. 23 cm below soil surface 8. 6 cm below soil surface 9. On forest floor 10. 5 cm above soil surface 11. 40 cm above soil surface on southwest side

APPENDIX D

Moult progression of *Microtus* in the study area

From the 340 flat skins examined, I discerned three different moult patterns representing the juvenal, post-juvenal and adult moults (Figs. 74a and 74b, pp. 196-197).

The juvenal moult began when a vole reached the weight of approximately 20 gm. The hair on the sides was the first to be affected (skin 1). The moult progressed ventrally and anteriorly along the sides of the body and head (skin 2). Then the dorsal surface of the back and finally the top of the head began to moult (skins 3 and 4). The sides and venter were the first areas to become prime (skin 4). Then the mid-dorsal region became prime (skin 5), leaving only two thin unprime stripes down the sides of the head and body (skins 6 and 7). Small patches on the rump were usually the last areas to become prime (skin 8).

The post-juvenal moult appeared to commence shortly after the juvenal moult was completed. The progression of the post-juvenal moult was quite different from that of the earlier moult. The dorsal surface of the head was the first area affected by this moult (skin 9). Shortly afterwards the mid-dorsal surface of the back began to moult (skin 10). Then the top of the head became prime, followed closely by the back (skins 11 and 12). Meanwhile the moult progressed down the sides toward the venter as two converging lateral stripes (skins 12 and 13). Two small patches on the neck were the last areas to moult (skin 14).

Skin 15 is from a subadult, yet its moult pattern does not conform to the typical post-juvenal moult progression. This skin appears to be a variant in which the mid-dorsal region and the venter moulted simultaneously rather than in sequence as depicted by skins 11, 12 and 13. Out of the 340 skins examined only four voles collected from the SKC plot displayed this atypical moult pattern.

In contrast to the regular progression of the juvenal and post-juvenal moults, the adult moult was highly irregular. The adults moulted in irregular patches all over the body (skin 16). These moults were noted throughout the year. The time of moult appeared to be an individualistic phenomenon which might have been related to other aspects of the animal's physical condition.

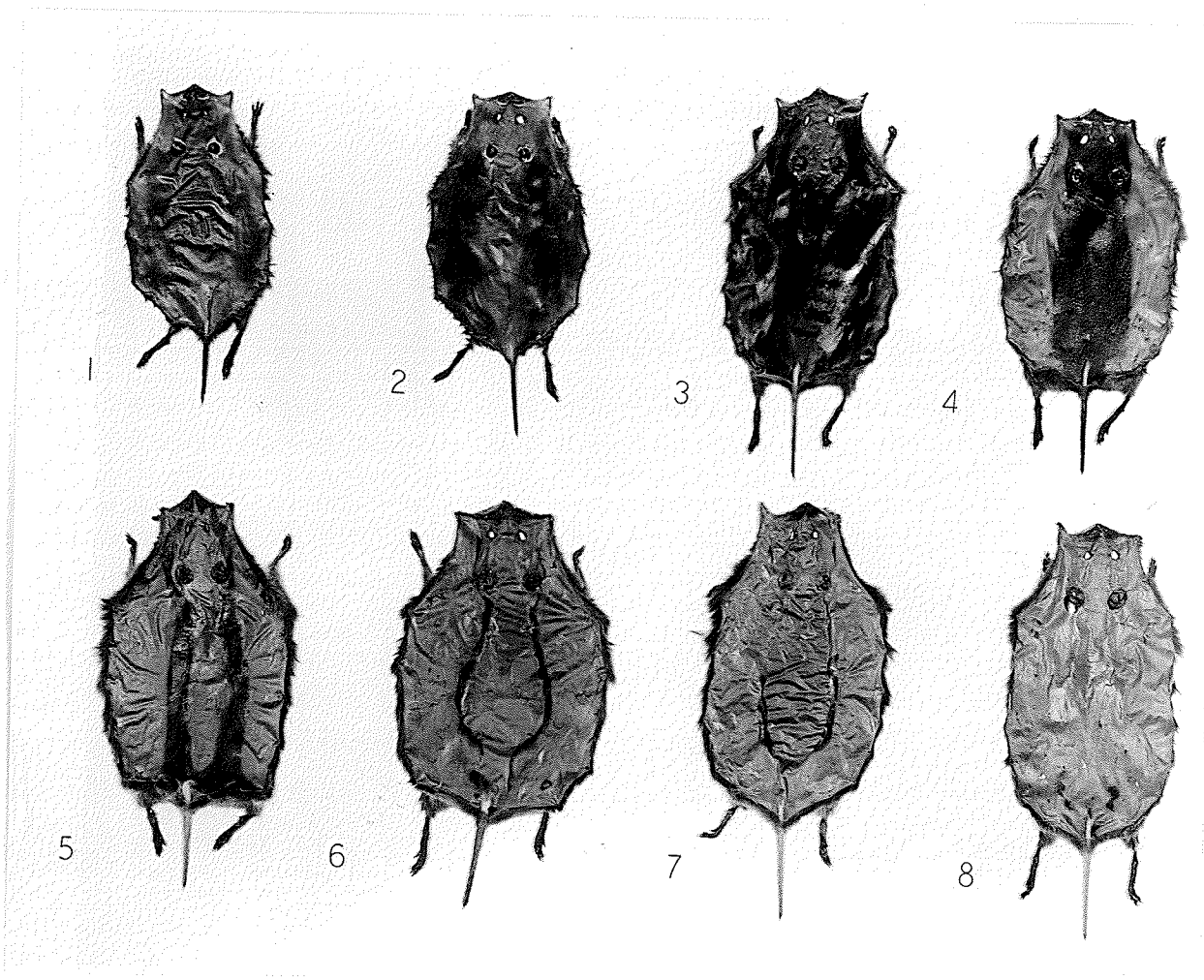


Fig. 74a. Flesh-side view of *Microtus pennsylvanicus* pelts showing the regular juvenal moult progression (skins 1-8).

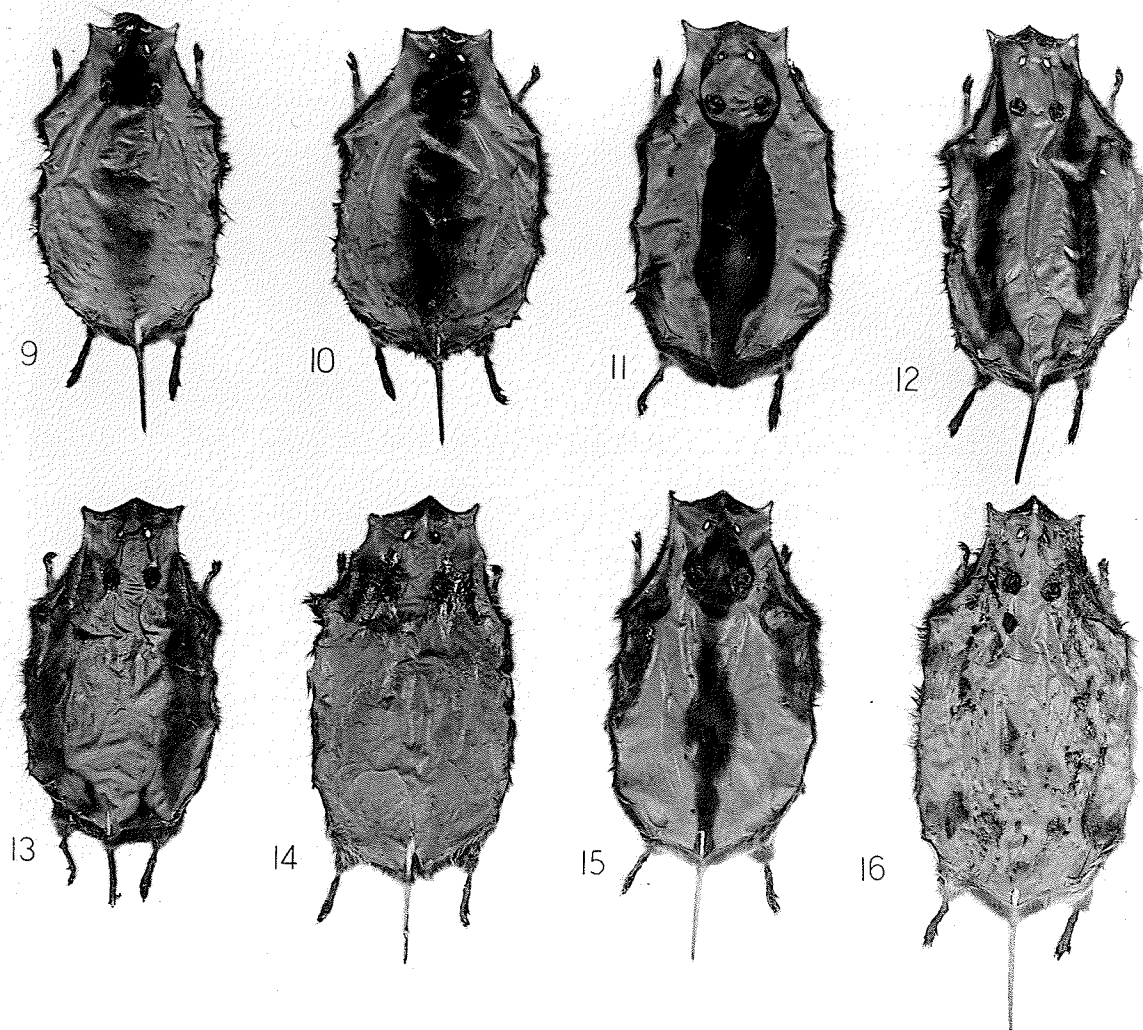


Fig. 74b. Flesh-side view of *Microtus pennsylvanicus* pelts illustrating three types of moult: skins 9-14 show the regular post-juvenal moult progression; skin 15 is from a subadult undergoing an atypical post-juvenal moult; skin 16 is from an old vole undergoing an irregular adult moult.

APPENDIX E

Annotated list of birds occurring in the study area

The status of the birds in the study area was determined using the following classification:

Uncommon: birds observed fewer than five times during the 18 months of field study (25 May to 30 August 1967 and 30 May 1968 to 22 August 1969).

Common: birds observed frequently in particular seasons of the year.

Extremely common: the most-obvious birds in the study area. They were seen and heard every day during the summer months.

Common Loon (*Gavia immer*): uncommon. One observed in Dildo Run in July 1968.

Leach's Petrel (*Oceanodroma leucorhoa*): common. Several specimens found on beach of Pyke Island (No. 39) on 31 May and 1 June 1967.

Wilson's Petrel (*Oceanites oceanicus*): common. Often seen among the inshore and offshore islands during the summer.

Great Blue Heron (*Ardea herodias*): uncommon. One seen flying over New World Island (No. 89) near Summerford on 8 June 1968. A few days later, another (or perhaps the same bird) seen flying in the same location.

King Eider (*Somateria spectabilis*): uncommon. Never seen from land. A flock of several birds seen flying over pack ice about 16 km north of Twillingate on 28 April 1969.

Surf Scoter (*Melanitta perspicillata*): uncommon. One observed off Inspector Island (No. 36) during summer of 1968.

Common Merganser (*Mergus merganser*): common. Several seen in Dildo Run near Chapel Island (No. 32) during summer of 1967. They were formerly more abundant, but eggging and hunting have reduced their numbers.

Goshawk (*Accipiter gentilis*): uncommon. One seen on Inspector Island near the end of June 1968.

Rough-Legged Hawk (*Buteo lagopus*): common. Fall and spring transient. Few were seen hunting in the vicinity of Trump Island (Nos. 82 and 86) between September and October 1968. They reappeared the following spring from 7-15 May 1969.

- Bald Eagle (*Haliaeetus leucocephalus*): uncommon. One seen flying over Trump Island on 28 January 1969. An adult seen perched in dead spruce on Trump Island on 5 February 1969.
- Osprey (*Pandion haliaetus*): uncommon. An adult and two young were seen flying over Inspector Island during midsummer 1967. Only one other individual was observed in the same area during that summer. J. Williams observed an osprey in the vicinity of Summerford on 1 August 1969.
- Pigeon Hawk (*Falco columbarius*): uncommon. One seen perched in *Larix* near North Harbour, Bay of Exploits on 24 July 1969.
- Semipalmated Plover (*Charadrius semipalmatus*): uncommon. Two seen on gravel beach of Pyke Island 27 August 1967, and two seen on shore of Camel Island (No. 8) 28 August 1967.
- Black-Bellied Plover (*Squatarola squatarola*): uncommon. One seen on sandy shore of small forested island (No. 52) in Dildo Run on 9 August 1967.
- Ruddy Turnstone (*Arenaria interpres*): uncommon. Two seen on Mile Island (No. 19) on 12 July 1968, and one seen on rocks off Inspector Island on 4 August 1968.
- Common Snipe (*Capella gallinago*): common. Often seen on Trump, New World and Chapel islands in bogs and alder patches. First arrivals in spring 1969 noted on 10 May.
- Spotted Sandpiper (*Actitis macularia*): extremely common. Bred on just about all islands in Notre Dame Bay. First arrivals in spring 1969 noted on 27 May.
- Greater Yellowlegs (*Totanus melanoleucus*): common. Summer and fall resident. Several seen individually and in small flocks.
- Glaucous Gull (*Larus hyperboreus*): uncommon. Few seen overwintering with great black-backed and herring gulls.
- Iceland Gull (*L. glaucoides*): uncommon. Few seen overwintering with other gulls.
- Great Black-Backed Gull (*L. marinus*): common. Year-round resident. Nested on cliffs of offshore islands. Moved into the inshore islands in late August and September, where they spent the winter.
- Herring Gull (*L. argentatus*): common. Year-round resident. Nested and wintered with great black-backed gulls. All gulls were hunted by the fishermen, particularly during the fall and spring.
- Black-Legged Kittiwake (*Rissa tridactyla*): common. Often seen over the offshore water of Friday Bay during the fall of 1968.
- Arctic Tern (*Sterna paradisaea*): common. Often seen associated with common terns among the inshore islands.

Common Tern (*Sterna hirundo*): extremely common. Summer resident. Nested on many of the small islands. First arrivals noted in spring during last week of May. Only a small portion of the eggs from the first brood were allowed to hatch, because lobster fishermen collected eggs until the close of the lobster season, 15 July. Large migration flocks began to form about 20 August. Most of the terns had left Notre Dame Bay by mid-September.

Common Murre (*Uria aalge*): common. Winter resident. Often seen in exposed bays and around offshore islands.

Thick-Billed Murre (*U. lomvia*): common. Winter resident out at sea. Observed around pack ice 16 km off Twillingate Island on 28 April 1969.

Dovekie (*Plautus alle*): common. Fall, winter and spring resident. Often seen in exposed bays and around offshore and inshore islands.

Black Guillemot (*Cephus grylle*): common. Year-round resident. Bred in crevices on cliffs of offshore islands. Often seen during winter close to inshore islands as well as in exposed bays.

Common Puffin (*Fratercula arctica*): common. Winter resident. Often seen on the exposed waters of Friday Bay.

Boreal Owl (*Aegolius funereus*): uncommon. One seen on Trump Island on 3 January 1969.

Belted Kingfisher (*Megasceryle alcyon*): uncommon. One seen on Chapel Island during summer of 1967. Another seen perched on spruce top on Pyke Island during last week of August 1967. Few seen perched on wires along roads of New World Island during summers of 1968 and 1969.

Yellow-Shafted Flicker (*Colaptes auratus*): uncommon. Few seen on forested islands in Dildo Run (Pyke and Inspector islands) during first week in August 1967. One seen by J. Williams on North Trump Island during August 1969.

Hairy Woodpecker (*Dendrocopos villosus*): common. Often seen on forested islands in the summer.

Downy Woodpecker (*D. pubescens*): common. Often seen on forested islands in the summer. However, hairy woodpeckers appeared to be more abundant in the area.

Yellow-Bellied Flycatcher (*Empidonax flaviventris*): uncommon. One seen on Pyke Island on 12 August 1967. J. Williams observed one near Virgin Arm on 15 August 1969.

Bank Swallow (*Riparia riparia*): uncommon. One seen by J. Williams on Hummock Island (No. 1) on 25 July 1969.

Barn Swallow (*Hirundo rustica*): uncommon. One seen flying over Trump Island on 28 October 1968.

- Tree Swallow (*Iridoprocne bicolor*): uncommon. One seen July 1969 on New World Island.
- Purple Martin (*Progne subis*): uncommon. Once during summer 1967 a few were seen flying over a small grassy island (No. 43).
- Gray Jay (*Perisoreus canadensis*): common. Year-round resident. Often seen on the larger forested islands but never observed on the small forested islands less than 8 ha.
- Blue Jay (*Cyanocitta cristata*): uncommon. One seen near Summerford during October 1968. J. Williams reported one at North Harbour on 24 July 1969.
- Common Raven (*Corvus corax*): common. Year-round resident. Often bred on cliffs among the gulls.
- Common Crow (*C. brachyrhynchos*): common. However, ravens appeared to be far more common in the area.
- Black-Capped Chickadee (*Parus atricapillus*): common. Year-round resident.
- Boreal Chickadee (*P. hudsonicus*): common. Year-round resident. More abundant than black-capped chickadee, especially during winter.
- American Robin (*Turdus migratorius*): common summer resident and uncommon year-round resident. One seen as late as 28 January 1969 in a cut-over meadow on Trump Island.
- Hermit Thrush (*Hylocichla guttata*): common. Summer resident. Seen occasionally on forested islands.
- Swainson's Thrush (*H. ustulata*): common. Summer resident. Nesting site noted on Big Cranpot Island (No. 15). Often seen on forested islands.
- Golden-Crowned Kinglet (*Regulus satrapa*): common. Year-round resident. Noted especially during winter on forested islands.
- Ruby-Crowned Kinglet (*R. calendula*): uncommon. Few seen during summer 1967 on forested islands.
- Water Pipit (*Anthus spinoletta*): uncommon. One seen on Mile Island on 24 August 1968.
- Northern Shrike (*Lanius excubitor*): uncommon. One observed hunting in tuckamoor on Trump Island on 26 February 1969.
- Common Starling (*Sturnus vulgaris*): common. Several seen around settlements on New World Island.
- Black-and-White Warbler (*Mniotilta varia*): common. Summer resident. Bred on Pyke Island during summer 1967.
- Yellow Warbler (*Dendroica petechia*): common. Summer resident.

- Myrtle Warbler (*Dendroica coronata*): common. Summer resident. Bred on Pyke Island in summer 1967.
- Black-Poll Warbler (*D. striata*): common. Summer resident. Bred on Yellow Fox Island (No. 12) in June 1967.
- Ovenbird (*Seiurus aurocapillus*): uncommon. One seen on Pyke Island on 15 August 1967.
- Northern Waterthrush (*S. noveboracensis*): common. Summer resident. Often seen on forested islands.
- Wilson's Warbler (*Wilsonia pusilla*): uncommon. One seen on Pyke Island on 15 August 1967.
- American Redstart (*Setophaga ruticilla*): uncommon. One seen on Pyke Island during summer 1967.
- Evening Grosbeak (*Hesperiphona vespertina*): common. Locally abundant in large flocks during winter. Flock of several hundred observed on Black Island (No. 78) in alder patch near deserted settlement on 24 February 1969.
- Pine Grosbeak (*Pinicola enucleator*): common. Year-round resident of forested islands.
- Common Redpoll (*Acanthis flammea*): common. Abundant in large flocks throughout the winter.
- Red Crossbill (*Loxia curvirostra*): common. Year-round resident.
- White-Winged Crossbill (*L. leucoptera*): common. Year-round resident. More abundant than red crossbills.
- White-Throated Sparrow (*Zonotrichia albicollis*): common. Summer resident. Often seen on forested islands.
- Fox Sparrow (*Passerella iliaca*): extremely common. Obvious on forested islands during summer.
- Swamp Sparrow (*Melospiza georgiana*): uncommon. One seen by J. Williams on 15 August 1969 near Virgin Arm.
- Song Sparrow (*M. melodia*): common. Summer resident.
- Lapland Longspur (*Calcarius lapponicus*): uncommon. One observed on Trump Island in October 1968.
- Snow Bunting (*Plectrophenax nivalis*): common. Winter resident. First arrivals noted 20 October 1968. Obvious in large flocks throughout winter.

APPENDIX F

Annotated list of mammals occurring in the vicinity
of the study area

Common Shrew (*Sorex cinereus*): J. D. Folinsbee recorded this species at Boyd's Cove during the winter of 1968-69; he also reported it on two small islands 10 km south of the study area in the summer of 1970.

Little Brown Bat (*Myotis lucifugus*): one specimen was collected approximately 6 km east of the study area at Horwood Pond by a local resident, W. Freak, during the summer of 1968. I observed a small bat which may have been the same species flying along the shoreline of Pyke Island (No. 39) during the night of 17 July 1967.

Varying Hare (*Lepus americanus*): this species was reported by locals to be present on most of the larger islands; I recorded hares on Upper Black, Hummock (No. 1), Shag Cliff (No. 6), Camel (No. 8), Yellow Fox (No. 12), Chapel (No. 32), Inspector (No. 36), Pyke, New World (No. 89), North and South Trump (Nos. 86 and 82) and Black (No. 78) islands. The local residents snared "bunnies" wherever they found them; the mainland just east of Hummock Island was a particularly productive area.

Red Squirrel (*Tamiasciurus hudsonicus*): in 1964 the Newfoundland Wildlife Service introduced two females and four males to Camel Island. These animals rapidly multiplied and spread over the entire island. In 1969 J. D. Folinsbee observed red squirrels on Birchy and Sivier islands which are situated west and southwest, respectively, of Camel Island.

Beaver (*Castor canadensis*): this species was numerous in the freshwater ponds on New World and Chapel islands. Occasionally beaver were sighted swimming among the islands by fishermen. I discovered two abandoned lodges in a freshwater pond on Shag Cliff Island which is at least 12 km from the nearest other pond of freshwater.

Red-Backed Vole (*Clethrionomys gapperi*): W. O. Pruitt introduced two males and one female to Camel Island on 8 July 1967, and an additional 17 animals were released on 6 August 1967. By summer 1968 the voles had multiplied at least ten-fold and had spread over the entire island.

European Bank Vole (*C. glareolus*): W. O. Pruitt introduced one male and one female to Yellow Fox Island on 18 July 1967, and on 23 August 1967 an adult female and her litter of five (approximately seven weeks old at the time) were also released there. By the summer of 1968 the population had greatly increased in number and had expanded over the entire island.

Red-Backed Vole (*C. rufocanus*): six adult males and one adult female were introduced by W. O. Pruitt to Big Cranpot Island (No. 15) on 7 July

1967. The following summer only a lone male was recaptured, indicating that the introduction had failed.

Meadow Vole (*Microtus pennsylvanicus*): this species was the most common mammal in the study area.

Muskrat (*Ondatra zibethicus*): this species was frequently observed in the freshwater ponds on New World and Chapel islands. Muskrats were trapped in the spring primarily for their pelts, but a few local residents trapped them for their meat as well.

Norway Rat (*Rattus norvegicus*): this introduced pest was common in the outports on New World Island but rare or absent on most of the other islands. I did observe rat sign on South Trump and Hummock islands, but the animals were definitely scarce.

House Mouse (*Mus musculus*): this species was also common in the villages on New World Island but otherwise rare. The only tracks I noted were on Black Island around an abandoned homesite during the winter of 1968-69.

Domestic Dog (*Canis familiaris*): small mongrel dogs known locally as "crackies" were numerous in the villages, but no sign was noted on the uninhabited islands.

Arctic Fox (*Alopex lagopus*): rarely a transient moved into the area on the arctic pack ice. A few years prior to my study an arctic fox lived on Glead Island (No. 14) for several months and visited the fishermen when they ate lunch ashore; the fox was killed when it approached the wrong fisherman.

Red Fox (*Vulpes fulva*): at times this species was very common throughout the study area, but at other times it was rarely seen. After freeze-up red foxes probably ranged over most of the islands. They were known to breed on several of the larger islands; I examined den sites on Yellow Fox and South Trump islands. During the field study I saw four foxes and examined an additional ten specimens which were trapped by local men. I noted the following colour phases among these foxes: 5 silver, 4 cross, 4 red and 1 black.

Black Bear (*Ursus americanus*): this species was rare in the study area. I received a few reports of bears on Chapel and New World islands, but I question the validity of these reports. I did find, however, fresh bear scat on a trail near North Harbour which is 3 km west of Exploits Island.

Ermine (*Mustela erminea*): E. Jenkins of Summerford reported weasels present on Chapel Island during the winter of 1967-68. I found sign of this species only on Upper Black, New World and Black islands. On the latter island in abandoned farm buildings, I discovered three weasel nests which were constructed of hay and bird feathers. An adult male and an adult female were captured at two of these nests; the male's nest was approximately 28 cm x 20 cm x 13 cm.

Mink (*Mustela vison*): eighteen animals were introduced to Chapel Island in 1950. I never observed mink or mink sign while in the field, but I did secure a specimen shot by J. Barnes of Summerford in December 1968 on the mainland west of Hummock Island; reputedly they were numerous in this region. L. Payne reported that a pregnant female was shot on Camel Island in April 1970.

Otter (*Lutra canadensis*): this species was fairly common among the islands in Bay of Exploits. I secured the skull of an adult specimen shot off Exploits Island in May 1969 and the carcass of a juvenile female which had drowned in a lobster trap near Camel Island on 3 June 1969. An otter slide was noted on Shag Cliff Island in summer 1967. On 15 January 1969 an otter swam into Sam Keefe's Cove on South Trump Island; the following day I followed an otter's trail through 1.5-m deep snow across the hills of South Trump Island. Earlier that winter I recorded otter tracks on Hummock and Upper Black islands. On several occasions in June and July 1969 an otter was observed fishing in Frog Martin Pond near Virgin Arm.

Domestic Cat (*Felis catus*): many animals resided in the outports and several roamed freely on New World Island, but I observed no sign of them on any of the other islands.

Harbour Seal (*Phoca vitulina*): in the past the islands of Dildo Run were the whelping grounds for a large population. Harbour seals, known locally as "dodders," rapidly began to dwindle in number about 10 or 15 years ago after the outboard motor came into popular use by the local fishermen. During the field study I never saw a specimen nor to my knowledge were any taken by sealers during the 1969 sealing season.

Ringed Seal (*P. hispida*): a few specimens were shot by sealers every spring. A. R. King of Cottle's Island who purchased most of the seal pelts taken by the men of New World Island (about 150 hunters) reported that he bought two adult ringed seals, known locally as "double jars," and five young, or "single jars," during spring 1969. I knew of two additional animals taken during that season. According to the sealers the ringed seal occasionally whelped on the low rocks off Exploits Island.

Harp Seal (*P. groenlandica*): this was by far the most common seal in the vicinity. Huge schools often numbering in the hundreds migrated through the study area in the spring. A. R. King reported that 1200 harp seals were taken in the vicinity of the study area during the spring of 1969. A few animals also migrated through the area during the winter; I obtained a "smutty harp" (see below) which was caught in a cod net off Glead Island on 24 January 1969.

Harp seals entered the bays and coves to feed on herring and other fish during the nights, but they headed out for the open sea as soon as they were disturbed by hunters in the mornings.

When hunted on the pack ice, seals were usually shot with rifles, but they were shot with breech-loading and muzzle-loading

shotguns when hunted from speed boats. Seals were also netted in cod nets set for this purpose at 40 to 60 fathoms; one fisherman reported that he had netted a harp seal at 190 fathoms.

The following is a list of names and age classes used by the local sealers when referring to this species:

1. "White coat": pure white natal coat, retained for first two to three weeks of life, pup confined to ice pan, weight approximately 10 kg.
2. "Raggy jacket": about three weeks old, pup in process of shedding natal fur, has left ice pan and entered sea, weight approximately 10 kg.
3. "Beater" or "young harp": four weeks to one year in age, has completely shed white coat, black-spotted pelt with silver-grey sides and venter and dark dorsum, pelt at most valuable stage of development, weight approximately 10 to 25 kg.

According to W. Boyde of Summerford, harp seals have whelped on the rocks off Exploits Island during the last few years due to a scarcity of pack ice in the vicinity, and, therefore, more "raggy jackets" and "beaters" have been shot than in the past.

4. "Nippy bellemmer": one-year old, pelt similar to "beater" except more silvery, weight approximately 35 kg.
5. "Two-year bellemmer": two years old, pelt similar to "nippy bellemmer," weight approximately 45 kg.
6. "Three-year bellemmer": three years old, pelt similar to "two-year bellemmer," weight approximately 55 to 70 kg.
7. "Turning harp": four years old, typical harp pattern beginning to form on dorsum, spots disappearing, weight approximately 75 to 85 kg.
8. "Smutty harp": considered by some to be variation of "turning harp," pelt all black with few brown spots, faintly visible black harp pattern on dorsum, sometimes confused with "blue hood" (*Cystophora cristata*).
9. "Old harp" ("dog" = male, "bitch" = female): five years or older, typical harp pattern present on dorsum, harp darker and more-pronounced on "dog" than on "bitch," weight approximately 110 to 180 kg.

Bearded Seal (*Erignathus barbatus*): usually one or two animals were shot every spring on the pack ice. C. Earle of Fairbanks East discovered the pelt of a bearded seal ("square flipper") on an ice pan near South Trump Island during the spring of 1968, but to his knowledge the seal had not been killed in the vicinity. A. R. King reported that he purchased the pelt of a young seal of this species in the

spring of 1969. His description of the seal, however, made me question his identification: about the size of a "bellemmer" harp with light and dark spots over the body and lacking a dark back. This specimen was possibly a young grey seal (*Halichoerus grypus*).

Grey Seal (*H. grypus*): this species was known by only a few sealers in the area. Reputedly it occasionally appeared in Green Bay which is approximately 55 km west of the study area. The animal reported by A. R. King as a "square flipper" may have been a grey seal.

Hooded Seal (*Cystophora cristata*): this species regularly bred on the pack ice many kilometres north of the study area. In some years the pack ice carried large schools of hooded seals into the Bay of Exploits; at such times this species was reported as far south as Lewisporte which is 17 km south of Camel Island. During many springs, however, these seals remained far offshore on the pack ice and rarely ventured into the study area. On 23 April 1969 I observed a single "young hood" (see below) along the edge of string ice 20 km north of the study area. A. R. King reported only one adult and four young taken by the sealers that spring.

The following are the names and age classes recognized by the local sealers for this species:

1. "White coat": unborn pup with prenatal white coat shed prior to birth.
2. "Young hood": pup born in spring, venter and sides pure white, dorsum silver-grey, about size of "two-year bellemmer." Unlike "bellemmer" harp seals, "young hoods" swim on bellies often exposing entire bodies including "scudders" (hind flippers).
3. "Blue hood": two-year old, entire body gun-blue.
4. "Hood": any hood seal three years or older.

Domestic Horse (*Equus caballus*): these animals were plentiful on New World Island where they were left to roam freely during the summer. Occasionally they were released on the islands in Dildo Run for the summer months. During the winter, horses were used for hauling firewood.

Domestic Pig (*Sus scrofa*): a few animals were raised in the region, but they were usually confined to small pens in the outports.

Moose (*Alces alces*): this species was common on the mainland especially west of the study area and occurred on some of the larger islands in Bay of Exploits and Dildo Run. During December 1968 I noted that four or five animals resided on Upper Black Island. Moose were occasionally seen swimming between the islands by the fishermen; in June 1968 I noted that one walked across Shellbird Island (No. 42) and then swam onto Inspector Island. Reputedly animals often occurred on Coal All (No. 27), Chapel and Dunnage (No. 75) islands,

but, due to the comparative ease of hunting moose on these islands, the populations were usually short-lived.

Caribou (*Rangifer tarandus*): the Newfoundland Wildlife Service introduced this species to Fogo Island, 20 km east of the study area, about 1963. On 17 July 1967 a buck in velvet was seen swimming from Farmers Island to the west end of Summerford, and later that day I saw him on the south shore of Farmers Island. This animal had undoubtedly emigrated from the Fogo Island herd. In former times caribou were seen on the bogs of the larger islands. S. Wheeler of Summerford told me that on one occasion more than 30 years ago approximately a dozen caribou were killed on a Chapel Island bog, but, since that time, none have resided in the study area.

Domestic Cow (*Bos taurus*): only a few animals were raised by the local residents and these were usually confined to the villages. An occasional cow, however, was released for the summer months on the uninhabited islands.

Domestic Sheep (*Ovis aries*): this species was commonly raised in the vicinity. Sheep were often seen roaming freely on New World Island. During the summer, some of the local residents also released their sheep on the uninhabited islands where they did considerable damage to the vegetation. About a dozen sheep resided on Glead Island during the summer of 1967, and ten were released on Inspector Island for the 1968 summer.

Domestic Goat (*Capra hircus*): these animals were raised by a few local residents. They were released on the uninhabited islands during the summer and, on a few islands, did considerable damage by overgrazing. Ten goats were released on Inspector Island during the 1968 summer.

White-Sided Dolphin (*Lagenorhynchus acutus*): these animals, known locally as "jumpers," were often reported in large schools in Friday Bay. I observed a school of at least 20 individuals leaping vertically out of the sea to a height of two or three metres on 26 October 1968 near Twillingate Island. I also noted a single individual near South Trump Island on 14 July 1969.

Pothead Whale (*Globicephalus melaena*): during the summers, local residents sometimes drove schools into the shoal waters of Dildo Run where the whales were butchered. Reputedly they were common in the area, but I never saw any during the field study. W. O. Pruitt found part of a skull on Inspector Island on 25 May 1966 and scraps of a carcass on island No. 53 on 12 June 1966.

Common Porpoise (*Phocoena phocoena*): this species was occasionally seen by fishermen in the study area. On 2 September 1968 I observed three common porpoises surfacing near Glead Island.

Common Finback (*Balaenoptera physalus*): this animal used to be commercially hunted from the whaling station near Port Albert which is about 4 km east of the study area. A skull of this species was noted on the beach at the deserted whaling station in 1967. These whales were occasionally seen by fishermen in Bay of Exploits and

Friday Bay. In the summer of 1968 the tail of a finback floated into Friday Bay. I was told that this animal had been killed off the northeast shore of New World Island.

Other Whales: B. J. Lincoln observed a whale approximately 15 m in length surfacing near Yellow Fox Island on 4 July 1968; it may have been a small finback or possibly a sei whale (*B. borealis*). On 5 July 1968 a whale about seven to nine metres in length surfaced three times only 30 m from me while I stood on the shore of Mile Island. This whale may also have been a sei, but I was not positive. Undoubtedly other species of whales occurred in the study area, but I never recorded them.

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