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Ecology

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POPULATION BIOLOGY AND ENERGETICS OF THREE SPECIES OF SMALL MAMMALS IN THE TAIGA OF INTERIOR ALASKA

A

DISSERTATION

Presented to the Faculty of the
University of Alaska in Partial Fulfillment
of the Requirements
for the Degree of
DOCTOR OF PHILOSOPHY

By
Paul H. Whitney, A.B., M.S.
Fairbanks, Alaska
May 1973

POPULATION BIOLOGY AND ENERGETICS OF THREE SPECIES OF SMALL MAMMALS IN THE TAIGA OF INTERIOR ALASKA

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ABSTRACT

Small mammals were trapped on six grids in the taiga woods near Fairbanks, Alaska. Live traps were checked at two-week intervals during the snow-free months and four-week intervals when snow was on the ground. The Steese *Microtus oeconomus* population reached a peak of 73 to 83 animals per hectare in September 1969. Numbers declined the following winter and no *Microtus* were captured until 1972 when the population density began to increase (Feist, pers. comm.). A sympatric population of *Clethrionomys rutilus* was not cycling and reached densities of 50 to 60 animals per hectare each year of the study. The density of *Zapus hudsonius* was usually 20 to 30 animals per hectare during June and July. Wet weight production for all three species was high when compared to production of other areas.

Survival was good for female *Microtus*, while female *Clethrionomys* had several periods of poor survival. In males, periods of low survival occurred during increasing and peak populations; these periods of low survival did not occur at the same time in both species. Nesting survival was poor in both microtines in July 1969, but remained low for the whole breeding season for *Microtus*.

Growth rates were maximal during different seasons for each year. Positive growth rates for the *Clethrionomys* population during January 1971, under 120cm of snow at -8°C subnivean temperatures cannot be explained by conventional physiological cause and effect relationships.

Average Daily Metabolic Rates were measured at regular intervals over a two year period. Winter and spring mean ADMR's ranging from

6.79 to 9.24 $ccO_2/g/hr^{-1}$ for the two microtines are twice estimated values reported in the literature. Seasonal maintenance productivities show that peak values for the Microtus (spring and summer 1969, 45 x 10^3 kcal per season per grid) were nearly equal to the peak values for the Clethrionomys (winter 1969-70, spring 1971, 47 x 10^3 kcal per season per grid).

Total body fat, water content and caloric value of fat and fat-free dry weight were also measured in order to calculate yearly caloric net production for natal, nestling and weaned animals. Nestling net caloric production for the Steese Clethrionomys population during 1969, 1.04 x 10^3 kcal per grid, made up more than 70 per cent of the yearly net production 1.49 x 10^3 kcal per grid. Nestling net caloric production for the Steese Microtus population during 1969, 2.32 x 10^3 kcal per grid, made up more than 60 per cent of the yearly net production, 3.89 x 10^3 kcal per grid. These values are very high in comparison to values in other habitats.

Niche dimension and breadth were investigated for the two microtines. The C. rutilus population in the Fairbanks area has a broad niche and is variable in several morphological, physiological and ecological characteristics. The M. oeconomus population, on the other hand, has a narrower niche and is more specialized than the C. rutilus population. It is hypothesized that niche breadth and dimension are a determining factor for microtine cycling. Current concepts of ecological productivity are also discussed and it is shown that current energy flow theory was inadequate for complete interpretation of results.

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INTRODUCTION

Ecology is now accelerating through a phase of descriptive energetics. Energetics of small mammal populations have been studied in many of the world's biomes: deciduous forests (Grodzinski, 1961; Drozdz, 1966), old-field grasslands (Golley, 1960; Odum et al., 1962); French, 1970), desert (Chew and Chew, 1970), subarctic taiga (Grodzinski, 1971), and arctic tundra (Pitelka, 1973). While ecosystems and their components have been related in numerous ways, the energy flow approach is said to be one of the most applicable because it provides a unifying framework. As a means of expressing the productivity of an individual organism or of all the organisms within an ecosystem, energy flow permits comparison of productivity within and between various ecosystems. Unfortunately, few studies have been able to interpret the comparisons. Problems facing the energetics ecologist are many, ranging from non-standardized techniques to a strong bias on the part of many that energetics is the basis of all ecosystem phenomena. In short, there has been little attempted to integrate other levels of ecology to help with ecosystem analysis.

Several works have served as invaluable reviews of the material with which we are concerned in this study. The Proceedings of the IBP Meeting on Secondary Productivity in Small Mammals (1971), Ecology: the Experimental Analysis of Distribution and Abundance (Krebs, 1972), Productivity of Terrestrial Animals (Petrusewicz and Macfadyen, 1970), and Population Cycles in Small Mammals: A Review (Krebs and Myers, 1973) have served as a base line to which I have continually referred.

In spite of the voluminous amounts of material in these reviews, I have noticed that physiologists often explain phenomena without reference to natural habitat, population biologists often attempt to explain variation without regard to physiological principles, and, moreover, few ecosystem ecologists attempt to explain variability in terms of the basic physiology and demography that regulate production dynamics. This study is based on the assumption that ecosystem properties, such as stability, cannot be completely understood from the energetics approach alone. Every existing ecological pattern may be presumed to have survival value under certain environmental conditions, and Cole (1954) concludes that the study of these adaptive values represents one of the most neglected aspects of biology. While time and space prohibit discussion of all possible ecological patterns, I have attempted to examine parameters of interest to the physiologist, population and ecosystem biologist.

The four main objectives of this research were: first, to describe the dynamics of energy flow in three species of small mammals, Clethrionomys rutilus, Microtus oeconomus and Zapus hudsonius; second, to describe the demographic changes which occur in these taiga small mammals and to relate these parameters to general population theory; third, to examine physiological processes in relation to theory developed for subarctic adaptation; and fourth, to integrate the first three objectives into an ecological strategy for taiga small mammals.

Figure 1. Location of Steese Highway grids, snap trap lines, plant sampling stations (circled numbers) and climatological stations. Grids A, B and E are live trapping grids and Grid F was snap trapped.

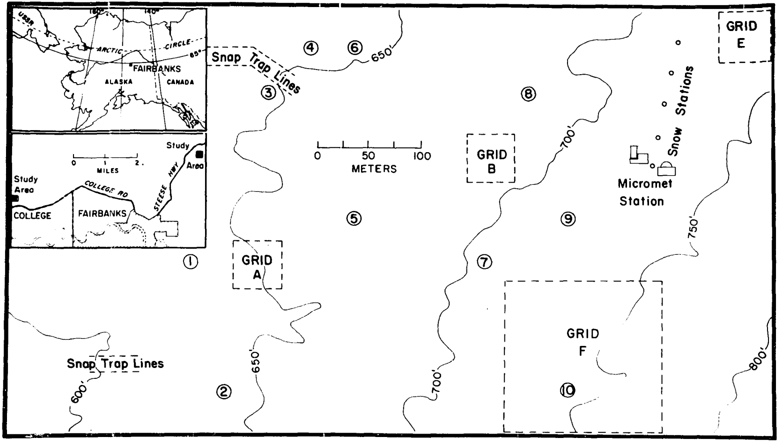
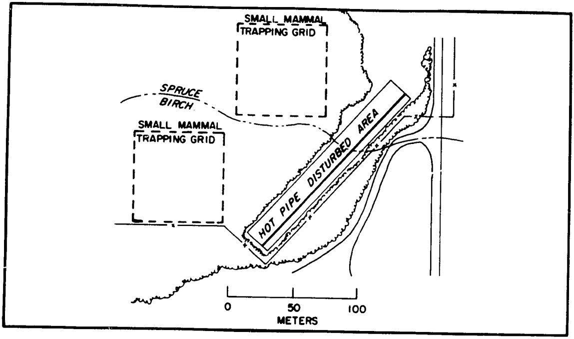

USSR
160°
140°
ARCTIC CIRCLE
65°
FAIRBANKS
ALASKA
CANADA
0 1 2.
MILES
Study Area
Study Area
COLLEGE RD
STEESE HWY
COLLEGE
FAIRBANKS
Snap Trap Lines
④
⑥
650'
③
⑧
GRID E
Snow Stations
0 50 100
METERS
GRID B
700'
Micromet Station
⑤
⑨
750'
①
GRID A
⑦
GRID F
Snap Trap Lines
650'
800'
700'
600'
②
⑩

Figure 2. College grids in relation to the hot pipe disturbed area, birch and spruce habitats.


SMALL MAMMAL
TRAPPING GRID
SPRUCE
BIRCH
SMALL MAMMAL
TRAPPING GRID
HOT PIPE DISTURBED AREA
0
50
100
METERS

METHODS

Data have been collected in such a way that, with minor modifications, they can be applied to the three main levels of ecology: the individual, the population and the community. While the data are applicable to these levels of ecology, detailed procedures necessarily obscure the overall picture of energy flow.

Whenever possible, methods recommended by the International Biological Program (IBP) have been employed. For those techniques not covered by the IBP, I have used accepted methods from the literature.

Climate and Study Area

The interior basin of Alaska where Fairbanks is located (Fig. 1) is generally described as having a continental climate (Watson, 1959) where extremes in nearly all climatic elements occur (Frost, 1934). Yet there is a striking climatic unity within the region exemplified by the correspondence of warm and cold periods at different stations throughout the area (Streten, 1969). On the mean climate maps the interior basin appears as the most extensive region of extremely low mean winter temperatures in the United States and provides a striking contrast to the milder winter temperature regimen of both southcentral Alaska and the Arctic Slope of the Brooks Range (Trabant, 1970).

The mean annual temperature is -3.4°C; July, the warmest month, has a 15.5°C mean temperature, and January, the coldest month, a -23.9°C mean temperature. Precipitation is low, with a yearly average of 28.7

cm, with a maximum in late summer (5.6 cm in August) and a minimum in late winter (0.6 cm in April). Annual snowfall averages 151 cm with an average accumulation of 74.4 cm. Snow is present on the ground for approximately six months. Early snowfalls in late September are not unusual. Snows falling after early October usually persist for the entire winter.

The regional vegetation of interior Alaska consists of stands of white spruce (Picea glauca) on both well drained soils and south facing slopes, with black spruce (P. mariana), larch (Larix laracina), and bogs on poorly drained lowland soils and on north facing slopes. Fire has been an important environmental factor, consequently, successional stands of quaking aspen (Populus tremuloides) and Alaska paper birch (Betula papyrifera) are common throughout the area (Viereck, 1970).

This study was carried out on three areas north of Fairbanks. The primary study area was located near 3 Mile Steese Highway (Fig. 11, 12 and 13) (SW 1/4, SE 1/4 Sec. 26, TIN, R1W, Fbxs. M.). This open birch area is typical of a middle (forty to sixty years since a fire) stage in forest succession. Similar areas are of widespread occurrence on the well drained uplands in the Chena Valley (Lutz, 1956). Ground cover (Fig. 11) was mostly blue-joint (Calamagrostis canadensis), bunch berry (Cornus canadensis), cranberry (Vaccinium vitis-idaea), horsetail (Equisetum sp.), prickly rose (Rosa acicularis) and fireweed (Epilobium sp.). On the southwest edge of the study area, the birch woods and under cover are abruptly replaced by black spruce with a ground cover of Labrador tea (Ledum groenlandicum), cranberry, and Sphagnum sp. moss. Excepting this lower edge, the area was typical south facing birch woods.

The Red Fox Area (approximately two miles north of the University) was similar to the Steese Highway Study Area. The only obvious difference was the predominance of highbush cranberry (Vibrnum edule).

Unlike the open Steese and Red Fox Area, the College Area (Fig. 6) was dominated by four arboreal species, with little opening between the crowns. A detailed cover and abundance analysis of the vegetation types on the College Study Area was done during the summer of 1970 (Anderson, 1970). The trees form a gradient from paper birch to black spruce and white spruce. The ground cover (Fig. 16) in the College Area birch stand was similar to the Steese Area, but lacked the blue-joint. Ground cover in the spruce woods was similar to the bog area on the Steese. The College Area was slightly north facing and underlain with permafrost. All areas were on the Minto Soil Series.

In addition to the small rodents, the following mammals were observed on the Fairbanks plots: Sorex cinereus, Sorex arcticus, Mustela rixosa, Mustela erminea, Vulpes fulva, Lepus americanus, Alces alces, Tamiasciurius hudsonius. Many species of small passerine birds were present and captured in live and snap trapping operations. Ruffed (Bonasa umbellus) and spruce grouse (Canachites canadensis) were common. The only predatory bird observed on the study areas was a single great horned owl (Bubo virginianus). Following the late summer rains, wood frogs (Rana sylvatica) were captured in snap traps.

Solar Radiation

Solar radiation was measured on the Steese Study Area (Fig. 1) during the 1970 growing season using a Weather Measure Mechanical Pyanograph which was placed in an open area with an unobstructed view of the sky. Additional records of solar radiation for all three years were obtained from Richard Barney of the Institute of Northern Forestry, University of Alaska.

Temperature

Air temperature and micro-environmental temperature in the areas utilized by small mammals were measured on the Steese Area from November 1969 to June 1971, using a Weather Measure Remote Two Point Thermograph. When snow was present, one probe was placed on the snow surface and the other was placed on the ground surface in the subnivean space. During the snow free time of the year, one probe was placed on the top of the litter layer and the other was placed in an apparently active runway.

Spacial variability in temperature was studied during the winters of 1969-70 and 1970-71. During the preceding summers, five Yellow Springs Instrument Company thermistors were placed in apparent runways, one at each of the five show stations on the Steese Area. The thermistor wires led from the runways and were tied to nearby trees above the anticipated snow line. Every two weeks subnivean runway and snow surface temperatures were measured. During the last half of the 1970-71 winter one thermistor tied in a birch tree was removed by a browsing moose, consequently data were taken from four stations for the rest of the winter.

Snow and ground surface temperatures at the College site were measured with a Yellow Springs Instrument Company Telethermometer at weekly intervals.

Snow Morphology

Snow measurements were made on the Steese study area with instruments designed by the Associate Committee on Soil and Snow Mechanics of the National Research Council of Canada (Klein *et al.*, 1950). Similar instruments have been used by Fuller *et al.* (1969) and Lent and Knutsen (1971). Snow hardness (break through pressure), snow density and snow depth were measured every two weeks (temperature permitting) at each of the five locations (Fig. 1). Care was always taken to sample in undisturbed areas.

On the College Study Area snow depth was measured every week. One snow density profile was made by Dr. Gunter Weller of the Geophysical Institute, University of Alaska, during the 1970-71 winter.

Live Trapping

Small mammal trapping was carried out in three general locations (Fig. 1). Four grids, A, B, E and F, were located on the 3 Mile Steese Study Area. Grid G was located approximately two miles north of the University on Red Fox Drive (Not shown on Fig. 1). Grids C and D were adjacent to the Biological Science Building on the West Ridge of the University of Alaska Campus. Each area was trapped according to the schedule in Table 1.

Table 1. Details of grid size, location and duration of trapping.

Location	Vegetation	Type of Trapping	Size and Interval	Number of Traps	Dates Trapped*
Grid A 3 Mile Steese	Open Birch	Live	100 stations at 5M intervals 64 stations 5M intervals	100-150 64	2 wk. intervals in snow free periods 4 wk. intervals when snow was present 1968-1971
Grid B 3 Mile Steese (control)	Open Birch	Live	100 stations at 5M intervals	100-150	2 wk. intervals in snow free periods 1969-1970
Grid E 3 Mile Steese (control)	Open Birch	Live	100 stations at 5M intervals	100	2 wk. intervals in snow free periods 1970
Grid F 3 Mile Steese	Open Birch	Snap	256 stations at 10M intervals	512	August 1969, May 1970 September 1970
Grid G Red Fox Drive (control)	Open Birch	Live & Snap	64 stations at 5M intervals	64,64,128	July 1969, June 1970 August 1970
Grid C College	Closed Canopy Birch	Live	64 stations at 10M intervals	64	2 wk. intervals in snow free periods 4 wk. intervals when snow was present
Grid D College	Spruce	Live	64 stations at 10M intervals	64	2 wk. intervals in snow free periods

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* Exceptions:
1) Did not trap when temperatures were below -30°C.
2) Did not trap January 1969 - March 1969.
3) Did not trap June 1970 - July 1970 due to road construction
4) Did not trap during some periods of the record snow fall of 1970-71.

Live trapping procedures were modeled after those of Krebs *et al.* (1969). Sherman traps (3 inch) were used in conjunction with nest boxes made from 48 oz tin juice cans (Fig. 6). These cans were squared off to fit onto the end of a Sherman trap with the back door removed. Insulation was provided by placing a 15 oz tin can inside the larger can and blowing polyurethane foam between them. A foam plastic coffee cup was inserted inside the smaller can to prevent the animals from making contact with the metal surface of the inner nest box.

Rolled oats were used for bait and the nest boxes were supplied with a half handful of grain and mattress cotton. All traps were covered by plywood squares (20 cm x 20 cm) (Fig. 5 & 6). These boards kept the traps cool in the summer and provided a subnivean space in front of the trap opening in the winter. Prebaited traps locked open with tongue depressors were left out on all grids. Traps were usually set within one meter of each station. When runways could not be found near the stake, traps would be moved up to two meters away. One or two traps were placed around each stake depending on animal density. No systematic attempt was made to move the trap after each capture. Each area was trapped for 2-4 days at the intervals noted in Table 1. At first capture each mouse was individually tagged in its right ear with a numbered fingerling fish tag. The following information was taken each time an animal was captured: tag number, location on grid, weight to the nearest gram and sex. Position of testes was recorded for the males and vagina perforate or not, nipple small, medium or large, pubic symphysis closed, slightly open or open for females. Records of ectoparasites and morphological variations were noted. If the mouse was recaptured during the same trapping period, only its tag number and location were recorded. These data were punched on IBM cards. A series of computer programs (Krebs, 1968) were used to analyze the data.

Snap Trapping

Grid F, on the Steese Study Area (Fig. 1), was sampled three times using the Standard-Minimum Method (Grodzinski, et al., 1966). Victor and Museum Special mouse traps (both seemed to be equally effective) were baited with peanut butter and two traps were placed unset at each station for five days. On the sixth day the traps were set and checked for five more days. Captured animals were placed into plastic bags and frozen.

Grid E on Red Fox Drive was snap trapped for five days starting August 26, 1970. The same prebaiting and checking procedure was used.

Eight other removal trap lines were run at various times and locations (Table 2). These areas were trapped to acquire additional animals for autopsy, to assess movement of tagged animals, to evaluate new areas for species composition and to provide animals for other laboratory studies at the Institute of Arctic Biology.

Autopsy

Snap trapped animals were kept frozen until autopsy. Each animal's body weight, adrenal weight, stomach weight and the following reproductive indices were recorded:

Table 2. Non-grid trapping sites. Dates and numbers of animals captured per session.

Location	Trapping method used	Date	Animals Captured
Steese 1	Live	July 11, 69	2 *Zapus* 9 *Microtus oeconomus*
Steese 2	Live	July 25, 69	1 Shrew 5 *Zapus* 7 *Microtus oeconomus* 4 *Clethrionomys*
Steese 3	Snap	Oct. 29, 69	2 *Microtus oeconomus* 2 *Clethrionomys*
Smith Lake 1 (College)	Snap	Oct. 31, 69	1 *Microtus pennsylvanicus* 10 *Clethrionomys*
Steese 1	Snap	Dec. 10, 69	Zero
Steese 2	Snap	Feb. 15, 70	Zero
Steese 3	Snap	Mar. 26, 70	Zero
Steese 4	Snap	Apr. 14, 70	1 Shrew
Deer Yard 1 (College)	Snap	July 1, 70	10 *Clethrionomys*
Smith Lake 1 (College)	Snap	July 17, 70	1 *Zapus* 10 *Microtus oeconomus* 5 *Clethrionomys*
Steese 1	Live	Aug. 20, 70	5 *Zapus* 2 *Clethrionomys*
Smith Lake 2 (College)	Snap	Aug. 22, 70	11 *Microtus oeconomus* 14 *Clethrionomys* 2 *Microtus pennsylvanicus*
Deer Yard 2 (College)	Live	Aug. 30, 70	5 *Clethrionomys*

For Females:

1. nipple size and lactation tissue: small, medium, large.
2. pubic symphysis: closed, slightly open, open.
3. vaginal orifice: perforate or not perforate.
4. placental scars: number.
5. embryos: number, crown-rump length of all embryos.
6. uterus: weight.
7. corpora lutea: number.

For Males:

1. testes: paired weight.
2. epididymis: large or small

Average Daily Metabolic Rates

Average daily metabolic rates (ADMR) (Grodzinski, 1966) were measured in *Microtus oeconomus*, *Clethrionomys rutilus*, and *Zapus hudsonius*. Animals were removed from the live trapping grids, brought into the laboratory, placed into the respirometer and at the end of the run returned to their capture station in the field. Most of the animals spent 48 hours in the metabolic chamber but a few were allowed to remain up to 96 hours. Voles were sampled from April 1969 to March 1971. Depending upon availability, eight animals of each species were measured each season.

Morrison respirometers in conjunction with an Esterline Angus recorder (Morrison, 1951) were used to determine ADMR's for 122 animals. The animal cages constructed of 1/8 inch stainless steel mesh were placed in stainless steel metabolism chambers and submerged in a constant temperature bath. The animals were supplied with rolled oats, water and cotton batting stuffed inside a No. 303 tin can. Stainless steel screen baskets filled with Barylyme, to absorb CO_2, lined two sides of the chamber. A stainless steel tray covered with 8 mesh calcium carbonate was placed under the cage to prevent excessive water vapor build up. For each run, ambient temperature (the water bath) and photoperiod (a fluorescent light) were set to simulate the field conditions from which the animals had just been removed. Due to the large incidence angle of solar radiation at Fairbanks, two hours were added to the true sunrise and sunset to simulate twilight time. The temperature of the bath was determined from subnivian and ground temperatures that were taken simultaneously in the field. Since the bath was not able to maintain temperatures much below -15°C, ADMR's were not measured during January 1970, when temperatures under the snow fell to -30°C.

Continuous nest can temperatures were recorded at the time ADMR's were being measured. The nest box was equipped with two thermocouples linked to a recorder. One thermocouple wire was taped to the roof of the nest box with the sensor bent at a right angle penetrating approximately one centimeter into the cotton nesting material. The other thermocouple was taped to the outside of the nest box with the sensor approximately four centimeters away from the nest can.

Freeze drying, Fat extraction and Calorimetry

Ninty-eight animals were subsampled for freeze drying and fat extraction. Animals, minus stomach contents, were cut into small (approximately 1 cm^3) pieces and freeze dried to a constant weight. The dry pieces were placed in extraction thimbles and subjected to petroleum ether soxhlet extraction (Odum et al. 1965) for eight hours. Following extractions the thimbles were dried at 80°C for six hours and reweighed.

Twenty-six animals were subsampled from the freeze dried animals for bomb calorimetry. Fat free pieces were ground in a Wiley Mill, made into pellets and bombed in a Parr Bomb Calorimeter. Ether was evaporated from the soxhlet extract sample under a stream of Nitrogen at 40°C. A Phillipson (1964) microbomb calorimeter enabled caloric determinations of pure fat. Acid corrections were made according to the usual procedure in bomb calorimetry.

Figure 3. Open paper birch stand, Grid A, February 1970. There was very little snow fall this winter. Note fireweed and grasses above the snow level. Sherman trap is being broken away from home-made nest box and contents are emptied into a bucket for processing.

Figure 4. Open paper birch stand, Grid A, April 1971. Snow has covered stakes seen in the following picture. No grasses or other herbage can be seen above the snow pack. Home-made scale designed by C. Krebs and B. Keller weighs a _Clethrionomys_ to the nearest gram.

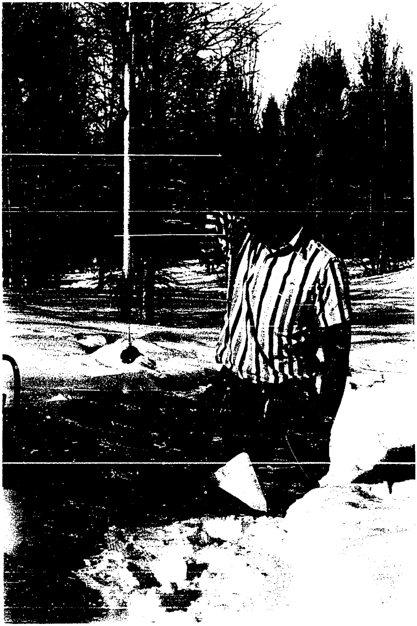

Figure 5. Open paper birch stand, Grid A, August 1970. Traps under boards can be seen next to the stakes. When snow falls, bending grasses over, more cover is provided in the subnivean space than in the dense paper birch stand (Fig. 6).

Figure 6. Dense paper birch stand, Grid C, September 1970. Sherman trap can be seen under board at trapping station. Ray Kendell holds two nest boxes (page 26) that have been squared off to fit onto the end of the trap.

RESULTS

Solar Radiation

Continuous records of solar radiation measured on the Steese and College* sites are presented in a condensed form (Table 3). It should be noted that these values are from pyanographs in open fields, hence representing maximum solar input. Since the College sites are entirely covered by tree canopy the actual energy influx should be modified accordingly when calculating primary productivity efficiencies in this area. The main purpose for giving data from two sites is to compare area wide variability in relation to yearly variability.

Table 3. Solar radiation summary. Solar radiation (wave lengths available to plants) in g cal/cm^2/day from Steese and College areas. All values are means, ± 1 standard deviation, calculated over approximately two weeks.

		May		June		July		August	
Area	Year	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-31
Steese	1969	-	-	531±124	506	435	361±127	-	-
Steese	1970	489	552	506±137	474	501	431±160	366	295±90
College*	1969	-	-	523±114	536	454	374±140	362	361±80
College*	1970	-	541	470±117	452	477	425±125	392	290±76
	Means	480	546	508	492	467	397	373	315

These values show general trends of maximum solar input from the end

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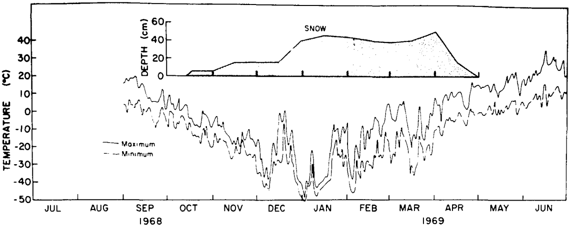
* College values were measured 1/2 mile north of the Grids C and D by R. Barney, Institute of Northern Forestry, University of Alaska.

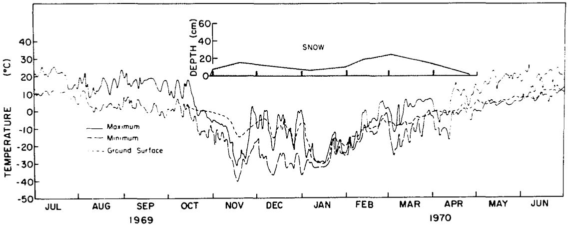
of May to the first of July. Smoke, due to forest fires, occurred over most of Alaska in July 1968, and is responsible for the decrease in values on both areas. The variation of these data due to cloud cover and smoke was large enough so that there is no significant difference between the mean values between areas and years for July 16-31 (F = 0.96, df = 2,56). While the variation in solar radiation decreased during the seaso (see August standard deviations vs June and July) the one F-test from July justifies lumping both years and sites together (see means Table 3). It is far more important to consider the variation in utilization due to annual differences in phenology. For example, birch leaves were out in late April, 1969, but were delayed until the third week in May, 1970. The start and end of the growing season is a very difficult parameter to determine considering the many species present, but based on the birch data and my other phenological notes, the growing season started at least two to three weeks earlier in 1969 than in 1970. The overall growing season, however, was not longer in 1969 since it ended two to three weeks earlier, as judged by coloring of fire weed and equisetum (i.e. lack of chlorophyll) and minimum daily temperatures below freezing (see Fig. 7). It could be significant to the mouse population that solar energy was being utilized for primary productivity two weeks earlier in 1969 than in 1970.

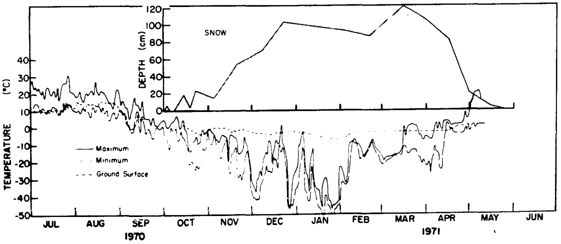
Temperature

Temperature data are analyzed in four periods of significance to small mammals: plant growing season, fall freeze-up, full winter and

Figure 7. Yearly maximum, minimum and ground surface temperatures in relation to existing snow pack. (a) = 1968-69; (b) = 1969-70; and (c) = 1970-71.


TEMPERATURE (°C)
40
30
20
10
0
-10
-20
-30
-40
-50
DEPTH (cm)
60
40
20
0
SNOW
Maximum
Minimum
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
1968
1969


TEMPERATURE (°C)
40
30
20
10
0
-10
-20
-30
-40
-50
DEPTH (cm)
60
40
20
0
SNOW
Maximum
Minimum
Ground Surface
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
1969
1970


TEMPERATURE (°C)
40
30
20
10
0
-10
-20
-30
-40
-50
DEPTH (cm)
120
100
80
60
40
20
0
SNOW
Maximum
Minimum
Ground Surface
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
1970
1971

spring thaw.

Plant growing season:

Continuous temperature data recorded on the Steese Area are shown in Figure 7. Temperatures during the 1969 and 1970 summers were essentially the same with the June 1969, being warmer than June 1970, and July 1969, being cooler than 1970.

Fall freeze-up:

Fall temperatures seem to be different between years. In 1968 the freeze-up was gradual with considerable freezing and thawing (Fig. 7). One should also note that ground and air temperatures fluctuated in unison during this period. By the time daily maximums dropped below 0°C, snow was on the ground. The 1969 freeze-up was rapid in comparison and was preceded by a warm September and October. When daily temperatures first fell below 0°C there was no snow on the ground. The following fall, 1970, like 1968, was gradual with freezing and thawing during the time of early snow falls. As can be seen in Figure 7, snow was accumulating by the time daily maximums dropped below zero.

The 1969-70 winter was one of the warmest on record while the winters before and after set many record low temperatures. Minimum daily temperatures fell below -40°C only on one day during this warmer winter while the previous and following winters had 25 to 30 days with below -40°C temperatures.

Another difference between the winters was the frequency of 0°C or above temperatures. After November, the number of thaws were five, ten, six for the three successive winters or about twice as many thaw conditions in the 1969-70 winter than in either of the other two.

Full winter:

During the 1970-71 winter, cold temperatures at the air snow interface were not accompanied by cold temperatures at the ground surface (Fig. 7 and 8). Warmer ground surface temperatures were also experienced during the 1968-1969 winter (Fig. 7a). During the 1969-70 winter which was relatively mild, the ground surface temperatures were relatively colder due to poor snow conditions. In mid-January 1970, when snow surface temperatures fell to -33°C, the temperature of the subnivean space was -30°C (Fig. 7b). In January 1971 surface temperatures fell to -52°C but the subnivean temperature fell only to -7°C (Fig. 7c).

Bi-weekly temperature measurements taken when snow was sampled are shown in Tables 4a and 4b. Temperatures were quite variable with subnivean temperatures often ranging six to eight degrees depending on the sample location along the transect. When comparing these data to the continuous records of temperature taken at the same time in an adjacent location, there were several days when the range of biweekly temperatures did not include either the maximum or minimum that were being continuously recorded, thus indicating subnivean temperature heterogeneity.

Spring thaw:

Spring temperatures in all three years showed similar mid-April fast warming trends. However the first two spring break-ups were markedly different from that of the last spring, in that maximum

Table 4a. Snow morphology and temperature data measured at the five stations on the Steese Area, 1969.

Date	Density			Hardness (gm/cm^2)			Temperature (°C)				
		Surface	Subsurface		Surface	Subsurface		Supranivean	Subnivean		
	N	$\bar{x}$	$\bar{x}$	N	$\bar{x}$	$\bar{x}$	N	$\bar{x}$	$\bar{x}$	Max	Min
Oct 18	1	0.09	-	1	0.5	-	5	9	2	3	1
Nov 1	15	0.08	-	15	0.5	-	5	1	-4	0	-7
Nov 18	12	0.11	-	15	0.5	-	5	-31	-15	-12	-19
Dec 6	15	0.16	-	15	14	-	5	-6	-4	-3	-5
Dec 21	15	0.17	-	15	12	-	5	-12	-11	-9	-12
Jan 5	15	0.18	-	3	5	22	5	-22	-14	-12	-16
Jan 28	15	0.16	-	15	2	-	5	-25	-16	-13	-21
Feb 11	10	0.16	0.18	3	33	10	5	-5	-7	-6	-8
Mar 2	10	0.17	0.20	3	700	47	5	-14	08	-7	-9
Mar 11	11	0.20	0.20	13	850	53	5	-7	-5	-3	-7
Mar 27	1	0.41	-	1	40	-	2	9	3	5	1
Apr 12	10	0.31	-	5	88	-	5	6	1	1	0

Table 4b. Snow morphology and temperature data measured at the five stations on the Steese Area, 1970.

Date		Density			Hardness (gm/cm^2)			Temperature (°C)			
		Surface	Subsurface		Surface	Subsurface		Supranivean	Subnivean		
	N	$\bar{x}$	$\bar{x}$	N	$\bar{x}$	$\bar{x}$	N	$\bar{x}$	$\bar{x}$	Max	Min
Oct 9	-	-	-	-	-	-	5	2	1	2	0
Oct 22	15	0.11	0.18	15	1	39	5	-15	-3	-1	-7
Nov 4	15	0.18	-	15	54	-	-	-	-	-	-
Nov 20	10	0.08	0.25	15	2	87	1	-8	-2	-	-
Dec 7	10	0.10	0.24	15	530	480	5	-7	-29	-26	-30
Dec 22	5	0.13	0.31	6	6	380	5	-2	-2	-1	-3
Feb 3	4	0.11	0.22	8	1	180	2	-30	-6	-6	-6
Feb 17	10	0.10	0.22	10	4	290	4	-6	-5	-2	-10
Mar 16	5	0.12	0.25	12	7	300	4	2	-4	-3	-7
Mar 31	10	0.16	0.24	16	7	640	4	-5	-5	-2	-8
Apr 16	2	0.40	0.48	9	1600	150	4	2	0	0	-1

temperatures following break-up in 1971 remained close to freezing for several weeks and reached 15°C three weeks later than in the previous springs. Temperature data collected at the College Area varied little from those at the Steese Area.

Temperature values for the three years can be summarized as follows: the second winter, even though one of the warmest on record, was probably the most severe for animals living under the snow. Fall freeze-ups were similar, but twice as much freezing and thawing occurred during the 1969-1970 winter. Cool temperatures in April 1971 delayed the spring thaw by three to four weeks.

Snow Morphology

Depth:

Snow cover values for the 1968-69 winter were taken from the Fairbanks Airport Local Climatological Data Sheets published by the U.S. Department on Commerce (Fig. 7a). The validity of comparing Airport snowfall to the Steese snowfall was evaluated by comparing data for one subsequent year on both areas. Results of such comparisons show good correlation with differences in depth never being more than 5 cm for any two week period. Early snow accumulation in 1968-69 was slow, with mid-December snow developing a 45 cm cover that was only slightly increased to 50 cm in late March. While this winter was particularly cold after the first of the year (record lows, -56°C, were set during the first two weeks of January), the average snow accumulation kept subnivean temperatures above -10°C (Fig. 7a).

Field snow measurements were started on the Steese Area in late October 1969. Initial accumulations were similar to the previous winter, however additional snow did not fall during the coldest part of the year. The cover decreased to 6 cm, resulting in little insulation for the subnivean space during the coldest part of the year. New snow in mid-February was exposed to much freezing and thawing and the eventual maximum cover was only one half the depth of the previous winter (Fig. 7a and 7b). All of the snow was gone by the end of April, similar to the previous year.

In contrast to the 1969-70 winter, when the lightest snowpack on record was measured in interior Alaska, the winter of 1970-71 may well be marked as the season of heaviest snow cover for many years. An early October snowfall melted within four days but by mid-October, enough snow had fallen, melted and fallen again to equal the greatest depth of the year before. Snow continued to come in copious amounts on all but the coldest days until maximum depth, 118 cm, was reached in mid-March. This depth was five to six times that of the previous year and well over twice the 1968-69 winter. Cool weather during April prolonged the period of snowmelt and all of the snow did not disappear until late May, nearly a month later than in the previous years.

Snow depths on the College Area averaged within 6 cm of those on the Steese and therefore snow depths on these two areas will be considered the same.

In summary, snow depths over the three years studied varied from a record minimum in 1969-70 to a record maximum in 1970-71, with an average snowfall in 1968-69.

Density:

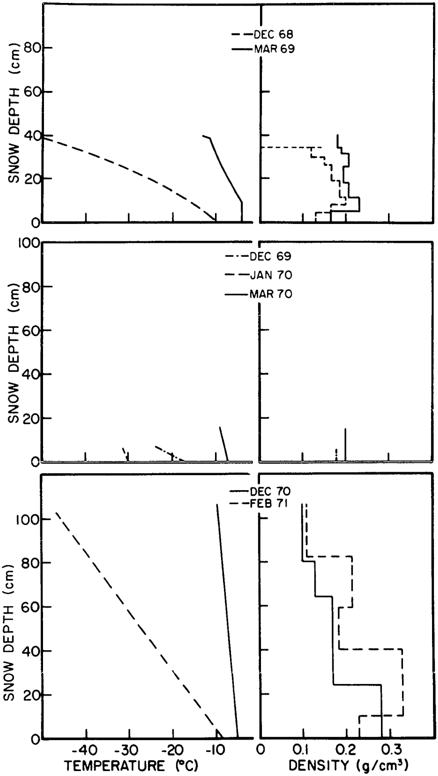
Snow density and snow density profiles are the most useful measurement made during the snow sampling. They are considered to be useful measurements because density is related to many aspects of snow morphology: structural aspects of snow cover, insulation, shape and packing of grains and modification of the structure by melt.

Density was not measured during the 1968-69 winter. Trabant (1970) who made measurements at nearby locations in Fairbanks (Goldstream Valley), summarized his intensive work for the 1968-69 winter with the following generalization. There were few melts (i.e. crusts), which resulted in a uniform insulative layer of low surface density and (well developed) hoar frost formation. Temperature gradients indicate that the snow cover provided excellent insulation with -50°C temperatures at the surface and -7°C temperatures at the ground-snow interface (Fig. 7a and 8a).

Density measurements for the 1969-70 winter are presented in Table 4a and Fig. 8b. Data are limited due to the physical size of the snow-tube instrument in relation to the thin layer of snow. This winter had 10 thaw periods producing many iced layers and melt crusts in the snowpack. Following thaws in late November, 1969, surface densities increased approximately 45 per cent and did not change for the rest of the winter. Density gradients through the snow were minimal (Fig. 8b).

Surface densities in the 1970-71 winter fluctuated throughout the winter depending on whether there had been a recent snowfall (Table 4b).

Figure 8. Temperature gradient through snow in relation to snow density. (a) = 1968-69 (Trabant, 1970); (b) = 1969-70; and (c) = 1970-71.



--DEC 68
—MAR 69
-·-DEC 69
--JAN 70
—MAR 70
—DEC 70
--FEB 71
SNOW DEPTH (cm)
0
20
40
60
80
100
-40 -30 -20 -10
TEMPERATURE (°C)
0 0.1 0.2 0.3
DENSITY (g/cm³)

Subsurface densities early in the winter increased to a December high of $0.31 g/cm^2$ (Table 4b). At this December sampling period, the increasing density gradient of the snow indicated little sublimation from lower layers and recrystallization in upper layers, i.e. hoar frost buildup (Fig. 8b). Following extreme low temperatures in January, temperature gradients through the snow resulted in hoar frost formation and a better developed subnivean space. Once the hoar crystals had increased in size, to about 1 cm long, icing on the ground surface was decreased.

The snow started melting on the surface by mid-March, yet the subnivean space was dry until late April when the snow pack became wet throughout. Some of the melt was absorbed by the dry soil but the rest of the melt produced the highest recorded runoff.

The subnivean space was not noticeable in 1970-71 until January, however the space was well developed in December 1968 (Fig. 3a, note low density at 0.8 cm indicating hoar frost development). Hence, the first and last winters had a well developed depth hoar while the second winter was without a lower density layer as well as a temperature gradient. These density and temperature gradient data indicate that the second (1969-70) winter was the most severe for small mammals. The third winter had a thick snow cover but due to the delayed hoar frost formation, I would classify this winter as more severe than the first: 1968-69 optimal, 1970-71 near average, 1969-70 poor.

Break through pressures:

Break through pressures (BTP) or snow hardness affect the mouses' environment in two places: one at the ground-snow interface and secondly (indirectly) at the snow-air interface. Surface-air hardness was extremely variable (Table 4a and 4b) and represents little more than newly fallen snow and weathered snow. High hardness values from wind blown surface and melting decrease gradients through the snow and result in poor hoar frost formation (Trabant, 1970). As was noted earlier, good subnivean conditions for small mammals require hoar frost formation. Newly fallen snow had a fluffy appearance and a very low density. Observations of mice released on different snow surface conditions indicated that mice require a BTP of at least $5 g/cm^2$ to stay on the surface. On fluffy, newly fallen snow, with BTP values below $10 g/cm^2$, Clethrionomys would attempt a few steps and then burrow. In comparison, when snow hardness values were above $10 g/cm^2$, mice would run across the surface to a nearby tree.

Subsurface BTP (Table 4a and 4b) were taken to gain a quantitative index of the mouse tunneling potential at the ground surface interface. The thin snow cover early in the 1969-70 winter did not lend itself to measuring a distinct subsurface BTP with the instruments available. As the depth increased to 20 cm, subsurface BTP's were low, indicating some some depth hoar frost formation later in the winter. Horizontal BTP at "mouse level" were five to ten times greater in the 1970-71 winter than in the 1969-70 winter. This may indicate that mice would have greater difficulty making new tunnels in the snow-ground interface in spite of the heavy insulative snow cover.

In summary, few thaws during the 1968-69 winter contributed to the development of fragile depth hoar (Trabant, 1970). The 1969-70 winter had low subsurface BTP compared to the 1970-71 winter. BTP data does not alter the order of severity of the three winters (to a mouse) but does show that the deep snow year 1970-71 was, in one way, more severe than the year of little snowfall.

Population Density

In this study, determination of population density depended upon a knowledge of both the number of individuals and the size of the area being studied. On grids A & B, density determinations also depended on converting density values based on reduced 8 X 8 grids (see Methods, Table 1) to those based on the 10 X 10 (snow free period) grid size.

Numbers present:

From the beginning of this study I assumed that capture-recapture estimations would be invalid due to non-random sampling (randomness is tested below). Thus I adopted Krebs' (1966) method of direct enumeration. Traps were placed at 5 m intervals as recommended by Polish IBP small mammal ecologists. Prebaiting procedures were employed (Krebs, 1966) in an attempt to capture all animals present. Minimunumbers present at time t can be calculated two ways using the above trapping procedure. Krebs (1966) added previously marked individuals caught after t but not at that time, to the number actually caught at time t. He assumed that these animals were present at time t but just not caught. Results using this method, N_1, are plotted in Figures 11, 12 and 13. Lidicker (1966) calculated minimum numbers, N_2, a little differently. He assumed that one half of those marked individuals which were released during the previous (t-1) trapping periods, but never again caught on the grid are also part of the population during the interval that the trapping effort represents, t. These animals (1/2 x number released at [t-1] but not caught again at t are added to Krebs' minimum number. Lidicker assumed that this addition compensated for individuals which remained for more than two weeks after their last capture. Results using Lidicker's method averaged 1.4 animals more per trapping interval than those using Krebs' method.

The effectiveness of this type of live trapping effort can be evaluated by two indices of trappability (Krebs et al, 1969). The first index, snap trapping the area at the end of this study, was not feasible since the trapping program was being continued by other investigators. The second index, comparing the actual catch in each trapping period with the number of animals known to be alive on the area, has been used to obtain a range of maximum values of trappability (Table 5).

Lidicker's minimum number estimate, N_2, gives trappability percentages (Actual Number Captured/N_2) from a minimum of 73 per cent for Microtus to a maximum of 89 per cent for Clethrionomys (Table 5). Krebs' trappability percentages (Actual Number Captured/N_1) are higher, ranging from 84 per cent for Clethrionomys and a maximum of 99 per cent for Microtus (Table 5).

A basic assumption of the Jolly (1965) procedure for estimating animal numbers from live trapping data is that all animals in the trappable population have equal probabilities of capture. The assumption

Table 5. Trappability of C. rutilus and M. oeconomus on Grid A. Trappability as measured by Krebs *et al*. (1969), is the percentage of mice known to be alive which were actually caught. The minimum number known to be alive was calculated two ways: min N_1 used Krebs' *et al*. (1969) and N_2 used Lidicker's (1966) method.

Clethrionomys rutilus

Period	min N_1	min N_2	Trappability 1	Trappability 2
10/68 - 3/69	69	74	90%	84%
7/69 - 9/69	159	182	95%	83%
8/69 - 5/70	61	74	97%	80%
6/70 - 10/70	85	94	99%	89%
12/70 - 2/71	55	61	84%	76%
3/71 - 7/71	132	143	96%	89%

Microtus oeconomus

Period	min N_1	min N_2	Trappability 1	Trappability 2
10/68 - 3/69	33	39	91%	77%
4/69 - 9/69	262	298	99%	82%
10/69 - 5/70	43	52	88%	73%

of equal capture probability of the marked and the unmarked segments of the population is tested using the method of Leslie *et al*. (1953). Since this method can only be tested in a non-breeding population in which no immigration is occurring, Grid A data from the 1969-70 winter is the only suitable area and time. Live trapping data (Fig. 16b) indicate that there is no breeding during this period. Movement distances between capture periods, an index of immigration do not indicate a decrease in immigration during the weeks when no breeding occurred (Fig. 21). The distribution of Microtus and Clethrionomys recaptures (wk 50 -

wk 76), are listed according to the week they were first marked and released (Table 6a).

From Tables 6a and 6b, expected numbers of marked and unmarked animals can be calculated for each sampling period according to Leslie et al. (1953). The expected and observed values were compared using chi-square analysis (Table 7a and 7b).

Unlike the results from Krebs (1966) and Leslie et al. (1953) over one half of the expected values for Clethrionomys were greater than the observed values. The chi-square values given in Table 7a indicate that insufficient evidence exists to reject this. Hence this method does not indicate a systematic bias favoring the recapture of marked individuals. Assuming that the lack of bias applies to all other times of the year, estimates of the total numbers present were made for Grid A using the Jolly Model. Estimates averaged 1.6 animals more per trapping period than the Krebs, N_1, values plotted on Figure 7a. However, there was one trapping period in the middle of August, when the Jolly Model overestimated the minimum numbers present by 11 animals. This estimate was not subsequently used for minimum productivity calculations.

Microtus data from the same period, Table 7b, indicate the null hypothesis is false and there is a difference between expected and observed. Therefore the Jolly method will not be used to estimate animal numbers for the Microtus population.

Effective area:

The second variable in density calculations, the effective area is at least as difficult to measure as absolute numbers. Recent studies

Table 6a. Distribution and recaptures of _Clethrionomys_ tallied according to the week first marked (Leslie _et al._, 1953).

Clethrionomys

Week of Recapture

Week when first marked*	50	54	58	62	66	72	76	Total Recaptures
1-48	8	3	1	1	1	1	1	16
50		6	4	4	3	3	1	21
54			2	2	0	0	0	4
58				2	2	2	1	7
62					2	2	2	6
66						0	0**	0
72							0	0
Total unmarked	14	5	3	4	0	1	1	
Total catch	22	14	10	13	8	9	6	82

Table 6b. Distribution and recaptures of _Microtus_ tallied according to the week first marked (Leslie _et al._, 1953).

Microtus

Week of Recapture

Week when first marked*	50	54	58	62	66	-	-	Total Recaptures
1-48	10	2	1	0	0***			13
50		2	2	2	0			6
54			1	1	1			3
58				1	0			1
62					2			2
Total unmarked	5	8	2	4	2			
Total catch	15	12	6	8	5			46

Footnotes for Tables 6a and b:

* To convert week number to date, see Table 42. Week 50 was during late September 1969.

** Since there may be some question about the zero cells in Table 6b, the same procedure was performed only on weeks 54, 58, 62 and 66. The χ^2 was 5.44, df = 3, $0.20 > p > 0.100$. The result is the same as dropping a degree of freedom for each expected value less than three.

*** The same recalculation was performed for the Microtus population excluding wk 50, which decreased the number of cells with values of less than three. This resulted in a χ^2 of 11.90, df = 3, $0.010 > p > 0.005$.

Table 7a. Tests for the absence of dilution in the non-breeding season for the Grid A *Clethrionomys* population.

Clethrionomys Grid A

Week*	Marked Observed	Marked Expected	Unmarked Observed	Unmarked Expected
50	8	4.29	14	17.71
54	9	7.63	5	6.37
58	7	6.32	3	3.68
62	9	9.72	4	3.28
66	8	8.00	0	0
72	8	9.00	1	0
76	5	6.00	1	0

$\chi^2 = 5.31$

df = 3

$0.250 > p > 0.100$

Table 7b. Tests for the absence of dilution in the non-breeding season for the Grid A *Microtus* population.

Microtus Grid A

Week	Marked Observed	Marked Expected	Unmarked Observed	Unmarked Expected
50	10	4.24	5	11.76
54	4	5.71	8	6.29
58	4	3.70	2	2.30
62	4	5.79	4	2.21
66	3	5.00	2	0

$\chi^2 = 15.94$

df = 2

$p < 0.005$

---

* To convert week number to date, see Table 42. Week 50 was during late September 1969.

have placed great emphasis on marking procedures for estimating effective areas trapped (Smith *et al.*, 1971; Ryskowski, 1971). The same sort of information gained from radioisotope tagging and stained bait could have been obtained by snap trapping a grid of marked animals; however, as mentioned above the continuation of live trapping ruled out this possibility.

Four methods of estimating the effective trapped area are presented. The first method, Pelikan (1970), recommended at the Small Mammal Meeting at Oxford, 1970, was used on data from the 16 X 16, 10 m interval snap trap grid and no edge effect could be detected for *Clethrionomys* and *Microtus* (Table 9). Live trapping data analyzed in a similar way for *Clethrionomys* on Grid A (during the breeding season) detected an edge effect of 5 to 10 m and during the non-breeding season 0 to 10 m depending on the year examined (Table 9). The edge effect for the *Microtus* population on Grid A during the breeding season was within 10 m and was zero for both non-breeding seasons. Animals on grids B, C, D and E were not tested for edge effects, in addition calculations were not made when samples sizes were small. Table 8 shows two sample calculations for the snap trap grid F and live trap grid A.

Smith *et al*. (1970) assume that the probability of capture should rise from zero as the grid is approached, increase to a maximum at the outer row of traps and decline to a level at which the probability of capture is constant. An assumption of no migration is required for proper use of this method. This assumption can be tested by plotting the ratio of accumulated captures in the outer rows to those in the remaining inner rows against each successive day of capture. If no migration occurs a horizontal line should result.

Table 8. Sample data and calculations for edge effect test (Pelikan, 1970). Expected and observed values are presented for concentric rings of snap trapped Grid F and live trapped Grid A.

Grid F No. of traps	Microtus expected	observed	Grid A No. of traps	Microtus expected	observed
60	63.54	83	36	39.6	56
52	55.06	54	28	30.8	36
44	46.59	42	20	22.0	22
36	38.12	38	12	13.2	9
20	21.65	16	4	4.4	2
28	29.65	27			
12	12.71	8			
4	4.23	4			
$\chi^2 = 9.69$			$\chi^2 = 9.58$		
df = 7			df = 4		
$0.250 > p > 0.100$			$0.050 > p > 0.025$		
null hypothesis: there is no edge effect; accept			null hypothesis: there is no edge effect; reject		

Snap trapping results on Grid F during August 1969 are presented in Figure 9. The line for the one outer row/inner rows shows an initial dip but the last three days closely approximate a straight line. The dip in the two outer rows line is much less noticeable and a horizontal line is approximated. The three outer rows show a negative slope that indicates migration. It should be noted that three data points are

Figure 9. The accumulated number of captures in the outer rows divided by those in the remaining inner rows each trapping day on Grid F. (These data were used to detect migration onto the grid as proposed by Smith *et al.*, 1970).

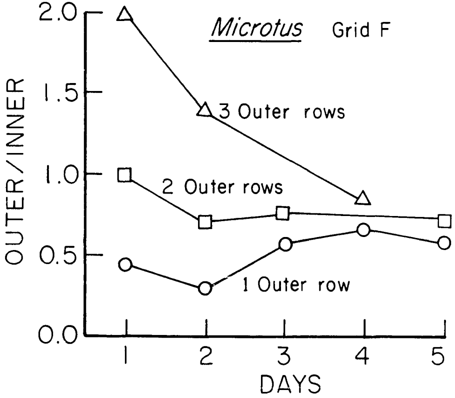

Microtus Grid F
OUTER/INNER
2.0
1.5
1.0
0.5
0.0
3 Outer rows
2 Outer rows
1 Outer row
1
2
3
4
5
DAYS

Table 9. Summary of chi-square testing for edge effect using concentric squares. (Pelikan Method, 1970)

Live Trapping

Species	Time Week*	Breeding Status	χ^2	df	> p >		edge
Microtus	2-30	NB	2.70	2	0.250	0.100	0 m
Microtus	42-48	B	9.58	4	0.050	0.025	
eliminate outer row			9.01	3	0.050	0.025	
eliminate 2 outer rows			3.10	2	0.100	0.050	10 m
Microtus	54-86	NB	0.64	2	0.750	0.500	0 m
Clethrionomys	2-30	NB	2.70	3	0.500	0.250	0 m
Clethrionomys	42-48	B	73.61	3	0.005		
eliminate outer row			5.53	1	0.025	0.010	10 m
Clethrionomys	54-76	NB	9.56	2	0.025	0.010	
eliminate outer row			7.40	1	0.010	0.005	10 m
Clethrionomys	116-125	NB	7.95	2	0.025	0.010	
eliminate outer row			8.95	1	0.025	0.010	10 m
Clethrionomys	134-146	B	13.50	3	0.025	0.010	
eliminate outer row			1.7	2	0.500	0.250	5 m

Snap Trapping

Microtus	Aug 1969	B	9.69	7	0.250	0.100	0 m
Clethrionomys	Sep 1970	B	3.68	4	0.500	0.250	0 m

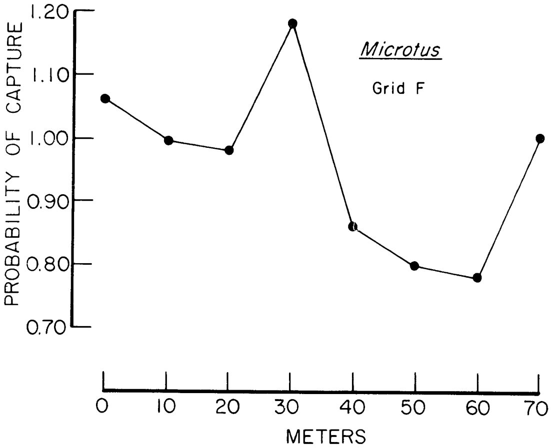
* to convert week to date, see Table 42.

missing due to lack of captures on the last three days. Moreover, 70 per cent of the data are presented by the three points for the first day. Hence the slight positive slope for the "one outer row" curve indicates immigration, but the lack of a positive slope for the other curves suggests that the initial dip merely represents an edge effect and perhaps a movement from the inner part of the grid.

Probabilities of capture were calculated for Clethrionomys and Microtus (assuming there was no immigration) for the times and breeding intervals. The data from the ten stratifications examined all failed to show inflection points as the theory (Smith et al., 1970) predicted there should be. Figure 10 shows a sample plot. Furthermore the maximum probability of capture was not on the outer row but well within the edge of the grid. Hence the Smith et al. (1970) method proved to be unsuitable for the animals in this study.

Assessment lines in conjunction with trapping grids have been suggested by Smith et al. (1971) to be the only suitable method for calculating effective trapped area with confidence intervals. Assessment lines on snap trap Grid F and live trap Grid A did not capture animals. In other words when these lines were first used, only seven animals were captured out of 2560 trap nights on the grid and no animals were caught in the assessment line. At the same time, May 1970, only one animal was captured on Grid A and no animals on the assessment lines. The assessment lines were not put in again after Grid A was shifted (about 75 m, see Methods). Feist (pers. comm.) has resumed trapping the assessment lines on Grid A and greater animal densities have

Figure 10. Number of animals caught divided by the number of traps (probability of capture) as a function of the distance of the traps from the outer edge of Grid F. (These data do not indicate an edge effect outside of the snap trapped grid.)


PROBABILITY OF CAPTURE
1.20
1.10
1.00
0.90
0.80
0.70
Microtus
Grid F
0
10
20
30
40
50
60
70
METERS

yielded animals in the lines.

Lidicker's (1966) method for determining the effective trapped area from a study of the distribution of individual two-week recapture distances was used to analyze Grid A between period movement data. Samples of movements grouped in frequency distributions are presented for Grid A in Table 10.

Table 10. Frequency distributions of movements between capture periods. These are samples of frequencies that were used to estimate edge effects according to Lidicker (1966).

Weeks* 32-50	*Microtus* Breeding	Weeks* 134-146	*Clethrionomys* Breeding
Meters		Meters	
0-3	8	0-3	1
3-6	12	3-6	7
6-9	10	6-9	4
9-12	16	9-12	10
12-18	11	12-18	9
18-30	20	18-30	15
30-48	8	30-48	4
over 48	1	over 48	

* to convert week number to date, see Table 42

Unlike the Pelikan Subtraction Method which gives some zero edge effects, the Lidicker Method always shows an edge. When data from those periods that are common for the two methods are compared (Table 9 vs Table 11), the Lidicker Method (averaging 100% and 50% effeciency) gives an edge that is most commonly 1 to 10 m greater. The edge effect for breeders is equal to or greater than the non-breeders. There is no obvious difference between edge effects when comparing *Clethrionomys* and Microtus for the same time periods. However, the edge effect seems to be greater for Clethrionomys in week 98-106. This corresponds to the absence of Microtus and a marked increase in both between and within period movements.

Table 11. Edge effects detected using Lidicker's (1966) method.

Clethrionomys

Weeks*	Breeding Condition	100%	50%
2-30	B	15 m	7 m
2-30	NB	11 m	5 m
32-50	B	15 m	7 m
32-50	NB	15 m	7 m
98-106	B	24 m	12 m
98-106	NB	20 m	10 m
134-146	B	20 m	10 m

Microtus

Weeks*	Breeding Condition	100%	50%
2-30	B	-**	-**
2-30	NB	12 m	6 m
32-50	B	15 m	7 m
32-50	NB	15 m	7 m

*to convert week number to date, see Table 42. Week 2 was during mid-October.

**Samples of less than ten were not analyzed.

Note: Weeks 50-98, 106-134 represent 4 week trapping intervals and wer not analyzed.

Unfortunately these results from the four methods presented are of limited use in calculating the effective trapped area. To be on the conservative side, I have chosen to assume a 10 m edge effect for all times and conditions. When calculating the effective area trapped, the corners of the grids were rounded off (i.e. quarter circles).

Density:

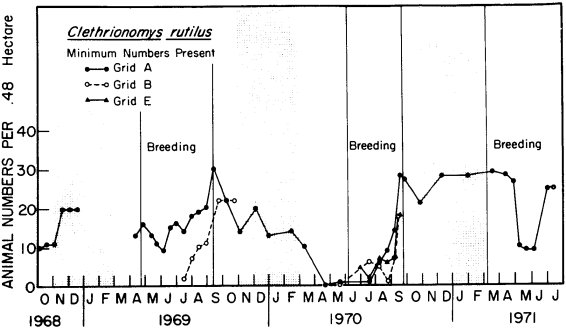
Variations in population density have been plotted as minimum numbers (Krebs, 1966) for the Steese and College grids (Fig. 11 and 12). Figure 13 shows the breakdown of male and female density for Clethrionomys and Microtus. Microtus numbers were not plotted for the College grids due to their brief occurrence in July, 1970. Density is discussed separately for each species.

Clethrionomys. The Steese Grid A was the only grid trapped in 1968. The Clethrionomys overwintered at an approximate density of 20 animals per 0.48 hectare (42/ha). The initial increase in November 1968, is believed to be due to immigration and/or poor sampling success in the early stages of the study. Numbers were maintained during the winter with only a slight decrease which lasted until June 1969, when recruitment started. Figure 13a indicates that this first increase in September 1969 was due to both males and females. The density on Grid B increased at a lower rate and later than the density of the Grid A population. These data indicate that the phenomena described above were not just localized events. Numbers from the 16 x 16 station snap trap Grid F (Table 12) show 17 animals per 0.48 hectare (35/ha) which agrees well with the simultaneous density of 37 animals per ha on live trap Grid A. Such a good correlation would not be apparent if edge effects for Grid F and Grid A had not been examined.

The peak in the population on Grid A was very short lived and was followed by a relatively rapid decrease which lasted until November 1969. Trapping under the snow at four week intervals on a reduced 8 x 8 grid

Figure 11a. Population changes in <u>Clethrionomys</u> on Steese Grids A, B and E. Winter months are shaded and vertical lines mark the length of breeding periods.

Figure 11b. Population changes in <u>Microtus</u> on Steese Grids A, B and E.


Clethrionomys rutilus
Minimum Numbers Present
Grid A
Grid B
Grid E
Breeding
Breeding
Breeding
ANIMAL NUMBERS PER .48 Hectare
0
10
20
30
40
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
1968
1969
1970
1971

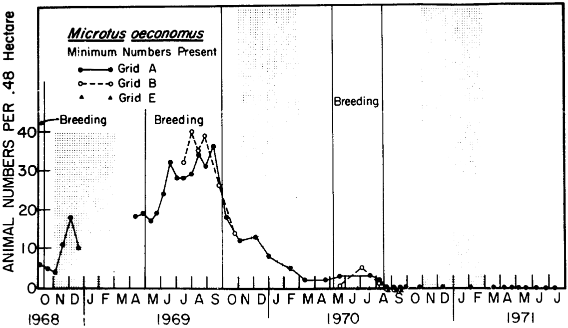
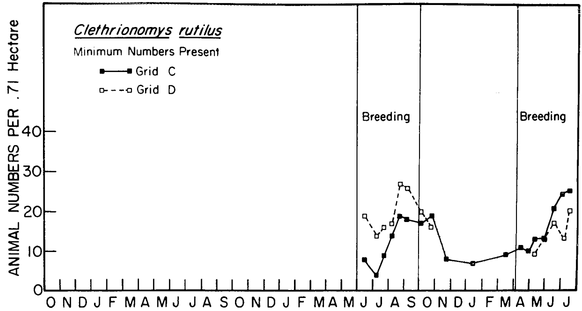

Microtus oeconomus
Minimum Numbers Present
Grid A
Grid B
Grid E
Breeding
Breeding
Breeding
ANIMAL NUMBERS PER .48 Hectare
0
10
20
30
40
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
1968
1969
1970
1971

Figure 12a. Population changes in *Clethrionomys* on College Grids C and D. Winter months are shaded and vertical lines mark the length of breeding periods.

Figure 12b. Population changes in *Zapus* on Steese Grids A, B and E.


Clethrionomys rutilus
Minimum Numbers Present
Grid C
Grid D
Breeding
Breeding
ANIMAL NUMBERS PER .71 Hectare
0
10
20
30
40
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J

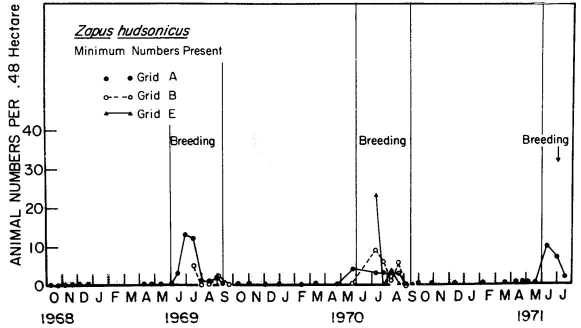
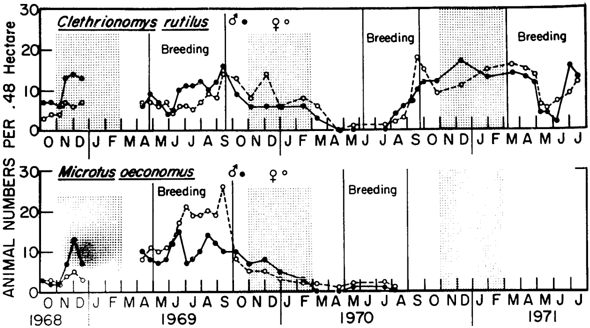

Zapus hudsonicus
Minimum Numbers Present
Grid A
Grid B
Grid E
Breeding
Breeding
Breeding
ANIMAL NUMBERS PER .48 Hectare
0
10
20
30
40
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
1968
1969
1970
1971

Figure 13. Population changes in males and females on Steese Grid A. Winter months are shaded and vertical lines mark the length of breeding periods. (a) Clethrionomys; (b) Microtus.


ANIMAL NUMBERS PER .48 Hectare
Clethrionomys rutilus
♂ ● ♀ ○
Breeding
Breeding
Breeding
Microtus oeconomus
♂ ● ♀ ○
Breeding
Breeding
0
10
20
30
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
1968
1969
1970
1971

indicated that the population remained stable until April 1970. The reader must be reminded that the animal numbers captured during this snow covered period have been extrapolated to a 10 x 10 grid size, hence the apparently large decrease in March-April 1970 numbers is accentuated by this conversion.

Numbers remained low until early August 1970, when the density increased very rapidly on all the Steese live trap Grids (A, B and E). This increase was noticeably more rapid than the increase to peak density in 1969. One *Clethrionomys* was captured by snap trapping on the 16 x 16 Grid F during the low population density in May-June 1969. During the September peak, the 16 x 16 Grid F had a density of 28 animals per 0.48 hectare (58/ha), the same as the estimate on Grid A.

Again the numbers of animals remained stable over winter but above the density in the previous winters studied. A significant decline occurred in early May 1971, and low numbers persisted for at least six weeks. Numbers increased very rapidly to about 25 per 0.48 hectare (52/ha) by late June. There were no other Steese grids trapped in 1971 to see if the May decline was area wide.

The 8 x 8 station grids C and D on the College site were first trapped in June 1970. Density on Grid D in the spruce forest was lower than that in the Grid C in the dense birch forest, yet neither was as low as the populations on Steese Grids A, B and E. As on the Steese both Grids C and D showed an increase until late August, however neither of the College grids reached the peak density that was simultaneously present on the Steese. Winter trapping on the 8 x 8 grids with 10 m between traps missed some animals that may have overwintered on the grid. This is indicated by the slight increase in numbers just after melt off. I feel it is significant that the spring 1971, rapid dip in numbers seem on Grid A was not apparent on either of the College grids. It is unfortunate that snow density was not being measured on Grid C.

Microtus. Overwintering density on the Steese Grid A (Fig. 11b) was approximately 15 animals per 0.48 hectare (31/ha). By late May 1969, both males and females continued to increase until late June 1969, when the density leveled off at approximately 28 animals per 0.48 hectare (58/ha). A final increase in female numbers pushed the population to a peak of 35 animals per 0.48 hectare (73/ha). Live trapping on Grid B indicated a slightly higher peak density (40/0.48 ha, 83/ha). Grid F was snap trapped when the density on Grid A was 29 animals per 0.48 hectare and 36 animals on Grid B. The converted (to 0.48 ha) values from Grid F indicate a _Microtus_ density of 31 animals or about halfway between the Grid A and Grid B values.

Declines on both Steese grids occurred simultaneously and were quite rapid until the first snow fall. Numbers stabilized but gradual losses continued through the winter until March 1970 when occasional transients and only one resident female occupied the area. All Steese Grids A, B and E showed zero _Microtus_ in late August 1970. The fall September 1969 decrease was not found in both sexes. Female numbers (Fig. 13b) were nearly twice male numbers during the summer and fall. By early September female numbers fell below male numbers and remained so through the winter. Snap trap Grid F appeared to be at a low density in May-June 1970, and

September 1970 as was seen on the live trap grids.

Zapus. Zapus only occurred on the Steese Grids A, B, E and F. Peak numbers 21 to 42/ha occurred during June and July of each year. Dynamics of Zapus numbers have been discussed elsewhere (page).

To summarize, Microtus reached a peak population density in 1969, declined over winter and did not increase again until 1972. However, Clethrionomys reached a peak population each year studied.

Table 12. Summary of snap trap data collected on Grid F. T indicates total numbers for each species captured on all five days. N equals the estimate of animals using the Janion et al. (1968) Method.

	Day 1	Day 2	Day 3	Day 4	Day 5	T	N
July-August 1969							
Clethrionomys	7	4	4	2	1	18	22
Microtus	68	52	6	8	9	143	159
Shrews	52	28	16	7	18	131	141
Zapus	0	0	0	0	1	1	-
May-June 1970							
Clethrionomys	1	0	0	0	0	1	-
Microtus	1	0	0	0	0	1	-
Shrews	0	0	1	0	0	1	-
Zapus	4	0	0	1	0	5	-
September 1970							
Clethrionomys	9	14	4	4	1	32	36
Microtus	0	1	0	0	0	1	-
Shrews	7	6	3	2	1	19	20
Zapus	0	0	0	0	0	0	-

Survival

Survival rates in the trappable population of Clethrionomys and Microtus on Grid A are presented in Fig. 14 and for all other grids in

Figure 14. Per cent surviving per 14 days for males and females on Grid A. Vertical lines indicate breeding periods and shaded areas are winte months. (a) *Clethrionomys*; (b) *Microtus*.

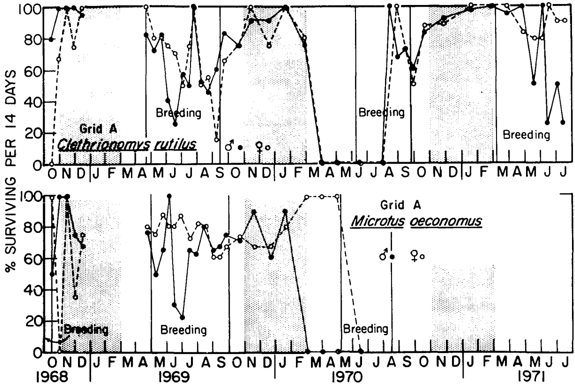

% SURVIVING PER 14 DAYS
100
80
60
40
20
0
Grid A
Clethrionomys rutilus
♂● ♀○
Breeding
Breeding
Breeding
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
Grid A
Microtus oeconomus
♂● ♀○
Breeding
Breeding
Breeding
1968
1969
1970
1971

Table 14. These rates are calculated by counting the number of animals surviving a two week period. If the capture interval was over two weeks, conversions are made to a two week period assuming a linear decrease in numbers. Missed animals that were subsequently recaptured are counted as present. When grid size was reduced to 8 x 8 m, in mid-September (*t*), survival rates were calculated by only counting animals at (*t*-1) that were on the smaller area 8 x 8 portion of the 10 x 10 grid. Nestling survival has been estimated in the Nestling productivity section, p. .

Clethrionomys:

Grid A. Five periods of poor survival (50 per cent or lower) are outlined in Table 13.

Table 13. Generalized periods of low survival (50 per cent or lower). These periods apply also to both Clethrionomys and Microtus.

Period	Months	Year
1	June to early July	1969
2	August to early September	1969
3	March	1970
4	September	1970
5	June and July	1971

All other periods, including the three winters (Nov.-Feb.), are considered to have high survival rates.

Spring and early summer survival were reduced in all three years (periods 1, 3, and 5) but not in similar ways. The Clethrionomys

Table 14. Minimum survival rates per 14 days for populations not in Fig. 14a and b. Sample sizes in parentheses. Weeks not listed have zero survival. Dashes indicate failure to capture animals. All two week periods were not trapped on all grids. (*Week numbers are converted to dates in Table 42).

	CLETHRIONOMYS								MICROTUS	
	Grid B		Grid C		Grid D		Grid E		Grid B	
Week*	Male % (n)	Female % (n)	Male % (n)	Female % (n)	Male % (n)	Female % (n)	Male % (n)	Female % (n)	Male % (n)	Female % (n)
42-44	100 (1)	100 (1)							33 (12)	73 (15)
44-46	60 (5)	100 (1)							81 (16)	73 (22)
46-48	38 (8)	100 (2)							82 (17)	90 (20)
50-52	100 (5)	91 (6)							71 (17)	66 (22)
54-56	100 (4)	70 (10)							72 (9)	79 (7)
90-92			70 (5)	66 (3)						
92-94					44 (9)	60 (10)				
94-96	0 (8)	- -	66 (3)	100 (1)	50 (8)	87 (7)	40 (5)	- -		
96-98			50 (6)	66 (3)	88 (8)	67 (9)	100 (2)	- -		
98-100	0 (7)	0 (1)	57 (7)	75 (8)	40 (10)	43 (7)	60 (5)	50 (2)		
100-102	- -	100 (1)	29 (7)	25 (12)	50 (10)	59 (17)	25 (4)	50 (2)		
102-104	100 (4)	66 (3)	75 (6)	88 (13)	72 (9)	92 (18)	100 (3)	50 (4)		
106-108			100 (5)	90 (14)	60 (5)	88 (17)				
110-112			80 (8)	74 (15)						
116-118			100 (5)	93 (8)						
124-126			98 (5)	100 (7)						
130-132			80 (5)	92 (7)						
134-136			67 (6)	75 (8)						
136-138			80 (5)	100 (7)						
138-140			88 (8)	100 (7)	100 (3)	86 (7)				
140-142			86 (7)	100 (8)	50 (8)	83 (6)				
142-144			42 (12)	66 (9)	40 (10)	63 (8)				
144-146			29 (14)	36 (11)	63 (8)	60 (5)				

population declined in spring 1970, whereas the population that overwintered the 1968-69 and the 1970-71 winter declined in early summer. These periods (1 and 5) of low early summer survival are the only two when survival differed between the sexes. Low numbers of males occurred earlier than did low numbers for females. All other differences between males and females have been considered non-significant (see Discussion). The remaining two periods (2 and 4) of poor survival are considered to be late summer, 1969 and 1970, and will be discussed in more detail below.

The periods (excepting period 3) when survival on Grid A decreased to the 50 per cent level or below are characterized by differences in age (weight) class. During the period 1 low, male and female subadults (13-17 g) accounted for 82 per cent of the loss. During period 2, losses occurred in all sex and age classes but more heavily in subadult and juvenile females. Fifty per cent of the September, 1970, period 4, dip was due to disappearance of subadult females while 60 per cent of the June-July 1971, period 5, dip was due to the disappearance of subadult males.

Grids B and E. Low survival rates on Grid B corresponded with the low survival rates on Grid A during period 2. However, losses seem to have been present in both sexes and all age classes. The absence of animals during May 1970 on Grid B indicates that the poor spring survival (period 3) was area wide. The additional data from Grids B and E in 1970 also show a late summer low, period 4. Losses were greater in males (relative and absolute, no males survived) than females.

Unfortunately these auxiliary grids were not being trapped during the spring lows.

Grids C and D. Differential survival between sexes was not apparent on Grids C and D. Two low periods (50 per cent surviving or less) occurred on both grids. The first period of low survival was late summer which occurred on Grid D about two weeks before Grid C. Overwinter survival was good on Grid C. Grid D was not trapped between November 1970, and March 1971, yet nine out of the 16 Clethrionomys survived this five month period. When converted to survival on a two week period, survival is approximately 95 per cent. There were no differences in age class survival on Grid C and/or Grid D during the August-September 1970, period 4, low. Yet on Grid C, July 1971, period 5, no male juveniles or subadults survived. Losses on Grid D (period 5) were two weeks earlier than on Grid C.

In conclusion, overwinter survival was good on all grids for which data are available. Low survival is grouped into five periods and lows on various grids within a period were up to four weeks apart. Differential survival of the sexes was observed on Grid A in two early summer periods (1 and 5). Differential survival of the age classes occurred on most grids during most low periods but data on one grid tended to contradict that of a neighboring grid more often than not.

Microtus:

Grid A. The survival rate in Microtus was similar for males and females excepting June when no trappable male subadults survived. The near disappearance (period 3, zero survival) of the Microtus population occurred about a month earlier than the *Clethrionomys* population. Female survival was good in March-April-May 1970, but this was due to one animal. After January there were no *Microtus* recaptures until June 1971.

Grid B. Grid B trapping in 1969 was started during the period 2 low on Grid A and was ended before the period 3 low. Excluding the period 2 low, survival was as good on Grid B as it was on Grid A from late July to October 1969. The absence of *Microtus* in traps during May 1970, supports the contention that an area wide low of *Microtus* existed after the spring 1970 decrease. In conclusion, survival percentages on Grids A and B agree for the periods of overlap. Low periods of survival on Grid A were summer 1969 (period 2) and winter 1970 (period 3).

Grid C. While substantial numbers of *Microtus* were captured on Grids C and D in the first week of trapping in June 1970, fewer than 5 per cent of these animals were ever recaptured.

Reproduction

While a great many numbers were generated from external reproductive indices, one must realize that these results will ultimately be compared and contrasted to the reproductive parameters determined by autopsy.

Length of breeding season:

Clethrionomys. The lengths of the breeding season for adult *Clethrionomys* are summarized in Figure 15a for males and Figure 15b for females. When live trapping was started on October 2, 1968, the *Clethrionomys* population was in a non-breeding condition and remained so until the following April, 1969. Within a two month period, all of the adult males were scrotal (testes descended) and remained so until the end of August, when the adults stopped breeding rather abruptly. Females were in breeding condition for a shorter period of time as judged by a perforate vagina and medium or large nipples and the presence of active mammary tissue. The peak of breeding was reached in mid-summer and then decreased due to recruitment of immatures. Breeding conditions ended a week or two earlier in males.

The following year, 1970, adult males reached breeding condition sometime after mid-May. The exact date of onset was not observed due to the inability to trap for a six week period (gravel road construction) in the spring. Females were not breeding by early July (when live trapping was resumed), but by the end of the month adult females started to breed; all females were breeding two weeks later (early August). As in the first year (1969) the females had stopped breeding by the end of September resulting in a short breeding season. One adult and one subadult remained scrotal into October but the majority of the males had ceased to show signs of breeding by the same time as in year 1.

During 1971, unlike 1969 and 1970, breeding under the snow was well underway by March. Additional evidence of early breeding under the snow was the two litters born in the metabolic chambers in late March and early April. Trapping was not continued to the end of the 1971, breeding season.

Reproduction data from other live trap grids (B, C, D & E) correlate with the results described for Grid A. There are numerous occasions when breeding indices started or ended a month earlier or later on one grid than another but none of these exceptions discount the conclusion that: 1) There was no winter breeding (November - February), 2) There was a substantial delay in breeding in the second year, 1970, and 3) Breeding under the snow (see Fig. 7c for the length of snow cover) occurred during the spring of 1971.

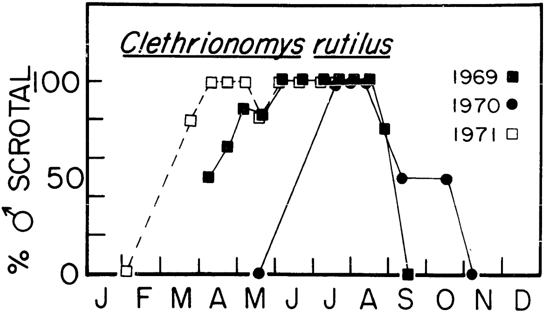
Microtus. The initiation of the breeding season for Microtus adult males during 1969, was delayed when compared to the Clethrionomys population on the same area. The delay in breeding condition was much more noticeable in the males than the females. The breeding activity in Microtus ceased at the same time Clethrionomys stopped breeding, about mid-September (Fig. 16b).

In 1970, there was only one adult male Microtus on Grid A and he was scrotal in mid-May.

Reproductive data on Grid B were very similar to that on Grid A 1969 and 1970. Microtus occurred on Grids C and D for a very short time in the middle of the 1970 breeding season, hence data on these animals are not applicable to evaluating the extent of the breeding season.

Zapus. Reproductive data of Zapus males are difficult to interpret for there seems to be no obvious external change in size of testis when they are breeding. Lactation information indicated that breeding started in all three years within a two week period from late-May to mid-June seemingly independent of when the females first appeared in the traps after hibernation. The drop in breeding intensity in the middle of the season and a subsequent increase suggest that the Zapus produced two

Figure 15. Length of breeding season and breeding intensity in adult Clethrionomys. (a) males; (b) females. Note delay in the 1970 males and females.


Clethrionomys rutilus
% ♂ SCROTAL
100
50
0
1969 ■
1970 ●
1971 □
J F M A M J J A S O N D

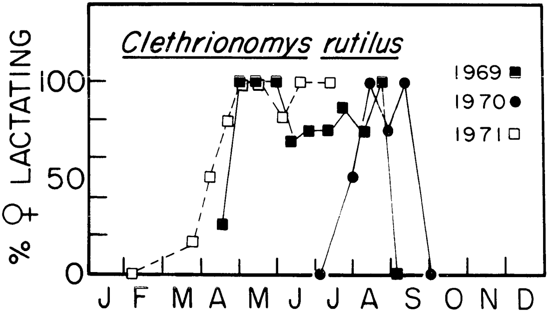
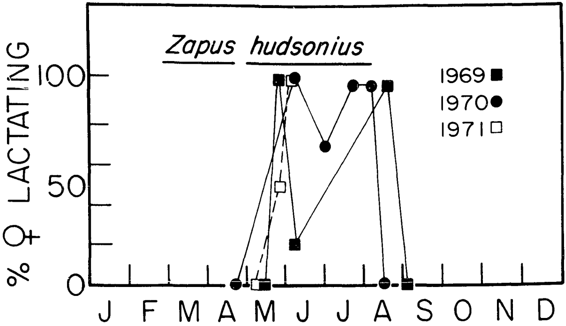
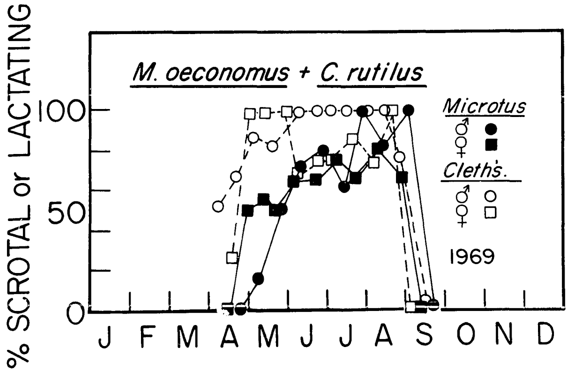

Clethrionomys rutilus
% ♀ LACTATING
100
50
0
1969 ■
1970 ●
1971 □
J F M A M J J A S O N D

Figure 16a. Length of breeding season and breeding intensity in Zapus, Note mid-season dip which may indicate two litters per year.

Figure 16b. Comparison of the length and intensity of breeding between the 1969 Microtus and Clethrionomys populations. Note the gradual increases in Microtus breeding intensity.


Zapus hudsonius
% ♀ LACTATING
100
50
0
1969 ■
1970 ●
1971 □
J F M A M J J A S O N D


M. oeconomus + C. rutilus
% SCROTAL or LACTATING
100
50
0
Microtus
♂ ●
♀ ■
Cleth's.
♂ ○
♀ □
1969
J F M A M J J A S O N D

litters (Fig. 16a). The two years, 1969 and 1970, of data on cessation of breeding indicate that breeding ends rather abruptly in mid-August (Fig. 16a).

The onset of breeding can also be estimated by knowing the date when juveniles first appear. Excepting Clethrionomys during 1971, appearance of juveniles correlates well (never more than two weeks difference) with the external reproductive indices in all species on all grids. The exception is interesting in that it occurred on both the Steese Grid A and the College Grid C during spring of year 1971. Juveniles did not appear on Grid A until June 22. This would indicate that insemination occurred on approximately May 7. External reproductive data and the new born litters in traps and the metabolic chambers indicate breeding had started six to seven weeks earlier than May 7, i.e. late March.

Intensity of breeding:

The external indices of reproduction can be used to estimate relative changes in breeding intensity. In a later section, autopsy information on litter size, testis size, pregnancy rates etc. will be analyzed and the results of these two methods are evaluated in the discussion.

Trends in intensity of breeding within breeding seasons were observed for the Microtus population during 1969 (Fig. 16b). A steady increase in reproductive intensity occurred as the population density increased. This gradual increase is unlike that of the Clethrionomys that reached 100 per cent breeding intensity in a shorter time.

A total of thirty-eight chi-square tests were applied to the breeding intensity information to test homogeneity for each species between years and to test for homogeneity of each species within a year or between grids (Krebs _et al._, 1969). The external reproductive indices for adult _Clethrionomys_, _Microtus_, and _Zapus_ were all homogeneous (tests were not made when sample sizes were not large enough to give an expected value of three or more). Heterogeneity was observed only in the subadults of _Microtus_ and _Clethrionomys_ as listed in Table 15.

The differences in Table 15 can be inversely related to density in the breeding season. The rapidly increasing high density _Clethrionomys_ population on the Steese grid in 1970 had a lower subadult breeding intensity. This tendency also holds between years when the density was low in the spring of 1971 the subadult males on Grid A showed an increase in intensity.

Table 15. Significant differences in breeding intensity between years and trapping areas. The differences can be inversely related to density.

Species	Interval	Breeding Parameter	Age	Year or Grid	χ^2	df	Reason
Clethrionomys	Between Years	Testes	Subadult	A	19.3	2	1971 high
		Testes	Subadult	C	3.8	1	1971 high
	Within Years	Vagina	Subadult	1970	6.1	2	Steese lower than College
Microtus	Within Years	Vagina	Subadult	1969	4.6	1	Grid A high

To summarize, data on length and time of the breeding season as measured by external reproductive indices seem to be independent of population numbers in the Clethrionomys and Zapus populations. Microtus numbers during 1970, are too scanty to make conclusions relating density to the length of the breeding season. Breeding intensity was mostly homogeneous between grids and years for all species. The four significant exceptions were in the subadult population, indicating an increased reproductive output in less dense populations both between grids and between years.

Growth

Growth is expressed in three ways: body weight distributions for each trapping period, individual growth followed over several trapping periods and weight class growth rates. The first two analyses are more generalized to give the reader a feel for the trends in growth, while the latter method is used to look into the details and quantify the growth trends.

Body weight distribution:

Clethrionomys. Body weight distributions are graphed for Clethrionomys males on Grid A, (Fig. 17). The female data is more variable than the male data but the same trends are apparent.

From October to December 1968, animal weights on Grid A decreased to a mean of 16 g (15 g for females). When trapping was resumed three months later, the animals had already started to grow; males started two to four weeks earlier than females. Only 12 per cent of the animals

Figure 17. Body weight distribution of Clethrionomys - Grid A. Each small square represents one vole.

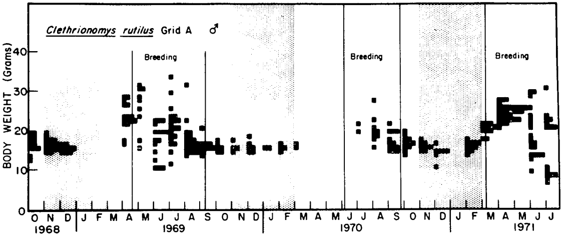
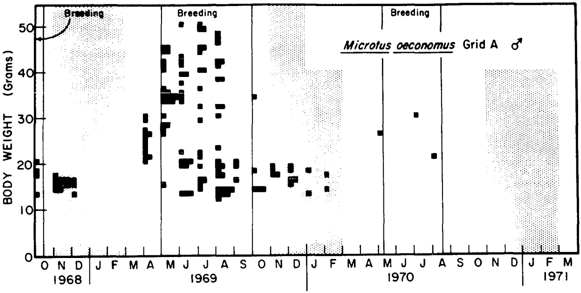

Clethrionomys rutilus Grid A ♂
Breeding
Breeding
Breeding
BODY WEIGHT (Grams)
0
10
20
30
40
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
1968
1969
1970
1971

Figure 18. Body weight distribution of Microtus males from Grid A. Each small square represents one vole.


Breeding
Breeding
Breeding
Microtus oeconomus Grid A ♂
BODY WEIGHT (Grams)
0
10
20
30
40
50
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M
1968
1969
1970
1971

remained in the overwintering weight class (13-17 g). During the breeding season, the mean male body weight increased to 19 g (21 g for females). Grid B with a low breeding density, lacked the heavier males that were present on Grid A. By September when breeding had ceased and total numbers of animals were decreasing, the overwinter distribution of body weights was again very narrow, with a mean weight of 15 g for males. Few males were captured during the spring, 1970. When males appeared on Grids A, B and E in July, 1970, they were already out of the subadult weight class. However, larger animals (over 24 g) were not seen on the Steese grids this summer. One third of the males on the College Grids C and D were over 24 g. The following winter, 1971, body weights decreased to a mean of 15 g (16 g for females) on the Steese and College grids. By February 1971, body weights started to increase first on Grid A and about a month later on Grid C (College). As in the 1969 spring, males started to grow about two weeks earlier. The increase in body weight in 1970 was unlike 1969 on both the Steese and College areas: there were no juvenile or subadults (judged by weight) in April and May, 1970.

To summarize: Increases in the range of body weight occurred in winter, spring and summer periods, which was followed by a narrow distribution during the late fall and early winter months.

Microtus. Body weight distributions are presented for male Microtus on Grid A (Fig. 18). As the animals went into the 1968-69 winter, their body weights gradually decreased to levels below that expected for their age. Approximately 90 per cent of the animals fell into the juvenile weight class; tagging showed that these animals were at least four to eight weeks old. (See discussion of Dehnel Phenomena.) Growth in the overwintered animals had already started when trapping resumed the following spring. There was a wide range in weight distributions through the summer into August. This was due to an increase in body weight and recruitment of light-weight young. Overwinter (1969-70) weights on Grid A were a little lower than those recorded the previous winter: males 18 g (females 17 g). The few animals that were captured the following summer showed only a slight increase in body weight with no males over 33 g. Only two males were captured in August on Grids A and B; for the duration of the study no more Microtus were captured.

The year after the high on the Steese, body weight distribution on the College grids indicate a distribution similar to that during the previous year on the Steese. The very heavy animals (45-50 g) were not present but several animals were over 30 g and several light animals were captured, a phenomena that did not occur on the Steese in 1970.

Zapus. Body weight data for Zapus has been combined for all three grids. During the 1969 and 1970 summer months there was a slight increase in the range of body weights. Animals trapped in the first part of 1970 weighed 15 to 16 g. Animals were observed going into hibernation (i.e. failure to recapture) at a wide range of weights from 12 to 37 g. (See Zapus discussion for further detail of initial hibernation weight).

Selected individual growth rates:

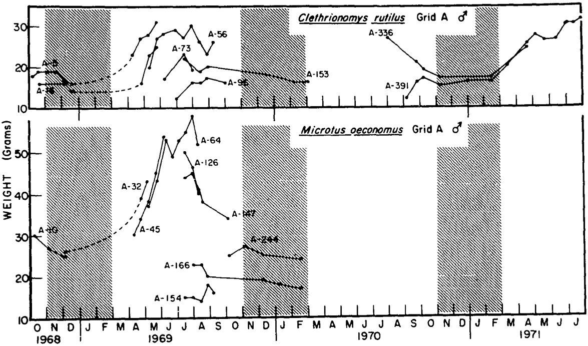
Clethrionomys. In Fall 1968, males on Grid A (Fig. 19a) had weight losses of two to three grams by the start of winter. By May, 1969, (when the snow was melting) rapid growth rates had started in overwintered animals (A-5, A-16) young of the year also experienced good growth (A-73, A-96). Peak weights of the overwintered animals were seven to fourteen grams greater than the young of the year. Both overwintered animals and young of the year lost weight in the fall. Overwintered (1969-70) animals (A-366) lost one third of their body weight; the loss of weight by the young of the year (A-391) was considerably less but present. It is important to note that there were no recorded overwinter (1968-69) animals that lived past August 1969.

The exact date when growth started in 1970, could not be determined due to the scarcity of animals during late winter and spring. By late July 1970, overwintered (1969-70) animals had reached peak weights; these peak weights were about ten grams lower than the same age class the previous year.

Growth started early in 1971, animals A-366 and A-391 (Fig. 19a) are examples of weight increase during late February or early March. Peak weights were once again in the 25 to 30 g range. Recruitment in 1971 was very poor until July, hence growth data for the young of the year are not available.

To summarize: Growth rates started to increase in late February 1971, March 1969, and about May 1970. Young of the year (1969) had lower peak weights than the overwintered animals. Heavier animals

Figure 19. Selected growth curves for individual male animals on Grid A. (a) *Clethrionomys*; (b) *Microtus*.


Clethrionomys rutilus Grid A ♂
A-56
A-73
A-153
A-95
A-336
A-391
Microtus oeconomus Grid A ♂
A-64
A-126
A-32
A-147
A-10
A-45
A-244
A-166
A-154
WEIGHT (Grams)
10
20
30
40
50
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
1968
1969
1970
1971

lost weight from late summer through the fall and winter.

Microtus. Microtus (Fig. 19b) also lost weight as they entered the 1968-69 winter (A-10). By April 1969, growth had already started and gains of 2.5 g per week (A-64, A-45) were not unusual. This rapid growth was similar for all the overwintered animals. In July, during the peak of the plant growing season, weight losses were equal to the increases a few months previous. Recruits during July (A-154) did not show the growth rates that occurred earlier in the year by overwintered animals. On both Grids A and B the maximum weight reached by a recruit was 31 g. This was an exception and all other males of the year weighed less than 22 g. It is difficult to classify animals such as A-244 and A-166 as young or old. Without earlier captures one cannot be sure if they are young of the year that had slightly higher asymptotic weights or overwintered animals that either lost 40 to 50 per cent of their weight or reached a low asymptotic weight. Weight was gradually lost through the winter. No recaptures were made after February, 1970.

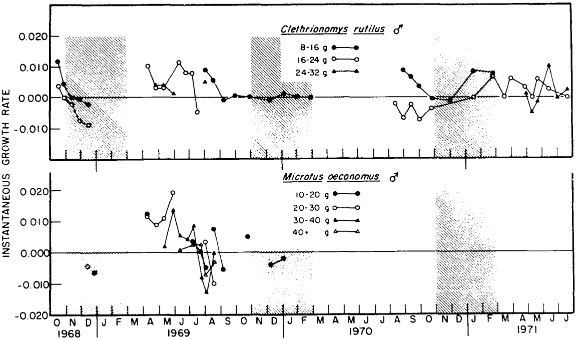
Zapus. This type of analysis is not applicable to Zapus for there were so few multiple captures in one season.

Instantaneous relative growth rates by weight class:

Instantaneous relative growth rates are graphed according to weight class for Clethrionomys in Fig. 20a and for Microtus in Fig. 20b. Each point represents the mean growth rate for all individuals in each weight class. This analysis is useful for analyzing the quantitative details of growth which will be used to calculate productivity.

Clethrionomys. Grid A, B and E animals in the 8 to 16 g weight

Figure 20. Instantaneous relative growth rate by weight class. Each point represents the mean growth rate for all individuals in each weight class. (a) *Clethrionomys*; (b) *Microtus*.


INSTANTANEOUS GROWTH RATE
Clethrionomys rutilus ♂
8-16 g
16-24 g
24-32 g
Microtus oeconomus ♂
10-20 g
20-30 g
30-40 g
40+ g
0.020
0.010
0.000
-0.010
-0.020
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
1968
1969
1970
1971

class were still gaining weight in October 1968. When trapping resumed in April 1969, few animals were left in the 8-16 g weight class but the ones that were had very high growth rates. The males started to grow two to four weeks earlier than did the females. By May, all animals had either grown out of this weight class or had left the population. By early August recruits entered the 8 to 16 g weight class and these animals decreased their growth rates to a constant near zero over the winter. This decrease occurred at least two months earlier than in 1968. Immigrating young had positive growth rates in August 1970, which decreased to zero in October, 1970. This zero growth rate or stable overwinter body weight was reached a month later during 1968 but a month earlier during 1969. By mid-January, overwintered animals in the 8-16 g weight class were experiencing positive growth rates and all animals had grown out of this class or had left the population by March. One recruit was recaptured in early July and its growth was positive.

The 16 to 24 g weight class growth rates decreased earlier and had lower rates than the 8-16 g weight class in 1968. When trapping resumed in 1969 most of the males had grown into the 16-24 g class and experienced positive rates until mid-July when these animals left the population. In 1970, the 16-24 g males steadily lost weight until January (while no animals were captured in January, growth rates are plotted for animals that were captured in December and recaptured in February) when growth rates increased. Growth was unstable until the end of the study.

Heavier weight males, 24-32 g, were present only in 1969 and 1971 (excepting one animal in 1970). It is interesting to note that both the 24-32 g and the 16-24 g animals decreased their growth rates in May 1971, when snow was melting, yet this did not occur in 1969 during spring break up.

The main difference between Grids C and D and Grids A and B is the presence of heavier animals during the 1970 summer. Males in the 8-16 g class experienced zero to positive growth rates from June (and most probably April and May) to November when overwinter stability was reached. All males grew out of this class by late February or early March. One recruit was captured in July from the 0-8 g weight class which had a very high rate: 0.038 g/g/day (compare to Fig. 20).

Heavier animals (24-32 g) on Grids C and D had positive growth rates in late July and early August 1970. As winter approached animals on Grid C exhibited a slight negative growth rate and animals on Grid D possessed a larger negative growth rate. Males did not overwinter in this heavier weight class.

<u>Microtus</u>. <u>Microtus</u>, a heavier animal, is analyzed in five, 10 g, weight classes (Fig. 20b). By April 1969, overwintered animals had started to gain weight. The few males left in the 10 to 20 g weight class had good growth rates and as these animals grew into the 20-30 g class. By July most of the overwintered animals were all in the 30-40 g class and still growing into the 40 g and above class. By late July, growth rates in the recruits and the 30-40 g weight class decreased. Within the next two to four weeks all of the heavier weight classes experienced negative growth. The second groud of recruits that reached the trappable population (i.e. left the nest), decreased growth rates

even more rapidly than the first. A possible third cohort in October presumably lost weight as soon as it entered the trappable population. The same patterns of growth rates were observed on Grid B, especially the decreases in all weight classes in late-July and August.

Movement

The trapping procedures used in this study yielded four types of movement-related data. One aspect of movement, effective trapped area has already been presented in the density section (p. 52). The three movement parameters covered in this section are: (1) between trapping period mean movements, (2) within trapping period mean movements, and (3) intergrid movements or dispersal.

Clethrionomys:

Between period movement. Movements on one grid from the first capture point of one period to the first capture point of the next are termed "between period movements". The mean length of movement has been calculated for each breeding period as well as the sum of lengths of movement during all the non-breeding periods for Clethrionomys (Table 16).

The breeding season mean for all animals, 16 m, was very similar to the mean for all movements during the non-breeding season, 14 m. Female movements for the breeding and non-breeding seasons (13 m and 14 m respectively) were also quite similar. Male movement length during the breeding season (18 m) was slightly longer than the non-breeding (15 m) as well as being greater than that of the females.

Adult and subadult movements for the total breeding and non-breeding periods were similar except for that of adult males in 1970 which were larger. A mean movement length of 28 m for these adults was almost twice all other breeding season movements which ranged from 11 to 17 m.

Although the movement data on Grids B and E are based on much smaller sample sizes than that from Grid A, the data suggest that the movement patterns for males and females are similar for all three girds. For example the mean movement during the 1969 breeding season on Grid A was 15 m for 65 animals and 6 m for 10 animals on Grid B.

Mean movement lengths on Grid C was 39 m for males and 25 m for females approximately twice as large as the means from Grid A. Male movements during the breeding periods (40 m for 1970 and 34 m for 1971) were substantially longer than the non-breeding season mean (21 m). The opposite was the case for females which had a greater non-breeding mean movement length of 35 m compared to 28 m and 23 m for the two breeding seasons. Grid D movements were similar to but on the whole shorter than those on Grid C (except for male movement in 1971 which was greater).

Between grid comparison of movements were made for males and females by reproductive seasons. Chi-square analysis (Table 17) showed two significant differences: (1) male movements on Grids C and D were longer than on Grid A in the 1971 breeding season and (2) female movements on Grid C were longer than movements on Grids A, B, D and E in 1970.

Since there appeared to be trends in movement within each breeding period, mean movement lengths have been plotted for male and female Clethrionomys on Grid A (Fig. 21). During each breeding season, male

Table 16. Mean length of movement between trapping periods for adult males and female Clethrionomys. Movements were measured from first capture point of trapping period (*t*) to first capture point of trapping period *t*+1.

	Year	Breeding Status	$\bar{x}$ Distance in meters (M)	(N)	$\bar{x}$ Distance in meters (F)	(N)
GRID A:	1969	B	17.4	(36)	10.9	(29)
	1970	B	28.2	(10)	13.6	(10)
	1971	B	15.3	(43)	13.5	(40)
	All years	NB	14.3	(72)	13.8	(41)
GRID B:	1969	B	14.5	(7)	18.8	(3)
	1970	B	32.7	(5)	13.9	(3)
	All years	NB	14.1	(7)	13.9	(6)
GRID C:	1970	B	44.0	(14)	27.6	(11)
	1971	B	34.1	(21)	23.2	(31)
	All years	NB	21.4	(8)	35.2	(8)
GRID D:	1970	B	25.0	(15)	21.2	(16)
	1971	B	38.5	(8)	24.4	(9)
	All years	NB	19.1	(4)	19.2	(20)
GRID E:	1970	B	29.1	(6)	11.8	(4)

movements increased and then markedly decreased. The same phenomena may have occurred in females but is less noticable. These decreases within the breeding seasons seem to have occurred in a similar manner each year: male movement increased sooner and was longer than the female movement. When movement decreased male values were once again close to those of the females. One should also note the increase in variability of movement during the 1970-1971 breeding seasons as compared to the 1969 breeding season. On Grids C and D, the 1970 breeding season was also characterized by a marked male movement decrease in late August. Females reached a low in late July. There were no decreases in male or female movement lengths in 1970.

Table 17. Chi-square analysis for differences in Table 16 movements.

		Males			Females		
Year	Season	χ^2	df	p	χ^2	df	p
1969	B	1.34	1	$0.250>p>0.100$	3.75	1	$0.100>p>0.050$
1970	B	9.47	4	$0.100>p>0.005$	4.50	4	$0.050>p>0.025$
1971	B	17.45	2	$0.005>p$	4.50	2	$0.250>p>0.100$
1971	NB	3.30	3	$0.250>p>0.100$	23.18	3	$0.005>p$

Within period movements. Mean movement lengths within each trapping period for male and female Clethrionomys appear in Fig. 22. These are the only data presented for within period movement. Since the factors influencing movement length are somewhat different from those affecting between period movement (Krebs, 1966), data in Fig. 22. are presented strictly for comparative purposes with Fig. 21. The similarities between these two figures are striking for the three breeding seasons. For example, in 1970 both methods showed a marked increase in male movement. Both adults and subadults were responsible for the peak in movement but the subadult movement shortened two to four weeks before the adult movement length shortened.

Microtus:

Between period movements. The mean lengths moved between periods are summarized for male and female Microtus (Fig. 23). During the 1969 breeding season there was a steady increase in male movement until late July when trap revealed movements showed a 46 per cent decrease. Movements increased for a month then decreased in mid-September. The first decrease was due to the adults that remained on the grid. The second decline was due to an absence of adults and was a time of shorter subadult movements. Female movement (adult and subadult class) steadily increased throughout the breeding period. The highest values were measured under the snow in November and December 1969.

Grid B movement data were only available for the last half of the breeding season. While female movements are similar to those on Grid A, male movements are only half those of males on Grid A.

Four points can be summarized from between period movements. First, Microtus and Clethrionomys mean distanced moved between periods are very similar. Second, the means for Grid B and E agree with the ones for Grid A. Males on Grid C had longer moves in the 1971 breeding season and females on Grid C had longer moves in the 1970 breeding

Figure 21. Mean lengths of movement between trapping periods for male and female Clethrionomys on Grid A. Movements were measured from first capture point of trapping period *t* to first capture point of trapping period *t* + 1.

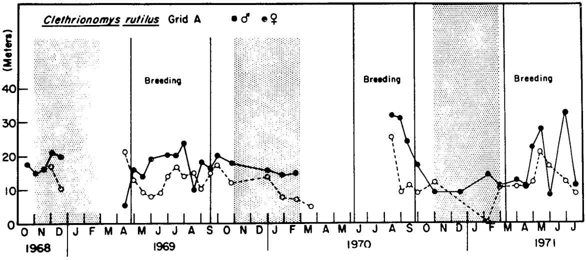

Clethrionomys rutilus Grid A
● ♂ ● ♀
(Meters)
40
30
20
10
0
Breeding
Breeding
Breeding
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
1968
1969
1970
1971

Figure 22. Mean lengths of movement within trapping periods for male and female Clethrionomys on Grid A.

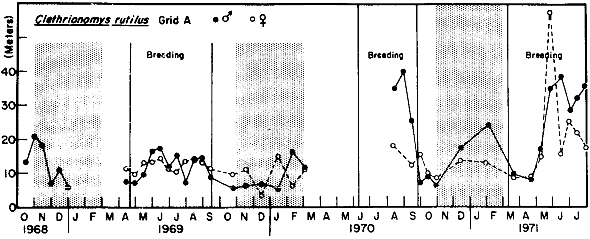
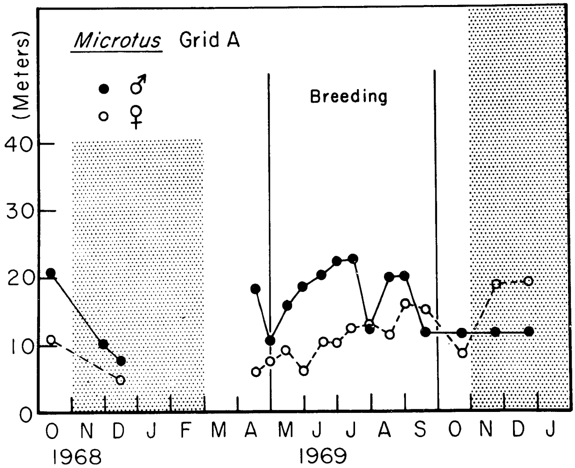

Clethrionomys rutilus Grid A
● ♂ ○ ♀
(Meters)
0
10
20
30
40
Breeding
Breeding
Breeding
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
1968
1969
1970
1971

Figure 23. Mean length of movement between trapping periods for male and female <u>Microtus</u> on Grid A.


Microtus Grid A
● ♂
○ ♀
(Meters)
0
10
20
30
40
Breeding
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
1968
1969

season. Third, trends within breeding seasons showed similar decreases in male movement for *Microtus* and *Clethrionomys*. *Clethrionomys* movement decreases (1970 and 1971 in the absence of *Microtus*) were approximately twice those in 1969 for within and between period movement length means. Fourth, the decreases in male *Microtus* movement were due to adults that remained on the grid while *Clethrionomys* male decreases were due to all weight classes.

Dispersal

Intergrid movement was used as an index of dispersal. Table 18 lists all intergrid movements for *Clethrionomys*, *Microtus* and *Zapus*. Movements are calculated from the point of the last capture before each move to the first capture after the move. Intergrid movements have been divided into all possible two way dispersals. The direction of the disperal is given by an arrow (Table 18).

Clethrionomys:

Thirty-four moves between grids were observed for *Clethrionomys*. Half occurred on the Steese area and the rest on the College area. Moves on the Steese were at least 100 m and up to 400 m while ten intergrid moves on the College area were under 100 m. It is interesting that all movements between Grids C and D that were under 100 m were followed by a return movement to the grid of origin. There were no return movements detected on the Steese grids. In the following analyses and in Table 18, only those moves over 100 m are considered.

Fifteen of the seventeen dispersals on the Steese grids were made by males. This difference was significant, $\chi^2 = 8.48$, df = 1, $0.005 < p$. The two females that did disperse were non-breeding subadults while the subadult males that dispersed were breeding. On the College area there was no significant difference in the sex of dispersing animals, $\chi^2 = 0.100$, df = 1, $0.900 > p > 0.750$.

Following the week 44 trapping period in late July 1969, during the density increase, five out of the seven adult males present on Grid A dispersed. The average body weight of animals that dispersed was 20 ± 2 g while the body weight of the single male that survived to the next trapping period was 29 g. All of these seven animals had been on Grid A for a minimum of two trapping periods before dispersal. These sample sizes are too small for statistical comparison but there is a trend for lighter weight breeding adults to disperse. Approximately a month after the immigration from Grid A, four *Clethrionomys* left Grid B. Three of these were light weight breeding males and one was a non-breeding subadult female.

There were seven dispersals greater than 100 m on the College Grids, five of which occurred in September and October 1970. Both sexes as well as all weight classes were represented in the animals that dispersed. All animals that were present on one grid for at least three trapping periods before dispersal were subsequently caught only once after the movement. However, those animals that were captured at least twice after dispersing had been captured only once before dispersal.

Microtus:

Microtus were only observed dispersing on the Steese grids.

Table 18. Intergrid movements for *Clethrionomys*, *Microtus* and *Zapus*. Movements are calculated from the point of the last capture before each move to the first capture after the move. Arrows indicate direction of move between grids. A = adult, Sa = subadult, J - juvenile.

Clethrionomys

Animal #	Before* week #	After week #	Sex	Age	A-B	A-E	A-F	B-E	B-F	F-E	C-D
A 45	44	44	M	A	→						
A 45	44	46	M	A					→		
A 70	44	46	M	A			→				
A 85	44	46	M	A			→				
A 140	44	46	M	A			→				
A 142	44	46	M	A			→				
A 160	44	46	F	Sa			→				
B 63	46	60	M	A	←						
B 72	46	62	M	Sa	←						
B 102	56	96	M	A	←						
B 97	56	72	F	Sa	←						
A 296	90	92	M	A				←			
A 365	90	92	M	A	→						
A 271	94	98	M	Sa		←					
C 12	92	92	M	A							→
C 4	92	92	M	Sa							→
C 32	102	102	M	Sa							→
D 56	102	114	F	Sa							←
A 310	102	104	M	J						←	
B 312	104	108	M	Sa		←					
B 136	104	112	M	Sa	←						
D 68	104	106	F	J							←
D 58	110	130	F	Sa							←

---

* See Table 42 for week number conversion to date.

Table 18. Continued

Microtus

Animal #	Before week #	After week #	Sex	Age	A-B	A-E	A-F	B-E	B-F	F-E	C-D
A 134	40	42	F	A			→				
B 2	42	46	F	A					→		
B 6	42	46	M	Sa					→		
B 25	42	46	M	A					→		
B 5	44	46	M	A					→		
B 30	44	46	F	A					→		
B 46	48	66	M	Sa	←						
B 48	48	66	M	Sa	←						
A 263	86	86	M	A			→				
Zapus											
A 99	40	94	M		→						
A 107	40	42	M		→						
A 114	40	94	F			→					
A 132	40	94	M			→					
B 27	42	142	F						→		
A 176	42	142	M		→						
A 177	44	94	M		→						
A 195	46	94	F		→						
B 86	48	144	F						→		
A 127	86	94	M		→						
A 206	86	94	M			→					
A 99	94	94	M					→			
A 206	94	94	M					←			
E 269	94	144	M					←			
E 285	94	142	M					←			
B 31	94	142	M						→		
B 127	96	144	M						→		
E 270	98	100	F					E→Ax			
E 299	100	102	M					←			

Extensive live trappings (1000 trap nights) were carried out on lines surrounding the College grids (see Table 2) in an attempt to pick up the 21 Microtus that disappeared in July, 1970. No marked or unmarked Microtus were caught on these lines but three out of 20 Clethrionomys captured had marks. These three marked Clethrionomys are not included in Table 18 because the information on the animal's number, sex, weight, etc., was lost. Microtus were present in substantial numbers throughout the study about 800 to 1000 m east of the C and D grids in low-lying fields around Smith Lake (800 to 1000 m NW of the area covered in Fig. 1). Tagged animals were never found during snap trapping in this area (Table 2). Nine Microtus were observed to have dispersed on the Steese grids. Six of these animals were caught during July 1970. The three females were breeding adults that weighed 35 g or more while the males ranged from 17 to 51 g. In early September two more subadults left Grid B. Eight out of nine Microtus emigrations were from Grid B during July to September.

Zapus:

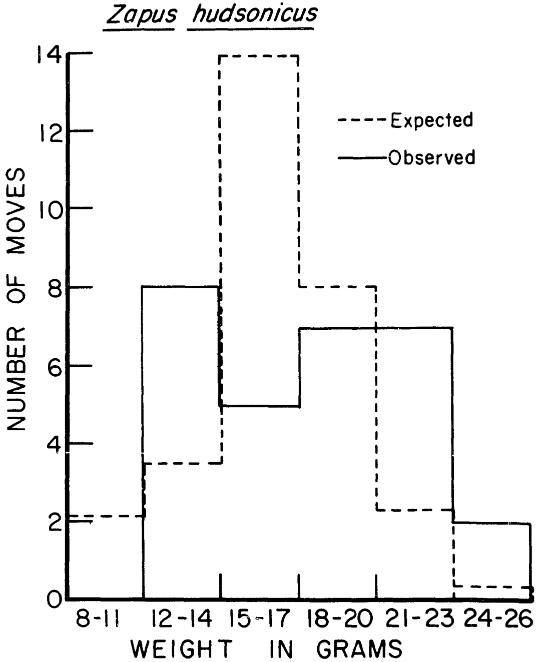
Of the 77 Zapus live trapped, 39 animals were recaptured at least once. There was a total of 55 recaptures, 22 were within the two snow free seasons, while 33 were between seasons or over a hibernation period. There was therefore, an equal or greater chance of recapturing a Zapus the following year. This applies to males as well as females, $\chi^2 = 0.032$, df = 1, $0.990 > p > 0.975$).

Intergrid movements were measured for 20 of the 39 recaptured Zapus. Neither sex was more likely to move long (Intergrid) or short (Intergrid) distances, $\chi^2 = 0.069$, df = 1, $0.97 > p > 0.95$). In addition 45 per cent of the movements measured from before to after hibernation were between grids. Therefore it is concluded that either sex had an equal chance of being recaptured before or after hibernation regardless of the distance moved.

While there is an equal chance for an animal to be recaptured in the same season or the next, there appears to be a greater chance for animals to be recaptured the next year if they were last caught in July as compared to September. Twenty-one dispersing animals were last caught in July versus eight last caught in September. This phenomena is not as pronounced when one recalls that many more animals were caught in July than September (67 captures versus 26 captures), yet 25 per cent more were last captured in July than would be expected from the percentage of captures in July, the difference however is not significant, $\chi^2 = 3.13$, df = 1, $0.10 > p > 0.05$.

Animals are just as likely to make a long move as a short move but another interesting phenomena appears when long and short movers are divided into three gram weight classes. The weight frequency distribution of the animals that made long movements was the same as would be expected when compared to the weight frequency distribution of all animals captured. However, the weight frequency distribution of those animals that made short movements was significantly different than the weight frequency distribution of all _Zapus_ caught (Fig. 24), $\chi^2 = 12.13$, df = 5, $0.05 > p > 0.025$. Figure 24 has been interpreted to mean that 15 to 17 g animals are dispersing, resulting in fewer moves of those animals left

Figure 24. Number of _Zapus_ short (intragrid) moves for each three gram weight class (solid line) are compared to the number of _Zapus_ short plus long (intergrid) moves for each three gram weight class (dashed line).


Zapus hudsonicus
NUMBER OF MOVES
14
12
10
8
6
4
2
0
8-11
12-14
15-17
18-20
21-23
24-26
WEIGHT IN GRAMS
----Expected
——Observed

on the gird.

To summarize: (1) All Clethrionomys intergrid movements under 100 m on Grids C and D were followed by a return to the grid of origin. (2) There was a tendency for light weight breeding Clethrionomys males to disperse on the Steese Grids. (3) Both Microtus and Clethrionomys had the highest number of dispersals during the later part of the breeding season during the population increase and peak. Four points can be summarized from Zapus dispersal: (1) There was an equal or greater chance of recapturing a Zapus the same or following year, (2) Either sex had an equal chance of a long or short move within or between seasons, (3) There was a tendency for animals being recaptured the next year if the animal was last captured in July vs September, and (4) Animals making shorter moves did not fit the expected weight frequency distribution (Fig. 24), thus indicating that 15 to 17g animals were dispersing.

Autopsy

Since snap trapped animals will be used to extrapolate fat, caloric and reproductive information to the live trapped population, one must ask if the live and snap trapped animals are samples of the same population. This section will first be concerned with, evaluating the question of whether the snap trapped and live trapped populations are similar enough to allow extrapolation and second, the basic analysis of autopsied mice. Autopsy sample sizes were 288 Microtus oeconomus, 100 Clethrionomys and 17 Zapus.

Body weight:

Body weight distributions, in four gram intervals, for autopsied male Clethrionomys, Microtus and Zapus are presented in Table 19. No animals were captured in winter snap trap lines, the animals that appear under September, 1969 - April, 1970, are winter live trap fatalities. (The validity of extrapolating from these live trap fatalities is questionable but these animals are the only data available from winter populations.)

Clethrionomys. Mean body weights for Clethrionomys (Table 19) are similar for June-July of 1969 and 1970 (19.9 g and 22.0 g, respectively). This similarity also holds for breeding stratification (breeding 1970, N = 12, 19.8 ± 4.1; breeding 1969, N = 8, 20.9 ± 2.0; t' = 0.57 for 7df and 12df; non-breeding 1970, N = 19, 16.6 ± 1.6g; non-breeding 1969, N = 4, 17.0 ± 0.8; t' = 1.38 for 3df and 19df).

The mean weights of snap trapped animals were similar to the mean weights of animals caught on all live trap grids. For example, weights on live trapped Grid A during the 1969 breeding season, 20.1 g, is very close to the mean snapped weight, 19.6 g, for the same period. However, the body weight distributions for snap trapped and live trapped groups were not the same during this period. None of the snap trapped animals caught in 1969 had weights less than 15 g or more than 24 g, while 58 per cent of the live trapped animals were above or below the 15 g to 24 g range. The following year, 1970, there were few heavy or light animals captured in either the live traps or the snap traps.

Microtus. When determining if year to year differences exist in

Table 19. Male body weight distribution, in four gram intervals, for autopsied _Clethrionomys rutilus_, _Microtus oeconomus_ and _Zapus hudsonius_.

Microtus

body weight (g)	1969					1970				
	May	June	July	Aug	Sept-Apr	May	June	July*	Aug*	Sept
0-10			2	1				3		
11-14			10	9						
15-18			27	24				3	1	
19-22			11	11				1	3	
23-26						1				
27-30					1		1			
31-34						2				
35-38										
39-42			1	1			1			
43-46	1	1	3	2						
47→		1	1	3				2		

Clethrionomys

body weight (g)	May	June	July	Aug	Sept-Apr	May	June	July*	Aug*	Sept
0-10					1					
11-14					1				2	2
15-18			1	4	3	1		3	2	13
19-22		1	1	4				3	2	3
23-26			3					1		
27→									1	

Zapus

body weight (g)	May	June	July	Aug	Sept-Apr	May	June	July	Aug	Sept
0-10										
11-14				1						
15-18				1		6	5	1		
19-22							3			

* Column totals do not correlate with data for both sexes in Table 2.

means and distributions of body weight for Microtus, it must be remembered that all the 1969 samples were from the Steese Area and all but two of the 1970 samples were from the College Area. The mean body weight for snap trapped animals seems to be different for the two year: 20.1 g in 1969 and 29.7 g in 1970. The non-breeding portions of these two populations (15.8 ± 4.6 g, N = 8, 1970; 16.0 ± 2.7 g, N = 61, 1969) do not cause this difference (t' = 0.072, df = 7 and df = 60), but the breeding populations do (36.3 ± 9.2 g, N = 7, 1970; 45.7 ± 5.1 g, N = 12, 1969; t' = 2.41 for 6 df and 11 df or t' = 2.18 for 19 df). The 1969 Steese sample is typical (Chitty, 1952, and many others) of a peak microtine weight distribution with few middle weight (23 g to 34 g) and many light (15 g to 22 g) animals. The 1970 population conversely has proportionately more middle weight and fewer light weight mice.

The distribution of body weights of snap trapped animals agrees very well with that of live trapped animals on Grid A for 1969. A chi-square goodness of fit indicate that there is no difference between body weight distribution for Grid B* and snap trapped animals $\chi^{2**} = 0.2$, df = 2, p = 0.9. The scarcity of Microtus on Grid A, B and E in 1970, make a comparison of distribution difficult, but the heavier weight animals on the College Area grids suggest that the populations are

---

* Grid B was used because the sample sizes are closer to those of the snap trapped animals.

** All weight classes above 39 grams were pooled and classes with zero were excluded.

demographically differen from those on the Steese (see Discussion, G & H declines). The heavier Microtus in the College Areas were evident in both the live and snap trapped samples.

Zapus. Insufficient snap trap data in 1969 did not permit comparison with live trapping data. In 1970, snap traps did not catch light weight animals. This was most noticeable in August 1970, when the Zapus young were well represented in the liver trapped population.

To summarize, the snap trapped and live trapped samples are similar, excepting the failure of snap traps to catch lighter weight Clethrionomys in 1969, heavier weight Clethrionomys in 1969, and light weight Zapus in 1970. Snap trap data as well as live trap data indicate that the Microtus population in 1969 was demographically different from that in 1970, while the Clethrionomys populations were similar in both years.

Number of embryos and uterine scars:

Clethrionomys. Few Clethrionomys were observed with embryos. The average for nine animals was 8.1 (range 4 to 11 embryos). Uterine scars in obviously pregnant and non-pregnant females averaged 12.3 for the eight individuals examined. The discrepancy between the average number of embryos and scars suggest resorption of embryos or post-implantation loss. Of the nine animals with embroys, there was an average of 3.7 resorptions. Sample sizes do not allow comparison between years. Preimplantation losses were not determined.*

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* Corpora lutea were counted; however, freezing and lack of experience in distinguishing lutea from mature follicles (M. Modafferi, pers. comm.) caused me to doubt much of the data.

Microtus. Even fewer Microtus were observed with embryos. The average number of embryos for the seven females was 6.8, while the average number of uterine scars for 23 individuals was 6.4. The similarity of these two numbers indicates few absorptions. Furthermore, only one embryo, of the seven females examined, was being resorbed.

Zapus. Two Zapus had six embryos apiece. No scars were observed in any of the other females.

Testes weight:

Following the method of Keller and Krebs (1970) males were divided into breeders and non-breeders and regression analyses were run between body weight and testes weight. The results are listed for all three species in Table 20.

Clethrionomys. Only the data for non-breeders during the summer, 1970, showed a body weight - testes weight regression that was significantly different from zero ($t = 3.48$). Therefore covariance analyses (Kelkr and Krebs, 1970) were not used for investigating possible seasonal differences in the testes weight data (Table 20). As an alternative, mean testes weights were compared using the t' test for samples with unequal variances. Mean body weight of the breeders is significantly different from that of the non-breeders: $t' = 4.80$, df = 3, 8 for 1960; $t' = 2.58$, df = 11, 18 for 1970. In addition the breeders testes weight was significantly different from the non-breeders testes weight: $t' = 26.95$, df = 3, 8 for 1969; $t' = 8.63$, df = 11, 18 for 1970. These statistics ignore the fact there is a biologically realistic overlap in the body weight of breeders and non-breeders during the summer. For

Table 20. Testes weight and body weight for *Clethrionomys* and *Microtus* by season and year.

Clethrionomys

Breeding	Season	Year	No.	r	Testes wt. mean (mg)	S.D.	Body weight mean (g)	S.D.	Slope
N B	Summer	1969	4	-0.95	13	7	17.0	0.8	-8.50
	Summer	1970	19	-0.64	11	4	16.6	1.6	-1.50
	Fall	1969	3	--	7	2	18.0	0.0	--
	Fall	1970	9	0.02	17	3	16.6	1.0	0.04
B	Summer	1969	8	0.38	498	52	20.9	2.0	10.21
	Summer	1970	12	0.56	409	157	19.8	4.1	25.20

Microtus

Breeding	Season	Year	No.	r	Testes wt. mean (mg)	S.D.	Body weight mean (g)	S.D.	Slope
N B	Summer	1969	61	-0.14	8	3	16.0	2.7	-0.15
	Summer	1970	8	-0.71	9	5	15.8	4.6	-0.71
B	Summer	1969	12	0.67	194	55	45.6	5.1	7.28
	Summer	1970	7	0.50	164	43	36.3	9.2	2.34

example, in Summer 1969, fertile males with testes weight of 450 mg weighed as little as 17 g while non-fertile males weighing 17 g and 18 g had testes weight less than 20 mg. Thus animals with the same body weight can have testes weights that are more than three standard deviations apart.

During the fall of both years, testes weights were the same. I believe, however, that the fall populations were made up of these two types, for example, animals as A-336 (Fig. 19) that lost up to 30 per cent of their body weight also went from scrotal to non-scrotal conditions.

Microtus. In Microtus, two of the body weight - testes weight correlation coefficients, were significant (Summer 1970, t = 2.48, NB; Summer 1969, t = 2.86, B). There was no overlap in body weight between the breeders and non-breeders. The significant difference between body weights of these two classes seem to be biologically realistic: t' = 19.60, df = 11, 60 Summer 1969; t' = 5.35, df = 7, 6 Summer 1970. The non-fertile Microtus weighed far less (more than three standard deviations from the mean) than the fertile males. The fertile males from 1970 were slightly lighter in both body weight and testes weight, but only significantly in body weight: t' = 2.43, df = 6,11.

Zapus. The Zapus data showed no significant correlation between body weight and testes weight. All of the male animals seemed fertile and capable of breeding.

Maturity:

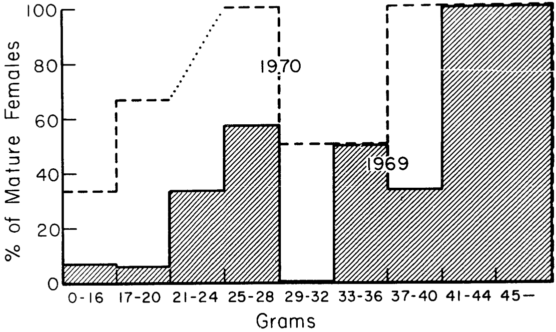
Median weight at sexual maturity was used as an index of age at sexual maturity for comparison between seasons and years. Female maturity was determined by the presence of corpora lutea or dark uterine scars. (Female weight was not corrected by removal of extra weight due to pregnancy.) Male maturity was determined by the testes size and secondarily by the enlargement of the cauda epididymus. There was never a discrepancy between these two parameters.

Clethrionomys. Female and male Clethrionomys had the same median body weight at sexual maturity (Mann-Whitney U-Test, Tate and Clelland, 1957, p. 87-91), .05 = 9, T = 18 for 1969 and 1970 females; for 1969 and 1970 males, .05 = 58, T = 80 for males and females pooled, Z = 0.98, p - 0.161. The median weight for all Clethrionomys was 21 g (95% confidence limits 22, 18). No animals from fall or winter samples were mature.

Microtus. There was no significant difference between Microtus female median weight at maturity between 1969 and 1970 (Mann-Whitney U-Test Tate and Clelland, 1957, p. 87-91, Z = 0.59, p = 0.28). The two groups were combined: the resulting group had a median weight at sexual maturity of 34 g (95% confidence limits, 25 to 37; n = 33). While the above test showed no difference in median body weight in females between years, Figure 25 indicates that a lower percentage of 13 - 32 g individuals matured in 1969 as compared to 1970.

Male median weights between years were significantly different p = 0.10 but not at p = 0.05; the 1970 males were lighter than those for 1969. The two animals in the 1970 sample from the Steese weighed 31 and 32 g and had the lightest weights of all mature animals. This is a very small sample size; but weights of these males seemed to be considerably

Figure 25. Per cent mature Microtus females in each four-gram body weight class. Dotted sloped line indicates that there were no females caught in this weight class in 1970.


100
80
60
40
20
0
% of Mature Females
1970
1969
0-16
17-20
21-24
25-28
29-32
33-36
37-40
41-44
45—
Grams

lower than the median weight (44 g) of the College animals. When the weights of the 1969 and 1970 males are combined the median weight at sexual maturity is 44 g (95% confidence limits, 39 to 48 g; n = 19). Only one Microtus captured in the fall and winter was sexually mature.

The following trends are evident from the sexual maturity data for Microtus: 1) Fewer light weight females were mature in the summer peak of 1969, 2) Males matured at a heavier median body weight than females, especially in the 1969 peak population, 3) Microtus males in 1970, from the College and Steese Area had nearly significant lower body weights at sexual maturity, and 4) Most animals were not mature in fall, winter or early spring.

Zapus. As noted by Quimby (1951), Zapus males are difficult to class as mature or not mature. All males captured seemed mature. Four of the six females were mature.

Pregnancy rates:

One of the major difficulties in determining pregnancy rates is to determine what proportion of the population is potentially mature. Two ways have been used to determine maturity: 1) By the weight above which most pregnancies occur, and 2) By the presence of corpora lutea.

In addition the weight above which pregnancies occur will be compared to live trap pregnancies. (Snap trapped animal weights were not corrected for embryo weights.) This comparison will be checked by making corrections for embryo weight in both live and snap trapped animals, i.e. corrected body weights of females with embryos and or corpora lutea will be compared to weights of live trapped females two weeks before or two weeks after pregnancy.

Clethrionomys. Live trapped and snap trapped pregnant animals were all 24 g or heavier. The heaviest litter in utero observed in the study was 6.3 g. Hence live trapping and snap trapping analyses using the first method would indicate that there is little chance that a Clethrionomys lighter than 18 g could be pregnant. However, when the presence of corpora lutea is used as an index of maturity the lower weight limit is reduced to 12 g, with 30 per cent of the snap trapped animals having weights less than 18 g. Weights of 14 live trapped females (Grid A), two weeks before externally observed pregnancy, were used as a comparison to the snap trapped animals whose weight was corrected for pregnancy related tissue. The median weight gain by pregnant females for two weeks was 9.0 g, the most spectacular being an increase from 11 g to 25 g in June, 1971. On the basis of this method, in addition to methods utilizing changes in lactation and opening of the pubic symphysis, all animals above 11 g could be mature.

Using the corpora lutea method, three of four or a 75 per cent pregnancy rate was observed in mature snap trapped Clethrionomys in June and July 1969. Six of eleven females were pregnant in 1970. There is not enough data for comparison between years. The pooled snap trap pregnancy rate for both years was 63 per cent in June and July. According to Keller and Krebs (1970) if 100 per cent of the females were pregnant, only 71 per cent would be observed as being pregnant due to the inability to detect the earlier days of gestation. Applying this logic to the snap trap data the corrected percentage would be 88 per cent.

Microtus. A comparison of body weight distributions for pregnant animals in the live trapping sample with those in the snap trapping sample indicate that lighter animals are pregnant in the snap trap sample. Snap traps failed to catch any 49 to 60g gravid females during June through September 1969. Eighteen females were considered pregnant during the breeding season from April to October 1969. This was determined by using weight gains (median 7g) in a manner similar to that done for Clethrionomys. Weights of these pregnant females two weeks before or after pregnancy ranged from 15 to 42g. Maturity as judged by corpora lutea indicated that animals could become pregnant at 12g, but based on data presented in Figure 24, 17 to 20g might be a better cut off point for maturity. In 1969 the number of pregnancies from June to August was $\frac{8 \text{ preg.}}{32 \text{ mature}}$ (22 per cent or 31 per cent corrected). The following year had a higher percentage of pregnancies for the same period $\frac{8 \text{ preg.}}{26 \text{ mature}}$ (31 per cent, 44 per cent corrected). The raw ratios are not significantly different $\chi^2 = 0.403$, df = 1, $p < 0.05$.

To summarize, corpora lutea seemed to be the best way for determining maturity in the populations. Based on the corpora lutea method, pregnancy rates of 88 per cent for Clethrionomys and 38 per cent for Microtus were observed.

Average daily metabolic rate

The graphs (Fig. 25 thru 29) of metabolic rate over time are a condensed form of the copious amounts of data generated by Average daily metabolic rate (ADMR) techniques. Table 21 summarizes the mean ADMR in

$cc0_2/g\ hr^{-1}$ for each species by season. The standard deviation for each animal's ADMR is assumed to be a good index of the amplitude of oscillations over time. Means of these standard deviations have also been summarized for each season. The frequency of the oscillation in ADMR has been measured on a subsample (54) of the total (98) runs. In addition to these physiological parameters, survival of the animals, whose ADMR was measured, is compared to the survival of all animals from the appropriate season and grid (Table 23).

ADMR's were determined on a total of 98 animals during all seasons. The body weights of the analysed animals are representative of the field weight classes present at the time of sampling. Temperatures (excepting spring 1969 and winter 1970) correlate well (by inspection) with ambient field temperatures. Differences in ADMR's between sexes were tested for all species for each season (on sample sizes of seven or greater). No significant differences were detected. Seasons from 1969 were tested against the same seasons in 1970, and the only significant differences in ADMR's were found for spring samples of both Clethrionomys and Microtus ($t' = 9.26$, $p < 0.001$, df = 4; $t' = 7.16$, $p < 0.001$, df = 6). These differences can be explained by the high +15°C temperatures of the water bath in 1969 compared to the cooler ambient temperatures in the field. Since the ADMR's measured at +15°C in spring 1969 do not represent ambient, they will not be used in calculating maintenance energy of the population. However, the results from this period are methodologically signficant and will be used to examine weight vs metabolic rate.

Figure 26. ADMR for a Clethrionomys run on June 25, 1969, at +15°C. The animal was a 20-gram breeding male. Lights were left on for the whole run.

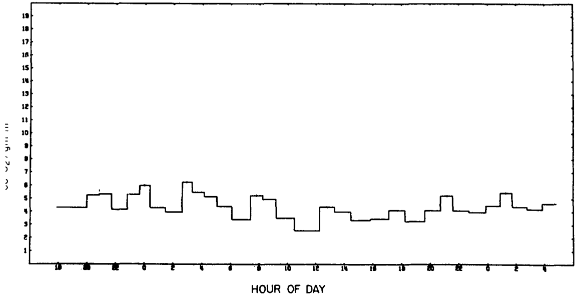

19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
18
20
22
0
2
4
6
8
10
12
14
16
18
20
22
0
2
4
HOUR OF DAY

Figure 27. ADMR for a Clethrionomys run on March 14, 1970, at -7.5°C. The animal was a 16-gram non-breeding male. Photoperiod is indicated on the axis.

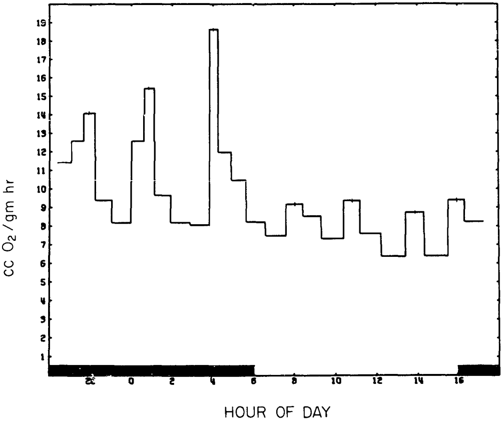

CC O2 /gm hr
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
22
0
2
4
6
8
10
12
14
16
HOUR OF DAY

Figure 28. ADMR for a Microtus run on May 28, 1969, at +15°C. The animal was a 45 g breeding male. Lights were left on for the whole run.

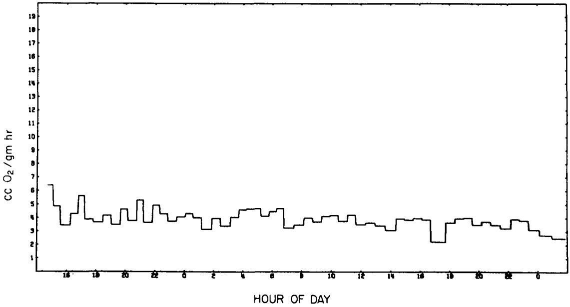
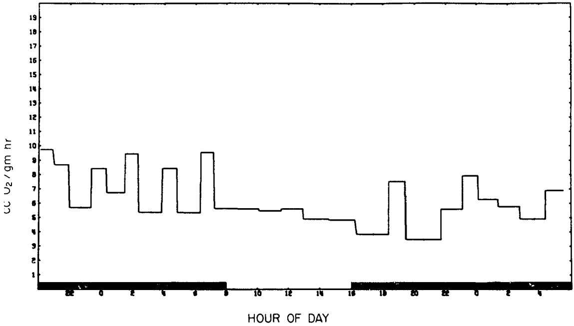

CC O_2/gm hr
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
16
18
20
22
0
2
4
6
8
10
12
14
16
18
20
22
0
HOUR OF DAY

Figure 29. ADMR for a Microtus run on October 27, 1969, at 5°C. The animal was a non-breeding female. Photoperiod is indicated on the axis.


cc O2 / gm hr
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18
17
16
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14
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12
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8
7
6
5
4
3
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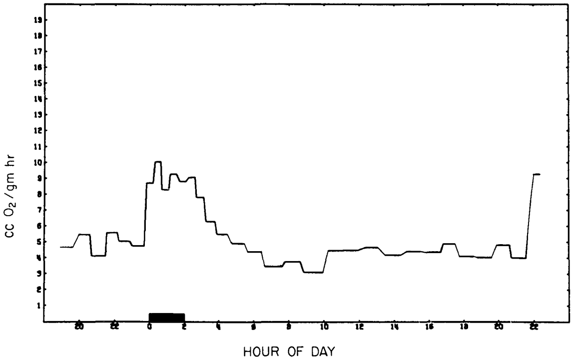
1
22
0
2
4
6
8
10
12
14
16
18
20
22
0
2
4
HOUR OF DAY

Figure 30. ADMR for a Zapus run on June 28, 1970, at 15°C. The animal was a 16 g non-breeding male. Photoperiod is indicated on the axis.


19
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3
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CC O_2 /gm hr
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HOUR OF DAY

Differences in ADMR's due to age class (body weight) have been examined for those seasons that have more than one age class present and where a sample size is large enough for stratification. Combined spring and summer 1969, samples for Clethrionomys and for the Microtus (all were run at +15°C) were tested for age class effects. Clethrionomys body weight (x) vs metabolism (y) $cc0_2/g\ hr^{-1}$ give a regression $y = 5.54 - 0.029 X$, $r = -0.18$, which is not significantly different from zero ($F = 0.30$, $df = 1,9$). The variability that prevents this equation from differing from zero, as theory says it should (Hoar 1964, Prosser 1967), can be removed by excluding breeding males, especially the larger ones. However I have no evidence to doubt these values. Instead I would prefer to reverse the problem by saying that the adult potentially breeding males are the most variable in terms of metabolic rate. Hence body weight (age class) will not be taken into account for calculating maintenance production. The Microtus regression $y = 5.81 - 0.048 X$, $r = 0.64$, is significantly different from zero ($F = 11.31$, $df = 1,16$). Age for Microtus will be taken into account for the overall picture of energy flow. The regression correction will be used only for the spring and summer 1969, since these are the only seasons with more than one age class (see Fig. 18). When these data are plotted as metabolism per individual per hour, rather than per gram per hour, the resulting regression slope should equal the classical 0.70 as seen in the Metabolism = k Weight $^{0.70}$ equation (mouse to elephant curve, Brody 1945). It is important to note that the slopes for Clethrionomys (4.64) and Microtus (2.88) are at least four times that expected.

Table 21. ADMR for *Microtus oeconomus*, *Zapus hudsonius* and *Clethrionomys rutilus*. The mean body weight, mean temperature and mean amplitudes are given for each season. Note that spring 1969 and winter 1970 temperatures were not the same as prevailing field temperatures.

Species	Season	No.	$\bar{x}$ Body Wt.	σ	$\bar{x}$ Temp	$\bar{x}$ ccO_2/g h^{-1}	σ	$\bar{x}$ amplit	σ
Microtus	Spring 1969	7	33.9	7.8	+15	4.28	0.88	0.84	0.31
	Summer 1969	11	29.3	15.6	+15	4.36	1.05	0.87	0.38
	Fall 1969	8	19.9	6.5	+ 8	5.46	1.29	1.05	0.43
	Winter 1969	3	16.7	2.1	- 3	7.26	1.50	1.75	0.54
	Spring 1970	2	16.5	2.1	- 6	8.00	0.33	1.74	0.11
	Summer 1970	4	23.3	6.4	+10	4.24	1.17	1.62	0.80
Zapus	Summer 1969+70	8	14.3	4.0	+14	4.94	1.22	2.01	1.03
Clethrionomys	Spring 1969	7	20.3	6.3	+15	5.08	1.18	0.78	0.32
	Summer 1969	4	24.3	6.8	+15	4.61	0.79	0.89	0.47
	Fall 1969	8	16.8	3.2	+ 8	4.90	1.16	1.37	0.72
	Winter 1969	5	15.8	2.2	- 6	6.79	0.62	1.47	0.34
	Spring 1970	4	13.5	1.7	- 8	9.24	0.48	1.86	0.54
	Summer 1970	4	25.8	3.8	+ 8	4.07	1.08	1.19	0.64
	Fall 1970	7	23.7	8.3	+ 8	4.52	1.21	0.90	0.13
	Winter 1970	16	15.6	1.6	- 6	7.30	1.39	2.09	0.80

An index of the amplitude of the ADMR is the standard deviation of the mean of the separate oxygen measurements during the 24 hour runs. As the following regression indicates, amplitude (x) seems to be inversely proportional to the temperature (y) at which the animals were run: *Clethrionomys* $y = 27.44 - 18.95x$, $r = 0.92$, *Microtus* $y = 32.4 - 21.23x$, $r = 0.99$. There is one significant exception to these trends, *Microtus* summer 1969, and summer 1970, differ significantly $t' = 4.00$, $df = 7$, $p < 0.01$. According to the regression trends above, the summer 1970, value is high. This suggests that the activity patterns of the animals from this time came in more energetic bursts.

The measurement of the frequency of the cycles in oxygen consumption seen in the ADMR plots is the most subjective parameter of the metabolic output to measure. The frequency of such cycles (referred to as oscillations above) have been the subject of much discussion but few data have been published citing the presence and absence of such cycles. Pearson (1962) attributed variation in cycle frequency to seasonal changes. However, runs as shown in Figure 26 and 28 that failed to show distinct 2-4 hr patterns do not substantiate Pearson's hypothesis of greater frequency in summer than winter. The fact remains that only one *Zapus* showed a cycle in ADMR and 23 per cent of the *Microtus* and *Clethrionomys* failed to show cycles of relatively constant period length. One must keep in mind that while fluctuations are almost always present, not all runs have cycles with frequencies that approach two to four hours. It is for this reason that I refer to these "cycles" as oscillations. Frequencies of those oscillations that showed two to four hour cycles were analysed for light and dark periods.

Table 22. Analysis of frequencies in metabolic oscillations measured during light and dark time.

Species	% showing 2-4 hr oscillations	Light Periods Mean Frequency ± S.D.	Dark Periods Mean Frequency ± S.D.
Clethrionomys	77	3.65 ± 0.38	2.33 ± 0.33
Microtus	83	3.40 ± 0.50	2.57 ± 0.35
Zapus	14	2.80 -	- -

The frequencies between light and dark periods are significantly different for both Clethrionomys (Fig. 27) and Microtus (Fig. 29) (t' = 2.9, df = 21, t' = 4.7, df = 9). Zapus showed little evidence of a shorter cycle, however, a 24 hour cycle was more apparent with or without dark periods (Fig. 30). The two microtines showed 24 hour cycles in only 26 per cent of the runs examined.

Several animals were run, released, recaptured and run again but only one of these animals was run at the same temperature both times. The ADMR's of that particular Microtus were 3.41 $cc0_2/g\ hr^{-1}$ and 3.79 $cc0_2/g\ hr^{-1}$, an 11 per cent difference which is relatively small compared to the 19 per cent difference between the spring 1969, mean of all animals 4.23 $cc0_2/g\ hr^{-1}$ and the upper standard deviation 5.16 $cc0_2/g\ hr^{-1}$. While more duplicate runs would have been desirable, this animal must serve as the empirical basis that the variability expressed in ADMR measurements which are over ten per cent has biological significance.

Two Clethrionomys produced litters while in the respirometer, one at +7.5°C and the other at -7.5°C. Neither of the ADMR values were ten per cent higher than the ADMR of animals similar in body weight. In fact, the ADMR of one of the littering females was 22 per cent lower than the average of other animals of similar weight.

The possibility exists that the act of removal of an animal from the population (measuring its ADMR in the laboratory and subsequent release) has an effect on the animals' chance for subsequent survival. Survival rates of those animals taken to the laboratory were compared with the survival rates of the whole population for the same seasons (Table 23). Chi-square tests showed only one significant difference: Microtus fall 1969, $\chi^2 = 8.24$, df = 1, $p < 0.005$. In addition, Microtus from summer 1969 were very close ($\chi^2 = 3.63$, df = 1, $p < 0.06$) to having significantly different survival rates. Further examinations of these two periods showed that the poor survival of the ADMR animals on a seasonal basis (seven animals out of eleven not being recaptured one season and zero out of seven the other) had little effect on the two week survival rates.

To summarize, this section provides rates for energy fluxes leaving the population that will be used for building an energy budget for the three species of mice. In addition, several other parameters of ADMR were examined for the first time from animals measured directly from the field. Clethrionomys, especially adult males, showed variability in metabolic rate - weight relations while the Microtus were more predictable for this parameter of metabolism. Hence a single but highly

Table 23. Comparison of the survival rates for those animals studied in the laboratory and the survival rates of the whole population for the same interval.

	Clethrionomys		Microtus		Zapus	
Season	Metabolism	Whole Population	Metabolism	Whole Population	Metabolism	Whole Population
Spring 1969	66%	66%	43%	47%		
Summer 1969	40%	43%	27%	75%		
Fall 1969	81%	72%	0%	67%		
Winter 1969-70	95%	93%	100%	88%		
Spring 1970	0%	17%	0%	0%		
Summer 1970	40%	60%	0%	0%	56%	57%
Fall 1970	57%	67%				
Winter 1970-71	72%	63%				

variable metabolic rate will be regulating the maintenance flux from the population for the *Clethrionomys*.

Body Composition

Ninety-eight individuals of the three species, *Clethrionomys*, *Microtus* and *Zapus*, were prepared for body composition analysis. Poor success in snap trapping under the snow and when animals were scarce left several seasons with a sample size that was small or zero. Data derived from individuals which died in live traps were included for those seasons with small samples, Table 24a, b and c (the number of live trapped animals are in parentheses below the total for each season). Equal numbers of males and females were analysed for each season, excepting *Clethrionomys*, fall 1969 (6 females, 1 male).

Six parameters were calculated from each animals' wet weight, dry weight and fat weight making a total of nine parameters (Table 24). The variances about the means for males and females were significantly different for all three species (F-test; Steele and Torrie, 1960, p. 83). There were no significant differences between the means of all the parameters for males and females (t'-test, Steele and Torrie, 1960, p. 81). Eighteen two-way analyses of variance were run for *Clethrionomys* and *Microtus* body composition parameters. Linear models and design matrices were set up and analysed by computer program Biomedical Package 05V. Results of these tests for differences between breeders and non-breeders, various seasons and the interaction of breeding status and season are listed in Table 25. As one would expect the wet weight,

Table 24a. Body composition data stratified by season and breeding condition (a) *Clethrionomys rutilus*. Ratios are given as per cents.

Stratification	N	Wet g	Dry g	Fat g	H_2O g	$\frac{H_2O\ g}{Wet\ g}$	$\frac{Fat\ g}{Dry\ g}$	Fat free g	$\frac{Fat\ free\ dry\ g}{H_2O\ g}$	$\frac{Fat\ g}{Fat\ free\ dry\ g}$
Breeding	20	20.1 ±5.8	5.73 ±1.63	0.71 ±0.35	14.3 ±4.3	71.4 ±2.6	12.49 ±4.20	5.04 ±1.47	35.3 ±4.9	14.52 ±5.47
Not Breeding	22	14.5 ±2.7	4.60 ±0.94	0.56 ±0.35	9.9 ±1.9	68.2 ±3.4	11.85 ±4.95	4.04 ±0.71	41.5 ±7.0	13.79 ±6.55
Late Fall 1968	4 (4)	12.8 ±2.4	4.28 ±0.38	0.30 ±0.19	8.5 ±2.0	66.1 ±3.3	7.30 ±4.90	3.98 ±0.55	47.6 ±6.0	8.08 ±5.53
Summer 1969	9 (2)	17.8 ±3.2	5.26 ±0.97	0.61 ±0.24	12.5 ±2.2	70.4 ±1.1	11.90 ±4.78	4.65 ±1.00	37.0 ±2.2	13.83 ±6.22
Fall 1969	6	16.4 ±2.7	5.43 ±1.28	0.77 ±0.50	11.0 ±1.5	67.2 ±2.3	13.25 ±4.92	4.67 ±0.84	42.4 ±2.7	15.60 ±7.11
Winter 1969	3 (3)	11.4 ±1.2	3.99 ±0.10	0.35 ±0.16	7.4 ±1.1	64.7 ±3.6	8.83 ±4.28	3.64 ±0.25	50.0 ±6.4	9.87 ±5.22
Summer 1970	12	20.0 ±7.8	5.71 ±2.28	0.71 ±0.41	14.7 ±5.6	72.2 +2.8	12.48 ±3.49	4.99 ±1.95	33.9 +5.6	14.42 +4.58
Fall 1970	8	17.5 ±2.8	5.11 ±0.75	0.78 ±0.26	12.4 ±2.3	70.6 ±2.6	15.02 ±3.63	4.34 ±0.65	35.7 ±4.0	17.89 ±5.4

Table 24b. Body composition data stratified by season and breeding condition (b) *Microtus oeconomus*. The total seasonal numbers do not add up to 44 because two, Spring 1970, animals were not included. Ratios are given as per cents.

Stratification	N	Wet g	Dry g	Fat g	H_2O g	H_2O g / Wet g	Fat g / Dry g	Fat free g	Fat free dry g / H_2O g	Fat g / Fat free dry g
Breeding	27	32.9 ±10.3	9.23 ±2.79	1.11 ±0.51	22.7 ±7.6	71.0 ±1.9	12.07 ±4.26	8.12 ±2.49	35.8 ±3.0	13.97 ±5.45
Not Breeding	17	19.0 ±9.6	5.63 ±2.96	0.64 ±0.39	13.4 ±6.7	70.6 ±3.6	11.46 ±3.34	4.99 ±2.61	37.2 ±7.1	13.09 ±4.14
Fall 1968	3 (3)	18.1 ±6.7	6.01 ±1.78	0.69 ±0.11	12.1 ±5.1	65.8 ±5.6	11.73 ±1.59	5.33 ±1.67	46.2 ±11.7	13.30 ±1.99
Summer 1969	22	27.6 ±11.7	7.89 ±3.41	0.85 ±0.50	19.7 ±8.3	71.5 ±1.6	10.78 ±3.88	7.04 ±3.01	35.6 ±3.0	12.26 ±4.71
Fall 1969	4 (2)	22.3 ±9.8	6.89 ±3.15	0.92 ±0.60	15.4 ±6.7	69.5 ±1.3	13.20 ±5.42	5.98 ±2.78	38.3 ±3.9	15.50 ±7.25
Summer 1970	13 (1)	29.1 ±13.9	8.31 ±3.87	1.11 ±0.56	20.8 ±10.1	71.4 ±2.5	13.46 ±3.05	7.20 ±3.40	34.7 ±3.7	15.71 ±4.20
Average(Pooled)	44	26.9 ±11.8	7.84 ±3.34	0.93 ±0.51	19.1 ±8.5	70.8 ±2.6	11.84 ±3.90	6.91 ±2.95	36.5 ±5.0	13.63 ±4.95

Table 24c. Body composition data stratified by season and breeding condition (c) *Zapus hudsonius*. Ratios are given as per cents.

Condition	N	Wet g	Dry g	Fat g	H_2O g	H_2O g / Wet g	Fat g / Dry g	Fat free g	Fat free dry g / H_2O g	Fat g / Fat free dry g
Breeding		16.8 ±3.3	5.27 ±0.82	0.81 ±0.21	11.6 ±2.6	68.3 ±2.8	15.51 ±3.53	4.46 ±0.79	38.7 ±5.1	18.55 ±4.93

Table 25. F statistic summary for 2-way ANOVA of body composition values presented in Table 24.

Species Stratification	Significance level	Degrees of Freedom	F Values								
			Wet g	Dry g	Fat g	H_2O g	H_2O g / Wet g	Fat g / Dry g	Fat free g	Fat free dry g / H_2O g	Fat g / Fat free Dry g
<u>Clethrionomys</u>											
Breeding	4.21	1,27	12.84	19.60	7.41	9.91	5.96	0.07	8.73	0.22	0.23
Season	2.96	3,27	0.16	1.40	2.50	0.08	8.34	1.28	1.22	2.48	1.54
Interaction	2.96	3,27	1.05	1.27	2.92	0.98	0.93	2.42	1.54	0.66	2.92
<u>Microtus</u>											
Breeding	4.16	1,31	21.42	22.53	13.45	20.43	1.76	0.04	22.07	1.40	0.07
Season	4.16	1,31	0.02	0.01	1.45	0.02	0.06	3.40	0.02	1.12	3.50
Interaction	4.16	1,31	2.04	3.16	4.44	2.08	2.34	0.46	2.65	1.57	0.62

dry weight, fat weight and fat free weight were significantly different between breeders and non-breeders. These differences have been described in the live trapped population as well. Those parameters that prove to be the most interesting both physiologically and ecologically are the ratios of body composition. The rest of the section will discuss three of these ratios:

1) $\frac{H_2O\ g}{\text{Wet Wt g}}$ = Water Index = WI

2) $\frac{\text{Fat Free Dry Wt g}}{H_2O\ g}$ = Maturity Index = MI

3) $\frac{\text{Fat g}}{\text{Fat Free Dry Wt g}}$ = Fat Index = FI.

Clethrionomys. The water index, WI, was significantly different for breeders and non-breeders (F = 5.96, df = 1,27) and between seasons (F = 8.34, df = 3,27). Since the proportion of water is not constant with weight, the dry matter must also vary by season and breeding condition. Hence, when calculating the caloric value of the live trapped population one must not assume that the calorie-containing dry matter makes up the same proportion in the non-breeding animal as it does in the breeding animal. Two conversion equations for wet weight (x) to dry weight (y) have been calculated: for breeders $y = 0.31 + 0.27x$ and non-breeders $y = 1.93 + 0.45x$.

Seasonal differences in the maturity index, MI, are close to being significant and thus will be examined in more detail (F = 2.48, df = 3,27; significance = 2.96). Seasonal regression equations and correlation coefficients are shown in Table 26.

Table 26. Seasonal regression equations and correlation coefficients (r) for _Clethrionomys_ water weight (x) and Fat free weight (y). High correlation coefficients indicate that all individuals are chemically mature (Bailey _et al._, 1960).

Season	N	Regression equation	r
Fall 1968	4	$y = 4.98 + 3.39\ x$	0.94
Summer 1969	9	$y = 2.51 + 2.15\ x$	0.97
Fall 1969	7	$y = 3.12 + 1.68\ x$	0.96
Winter 1969	3	$y = 1.74 + 2.50\ x$	0.53
Summer 1970	12	$y = 1.17 + 2.71\ x$	0.98
Fall 1970	8	$y = 1.29 + 2.97\ x$	0.87

Those seasons with sample sizes greater than four were subjected to an analysis of covariance. The null hypothesis that there is no difference in slope of these regressions was not rejected ($F = 1.04$, $df = 3,32$). In addition adjusted means of fat free weight were not significantly different ($F = 1.35$, $df = 3,31$).*

Lack of difference in MI between breeding conditions in conjunction with low correlation coefficients between water weight (x) and fat free dry weight (y) ($y = 1.56 + 0.25x$, $r = 0.67$ for non-breeders; and $y = 0.25 + .34x$, $r = 0.78$ for breeders) suggests that breeding animals are not necessarily mature in terms of body composition (Bailey, Kitts and Wood, 1960). The seasonal expression of this phenomena (if any) is not in low correlation coefficients but slope.

The summer and fall increase for both the fat index, FI, and the fat weight of Clethrionomys is not continued through the snow covered months. In other words the smaller samples from the snow covered months do not indicate an increase in fat during the winter. This lack of fatness is not consistent with winter values for more temperate species (Hayward, 1965; Sawica-Kapusta, 1970) which show a winter increase in fatness. An immediate explanation could be that all animals used in these winter samples are live trap fatalities, therefore one might suspect that the trapping fate has influenced the results. While there is doubt about the biological validity of these late fall and winter

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* As a check on the ANOCV a **t** test between summer 1969 and summer 1970 means resulted in a very low value for the test statistic ($t = 0.91$).

values; the weight losses in the fall (see Growth Section, Fig. 20) should not result in fat animals. For further analysis of this problem see discussion on Dehnel's Phenomena, p. 200.

The interaction between breeding and season for FI is very close to significance and inspection of this interaction shows that non-breeders in the summer of 1970 lack fat. This agrees with Hsia's (1963) index of relative fatness for Clethrionomys rutilus in China.

Microtus:

The five mean weights are significantly different for breeders and non-breeders as expected from live trapping data. In addition there are no differences in the means of the five ratios of body composition.

As in the Clethrionomys there is no difference in the MI, however, high r values for breeders and non-breeders suggest physiological maturity for both groups. (Water weight (y) vs fat free dry weight (x) for breeders: $y = 0.97 + 2.48\ x$, $r = 0.97$ and for non-breeders: $y = -0.73 + 2.89x$, $r = 0.95$). These results are interpeted as another index of delay in breeding status (see Reproduction Section, p. 76 and the Autopsy Section p. 109).

It is interesting to note the significance of the interaction term for fat weight. ($F = 4.44$, $df = 1,31$). This interaction suggests a possible depletion of fat in breeders 0.94 ± 0.46g during the 1969 peak population as compared to 1.47 ± 0.39 in the lighter weight 1970 breeders.

Zapus:

Body composition data has been pooled for both summers. The small sample size in 1969 (two animals) prevents comparison between years. It would be most convenient if *Zapus* could be analyzed along with summer *Clethrionomys* for calculating caloric net productivity. (Dry weights for both species are similar during summer. *Zapus* pooled 5.27 ± 0.82 grams, *Clethrionomys*, summer 1969 5.26 ± 0.97 grams). Unfortunately, the *Zapus* mean fat weight is significantly different from both summer *Clethrionomys* populations: t' = 20.6, df = 13,8 for 1969; t' = 8.05, df = 13,11 for 1970. The data presented in Table 24c will be used for calculating a separate energy budget for *Zapus*. Least squares fit regression for the MI is y = 8.36 + 0.72x, r = 0.39. This is the lowest correlation coefficient for all species. Females which could be judged as mature more easily than males resulted in a correlation coefficient of 0.78, hence the low values for both males and females could be a reflection of my inability to judge sexual maturity.

One can conclude that in both *Clethrionomys* and *Microtus* all body composition weights measured are significantly greater in breeders. Those ratios of body composition that show significance or very nearly so are the water, maturity and fat indices. Two way analyses of variance and regression techniques reveal several interesting interactions between breeding, maturity and seasonal effects.

Caloric value

Caloric values were determined for 26 animals of the three species (Table 27). Animals were selected from all seasons but the small sizes made analyses for differences between season, sex, and breeding condition rather speculative. There were no differences greater than five per cent between sex for calories per gram non-fat tissue for any of the species. However, there is a trend (18 percent difference) for Clethrionomys females to have higher caloric per gram of fat values than males. Since there are only two females, the significance of this difference was not tested.

Table 27. Caloric values for fat and fat free dry weight for Clethrionomys, Microtus and Zapus. Caloric values are means ± 1 standard deviation.

Species	N	Fat calories/g	Fat free calories/g
Clethrionomys	9	7514 ± 3127	4025 ± 164
Microtus	10	9208 ± 422	4073 ± 438
Zapus	7	8982 ± 520	4282 ± 246

An analysis of variance failed to reject the hypothesis that there is no difference between species in fat calories and fat free calories per gram (Fat calories: F = 1.37, df - 2,21; Fat Free calories: F = 1.63; df = 2,14). All stratification by season and sex failed to alter the above failure to reject. The apparent similarity is due to small sample sizes and large variability. Variability in the actual bombing (three samples were run for most individuals) was less than one per cent while individual variability was usually two or more times the measuring error (especially for Clethrionomys fat calories). Lack of significant differences between species was due to animal variability rather than experimental variability.

DISCUSSION

Productivity

This section of the thesis is based on the concept that ecological units may be analysed and related bioenergetically. However, energy flow is not necessarily the basic underlying concept of ecological systems. Such bioenergetic relationships are often expressed as models of energy flow through ecosystems. Models are often billed as ultimate problem solvers or general panaceas, therefore the word is used with hesitation. As a compromise, the term "empirical model" is used to denote that while these data are organized in a manner similar to many present day systems analysis models, the format is purely for descriptive purposes. Thus there is no intention to use these data to predict ecosystem, population or individual parameters.

Production data are presented in the discussion for they are essentially an integration of all the data in the result sections. Natal, nestling and weaned net production are the first to be discussed, respiratory or maintenance production of the nestlings and weaned animals follow. Average dDaily metabolic rates of pregnant females are used to calculate maintenance production of the weaned biomass and therefore include natal maintenance production.

Natal productivity:

Many formulas have been used for estimating the number of individuals born into a population. It would not be an exaggeration to say that almost every scientist who has measured natal production has used a somewhat different means (for a review of methods: Petrusewicz and

MacFadyen, 1970, p. 70-83). In this study natal productivity has been estimated using Formula 1:

Formula 1 $$v_r = \frac{L \cdot \overline{N}_p \cdot T}{t_p}$$ (Buyalska et al, 1968)

v_r = number of individuals born in T time

T = observation time (two weeks in this study)

$\overline{N}_p$ = mean number of pregnant females

t_p = duration of pregnancy

L = litter size

The formula is derived from the logic that $\frac{L}{t_p}$ is the mean number born during one day by a pregnant female; if there are $\overline{N}_p$ pregnant females, the mean number born during one day will be $\frac{L}{t_p} \cdot \overline{N}_p$ or $\frac{L\overline{N}_p}{t_p} \cdot T$ in T days or every two weeks. As a check on this method, $\overline{N}_p$ was plotted every two weeks and the area under the curve was integrated (assuming linearity) to yield the total number of pregnant female days. This value was multiplied by $\frac{L}{t_p}$ (the number of individuals born per pregnant female per day). These two estimating methods should and did produce the same numbers for maximum yearly production of new born.

A more direct method of determining the number of individuals born can be obtained from observation of external reproductive indices and growth rates. The following sets of observations furnish information regarding the minimum number of litters produced during a breeding season: an open pubic symphysis, a pregnancy bulge at time (t) followed by a weight loss and initiation of lactation at the next trapping period (t + 1); closed pubic symphysis at (t) followed by a slightly open

Table 28a. Summary of $\overline{N}_p$ (mean number of pregnant females) data for breeding seasons. These mean values were used in Formula 1 to yield estimated v_r. The estimated v_r is then compared the observed v_r. See text for calculation of observed v_r. (a) Clethrionomys rutilus, (b) Microtus oeconomus and Zapus hudsonius.

March April May June July August September October

Cleths 1969

Trapping Weeks	30		32		34		36		38		40		42		44		46		48		50
$\overline{N}_p$	2.5		5.0		4.5		3.5		2.5		3.0		3.5		3.5		6.0		4.0		1.5
estim. v_r	11.3		22.6		20.4		15.8		11.3		13.6		15.8		15.8		27.2		18.1		6.8
obser. v_r		0		16.2		8.1		8.1		8.1		8.1		16.2		16.2		16.2		0	

Cleths 1970

Trapping Weeks	96		98		100		102		104		106
$\overline{N}_p$	1.0		3.0		4.0		5.0		3.0		1.0
estim. v_r	4.5		13.6		18.1		22.7		13.6		4.5
obser v_r		8.1		0		24.3		8.1		16.2	

Cleths 1971

Trapping weeks	130		132*		134		136		138		140		142		144		146	
$\overline{N}_p$	1.0		4.0		7.0		6.5		6.0		6.0		7.5		9.5		10.5	
estim. v_r	4.5		18.1		31.8		29.4		27.2		27.2		34.7		43.1		47.5	
obser. v_r		0		0		16.2		32.4		0		40.5		0		24.3		48.6

data for the rest of the reproductive season is available from Dr. Feist.

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* Week 132 was not trapped on Grid A; these values are estimates from weeks 130 and 134.

Table 28b. Summary of $\bar{N}_p$ (mean number of pregnant females) data for breeding seasons. These mean values were used in Formula 1 to yield estimated v_r. The estimated v_r is then compared to the observed v_r. See text for calculation of observed v_r. (a) *Clethrionomys rutilus*, (b) *Microtus oeconomus* and *Zapus hudsonius*.

	March	April			May				June					July				August			September	October
Microtus 1969																						
Trapping Weeks			32		34		36		38		40		42		44		46		48		50	
$\bar{N}_p$			1.0		7.0		9.0		13.5		16.5		15.0		17.0		16.0		11.5		1.0	
v_r			3.7		29.9		33.3		50.0		61.0		55.5		63.0		59.2		42.6		3.7	
v_r				0		19.8		19.8		19.8		13.2		46.2		39.6		26.4		33.0		
Zapus 1969 + 1970																						
Trapping weeks											40 + 94		42 + 96		44 + 98		46 + 100		48 + 102			
$\bar{N}_p$											18.0		6.0		4.0		1.0		1.0			
estim. v_r											60.4		20.4		13.6		3.4		3.4			
est. v_r per 1 year**											30.2		10.2		6.8		1.7		1.7			

**these values are merely one half estim. v_r (see text).

pubic symphysis and initiation of lactation at (t + 1).

The mean number of pregnant females, $\overline{N}_p$, used to calculate estimated v_r, and observed v_r (using reproductive and weight data), are presented for Clethrionomys, Microtus and Zapus on Grid A for 1969, 1970 and 1971 (Table 28a). The other variables for the productivity formula are constant and are listed in the text for each species.

Clethrionomys. A mean litter size of 8.1 individuals was obtained from the autopsy section. Use of a mean litter size for all periods in all years ignores the phenomena of larger mean litter size with lower population density as shown for Clethrionomys by Patric (1962) and Zejda (1967). Krebs and Myers (1973) believe such a phenomenon is an exception rather than a rule.

The length of the gestation period, t_p, is the most difficult parameter to determine accurately in field populations. To my knowledge it is not known whether t_p varies with density and other demographic parameters in rodents. Assuming a constant value during the reproductive period, t_p, in this study could be anywhere from 16 days (more than the time between two trapping periods) (Koshkina, 1957: t_p = 16 days) to 28 days (greater than the time between two trapping periods but less than the time between three trapping periods). I have arbitrarily assumed a value of 25 days for t_p. While t_p may be equal to 16 days it is important to note that two periods between observed litters in 1969 were at least 42 days. Periods in other years were all between 16 and 27 days. In other words, while t_p may remain constant, pregnancy does not always immediately follow birth, i.e. variable post partum mating. This delay phenomena observed in 1969 is not taken into account in Formula 1 and may contribute to some of the discrepancy between the estimated and observed method (see Table 29, Clethrionomys, 1969). Numbers of newborn Clethrionomys in 1970 and 1971 are respectively smaller and larger than the number for 1969. The variability during the three years (Table 29) is most interesting when compared to the consistency in yearly peak density (Fig. 11a). The differences between 1969, 1970 and 1971 are best explained by the delay factor mentioned above, emigration, mortality and perhaps abortion.

Newborn voles were not weighed in this study (young found in the field were handled as little as possible). Koskina (1957) estimates newborn weights of 1.40 to 1.75 g and Morrison et al. (1954) 1.71 g. A value of 1.75 g was used in this analysis. Since 83.7 per cent of newborn weight is water, and calories per gram of the remaining dry tissue is 6000 (Sawicka-Kapusta, 1970), each individual produced was multiplied by 1740 calories (Table 29).

Microtus. The litter size for Microtus was 6.6 individuals (Autopsy Section, p. 114). This value agrees with the mean value of 6.4 cited by Bee and Hall (1956, p. 133). The gestation period was again assumed to be 25 days (Tast, 1966 and Zimmerman, 1965 observed values of 21 to 22 days). The weight of a newborn individual was extrapolated from Morrison et al. (1954) to 3.0 g. The mean number of pregnant females $\overline{N}_p$ was calculated for Microtus. Again it was assumed that perforate and lactating females were pregnant. Each

Table 29. Yearly individual production and caloric values of young.

	*Estimated v_r	**Observed v_r	Kcal/reprod. season
Clethrionomys			
1969	178.7	97.2	169.1
1970	77.0	56.2	98.7
1971	263.5***	162.0***	281.9
		Total =	546.7
Microtus			
1969	401.9	207.8	603.7
1970	6.4	0.0	0
1971	0.0	0.0	0
		Total =	603.7
Zapus			
1969	50.6		44.0
1970	50.6		44.0
1971	50.6		44.0
		Total =	132.1

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* Estimated v_r is calculated using Formula 1.

** Observed v_r is determined by inferring births from reproductive and weight loss data.

*** Values only represent part of the yearly production.

individual produced was converted to 2940 calories using data from this thesis. The number of calories produced by the Microtus population was two times greater than the highest Clethrionomys value. (Note: When Feist's data for the remainder of the season are available, the 1971 Clethrionomys natal productivity may be closer to that of Microtus v_r).

Zapus. Erratic movement patterns as indicated by between grid movement did not allow observation of individuals produced. Hence estimates using Formula 1 were the only recourse to measure v_r. Data from 1969 and 1970 were combined and $\overline{N}_p$ was calculated. $\overline{N}_p$ values estimated for the other two species were usually two times greater than the observed. Since the observed values were used for the other species, I attempted to approximate the observed value for Zapus by dividing the estimated v_r by two.

The litter size of 6.0 for Zapus was also taken from the Autopsy section. The gestation period was again assumed to be 25 days. Assuming that a newborn Zapus weighs the same as a Clethrionomys neonate (no data were available on birth weights of Zapus from Alaska), Zapus produced 44.0 kcal per year. This is approximately half of the lowest observed value for Clethrionomys. Zapus produced far more young than the microtines during the first of the breeding season. The Zapus peak natal productivity fell below both of the mid-season peak periods for the other two species.

Nestling productivity:

Very little is known about growth patterns of rodents from the time they are born until the first field capture. Laboratory growth information is available for Clethrionomys rutilus and Microtus oeconomus for this early period (Morrison et al., 1954) when the field populations are not available to conventional live trapping. Since it is generally recognized that laboratory growth does not realistically represent field growth, Bujalska and Gliwicz (1968) have used a correction factor to convert laboratory growth measurements to field growth. This empirical correction factor, 0.79, was derived from Ryszkowski and Truszkowski's (1970) data on litter growth of Clethrionomys in field nest boxes.

Survival of unweaned rodents is perhaps the least understood and most important parameter in production and population biology. Delong's index of juvenile survival is useful for comparing relative changes over phases of population cycles (Krebs 1966, 1970) and with modification is used below to estimate absolute juvenile survival. Litter production, v_r, is compared to the number of individuals appearing four to five weeks later in live traps. These data are summarized by four week intervals for Clethrionomys and Microtus (Table 30). It is very important to note that these 28 day groupings are not cohorts. The cohort analysis used by Ryszkowski and Truszkowski (1970) (who trapped every four to six weeks) was not applicable in this study. Since cohorts could not be clearly defined in this study, I feel that trapping on a four to six week schedule would make it even more difficult to separate cohorts. In addition, if the onset of breeding of the over-wintered animals was not synchronous (as in M. oeconomus, Fig. 16b) the cohort analysis used by Ryszkowski and Truszkowski (1970) should be cautiously interpreted.

Table 30. Instantaneous mortality rates for nestling *Clethrionomys* and *Microtus*. These values are calculated from the data in Table 28.

Animal Marked Date	Week	Number Born v_r	Number Surviving	Time Interval (days)	(u) Instantaneous Mortality Rate
Cleths					
June 1969	36-38	16.2	10	28	- .017
July	40-42	16.2	3	28	- .060
Aug.	44-46	16.2	10	28	- .017
Sept.	48-50	32.4	23	28	- .012
Oct.	54	16.2	5	28	- .042
Aug. 1970	98-102	8.1	7	42	- .001
Sept.	104-106	32.4	24	28	- .011
Oct.	110	16.2	3	28	- .060
1971					
May-June	140-142	48.6	2	28	- .117
June-July	144-146	40.5	22	28	- .022
		end of study still more production			
Microtus 1969*					
June	38-40	19.8	13	28	- .015
July	42-44	39.6	7	28	- .062
Aug.	46-48	59.4	17	28	- .048
Sept.-Oct.	50-54	67.0	9	42	- .048
Nov.	58	33.0	0	28	approx. - .125

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* Low density in 1970 and 1971 yield zero animals born, hence mortality rates cannot be calculated.

Production has been calculated using two formulas. The first (Formula 2) (in Petrusewicz et al., 1968), does not assume continuous production but treats it in steps much the way animals die:

Formula 2

$$P_T = \sum_{i=1}^{i=k} (\Delta N_T \Delta W_{T/2} + N_T \Delta W)_i$$

P_T = production in time T

ΔN_T = animals eliminated in time T

N_T = animals left at the end of time T

ΔW = weight increase of animals during time T

However, since growth is continuous, the formula (Formula 3) in Petrusewicz and MacFadyen (1970, p. 93) has been used for comparative purposes:

Formula 3 $P_T = B_o \left(e^{(q-n)T} - 1\right)$

B_o = initial biomass

q = instantaneous growth rate

n = instantaneous death rate

T = time interval for which above rate was calculated

The assumptions and discussion of these formulas are listed in the respective papers and are not reiterated here.

Clethrionomys. Instantaneous mortality rates, (u), (Table 30) are both above and below those in Ryszkowski and Truszkowski (1970) who used nest box monitoring for unweaned survival. Hence I do not feel the criticism against Zejda (that estimates of mortality without the use of nest boxes are too high) made by the above authors applies to these data. There were two interesting periods of high nestling mortality: first, the last litters of the year that should enter the traps in early October showed poor survival in both years; second, poor survival was apparent in May 1971, during the melt-off of a record snow fall. The high mortality in the middle of the summer of 1969, (which occurred in both microtines) was also interesting and could not be explained by weasel predation or unfavorable weather conditions.

Growth rates for unweaned Clethrionomys are not known to vary during the reproductive season (Bujalska and Gliwicz, 1968). Hence the following growth pattern has been used (Table 31).

Table 31. Growth rates for nestling *Clethrionomys rutilus*. Weight values are in grams. Growth rates are g/g/day.

Time	Birth	1wk	2wk	3wk	4wk
Weight	1.75	3.5	5.9	9.0	12.0
Instantaneous growth rates	0.099	0.075	0.060	0.041	

This pattern calculated from Morrison *et al.* (1954) does not reflect the accelerated rate of biomass increase found between the 12th and 18th day of life (Wojciechowska, 1970). Yearly caloric values of the nestling production (Table 33) are calculated using data from the section on body composition and caloric value. Thirty-two per cent of the production was dry biomass which had a caloric value of 4.42 kcal per gram.

The average weight of a juvenile first entering live traps in 1969 was 14 g (range from 18 to 17 g). This section only presents production to 12g. Since animals as small as eight grams were captured in live traps this section may overestimate the period of living in the nest.

As a check on the very high growth rate between the third and fourth week of life, a comparison is made for the instantaneous relative growth rate (Brody 1945) of two females first captured at 10 grams. These animals had growth rates of 0.038 and 0.024 (g/g/day) for the following two week period. These growth rates are similar to the rates for the third to fourth week (Table 31).

Microtus. Nestling survival in Microtus was high in June 1969, but by July there was very low survival. Unlike the survival pattern for Clethrionomys, high mortality continued to the end of the season when no animals survived from the last few litters (Table 30).

Growth rates in the unweaned litters were estimated (Table 32) by multiplying growth data from Morrison et al. (1954) by 0.79 (a correction factor derived from Bujalska and Gliwicz, 1968, for Clethrionomys).

Table 32. Growth rates for nestling Microtus oeconomus. Weight values are in grams. Growth rates are g/g/day.

Time	Birth	1wk	2wk	3wk	4wk
Weight	3.0	7.3	11.6	15.9	20.2
Instantaneous growth	0.126	0.066	0.045	0.034	

The average weight of juvenile Microtus first entering live traps was 16.5g (range 12g to 20g). Two animals captured in June at 13g had instantaneous relative growth rates of 0.047 and 0.034 g/g/day for the two weeks after the first capture. These growth rates were very similar to those between the third and fourth weeks of life as estimated from Morrison's et al. (1954) adjusted data (Table 29). It is important to note that July, August and September 15g young animals often showed no growth (Fig. 19b). Therefore, growth for 3-week-to 4-week-old animals will not be calculated in this section which assumes maximum growth in nestling individuals. Microtus nestling productivity values cover growth to 16 grams (15.9g). Since this was slightly less than the average first capture, nestling productivity will be slightly underestimated.

Thirty per cent of the production was dry weight which has a caloric value of 4.68 kcal/g. The caloric value (Table 33) for the nestling Microtus production in 1969 was more than double that of the Clethrionomys. Microtus caloric values for 1970 and 1971 were assumed to be zero or very near zero due to low densities.

Production values using Formula 3 were calculated for the Clethrionomys population in 1969 and 1970. Growth rates and death rates calculated on a four week basis gave answers that were 39.5 per cent lower than those given by using Formula 2. When weekly instantaneous growth rates were used (assuming constant instaneous death rates), production values using Formula 3 were only 18.5 per cent lower.

Difficulties arise with Formula 3 when mortality was high. High mortality values result in mathematically negative productivities which were biologically unreal for situations when growth was still positive. The 18.5 per cent lower values derived from Formula 3 may be a result of this biological imperfection in Formula 3. However, it is also possible that estimates from Formula 2 were high due to the assumption that mortality was constant over the interval of calculation. Hence, if mortality was lower in the younger animals (i.e. if there was better than average survival the first week of life), an overestimation could result from Formula 2.

Table 33. Yearly caloric values of nestling production for Clethrionomys and Microtus. Zapus values are included in trappable production values.

	Gms Production	Kcal Production
Clethrionomys		
1969	726.8	1,037.95
1970	455.6	644.83
1971	544.3*	-
Microtus		
1969	1,654.0	2,322.22

* This value is only for part of the growing season.

In conclusion, estimates of nestling productivity calculated on a monthly basis were twice as large for Microtus (during 1969) as they were for Clethrionomys (in 1969). In fact, the 1969 estimates for Microtus probably equalled the Clethrionomys three year total. Instantaneous mortality rates showed high values that can be explained by prolonged snow melt and irregular fall freezing and thawing. High nestling mortality also occurred in both microtines in the absence of predator sign or capture. The individual nestling productivity of Clethrionomys for 1969 and 1970 was 35 per cent and 38 per cent lower than natal individual production for Clethrionomys (meaning that 35 per cent of the natal production was realized at the end of the nest life) while individual Microtus nestling productivity during 1969 was 62 per cent lower, reflecting the greater mortality rates in the Microtus nests.

Trappable productivity:

Yearly production of the trappable population for Clethrionomys and Microtus are presented in Table 34. Zapus values (Table 34) include nestling as well as trappable (weaned) productivity. While these total yearly production data are informative for gross comparisons between years and species, it must be stressed that yearly values mask production dynamics i.e. rate, seasonal timing and magnitude. Theoretical aspects of the negative values in Table 34 will be discussed in more detail later (page 179), however, it should be noted that individual weight loss is responsible for such values. Negative values are not to be confused with elimination of production by death.

Each of the microtine populations were divided into six classes (juvenile, subadult and adults for each sex) and production was calculated for every trapping period using Formula 2. Zapus (recaptures) were divided into two classes (overwintered individuals and young of the year) and production was calculated on a seasonal basis.

Clethrionomys. Clethrionomys produced 286 kcal in 1969 of which 41 per cent was subsequently lost as weight. During 1970 production was poor; more weight was lost than was gained. The following year's data is incomplete but data through mid-July indicate 1971 was a highly productive year.

Table 34. Yearly caloric values of trappable production (weaned) for Clethrionomys, Microtus and Zapus.

	grams production wet	grams of wet wt lost	kcal production
Clethrionomys			
1969	209.0	(-) 87.5	287
1970	19.2	(-) 52.1	26
1971	347.0*	(-) 0.3*	469*
Microtus			
1969	672.8	(-)343.7	956
Zapus			
1970	166.33**	(-) 46.6**	264**

* Figures represent only a part of the season
** Figures represent nestling plus weaned animals

Microtus. Microtus production in 1969 (673 grams) greatly exceeded that of the Clethrionomys. Weight lossamounted to 51 per cent of the production.

Zapus. As mentioned in the previous sections, large movements of Zapus which resulted in irregular recapture patterns, made productivity calculations difficult. With this reservation in mind, seasonal Zapus production has been estimated using the following information. Overwintered Zapus emerge from hibernation at 15g. Galster (pers. comm.)

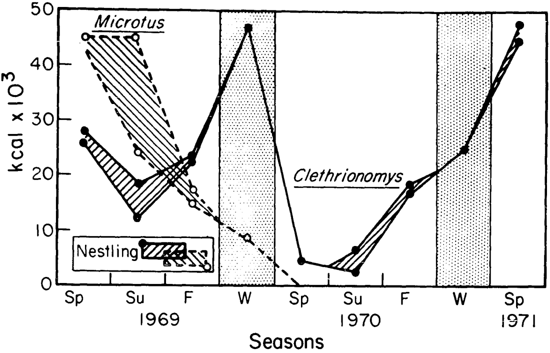
measured a mean value of 13.3g for seven laboratory Zapus in late April. (This date is one month before the earliest field capture. Galster's animals were captured in the Fairbanks area). Overwintered animals gained 17g by late August, hence entering hibernation at a mean value of 32g. Galster measured a mean value of 30g in laboratory animals. Since the heaviest young of the year going into hibernation was 20g (it is assumed that young animals do not have the same reserves as larger overwintered individuals) a separate calculation was made for young animals. The total production of unweaned plus weaned individuals was 499g for the three grids or 167g per grid. Caloric conversion was made using data from previous sections.

Respiration maintenance:

The cost of population maintenance has been estimated on a seasonal basis for the Clethrionomys and Microtus trappable and nestling populations (Fig. 31). Zapus maintenance was calculated for the 1970 summer (Table 35).

Clethrionomys. Seasonal maintenance was estimated by summing production for three age classes every trapping interval. Conversions from grams to calories were made using the mean cc 0_2/g hr^{-1} for each season. No correction was made for weight when more than one age class was present (see Metabolism section, p.121). Figure 31 shows seasonal changes for these periods when ADMR was measured. It is important to note that the three spring seasons represent moderate, low and high maintenance production. In addition, the 1969-70 and the 1970-71 winter represented periods of maximal and increasing production. Summer periods

Figure 31. Seasonal maintenance for the nestling and trappable populations of *Clethrionomys* and *Microtus*.


50
40
30
20
10
0
kcal x 10^3
Microtus
Clethrionomys
Nestling
Sp
Su
F
W
Sp
Su
F
W
Sp
1969
1970
1971
Seasons

are times of lowest maintenance production.

The cost of nestling maintenance was more than that of the trappable population in summer 1970 and over 50 per cent of the trappable population in summer 1969 (Fig. 31). However, on a yearly basis, nestling maintenance was less than 10 per cent of the trappable population (7.9 per cent in 1969, 9.4 per cent in 1970).

Microtus. A different method of estimating seasonal maintenance was used for *Microtus* than was used for *Clethrionomys*. The population was divided into five weight classes every trapping period for conversion to caloric value. Mean weights of each class were then used to estimate population respiration. The estimates for all weight classes were summed by season. Animals were present in spring and summer 1970, but lack of recapture data made it difficult to estimate the length of stay. While values for these seasons may not be zero, they are probably below 10^3 kcal. The production in the *Microtus* dropped significantly in late 1969 which made an interesting contrast to *Clethrionomys* (Fig. 31). Nestling production , in both absolute and relative amounts, was far greater than that for *Clethrionomys*, and temporarily offset the decline described above. The high level was not maintained through the winter.

Zapus. *Zapus* maintenance production was greates during the latter part of May through early August (Table 35). The rest of the year (8 months) *Zapus* was hibernating, using fat resources. Respiration maintenance during hibernation can be estimated using Morrison's formula for hibernators (Lyman and Dawe, 1960) or by calculating the caloric value of the fat stored when entering hibernation.

Table 35. Maintenance production in the nestling and trappable populations of Clethrionomys, Microtus, and Zapus. All values are x10^6 cal.

Species	Season	Maintenance Production Trappable	Maintenance Production Nestling
Clethrionomys	Spring 1969	25.58	1.937
	Summer 1969	12.37	6.646
	Fall 1969	22.33	0.883
	Winter 69-70	46.88	-
	Spring 1970	4.57	-
	Summer 1970	2.61	3.748
	Fall 1970	17.74	1.013
	Winter 70-71	25.26	-
	Spring 1971	44.60	2.489
Microtus	Spring 1969	43.563	1.768
	Summer 1969	24.843	22.015
	Fall 1969	15.329	2.509
	Winter 1969-70	9.968	-
Zapus	1970 4 Months	9.835	0.771
	(8 months Hibernation)	0.557	

By making the following assumptions, maintenance productivity can be calculated from existing fat reserves.

1. Two adults with 15g of fat and four young of the year with 8g of fat entered hibernation per grid. 64g of Zapus fat at 8982 calories per gram is used over the cold months per grid.

2. All the above animals survived the winter and they did not arouse during the 8 month period.

3. They depleted their reserves.

Having made these assumptions, the result is that 0.557×10^6 cal would have been used during hibernation. While such an estimation is very crude the range indicated by this figure gives one an idea of the low magnitude of maintenance. Metabolism during hibernation was approximately 1/30th to 1/40th of the active values. Morrison's formula estimates (using 8 months, 240 days, for the period of hibernation and 32g for weight) a 90 per cent reduction in basal rate ($M_B/8$: see Lyman and Dawe, 1960, Fig. 2, p. 78). If Zapus were only able to reduce metabolism to $M_B/8$, each individual would have to put on at least two to three times the amount of fat estimated above.

Synthesis-respiration maintenance. Loss of energy by respiration in field populations is one of the greatest single obstacles in the way of complete description of the energy dynamics of natural populations (Odum, Connell and Davenport, 1962). Since recent experimental field respirometric techniques had not reached sufficient refinement during the course of this study laboratory respiration studies serve as the basis for making inferences about respiration levels of mice in the field.

Corollaries of this assumption are listed in Petrusewicz and MacFadyen (1970, p. 128-139). While some of the assumptions (e.g. zero pCO_2 has no influence on respiration rate) could not be met, it is reassuring that many can be quantified by using a Morrison Respirometer (Morrison, 1951; Morrison and Grodzinski, 1968). The problem of the group and or the nest effect lowering metabolic rates have been studied by Wiegert (1961), Trojan and Wojciechowska (1968 a & b), Cotton and Griffiths (1967) and several others. However, a recent study of the insulating properties of nests and its effect on social temperature regulation in <u>Clethrionomys</u> by Gebczynska and Gebczynski (1971) show that there is no significant difference between metabolic rate of single individuals in nests as compared to grouped voles in nests. Therefore a single mouse in a nest box does not necessarily have a higher metabolic rate than it would if other mice were also present. Lack of social interaction while feeding, etc., may result in an even lower metabolic rate for single mice.

Thermocouples (constantly recording) indicate that ambient temperature did not vary over 2°C during a twelve hour period. However, the temperature of the nest could vary up to 20°C depending on whether the animal was in the nest or out.

According to Gorecki (1966) acclimation (Polish use acclimatization) can be a problem when animals are kept in the laboratory for more than five days before measuring O_2 consumption. Experiments to determine the effect of acclimation were not conducted with the Fairbanks animals but considerable time and expense were devoted to keeping animals in the laboratory for no more than three days (exceptions were made for a series of extended runs of six days. No apparent adjustment in O_2 consumption occurred over this extended time). One drawback of the Morrison Respirometer and all other closed systems is the problem of measuring the expense of locomotion. Lack of locomotion metabolism may result in an underestimation of the field energy requirements.

Maintenance production values for this study (Fig. 31) are quite different than values listed in the literature (examples are given below). The differences in yearly total values are not so great but the seasonal maintenance measurements indicate that the summer periods are the lowest times of the year with the winter being the highest. Studies that assume ADMR's to be low during winter (Hansson and Grodzinski, 1970, Microtus arvalis; Grodzinski, 1971, Microtus oeconomus and Clethrionomys rutilus; Gebczynska, 1970, Microtus oeconomus, and many others) did not measure ADMR, at prevailing winter temperatures and winter photoperiods, on winter acclimatized mice obtained directly from the field. (Also note that winter temperatures assumed by the above studies are much higher than those existing under the snow in the Fairbanks area.) The above authors believe winter metabolism is lower because the mice lack the burden of reproduction and that subnivean temperatures are relatively warm. However, subarctic winters actually impose conditions on small mammals that can only result in more expensive maintenance costs.

Every gram of dry food eaten by mice has to be warmed from approximately -10°C to approximately +40°C; at least 50 calories are needed for this process. An additional heat expenditure of 80 cal/g is required to melt ice (Kleiber, 1961, p. 117). Assuming that a winter mouse eats an amount of wet food equal to its own weight each winter day (Golley, 1960) and that 50 per cent of the food is water, an animal would have to expend at least 1.4 kcal per day just to warm food. This means a 20 per cent increase in ADMR over the summer.

Water in the food ingested may or may not be enough to compensate for water lost in breathing. The maximum amount of water that can be held at -2°C to -30°C (range of measured winter temperatures in the subnivean space, Table 4b, Fig. 4b) is only one tenth (Hodgman, 1958-59, p. 2420) the amount that can be held at +15°C (temperature at the ground surface in the summer). Until _in situ_ measurements are made of absolute humidity in vole nests during the winter, it must be realized that it is physically impossible for water vapor to be present at the levels of summer saturation in the subnivean space as Pruitt (1967) insinuated. Relative humidity may very well be high at these temperatures but absolute humidity must be very close to zero and of course it is this absolute value with which the voles must deal. Current studies of water turnover in these voles (Holleman, pers. comm.) in the College area will be of great assistance in calculating the amount of snow needed to replace water loss in the winter months. In addition to heating water and food to body temperatures, the small size of these voles will also be another reason for a higher metabolic rate per gram in the winter season. An additional factor that most likely increases field metabolism is the extra energy needed to move snow away from plants. This may be considerably important when snow morphological parameters result in high break through pressures in the subnivean environment. While the above discussion to justify the higher winter metabolic rates is speculative, it does serve the purpose of showing the need for field metabolism techniques.

The method used in incorporating metabolic data into an energy budget can also greatly influence maintenance energy estimates of field populations (Phillipson, 1963). It is important to note that the regression methods used by Grodzinski (1971) can give results different from those obtained when animals are measured throughout the year as they are captured. Phillipson noted that there could be as much as a 40 per cent difference between the two methods.

At the onset of the productivity section it was stated that energy was the basic unit which related all parts of an ecosystem. However, reference was also made to the equally important concept that energy flow is not necessarily the basis for understanding ecosystems, communities or populations. The latter concept is contrary to the theories of Odum (1968, 1971) and must not be left unjustified no matter how elementary the evidence.

Ecology is now in an active phase of descriptive energetics. It has been proposed that smaller studies will serve as building blocks of the large ecosystem models that will lead ecologists to the understanding of short and long term changes in ecosystem evolution. While many of these studies are thoroughly thought out and masterfully executed, there has been little mention of how the data may in fact contribute to the understanding of community or ecosystem function. In the past it has been standard practice to incorporate energetic data in ratios such as described by Kozlovsky (1968). These ratios of yield to energy flow or production to respiration are calculated on a yearly basis and are compared to ratios from other populations or ecosystems where the same methodology has been followed.

The question remains, how will individual bioenergetic studies lead to a better understanding of community and or ecosystem dynamics and evolution? It is, of course, meaningful to put upper and lower limits on various bioenergetic ratios just as it is useful to put upper and lower limits of the temperatures at which life can exist. However neither of these limits can contribute to the explanation of the dynamic processes that occur between the extremes. Perhaps it would be more appropriate to restate the above problem by saying that I do not know what many of the dimensionless ratios mean in terms of understanding the dynamics of ecosystem processes and I believe that I am not alone. Chew and Chew (1970) state: "Of course, it is uncertain what is the significance of a yield to energy flow ratio of 1.7% for P. eremicus compared to 1.2% for D. merriami." (Also see Alverson et al., 1970.) These ratios are certainly a succinct way of describing what has happened, however description is not the same as explaining why something has happened. To understand ecosystem dynamics, it is the explanations that are mandatory. In short, it seems that ecosystem ecologists with copious amounts of data are waiting for a skillful architect to put these blocks together and place before the scientific world new truths of ecosystem behavior and evolution.

In order to evaluate the probability of any one person or combination of people being able to gain insight about ecosystem function, one must look at the basic assumptions used when analyzing energetic data. For example, Wiegert (1965) in his classical energy dynamics study of grasshopper populations calculated the ratios as mentioned above and assumed that these ratios were important. He felt consumer organisms are ultimately dependent upon the transfer of energy from the primary producers, and it is therefore important to know the efficiency with which energy is transferred between trophic levels. Wiegert has since changed his trophic level approach but he still maintains that all energetic ratios are based on energy limitation of consumers. One may ask why such an obvious truism (energy limitation) should be doubted or as stated by Pitelka (1958) "it may be a strain on Occam's razor to suggest genetical hypotheses regarding fluctuation as long as more directly ecological explanation can be invoked and tested." Since the time of Darwin we have known that populations must be limited by their resources but as new genetical theory updated Darwin's idea of heritibility so has recent theory given credence to the theory that consumers are not proximally limited by their food supply. Proponents of such recent theory are far too numerous to list. They form a group often referred to as the self-regulatory school; the self-regulation concept is well recognized in current ecological text books (Andrewartha, 1971; Kormondy, 1971; Krebs, 1972). The self-regulatory school of is by no means the only school of population control nor is it necessarily the correct school; it merely represents another view of population regulation. In addition to the self-regulatory school, there is the biotic school of

Nicholson and Smith and the abiotic school of Andrewartha and Birch and many theories in between. The analogy of all population theory being a continuous spectrum is a gross oversimplification, but the point being made is merely that there are many different hypotheses of what regulates day to day population parameters. Moreover, food limitation as a controlling factor (as assumed by many ecosystem ecologists) is only one of the many different theories.

It is interesting to note that ecosystem ecologists are convinced that they are right in assuming that energetics is the basis of population regulation, even though a majority of population ecologists do not agree with them. Odum (1968, p. 14) states: "Many of the controversies about food limitation, weather limitation, competition and biological control could be resolved if we had accurate data on energy utilization by the population in question." While Odum's statement runs the risk of being an ecological tautology, I feel that if there is to be any communication between the population and ecosystem ecologists, further examination of his statement must be made. Odum's statement is general enough to allow several interpretations, one of which will be pursued below.

While Odum is advocating energy as the basic link of ecosystems, he seems to be willing to interpret population biology theories as expressions of energetic utilization. Systems theory has been developed to handle such an approach. Forrester (1961) has made use of a bow-tie concept that provides for regulation of energy flux at any point of energy transformation. Hence there is the possibility of utilizing population information whether it be behavioral, genetic, stress, predation or weather. It is important in such a scheme that any sort of integration of populations and ecosystems involves rate modification or dynamic information. In short, it is difficult to visualize attaining understanding of ecosystem phenomena without utilizing what is known about the dynamics of population structure and function.

As an alternative to the more conventional energetics approach, I have chosen to discuss the dynamic properties of the small mammal net productivity in the Fairbanks area. This will be first analyzed irrespective of the several possible driving mechanisms of population control. Following production dynamics the discussion will examine the properties of the three species of small mammal populations and finally a summary will consider the interaction between population phenomena and production phenomena and possible new approaches to understanding ecosystem stability.

Production dynamics:

Much of the basic theory of energy flow is already in text book form (MacFayden and Petrusewicz, 1970; Krebs, 1972) and requires no further discussion. However, it may be useful to review three equations used in this theory.

$$MR = NU + C$$
$$C = P + R + F + U$$
$$A = P + R$$

MR = Material removed from a previous level
NU = Proportion of MR not used
C = Proportion of MR consumed
P = Proportion of C used to build tissue (Net Production)
R = Proportion of C used for maintenance of tissue (Maintenance Production = Respiration)
F = Proportion of C eliminated as feces
U = Proportion of C eliminated as urine
A = Proportion of consumption that is assimilated

Each unit above is expressed in this study as calories.

It is important to note that the above equations have been previously quantified in the taiga system by Grodzinski (1971). Therefore I feel it necessary to briefly discuss those aspects of his study that apply to this study. Grodzinski's microtine population data were collected using three live trapping periods from May to August, 1963. Metabolism was measured on C. rutilus and M. oeconomus that were allowed to acclimate to laboratory conditions. Only summer ADMR values were measured. With a total of 31 C. rutilus and 7 M. oeconomus captured during the three periods in the summer of 1963, he calculated yearly net and gross microtine production. Grodzinski's values of yearly maintenance production were very close to the values obtained in this study for C. rutilus. It is significant that both of these studies resulted in the same yearly value but were based on two very different perspectives of population dynamics and maintenance respiration.

Annual net plant production was measured by subtracting the minimal standing crop value from the maximal. Such a procedure was not used in this study for the Steese plant clippings because the standard deviation of the mean dry weight for most species sampled was two to three times the mean value (unpublished data). No standard deviation values for vegetation production are given by Grodzinski. The food habits of C. rutilus and M. oeconomus studied by Grodzinski provide the most valuable data for this study. Cafeteria preferences, such as fresh aspen leaves in the spring, deserve warning, for (as noted in the population discussion to follow) C. rutilus has never been observed in aspen trees in the

Fairbanks area. Cafeteria tests are thus biased by introducing foods that are not naturally available to the animals. Stomach content analyses made by Grodzinski indicate that C. rutilus is more of a seeds eater than M. oeconomus which has a greater preference for greens.

While Grodzinski (1971) deals with all three of the equations on page 174, this study has only allowed accurate determination of the net productivity and the maintenance productivity. Calculations for the other equations would have to rely on values for F and U found in the literature, for these values were not directly determined. Since this has already been done by Grodzinski (1971), there is no need to repeat it again. Secondary production and respiratory energy loss together constitute population energy flow (by definition). These parameters of the field populations for each sampling period were used to construct Fig 31, 32 and 33. Figure 31 only shows seasonal values since ADMR's were not measured frequently enough to allow bi-weekly estimation of maintenance.

Peak production levels in Clethrionomys rutilus occurred in August and were followed by a decrease in productivity during the next two months. It is interesting to note that during the peak period in 1969 and 1970 weight loss was already taking place. The reader is reminded that such a phenomena is possible with some age (weight) classes of weaned animals gaining weight and others losing (Fig. 19; Growth section, p. 83). It is interesting to note that the initial loss of productivity in 1969 is due to subadults while smaller and larger (younger and older) weaned animals continue to produce. Larger animals

Figure 32. Grams produced and grams lost to respiration for the Grid A Clethrionomys population. Note that the ordinate is a log scale. The population has been stratified into three parts: natal, nestling, and weaned.

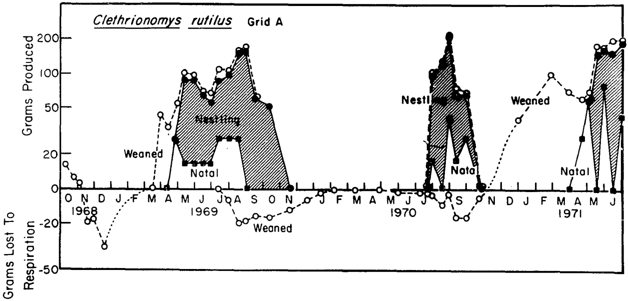
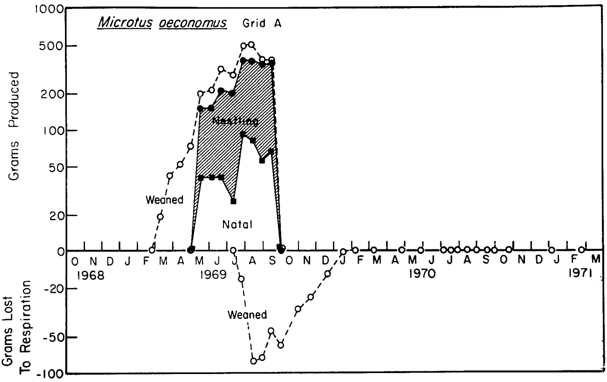

Clethrionomys rutilus Grid A
Grams Produced
200
100
50
20
0
-20
-50
Grams Lost To Respiration
Nestling
Natal
Weaned
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
1968
1969
1970
1971

Figure 33. Grams produced and grams lost to respiration for the Grid A _Microtus_ population. Note that the ordinate is a log scale. The population has been stratified into three parts: natal, nestling, and weaned.


Microtus oeconomus Grid A
Grams Produced
Grams Lost To Respiration
1000
500
200
100
50
20
0
-20
-50
-100
Weaned
Nestling
Natal
Weaned
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M
1968
1969
1970
1971

then start losing weight and in a few weeks the lightest animals start to lose. The production in 1970 is quite different from that in 1969 in that the young (juvenile weaned) animals that grew into the subadult class almost immediately started to lose weight. The resulting effect was energetic loss equalling production in the weaned population. Additional weight was lost by animals that immigrated onto the grids. Peak production and animal density were just as great as the year before and as the year after. These times of differential weight loss (growth was not prevented by shorter length of life or poor nutrition because some age classes were gaining weight while others were losing, etc.) are extremely important. They are examples illustrating the independence of population dynamics. In other words, the principle of energy limitation cannot explain why some weight classes gain weight while other weight classes lose weight. Moreover, weight losses in the mouse populations are a significant exception to general energetics theory as developed by MacFadyen and Petrusewicz (1970, p. 21). The definition equation for weight loss $L = G - P$ (L = Weight Loss, G = Total biomass produced, P = Production is faulty. The theoretical fallacy in the weight loss equation is classifying weight loss as negative productivity (e.g. when $G = 0$). While the concept of negative productivity is easy enough to grasp, negative productivity necessitates explaining negative turnover in the equation: $\Theta_p = \frac{P}{\bar{B}}$ (P = productivity, $\bar{B}$ = average biomass and Θ_p = production turnover). Parameters resulting from weight loss can only be explained as weight loss to respiration as labeled in Figures 32 and 33. In light of this finding, cumulative energy budgets as first proposed by Klekowski et al. (1967) render efficiencies meaningless as is stated below.

> However, where the energy budget is unbalanced, for example during periods of negative production (Petrusewicz, 1967) when an animal is either under-fed or starving and loses body weight, instantaneous efficiences cannot be calculated (Klekowski and Duncan, prepublication manuscript).

In this study however it seems unlikely that the animals are underfed or starving for they lose weight in the peak of the plant growing season. In short, conventional energetics theory is not applicable to this study. Moreover, it is proposed that ecologists carefully consider the use and meaning of energetic ratios.

1970 also stands out from 1969 and 1971 in that there was no weaned production (no production in overwintered animals) preceding the spurt of nestling growth. Weaned production of the overwintered animals preceded nestling production by four weeks in 1969 and by 16 weeks in 1971.

Nestling growth and survival is largely responsible for the overall shape of the production curve. The peak values of nestling production are approximately 140 ± 15g (range for all years) which is constant in light of the differing yearly intensities of natal production. It may be a coincidence but peak periods of nestling production always seem to follow a decrease in natal production.

Microtus production (Fig. 33) is characterized by an August peak that is twice that of the Clethrionomys fall peak value. However, production lost to respiration is four times greater than Clethrionomys. An additional contrast between species is that different weight (age) classes were responsible for the negative values in the *Microtus* weaned population. Subadults were the last to contribute to weight loss (loss of production) in comparison to the *C. rutilus* subadults that were first. *Microtus* were also different in that natal, nestling and weaned production simultaneously decreased very rapidly.

Production rates in the spring 1969, are similar for both microtine species (Fig. 31 and 32); both started production under the snow but the *Microtus* continued increasing until production was twice that of the *Clethrionomys*. This may be interpreted as evidence that *Microtus* out-compete *Clethrionomys* but in the absence of *Microtus* in 1970 the initial *Clethrionomys* growth phase was delayed several months. In 1971 in the absence of *Microtus*, *Clethrionomys* started production earlier but the rate of increase was lower.

There are very few studies where small mammal production rates have been measured. Most studies such as Grodzinski (1971) assume that turnover rates, density and body weights from the literature apply to the species studied. Yearly net production values calculated by Grodzinski (1971), 1,650 g/ha/yr, are roughly equal to the average of 1,511 g/ha/yr for 1969 and 1970. When data for the remainder of 1971 are made available by Feist, the average will probably be over 2,000 g/ha/yr. The average based on 1969 and 1970 data is about 48 per cent lower than the yearly hectare production (2,857 g/ha/yr) for an island population of *C. glareolus* (Petrusewicz *et al.*, 1968). Since the island only had *C. glareolus* living on it, Petrusewicz considered the values to be high but still within the range of already known values. It is interesting that Petrusewicz realizes the limited meaning of such comparison on account of the considerable difference in accuracy of empirical data and differences in methods of calculating production.

Microtus 1969 net productivity, 6,146 g/ha/yr, was higher than the island population mentioned above which is one of the highest values in the literature. However an average for three years (including the years with very low density) falls within the range of previously cited values. The average value for Microtus production on the Steese was three times higher than the value Grodzinski (1971) estimated for the spruce forest. Gebczynska (1970) found values similar to Grodzinski's (1971) and concluded the M. oeconomus has similar physiological characteristics over its entire range. Based on data from this study, I take exception to this statement.

The total rodent productivity for both microtines and the Zapus in 1969 gave a value of 8,890 g/ha/yr which was in excess of most values recorded in the literature. To this could be added a very dense population of shrews (approx. 75/ha), occasional flying squirrels, red squirrels and snowshoe hares whose population was in an increasing phase of abundance. Accurate energy flow data are not available for these latter species on the Steese area.

The most important conclusion to be gained from the net productivity results is that no two years were the same. This wide variability has been associated with several patterns of production rates. In comparison to other ecosystems, taiga small rodent production is above or at least within the range of already known values for other systems (Chew and Chew, 1970, desert; Gebczynska, 1970, peat bog; Golley, 1960, old field). It is stressed however that comparison of yearly production or averages over several years does little to elucidate differences between biomes. Problems of between biome comparisons due to variability in methodology have been discussed by almost every author reporting energy flow data. It is proposed that comparability between ecosystems and possible applicability of energy flow data to population theory can only be achieved through comparing production dynamics in a way that does not assume proximal energy limitation.

Demography

Clethrionomys:

Feeding. Clethrionomys rutilus is the "Peromyscus of the North" (Guthrie, 1965). As a seeds eater (Grodzinski, 1971; Bashenina, 1951), C. rutilus is quite different from the grazing C. rufocanus of Tast and Kalela (1971). C. rutilus is also more variable in many morphological characteristics (Koshkina, 1957; Curray-Lindahl, 1959). Tooth structure in C. rutilus is not as specialized as it is in Microtus sp. (Phillips and Oxberry, 1972; Guthrie, 1968), but C. rutilus still has grinding molars, a long small intestine and large caecum that permit utilization of low quality (herbage) foods that may be more available during poor snow conditions (Gorecki and Gebczynska, 1962). Hence it is postulated that when C. rutilus is sympatric with Peromyscus sp. as in the Great Slave Lake area of Canada (Fuller, 1969), the former fills the typical Microtus grazing niche. Furthermore, when C. rutilus is sympatric with Microtus it fills the niche of Peromyscus. If this is true, it may explain why C. rutilus is observed "cycling" in some areas (in the Microtus niche) and not "cycling" in other areas (in the Peromyscus niche). This assumes that the microtine "syndrome" as described by Krebs and Myers (1973) is an advanced evolutionary feature in the Cricetidae.

Clethrionomys habitat variability is one of the most noticeable natural history phenomena of the Fairbanks population. The species has been observed in every habitat type trapped in this study; this includes north and south facing spruce associations, all types of birch, poplar and alder associations, bogs and creek beds (Arvey, pers. comm.) and Clethrionomys even seems to fill the niche of the house mouse. Every report of mice in Fairbanks and College houses have been C. rutilus. Other reports of C. rutilus as the "house mouse of the north" have been cited by Manning,(1956), Tast (1968b) and Porsild (1945). Grodzinski (1971, p. 248) also makes reference to C. rutilus climbing trees as has been noticed in European C. rutilus (Koshkina, 1957). I have never observed red back voles in birch or aspen trees and Grodzinski's assumption is the only report for the Fairbanks and College area. Deans (pers. comm.) informed me that C. rutilus have been captured on white spruce in the Fairbanks area. Curray-Lindahl (1959) notes that C. rutilus is found in more habitat types in Sweden than is Microtus. Numbers in Sweden were highest in virgin pine forest and second growth pine forest where there were very low densities of other small mammals. As cited above, check lists from this study also agree in habitat variability but it is doubtful if avoidance of other species is the mechanism for such variability. Competition between Clethrionomys and Microtus has been well documented and is reviewed by Morris and Grant (1972). Therefore it appears unlikely that C. rutilus habitat variability results from passive avoidance as insinuated by Curray-Lindahl (1959).

There is also evidence for exclusion between Clethrionomys and Microtus in this study but my data on Clethrionomys do not support Morris and Grant's (1972) hypothesis for the mechanisms of exclusion. This is a detailed story and involves a completely different analysis of the demographic data than that presented thus far. It will suffice at this point to note that peak populations of Clethrionomys and Microtus occurred simultaneously on Grids A and B during 1969. Manning (1956) and Pruitt (1968) also noted that Clethrionomys occupied the same habitat but population peaks were in separate years.

Feeding and habitat observations have led to the hypothesis that Clethrionomys is filling the whole Cricetidae seeds eater niche (excepting Zapus for four months in the summer) in the Fairbanks area. Reference has been made to the variability of the seeds eater niche as compared to the specialized grazers niche (Baker, 1971) and it is the usual case for there to be several seeds eater species and only one grazer in most habitat types. Whatever the reason is for there being few seeds eaters in the Alaskan Interior, it is doubtful that lack of habitat variability is a factor. Moreover it seems that there would be a selective advantage for Clethrionomys to be as variable as possible to utilize the wide (Levins, 1968) available niche. It must be made clear that the discussion that follows will be giving evidence for the above hypothesis; this evidence should not be considered as a test, for it is the very same evidence that led to its development. While examination of this hypothesis is not one of the major goals of this study, I believe it provides a theoretical skeleton which could possibly relate the physiological and ecological observations to follow.

Survival. Survival values in this thesis have been referred to as minimal rates. The reason for this is that one can never be sure of catching all survivors from a cohort. As stated by Chitty and Phipps (1966), "minimal survival rates will be useful only in so far as marked animals remain on the area and continue to enter traps. Although we are unable to distinguish between losses through death, emigration, or a change in behaviour toward the traps, we shall assume, until there is evidence to the contrary, that a pronounced change in minimal survival rate is largely due to a change in survival". Since this statement was made, Myers and Krebs (1971) have gained some evidence to the contrary. This being, during increase phases in population density, low survival values can be largely accounted for by dispersal of animals. While dispersal was not the major emphasis of this thesis as it was in the above study, between grid movements indicate the same phenomena of increased dispersal during an increase in population density. However, since auxiliary grids were not being trapped on the Steese during the months when snow covered the ground, generalized dispersal indices (Table 18) only apply to snow free periods.

General survival patterns for Clethrionomys in this study, using live trapping and weight as an index of age, compare favorabl with those of Zejda (1961, 1967), Kaikasala (1972) and Ryszkowski (1971) using snap trapping and tooth morphology as aging indices. Adults survive through the early summer months but are gradually replaced by their young. However, a more detailed comparison of snap trap survival rate data is very difficult. For example, Ryszkowski (1971) calculates survival by comparing the estimated number of voles born each generation using spring snap trap data with corresponding numbers in the autumn population. The general trapping schedule as outlined by Ryszkowski was used for snap trapping a large 16 x 16 station grid (see Methods). If data collected in this way (see density results) were used to calculate survival, one would assume that survival was poor over winter 1969-70 and good from Spring to September 1970. As will be illustrated below much more detail is needed in order to untangle the intricacies of the demographic machinery behind such general trends. However, turnover calculations using snap trapping seem to be suitable for yearly gross energy budget calculations.

Year-long live trapping studies on _C. rutilus_ do not exist and there is a noticeable lack of survival data for _Clethrionomys_ in subarctic or arctic habitats. Fuller (1969) and Fuller _et al._ (1969) studied survival in _C. rutilus_ using snap traps during the fall, winter and spring in conjunction with summer live trapping. His interests were centered around winter survival and perhaps the major contribution of his study was integrating much of the Russian literature and winter data from the Arctic Aeromedical Laboratory in Alaska with current literature of population regulation (Fuller, 1967). Many conclusions below do not agree with many of Fuller's assertions. However, I do not assume to resolve all questions of winter survival in subnivean life forms.

Fuller's et al (1969) failure to capture C. rutilus in snap traps under the snow was considered to be an indication of poor survival. However, if one examines the differential in captures per 100 trap nights (5:1) that was used to indicate poor survival it is strange that an equal differential (13:3) was interpreted as variability in trap response. While there may have been poor survival over the whole winter as was indicated by the snap trapping effort on the 16 x 16 grid (Table 12), snap trapping does not seem to have the sensitivity to detect when survival rates are the lowest. Perhaps snap trap lines used in this study every month during the 1969-70 winter would be a better comparison to Fuller's work. Steese line trapping indicates that zero animals were captured in a declining C. rutilus population (Table 2). Figure 11a however, shows that live trapped densities during the same time (less than 400 meters away from the various snapped areas) were well above 10 per 0.48 hectare for the first three winter snap trappings and zero for the last. It is possible that winter snap trapping is better suited for the Great Slave Lake taiga. Yet snap trapping at its best (without appropriate calibration, Pettigrew and Sadlier, 1970; Yang et al., 1970) only yields relative densities. Therefore, conclusions drawn from survival and density using monthly snap trapping must be cautiously evaluated.

I was extremely fortunate to have three quite variable winters in contrast to Fuller's two similar winters. During the course of the study the smallest and heaviest snow packs were recorded. The first two weeks in January 1969 were the coldest on record with a mean temperature of -55°F (-42°C) while the next year's lowest temperature did not even reach -35°F (-37°C). This variability allows further evaluation of the hardship periods for voles. Three periods of hardship for vole survival have been proposed: 1) the onset of winter (Fall critical period of Pruitt, 1957), 2) the end of winter (Spring critical period of Fuller, 1967, and Dunaeva, 1948), and 3) full winter conditions (Pruitt, 1957; Beer, 1961). Fuller *et al.* (1969:p 42) proposed that the cold temperatures of the "full winter" were most severe for *C. rutilus*. As discussed above, the data upon which this conclusion was based provide only a "crude picture" (Fuller *et al.*, 1969) of density and survival interaction. Results from this study indicate that during extreme environmental exposure (January 1970, with subnivean temperatures at -30°C and only six inches of crusted snow cover) vole survival was very good, in fact better than most summer periods when temperatures were 10°C to 15°C at ground level (also observed by Koshkina, 1957). A decrease in survival in *Clethrionomys* did occur on the Steese (over a month after the above conditions) when there was more snow cover and higher (-10°C) subnivean temperatures. Hence, in this above particular "full winter" extreme case, survival was very good and gives a somewhat different impression from the *C. rutilus* in the Great Slave Lake taiga.

The following winter, 1970-71, with a record snow fall, was a marvelous contrast to the previous winter. Clethrionomys survival was again excellent through April. Growth had started in January and a majority of the animals were breeding by late March (note that breeding did not occur until there was a well developed subnivean space, Fig. 8c). However, in late April and early May, during an extended snow melt due to unseasonably cool weather, survival in males took a drop only to recover within the next two weeks. Survival in males then dropped even lower under milder June and July temperatures. The spring critical period therefore did not have a severe effect on adult survival. However, nestling mortality was extremely high during this period (Table 30). Figure 17 also shows a gap in the body weight distribution indicating poor recruitment into the trappable population. However, neither the short term moderate mortality nor the extremely poor survival of the first litter (typical of subarctic voles, Shvarts, 1962) prevented 1971 from being the most productive of all three years.

In reference to this conclusion it is significant that Krebs and Myers (1973) had access to my data and results before the completion of the thesis. There is one point on spring survival that must be corrected. Krebs and Myers state: "the period of poor survival at the start of the breeding season in the spring is typical of microtine populations and could not be tied to specific weather factors." As was noted above, breeding had started months before the spring critical period and survival was high when it started, so low survival cannot be correlated with the onset of breeding during spring 1971. This is one more instance in which C. rutilus differs from the typical "cycler". However, this correction does not alter Krebs and Myers' conclusion that survival during the spring critical period is not crucial to subsequent production, which is in contrast to Pjastolova (1971) and many others.

Low survival recorded during both falls (August and September of 1969 and 1970, i.e. well before freeze up and snow fall) indicate that low survival is definitely not limited to the fall critical period. In addition, low summer survival (June and July of 1969 and 1971) is characterized by very low male survival; however, the female survival is moderate to good. It was hypothesized that the low summer survival may have been due to emigration.

Nestling survival (Table 30) was high early in the breeding season (excepting 1971, as discussed above) with slightly lower values late in the season. The lowest nestling survival in Clethrionomys was in June 1969 and was not obviously correlated with any extrinsic factors. Nestling survival rates for other Clethrionomys species, Gliwicz et al. (1968), Bobek (1969), Ryszkowski and Truszkowski (1970) and Ryszkowski (1971) were calculated over much longer time intervals (from 32 to 90 days) than in this study (usually 28 days) and hence do not allow a comparison of differential survival through a breeding season. Krebs (1966) notes that juvenile survival (as well as adult female survival) was in fact the most important factor affecting population growth in Microtus californicus and in Indiana Microtus sp. populations. Krebs (1970) also notes that juvenile survival was in fact the most important factor affecting population growth. The periods for low nestling mortality are in peak and declining populations. In contrast, C. rutilus showed the poorest nestling survival in an early increasing phase. Once again C. rutilus does not behave as would be expected of a cycling species.

Krebs and Myers (1973) note that survival of adult females need only deteriorate 10 to 15 per cent per 14 days in order to produce a population decline. The 40 per cent decrease in early September 1969 (Fig. 14) is sufficient to start the over winter decrease in September 1970. An even greater similar decrease in survival; 50 per cent also caused a decline but the winter population did not continue to decline in density. While poor female survival may be sufficient to cause a decrease in numbers it is not necessary for a population decline in C. rutilus.

Prenatal mortality gives additional evidence that C. rutilus is not cycling. C. rutilus values (33 per cent) were observed to be five times greater than prenatal mortality of Microtus oeconomus in this study as well as several other Microtus species (Keller and Krebs, 1970; Stein, 1950).

To summarize, live trapping during the winter months is necessary to evaluate winter survival. Winter survival was good and survival patterns at other times of the year did not always coincide with the three proposed periods of hardship for voles. When low survival did occur during one of these hardship periods it had little effect on subsequent productivity. Survival patterns in weaned, nestling and natal animals indicated that C. rutilus is not cycling.

Reproduction. Reproduction information for *Clethrionomys rutilus* in past literature is based primarily on data obtained during the snow free periods of the year. Table 36 lists some estimates of the length of the breeding seasons:

Table 36. Recorded lengths of breeding seasons for *C. rutilus*.

Author		Location	Breeding Season	
Fuller	1969	Great Slave Lake	May	Aug. (3 yrs)
Grodzinski	1971	Fairbanks	May	August
Khlebnikov	1970	Sayan Mts.	winter breeding	
Koshkina	1957	Saligar taiga	May	end of Aug.
Koshkina	1965	Saligar taiga	late April	August
Manning	1956	Aklavik, NWT	April 20	Sept. 21
Rausch	1951	Anaktuvuk Pass	May	September
Sealander	1967	Fairbanks	May	August
Shvarts	1962	Yamal Peninsula USSR	May	August
Whitney	1973	Fairbanks	early March	mid Sept.

It is often difficult to compare estimates of such parameters as breeding season due to variability between years and location, however I feel that the information in Table 36 make it clear that the length of the breeding season for *C. rutilus* is quite variable from year to year. This is in contrast to the opinion of Shvarts (1962), who stated that microtines in the arctic breed at the same calendar date irrespective of environmental conditions. Hence interpretation of population, physiology and productivity data based on an assumed constant length of breeding season deserves re-examination. In addition, the presence of breeding females and no young in the trappable population (Fuller, 1969) is not always a sign of the beginning of the breeding season (see Reproduction Section, p. 76; Shvarts (1962) also mentioned common spring reproductive failure in the first litter of subarctic rodents).

The length of breeding seasons have been examined by: Quay (1960) who proposed temperature as a regulatory factor; Shvarts (1962) who considered regulation to be due to a delicate balance between light and temperature with the resultant dichotomy of responses leading to selection of animals which are not very responsive to either factor; and by Everenden and Fuller (1972) who indicated that the beginning of breeding season in C. gapperi is controlled by day length. The latter believe that more of the stimulatory short wave lengths may be transmitted through the weathered, melting snow commonly associated with the approach of spring. Hence years with different snow depths plus variability in break up may explain the variability in the timing of breeding seasons. Koshkina (1957) notes that breeding in the burnt areas starts earlier than in the spruce where the snow remains on the ground later in the spring. Sealander (1967) also feels that photoperiod is the key factor regulating the onset and cessation of the breeding cycle in Clethrionomys rutilus and supposes that changes in gonadal size are most probably influenced by photoperiod acting through the eyes (Hoffman and Reiter, 1966). Pinter and Negus (1965) have reviewed studies of photoperiod and reproduction in Microtus species and reach the general conclusion that food quality is a more important regulator of reproduction timing than photoperiod. If in fact photoperiod does regulate reproduction, the winter breeding observed in this study under 120 cm of snow and by Khlebnikov (1970) must represent some type of mechanism that overrides all of the extrinsic hypotheses above. The question remains, do

C. rutilus have the ability to regulate light levels through supranivean activity such as feeding on alder seeds in the snow pack, etc., or when building ventillation ducts from the subnivean space to the snow surface. In reference to Pinter and Negus (1965) it is interesting to note that the year 1971, when breeding started in March, was also characterized by positive growth rates (Fig. 20) and extremely high production rates (Fig. 32) in January and February prevailed. It is not possible that this growth was due to ingestion of high quality young plant shoots, for ground temperature were -7°C. Moreover, if food quality was good during 1970 (this is the crop year that mouse growth in spring 1971 was utilizing) it is difficult to imagine why growth ever stopped the previous fall. Krebs and Myers (1973) consider variability of length of breeding seasons as part of the microtine cyclic syndrome with a short breeding season occurring in the peak year. Whether or not C. rutilus in the Fairbanks area is a cycling microtine will be discussed in more detail below, however since 1971 seemed to be a peak production year (note that numbers were not necessarily peak, Fig. 11a) the early breeding season would favor exclusion of C. rutilus from the syndrome, i.e. length of breeding season supports the idea that C. rutilus does not "cycle" in the Fairbanks area.

A high fertility of arctic and subarctic species was noted by Rensch (1936). The biological importance of high fertility in the north is obvious to Shvarts (1962). He feels that in the far north the period of propagation and growth of the young is shorter than in other geographical zones and in order to compensate for shorter breeding seasons, litter size has been adaptively increased. This hypothesis is examined with the data in Table 37.

As with lengths of breeding season, litter size is a difficult parameter to compare between areas, years and different methods of sampling. For example, litter size has been shown to vary indirectly with population density in *Clethrionomys* (Patric, 1962; Zejda, 1967; Fuller, 1969) as well as directly (Koshkina, 1965). In addition the variability of values measured by the same or different scientists in the same area must caution one from too strict an interpretation.

Table 37. Recorded litter sizes for *Clethrionomys rutilus*.

Author		Litter Size	Location
Bee & Hall	1956	9.1 embryos	Umiat, Alaska
Fuller	1969	4.8 - 6.8 embryos	Great Slave Lake, NWT
Koshkina	1957	5.1 litter size 6.5 embryos	Kola Peninsula, USSR
Koshkina	1965	6.0 - 7.6 embryos	Salain taiga, USSR
Manning	1956	5.9 embryos	Tuktoyaktuk & Aklavik, NWT
Morrison	1954	6.7 litter size	Fairbanks, Alaska
Shvarts	1962	9.8 embryos	Yamal Peninsula, USSR
Whitney	1973	8.1 embryos	Fairbanks, Alaska

Data collected in Table 37 indicate that far north collections show the smallest litter size while taiga litter sizes can be larger or smaller. In comparison to more southern species of *Clethrionomys* (Ryszkowski, 1970, 4.8; Zejda, 1966, 4.9; Stein, 1950, 4.9; Bujalska and Ryszkowski, 1966, 4.9) there does seem to be a trend for larger litter size in taiga *C. rutilus*. However since there are no southern populations of *C. rutilus*, one can only say that over its range there is no latitudinal cline in litter size.

Female adult breeding intensity does not seem to vary over the population cycle (if one is present). In all years 100 per cent of the adult females are lactating. The female subadults do show variation (Table 15); but this is between habitat type, being more intense on Grid A and B on the Steese where breeding was occuring in a low density population. Autopsy data for Clethrionomys was not extensive enough for between year analysis but pregnancy rates in mature animals were 88 per cent based on pooled data for 1969 and 1970, which correlates well with the live trap data (Fig. 16b).

All of the adult males started breeding earlier in 1971 (Fig. 15a). Subadult breeding intensities show differences between years not shown by the females (Table 15). It is also interesting to note that animals of the same weight could have testes weights around 12 mg or around 450 mg. While body weights of these groups overlap several grams, the mean weights of the testes in each group are well over three standard deviations apart. This information is important to physiologists who have considered testes weights more than three standard deviations away from the mean as "aberrant". These data show that those values discarded by physiologists as aberrant are perhaps the key factors in relating their work to population theory of small rodents. The reason for such a bimodal distribution could relate to different types of animals being produced as the density is increasing. Myers and Krebs (1971b) have noted different genotypes of dispersing Microtus in increasing population density and Anderson (1970) refers to differences in generations. Live trapped animals were examined to determine if any differences in testes inhibition existed for those animals that remained on the grid as compared with those animals observed leaving the population. During July 23, 1969, all dispersing animals were breeding. These individuals represented all breeding males excepting the largest male. The animals that remained (besides the largest) were non-scrotal subadults. The weights of all these subadults that remained low through subsequent trapping periods and their breeding condition remained inactive. It is reasonable to suppose that differential breeding inhibition during the population increase existed. I feel that evidence presented above calls for further study into the possible heritability of reproductive inhibition in relation to the disperal process. Moreover, the observation that dispersing animals were in breeding condition supports the theory of r selection for island colonization as developed by MacArthur and Wilson (1968), Wilson and Bossert (1971), Krebs _et al_. (1973).

Maturity was also examined from a physiological point of view. Bailey, Kitts and Wood (1960) observed that the ratio of protein to body water (Maturity Index, Body Composition) increased exponentially with age until "chemical maturity" when the ratio remained constant. Studies of this ratio for different aged laboratory raised _Microtus arvalis_ were made by Sawica-Kapusta (1970). The ratio increased with age from 0.12 to 0.33 at thirty days of life without leveling off. They predicted that chemical maturity would be achieved after 30 days of age, perhaps together with sexual maturity. Maturity Index calculations for field captured *C. rutilus* indicate that chemically immature animals are not necessarily prevented from becoming sexually mature, thus indicating that the population phenomena of delayed sexual maturity may not be solely determined by age.

Sex ratios differed from 1:1 for two months in 1969 during the last phase of density increase (Fig. 13a). Males out numbered females which is not typical for population increases in cyclic microtines (Krebs and Myers, 1973). These data therefore provide additional evidence for *C. rutilus* not cycling in numbers or demographic parameters. The unbalanced sex ratio could have been due to greater male activity on the edges of the grid which would result in more male captures, however such an explanation is doubtful since the opposite trend in sex ratio was seen simultaneously for *Microtus* on the same grid. Since the sex ratio did not favor females during the population increase in Fall 1970, or Spring 1971, it can be assumed that unbalanced sex ratios are not sufficient and necessary for population increase in *C. rutilus* during the period of study.

Growth. Growth rates and body weights of arctic and subarctic animals have been the subject of debate on at least three different biological tangents: 1) interpretation of Bergman's Rule, 2) increased growth rates in arctic animals, and 3) growth as a parameter of microtine cycles.

1) Bergman's Rule: races from cooler climates tend to be larger in species of warm-blooded vertebrates than races of the same species living in warmer climates, has been a subject of formal debate since

Scholander (1955) and Mayr (1956) expressed a disagreement in interpretation. The focal point of the disagreement seems to be based on body size and cold adaptation. Scholander (1955) believed that insulation was the major adaptation to cold with body size relatively unimportant. Mayr (1956) did not necessarily argue for Bergman's Rule, but was more concerned with Scholander's idea of evolution resulting in only one significant adaptation. In short, body size was not considered to be of importance as an adaptation to cold.

Before this debate reached the literature cited above, Dehnel (1949) noted that arctic shrews in fact lost weight during the coldest parts of the arctic year. Dehnel did not explain this phenomena solely in terms of body weight - metabolic rate phenomena but integrated weight specific relationships with anatomical behavioral and ecological meaning. The theory, as Dehnel explained it (Mezhzherin, 1964), was that anatomical and behavioral characteristics of shrew feeding do not allow increased consumption to meet increasing homeothermic demands. Therefore the shrew was feeding at a maximal rate even in the most favorable parts of the year. According to the theory, shrews lose weight which allows them to maintain body temperature with the same rate of consumption. However, this weight loss is not believed to be a passive starvation phenomena. As noted by Mezhzherin and Melnikova (1966) the process of reduction in weight and dimensions of the animal's body during the winter is accompanied by processes reducing the measurement of the skull, inhibiting the activity of the endocrine glands, reducing the volume and weight of the brain and increasing the amount of hair per unit of body surface.

Since reduction of body weight by as much as 35 per cent is common to many subnivean mammals (chionophiles) one is led to believe that this ability is a cold climate adaptation (Fuller, 1969; Sealander, 1966; Kalela, 1957; Mezhzherin, 1964; Kaikusalo, 1972). Similar weight losses have been described for Clethrionomys in this study (Fig. 19). If this observed weight loss is an example of an adaptation to cold, the mechanism is not related to insulation but rather a change in body size. It is important that there is a reduction in body size during the winter rather than an increase. Even though per gram metabolic rate may be greater (seemingly disadvantageous for cold), the ecological savings of demanding less food from the environment might be more consequential (Kendeigh, 1969; McNab, 1972).

The main point of contention: evolution occurring on an ecological, behavioral and physiological basis must not be ignored. McNab (1972) seems to be the first to integrate ecological and behavioral relations into the Scholander-Mayr debate. He cites data on feeding behavior and ecological competition during times of limited food resource along with physiological arguments as evidence against Bergman's Rule. Fuller (1969) who measured weight loss in C. rutilus believes that the only advantage to being small would be in times of food shortage.

To summarize the discussion so far, it is apparent to many workers that the ability to lose body weight can be of significant importance for winter or cold survival. If the ability to lose weight is an adaptation to cold, this would be a mechanism in addition to insulation. The applicability of this theory to the microtines in this study is questionable. If the weight loss mechanism is an adaptation to cold or food shortages, why does it occur in the warmest parts of the year (from late July into the winter) when food resources should be at a maximum? While the cold adaptation argument used by the authors cited above makes sense, it does not apply to the phenomena as observed in this study.

In conclusion, two points must be examined in more detail before concluding that cold adaptation is not somehow related to the late summer and fall weight loss:

a) The weight loss phenomena observed in Clethrionomys and Microtus is driven by the same mechanism as proposed by Dehnel.

b) Is there a necessity of sharing a limited food resource as mentioned by McNab (1972)?

If weight loss is not related to cold, one must ask what is the cause? The only answer at this time is: that's what the animal does.

2) Increased growth rates in arctic and subarctic animals are believed to be an adaptation to a shortened breeding season (Shvarts, 1962). Small mammal data supporting this hypothesis have come primarily from laboratory experiments (Morrison et al., 1954; Shvarts, 1962). It would indeed be interesting to compare field growth rates from this study with data collected from other areas, however none exist. Another approach to testing this hypothesis is to examine peak growth rates in relation to season. Maximum instantaneous growths in

8 to 16 gram Clethrionomys are nearly the same (approximately 0.010) for all years, but the season in which these growths are maximized are different: October 1968, July 1969, August 1970, January 1971). Such a variation in peak growth can hardly be explained in terms of a strategy that used growth rates to take advantage of the short summers. Shvarts asserts that: "The biological basis for such a phenomenon (high growth rates in the arctic) is quite clear". To the contrary, cause and effect for peak growth rates in subarctic Clethrionomys is not clear.

3) On a third front, Krebs and Myers (1973) are interested in growth as a parameter of the microtine cycle "syndrome". Growth is considered an important aspect of the syndrome because "it is tied to the primary process of birth, death and dispersal. The size at sexual maturity is the most direct linkage between individual growth and the reproductive rate of a population."

Growth manifests itself in several ways in microtine cycles. For example, high body weights are considered to be a characteristic of the high population density phase of the cycle. Krebs and Myers see three ways in which this change in body size associated with density could be produced.

First, voles may simply live longer in the increase and peak phases and consequently achieve the maximum of their growth potential. Second, voles may grow faster in the increase and peak phases than in the decline phase, so that animals of equal age are larger in increasing and peak populations. Third, growth rates of juveniles and subadult voles may be the same in all years of the population cycle but asymptotic weights of adults may vary with cyclic phase. Any one or a combination of these three mechanisms could produce the observed heavy weight individuals of peak populations.

Krebs eliminates the first possibility using data from Chitty (1952), Zimmermann (1955) and Krebs (1964). The argument is that heavy animals of the peak year were on the average younger than the light animals of the decline phase. However, Krebs' (1966) data on expected length of life show that animals during the increase do in fact live longer. Data from this thesis do not support the first mechanism. Data in Figure 19 indicate that the older animal (A-336) from the previous year and the younger animal (A-391) both overwintered at the same weight. The older animal lost weight and the younger gained weight resulting in the same overwinter weight. Growth then began again in February 1971, (as early as January for other animals not in Fig. 19) with both animals growing at the same rate. The younger animal had plenty of time to grow to maximum weight but growth was delayed until late winter when all animals had peak growth rates. This is an example where the growth rates are independent of length of life, hence eliminating the first explanation as a sufficient one.

Krebs and Myers feel that the second and third explanation are difficult to separate. However, growth data for Clethrionomys in the dense population during the 1970-71 winter population show that rates may vary from negative to peak values, indicating no interaction with density. A more detailed analysis of correlation using existing data is needed to test this point.

The third explanation of equal growth rates but different asymptotic growth in part fits the Clethrionomys data. Figure 19 indicates that under the snow animals A-336 and A-391 had equal growth rates. The younger animal, that had a lower asymptotic weight in the fall, eventually equalled the maximum weights of the previous year. In an absolute sense, potential growth rates and potential aymptotic weights were equal in these two animals; however, the expression of these parameters were controlled differentially. As discussed under reproduction it is unlikely that cold temperatures, presence of snow, short photoperiod, or food could have proximally controlled growth parameters in the 1970-71 winter. The only feasible explanation is that changes in temperature, photoperiod or density and related population parameters, rather than absolute values, can be detected by these small mammals. In conclusion, it is important to note that the above analysis is not meant to provide an all or none explanation but rather it is an effort to find a sufficient and necessary explanation in relation to cyles. Such an analysis may not be appropriate if Clethrionomys is not cycling in the Fairbanks area.

Density data (Fig. 11a) show that the cycle (if it exists) could have a frequency of less than two years. Krebs and Myers (1973) would consider such an event as an irregular irruption rather than a cycle. They suggest that failure to show large animals in the peak density populations could also be an indication of a random irruption.

Data from this thesis indicate that such a clear-cut distinction cannot be made for Clethrionomys, i.e. while population densities are equal for each of the three years, lower body weights exist in the year of poor production (Fig. 17). During June-August, 1970, only one animal out of 26 weighed more than 24 g while at the same time the Clethrionomys populations on the College grids had one-third of the males in the 25 g and up class. The College grids did not have the extreme low numbers this summer as did the Steese grids (Fig. 12a). The heavy animals on the College grids were typical of the heavy animals on the Steese grids during the population increase in 1969 and 1971. It appears that the Steese Clethrionomys population was showing characteristics of the microtine syndrome but showing no variation in yearly density. The potential for such a population in studying the microtine syndrome is discussed by Krebs and Myers (1973). In conclusion, growth rates and asymptotic weights do not seem to differ within individuals; however, the timing of potentially equal growth parameters results in variable asymptotic weights which may be related to delayed maturity phenomena.

Movement and dispersal. Dispersal arguments have been dismissed from debates on population control for many years with the argument: if a population is at a peak density, there is no place to go, so how could emigration be important. The argument that there is no place to go was based on the assumption that voles filled every available space. However, Pearson (1960) using a clever photographic device, and Lidicker and Anderson (1962) using runway transects, hypothesized that seemingly uniform habitats were not being used in an homogeneous manner, leaving some areas unoccupied. With unoccupied areas there might be places to go, thus giving credence to emmigration.

Dispersal has been reported to be greatest in increasing populations and nil in declining populations (Myers and Krebs, 1971) and one may ask if the dispersal during the peak represents only part of the newly born animals while the others are colonizing the voids within the immediate area (Howard, 1960). The advantage of having a distinct segment of the population has been discussed by Anderson (1970), Gaines and Myers (1972), Myers and Krebs (1971b), and Krebs and Myers (1973). However, there seem to be two different mechanisms that could lead to such a phenomena. While Anderson (1964) and Howard (1960) give evidence and propose that demic structure may limit gene flow, Gaines and Krebs (1972) do not see evidence for grouping in Indiana _Microtus sp_. and dismiss the necessity to invoke demic selection.

Analysis of dispersal data in this thesis is limited by lack of genetic markers and small sized grids, but dispersal patterns for both species in the increasing phase (see dispersal results and growth discussions) indicate that the Krebs _et al_. (1973) analogy of island r and K selection (MacArthur and Wilson, 1968) is also applicable to taiga small mammals. Hence it seems that Mayr's (1956) statement: "population structure and dispersal are probably more important to species formation than purely genetic factors as mutation pressure," should be updated to read: "population structure and dispersal are genetic factors important to species survival and colonization, and are more important than other genetic factors such as mutation pressure." The mechanisms behind dispersal processes have yet to be worked out (Myers and Krebs, 1972).

Movement data within and between trapping periods is difficult to interpret due to greater probabilities for observing shorter moves on a grid as compared to longer moves. Mean values calculated here also tend to cancel out the effect of longer moves, hence making it more difficult to pick out possible heterogeneity in movement patterns. Moreover, smaller grids make it harder to notice (without radio tagging) longer movements followed by a return as compared to longer one-way dispersals (Brooks and Banks, 1971; Kaye, 1961; and many others). On Grids C and D which were rather closely situated it was found that all moves over 100 m were not followed by a return to the grid of origin.

Dice (1952) proposed that movement may be a regulatory mechanism that maintains stability in a community. If this were true, one might expect Clethrionomys to have moved more than Microtus. Such a trend or inverse trend was not observed. Between period movements were similar for Clethrionomys and Microtus.

Crawley (1969) stated that Clethrionomys sp. movement is greater just prior to and during the breeding season than at other times and gives several authors whose work supports this idea; Crawley then considers the above statement as an "established fact". While between and within movements are highest during the breeding season for all three years, pre-breeding season movement is far from being high in 1969 or 1971 (there is no data for 1970); in addition, winter movements under the snow in 1968 are equally as long as movements the next breeding season. In other studies where winter movement has been measured on red-backed voles (Beer, 1961; Blair, 1941) winter home ranges based on movement data are similar to summer home ranges. Clethrionomys movement after 1969 (Fig. 21) shows much more variability in the range of distances moved. This may be interpreted as a response to the absence of Microtus which may have altered movement patterns in Clethrionomys.

As was mentioned in the Zapus discussion, the movements recorded on the grids are representative of that portion of the population that is not dispersing, which may characterize shorter moving individuals which may result from K selection. Therefore, the long movements in the 1970, summer may represent the r selection dispersers colonizing a new habitat.

Density. Krebs and Myers (1973) assume that microtine populations that do not undergo cyclic density fluctuations are the exception and if any can be located, they would be exceptionally important to study. They feel that the burden of proof should be shifted to those who claim to have a non-cyclic population. Live trapping data indicate that Clethrionomys reached the same maximum density and peak net production for all three years studied. Data from Feist (pers. comm.) indicate that the Steese population was at the same peak density for the fourth year after which the study area was destroyed by a housing development. However, numbers alone are not enough to determine the absence of the cycle; for in the strictest sense of the word, there could still be a cyclic syndrome of other demographic parameters working within the above density limitations (Godfrey, 1956). Parameters of this syndrome have been discussed above and while there were many interesting delays in breeding and significant dispersal patterns, a majority of these parameters do not fit the cyclic syndrome as described by Krebs and Myers (1973). Such a population therefore represents a subarctic departure from the commonly assumed association between northern conditions and instability (Dunbar, 1968).

In the Fairbanks area Clethrionomys are both the Peromyscus and the Mus of the north. Red-backed voles, Clethrionomys, are filling a niche that is filled by several species in more southerly latitudes. In this sense of the word niche, the Clethrionomys occupy a broad niche (Levins, 1968:p. 41). Niche breadth is only one of the factors that are discussed. This thesis is only concerned with niche breadth and dimension. Niche overlap was mentioned briefly in reference to Morris and Grant (1972).

Niche breadth and niche dimension are of primary importance to the density discussion. Niche breadth is defined mathematically as:

$$B = \frac{1}{p_i^2}$$

B = niche breadth

p_i = the proper proportion of the species which is found in the environment i.

Unfortunately, the mosaic of vegetation types in the taiga ecosystem in addition to fluctuating populations in various habitats, rapidly leads to unmanageable complexity. For example, 1) how many distinct environments are there in the Steese trapping area or even the general Fairbanks area? 2) are these environments the same for all species? 3) how does one handle the dynamics of a fluctuating population? In short, the common problems of the field ecologist are tremendously complicated when compared to theory developed by Levins (1968) for fruitflies. However, the idea behind the formula seems to be valuable: "uniformity of a distribution over a presumed patchy environment indicates a broad niche" (Levins, 1968:p. 42). Clethrionomys are captured in most potential rodent niches in the Fairbanks area and therefore seem to have a broad niche.

If species divide their habitat among themselves on the basis of a single factor, niches can be represented along a single dimension. Unfortunately, there are no formal conventions that have been adopted for measuring niche dimension. However, Levins asks how many niche dimensions are there in a community and what is their importance? Since the answer to Levins' question in the taiga is not known, I have specifically chosen nine factors for measuring C. rutilus dimension:

1) C. rutilus coat color is quite variable (Manning, 1956) and the heritability of Clethrionomys coat variability (Drozdz, 1971) indicates a genetic basis.
2) Lactic dehydrogenase variability is very high (Whitney, Lyons, and Shaughnessy, unpublished MS).
3) Tooth structure is less specialized (Phillips and Oxberry, 1972; Guthrie, 1965).
4) Normal body temperature of C. rutilus is maintained over a wider range of temperatures than M. oeconomus (Morrison, 1960) and peak metabolism is twice that of M. oeconomus (Rosenmann, pers. comm.).
5) Fat content is extremely variable when compared to M. oeconomus.

6) Food preferences are more variable than M. oeconomus (Grodzinski, 1971).
7) Numbers are stable from year to year.
8) I would hypothesize that caecum and intestine morphology in C. rutilus is more variable than M. oeconomus.
9) I would predict that total heterozygosity of C. rutilus would be greater than that of M. oeconomus.

Whether these parameters are ultimately important is not known. Yet C. rutilus is a highly variable species in morphological, physiological, and genetical parameters. Since several other species of seed eating Clethrionomys fluctuate less than Microtus (Zedja, 1967; Koshkina, 1965), it is proposed that variability in niche dimension and a wide niche breadth may act as a buffer which ameliorates or alters the effects of many demographic parameters constituting the cycler's syndrome. As the "Peromyscus and Mus of the North", C. rutilus is not considered to be a cycler.

Microtus:

Feeding. Food habits of Microtus oeconomus were studied during the warmer snow free periods in 1963 by Grodzinski (1971). Cafeteria tests indicated that the Microtus exploited bulky foods and had a much more specialized diet than the Clethrionomys. Utilization of tree buds and leaves of both aspen and paper birch (particularly in summer) causes me to question the applicability of such tests to field conditions for I never observed a tundra vole in a birch or aspen tree in the Fairbanks area. Voles may have access to the buds from the snow surface but this would not be relevant to a summer diet. Comparison of Microtus and Clethrionomys utilization values also presents a problem when food consumption values (Grodzinski, 1971: Table 8) are summed. The total for Microtus was twice that of Clethrionomys. This may be related to the larger size of the Microtus but Grodzinski did not seem to take this into account. Stomach analyses yield better values for comparison between species and give a more accurate estimation of actual consumption in the field. Greens were preferred by Microtus (a greater percentage of animals had greens in their stomachs). Seeds and berries were also consumed in the field but consumptions of these foods were half that recorded for the Clethrionomys. As indicated by Guthrie (1965), Microtus tooth structure is specialized to handle a greens diet (also noted by Tast, 1966; Zimmerman, 1942). Since available food under the snow is most likely of poor quality and bulky (untested assumption for the Fairbanks area), Microtus should be well adapted to exploit such a resource. Kostian (1970) noted that Calamagrostis sp. is a very important food source for overwintering small mammals. This grass is in plentiful supply on the Steese area and I would suggest that a careful evaluation of this food source during several winters in relation to snow morphology would be a key study leading to understanding vole winter biology.

Habitat variability in M. oeconomus seems to be less than that observed for C. rutilus. Snap trapping and auxiliary live trapping data indicate that Microtus was absent from a greater proportion of places than Clethrionomys. In addition to the absences recorded in Table 2, the Microtus were only seen as transients on Grid C and D and were not captured on the Red Fox Drive plot. Pruitt (1968) also captured M. oeconomus in fewer plots (3 out of 7) than C. rutilus (6 out 7). One problem in interpreting Microtus distribution data in the Fairbanks area is the potential for confusing M. oeconomus with M. pennsylvanicus. While the difference between other sympatric Microtus species (e.g. M. pennsylvanicus and M. ochrogaster in Indiana) is quite noticeable using a combination of coat color, teat arrangement, and tail length, I was not able to find any distinguishing external characteristics. Rausch (pers. comm.) claims to be able to distinguish nose characteristics but I was not able to develop this technique. Tast (1968a) made the very interesting observation that M. oeconomus in Finland may occupy the rat niche and Kostian (1970) notes that the root voles are the animals found in cottages. This is a contrast to the Alaskan M. oeconomus that to my knowledge has never been observed in a Fairbanks home.

While M. oeconomus seems to be generally less variable than C. rutilus, this is not to imply that there was no morphological variability. During the population high there was a noticeable toe variation. As the animals were being examined some had one or several toes that were very definitely turned obliquely to the rest of the toes. The highest incidences were 19 per cent in May, 1969, and 10 per cent in mid-July, 1969. It is interesting that the first four animals observed with this variation were males and the last three in July were females. These two occurrences were separated by a six-week period. Oblique toes were also noted in Clethrionomys but no more than one such animal was ever observed per trapping period.

Voles and lemmings are noted for their periodic fluctuations. While the more mathematical definition of a cycle does not really apply to this phenomenon of variable amplitude and frequency the term has come to mean much more in the small mammal literature. It seems that the term cycle is now thought of as a syndrome of demographic parameters that are almost always associated with the periodic fluctuation in numbers (Krebs and Myers, 1973). The relatively short duration of this study did not enable me to evaluate M. oeconomus as a density cycling species. However, Feist's (pers. comm.) data shows that the Steese Grid A population increased again in 1972, three years after the 1969 peak. Yet this is only one parameter of a cyclic species. Further analysis of the population architecture must be examined in order to confirm cycling status of M. oeconomus. Hundreds of pages have been devoted to describing the syndrome of parameters accompanying microtine fluctuations (Krebs and Myers, 1973). Whenever possible, references to detail discussed in this review will not be reiterated. Their paper will rather serve as a standard to see if the M. oeconomus in the Fairbanks taiga is in fact a cycler.

Survival. Problems in sampling to determine survival rates have been discussed elsewhere (p. 186), yet it is important to remember that measured survival values are a function of both death and dispersal processes.

I was unable to find survival data for M. oeconomus in the literature that I could use for comparison with this study, but those values measured by Chitty (1952) for M. agrestis are very similar to the survival rates for the Steese population. Adult Microtus survived well (probability of survival per 14 days, about 0.7 to 0.9) but were gradually replaced by their young as the population increased in the summer. During the increase and peak phase of population growth, subadult male survival was very low. Following a brief period of dispersal, subadult survival was much better until February, 1970, when the population density was near zero. Female survival was not as labile as that of the males.

The declines described above was typical of a Type H decline (Chitty, 1962). However, all declines are not necessary over winter, as discussed by Keller and Krebs (1970). Examples of spring declines (Type M) are recorded by Chitty and Chitty (1962) and Newson and Chitty (1962). It is important to note that while the Steese population decreased over the winter period when climatological data indicated severe conditions, winter survival was as good as that observed in the summer months. In other words, the apparent sudden decrease in survival in February, 1970, for males and in June, 1970, for females (Fig. 14) is due to the death of the few animals left on the grid. Moreover, these animals had lived longer than most animals in the summer months.

Nestling mortality in Microtus (Table 27) was greater than in Clethrionomys during the peak population decline. This finding does not agree with Chitty and Phipps (1966) or Krebs et al. (1969). However, a more recent evaluation of juvenile (nestling) survival by Krebs (1970) using multiple regression analysis indicates that juvenile survival was highly correlated with, and thus is an important determinant of, population growth in *M. ochrogaster* and *M. pennsylvanicus*. Therefore, *M. oeconomus* nestling mortality in this study agrees with Krebs' (1970) conclusion that during the peak there is poor survival in the juvenile or nestling population.

Prenatal mortality in *Microtus* was very small (less than six per cent). The low percentage of pregnant females (33 per cent) resulted in very small sample sizes with which to evaluate this parameter with population change. It is generally agreed, however, that prenatal mortality is small and is not related to the population cycle of small rodents (Keller and Krebs, 1970; Mullen, 1965).

To summarize, female survival was good during the entire study while male survival, particularly that of subadults, was characterized by periods of low survival. Such a pattern is typical of microtine cycles (Krebs and Myers, 1973). Small sample sizes during the winter hinder classifying the Steese population decrease in numbers as a Type G or Type M decline; but high survival rates until the last few animals were not recaptured, strongly indicate good winter survival, even though the climatological conditions were quite severe.

Reproduction. The onset and termination of the breeding season for *M. oeconomus* is also variable (Table 38); however breeding lasting through the winter has not been observed. Tast (1968a) noted early breeding under the snow at the Kilpisjarvi study area and reproductive activity was also observed on the Steese Grid A (April, 1969) under a 20cm snow pack.

The same precautions for interpreting breeding season data as mentioned above for Clethrionomys must also be applied to Microtus. Moreover, limited references in the literature do not allow evaluation of the importance of changes in the length of the breeding season in relation to the population cycle.

Table 38. Duration of breeding in Microtus oeconomus.

Author	Year	Location	Duration
Bee and Hall	1956	Bettles, Alaska	June-August
Grodzinski	1971	Fairbanks, Alaska	May-August
Kostian	1970	Vassa, Finland	April-October
Shvarts	1962	Yamal, USSR	May-October
Tast	1968a	Kilkisjarvi, Finland	late Mar-Sept
Whitney	1973	Fairbanks, Alaska	April-September

Winter breeding has been associated with increasing lemming populations (Mullen, 1965; Dunaeva and Kucjeruk, 1941; Koskina and Khalasnky, 1962) and has been reviewed for Microtus by Keller and Krebs (1970). While winter breeding may be sufficient to cause peak numbers, it is not necessary as shown in this study for M. oeconomus. Chitty also recorded winter breeding in M. agrestis with no subsequent peak (cited in Krebs and Myers, 1973). This example is further evidence for winter breeding not being necessary for population peaks. As indicated above (p. 192) the effect of winter conditions on voles is not a simple one, especially in more northern species when breeding is usually started in the spring during snow melt. Data in Table 38 do not indicate a shorter breeding season in more northerly populations.

As suggested by Shvarts (1962) litter size in more northerly populations is larger (Table 39). In addition, litter size may be a function of altitude (as seen in Bauer's, 1953, animals), seasonal variation (Kostian, 1970; Tast, 1968a; Keller and Krebs, 1970; 15 to 25 per cent variation) and the variation associated with the size, age and parity of the mother (Kostian, 1970; 30 per cent). There is no data on litter size in relation to shorter breeding season (that consider the above sources of variability), that would be needed to evaluate Shvart's (1962) statement that larger litter sizes are associated with shorter breeding seasons in the north. Furthermore, survival from newborn Microtus to the breeding population is very poor (less than two per litter, Krebs and Myers, 1973; this study). In light of the high mortality rates, this suggests that increasing the litter size would be a very inefficient way to increase production.

Table 39. Litter size for *M. oeconomus*

Author	Year	Location	Litter Size
Bauer	1953	Alps, Austria	6.8
Bee and Hall	1956	Brooks Range, Alaska	7.8
Kostain	1970	Vassatown, Finland	6.7
Shvarts	1962	Yamal Peninsula, USSR	8.7
Stein	1950	Northern Germany	5.7
Tast	1966	Lapland, Finland	7.2
Whitney	1973	Fairbanks, Alaska	6.8
Wildhagen	1952	Southern Norway	5.7

Kostian (1970) reports the greatest breeding activity (per cent breeding) at the onset of the breeding season, whereas breeding in the 1969 Steese population started out gradually and reached peak intensity late in the season (August). Breeding intensity of live trapped animals could not be evaluated between seasons because the Steese population was low in 1970. The only difference between grids in 1969, was a significantly higher percentage of perforate subadult females on the more densely populated grid.

Krebs and Myres (1973) indicate that age at sexual maturity is variable in microtines and that changes in the rate of sexual maturity are a major factor related to population cycles. The statistical methods used for evaluating changes in sexual maturity did not show a significant difference between the Steese 1969 and Smith Lake 1970 female population. However, graphical analysis (Fig. 25) shows a delayed female maturity in 1969. Median tests did show that male mean weight at sexual maturity was significantly higher in 1969 which suggests a significantly greater delay in males. This was also noted in lemmings by Krebs (1964).

Sex ratio, being such an easily measured parameter, has been the subject of much discussion and has been reviewed by Myres and Krebs (1971a) in relation to population phenomena. By far the most interesting abnormal sex ratio is that observed in the wood lemming by Kalela and Oksala (1966). Ratios of 20 to 30 per cent males in the peak year were thought to be the result of more females being produced in the litters in the increasing phases and fewer females in the declining phase. According to this theory, the animals must have been sensitive not to absolute density but to the change in density. The Steese Microtus population also showed an equally low percentage of males during the two to three month increase and peak phases of population density. Reproduction ended just after the population started to decline, and it was at this time that the sex ratio returned to 1:1. While this was partly due to differential survival, sex ratio of litters from different phases are required to quantify the female producing mainly female theory of Kalela and Oksala. Rausch (pers. comm.) has observed the same chromosomal phenomena in laboratory M. oeconomus as Kalela and Oksala (1966) observed in the wood lemming.

As was discussed for Clethrionomys body composition parameters can be used as an index of maturity (MI). The MI ratio (grams protein to grams body water) showed no difference between breeders and non-breeders. In other words, while all the animals were physiologically mature some were breeding and some were not. It is important to remember that the delays in maturity observed thus far are the results of seasonal analysis. Further analysis into the mechanics of these seasonal parameters is needed to evaluate whether or not these delays are genetically selected or are just passive environmental tracking. In short, the question remains: are maturity delays a part of the syndrome or the result of some other mechanism as weather, food, predation, etc.? The answer to such a question is not an easy one and could involve any one or all of several mechanisms. Myers and Krebs (1971b) indicate that during population increase, there are demographic genotypes with a tendency for dispersal associated with higher reproductive potential leaving a more sedentary population with a lower reproductive potential. Hence, delayed maturity may be very closely linked (as an aspect of lower reproductive potential) to the causative role of population cycles. Zejda (1961, 1966, 1971) and Anderson (1970) believe that whole generations are responsible for delayed maturity; this phenomenon usually occurs at the end of the breeding season. This generation effect may or may not be a seasonal effect. While these two ideas are seemingly very different, one saying that there is continuous variability subject to differential selection and the other indicating cohort variability, it must be remembered that the maturity delay phenomena is being examined with two vastly different techniques. Zejda used snap traps and tooth ageing for comparison of demographic parameters from several adjoining areas. While he most certainly observed "premature termination of reproduction manifested in the age structure in the autumn", correlation of these phenomena to density dynamics are not as obvious. Snap trapping expressed by Zejda in per cent captures per trap has definite drawbacks (discussed p. 185-188) when used for density estimates. It would be very interesting to see if the variation from the cyclic syndrome (delayed maturity of generations and lack of peak body weights) would be as straight forward if Zejda used continuous live trapping rather than discontinuous snap trapping. In short, sampling technique may very well be at the root of the various types of delayed maturity. This problem cannot be overlooked for the _M._ _oeconomus_ in this study, the delayed maturity may very well be a function of inaccurate density estimates of the Smith Lake population; or this delay could be a function of a different habitat type rather than a different cyclic phase.

Growth. Growth has been studied in relatively few _Microtus_ species. The only growth data that I was able to find for _M._ _oeconomus_ were a few individual growth curves presented by Tast (1968a). It is interesting to note the amount of speculation about growth parameters on the basis of few data. Three aspects of growth were discussed for C. rutilus and this same format will be repeated for M. oeconomus: 1) weight loss, 2) weight changes during a cycle, and 3) Bergman's Rule.

A marked weight loss was observed in late July, 1969, and continued in all but the youngest animals throughout the winter. As shown in Figure 19 the larger animals that lost weight did not survive into the winter as did the younger, smaller animals. The potential energetic advantage of lower body weight in cold periods has been discussed for Clethrionomys (p. 200). Yet this weight loss started in late July and early August, 1969, and if this is a cold adaptation, it does not seem to be due to a passive environmental tracking of cold temperatures. Slight weight losses have also been observed during a winter decline in M. ochrogaster (Krebs, 1969) but these values are considered to be near zero rather than negative. Krebs must not feel that these negative values are characteristic of related to declining populations for the same phenomenon was also observed in M. pennsylvanicuswhen overwinter density was stable. It may be significant that the fenced (Grid B) M. pennsylvanicus population that was just starting to decline had greater weight losses than the unfenced population. (These weight losses were corrected to a standard 35g animal tend to overemphasize weight loss in both the fenced and unfenced areas). This could be interpreted to indicate weight loss due to overgrazing. However, as mentioned above this does not seem to be the case for the Steese population that continued high productivity six weeks after weight loss started. Weight loss, in contrast to body weight, does not seem directly related to population phenomena. Fuller's (1969) failure to find differences in body weight in C. glareolus may be related to weight loss phenomena rather than the cyclic syndrome.

As was evident in the Clethrionomys, all Microtus did not have similar asymptotic weights. Those animals that maintained a lower body weight were the animals that survived into and partially through the winter. It seems as if those animals that had heavier asymptotic body weights did not, or could not, reduce to a weight that would be energetically tolerable. Other interpretations of the lower asymptotic weights and decreased growth rates have been proposed by Krebs et al. (1973). In addition, the lighter weight animals may be the result of K selection. Such selection results in less efficient productivity. However, Roughgarden (1971) shows that K selection does not necessarily favor efficiency.

Negative growth rates before and during the density peak indicate that growth is not greatest in increasing and peak populations as would be expected of the syndrome (Krebs and Myers, 1973). When Krebs' et al. (1969) M. pennsylvanicus data and Krebs' (1966) M. californicus (Richmond Parr) data are examined for density growth rate relationships (within a year rather than between years) these microtines do not show peak growth in peak populations. This, however, was not the case for the M. ochrogaster population (Krebs et al., 1969) on the same area as the M. pennsylvanicus. While there are in fact larger animals in the peak population on the Steese Grids A and B in 1969 as compared to 1970, positive and negative growth rates are not so easily correlated with the syndrome.

Autopsy data provide body weights that indicate the presence of larger voles in 1970 that should be typical of a peak population. These larger animals (Table 19) are from the Smith Lake area (2km northwest of the College grids) and represent a rather small sample. Any one of three phenomena could account for these values: 1) an out of phase peak population, 2) a different type of decline than on the Steese, and 3) two peak years in a row. Live trapping is too rough an index to eliminate any of these possibilities. Lack of animals on the Steese in late 1970 and early 1971 followed by a recolonization in 1972 (Feist, pers. comm.) leads me to believe that there are pockets of Microtus that experience much different demographic patterns than the Steese population. While it is pure conjecture at this point, I would predict a much more stable population of Microtus in the Smith Lake area.

Comparison of body weight of Microtus from the Fairbanks area (58g max., snap trapped male) with that of M. oeconomus from the Gulf of Bothnia, Finland (Kostian, 1970, 98g max.), indicate still another exception to Bergman's Rule.

Movement and dispersal. When animals disperse from an area, one may suspect a change in the quality of the remaining population (Myers and Krebs, 1971). The significance and biases of between period movement in relation to population parameters have been discussed by Lidicker (1966), Krebs (1966), and Brant (1962). It will be assumed that grid measured movements are one way in which possible changes due to dispersal may be examined.

Heterogenous movement patterns within populations have been proposed by many authors (Howard, 1960; Myers and Krebs, 1972; Andrejewski and Wroclawek, 1962). Similar phenomena have been observed for the Microtus population. Six of the nin dispersing Microtus on the Steese were observed dispersing in July and this coincides with a sharp drop in male between period movement on Grid A and male and female between period movement on Grid B. This drop in movement may be due to dispersers (having a higher mean movement) leaving the grid. These changes in movement pattern occurred during peak population density a month or two before the decline in numbers. While low survival on Grid A correlates with the dispersing animals (dispersal was noted over a 6-week period, see p.102) and while a decrease in movement overlaps with the time when animals were dispersing, the low survival preceded the decrease in male movement by several weeks. This is an indication that low survival values may not be entirely due to dispersal.

Density. Following the 1969 peak on the Steese study area, numbers were very close to zero until the summer of 1972, when the population again began to grow (Feist, pers. comm.). The cycle was manifested in other parameters besides numbers. Thus this microtine fits the general picture predicted by the microtine syndrome as described by Krebs and Myers (1973). However, peak numbers were not present on the College and Red Fox areas in 1969. It has been proposed that Microtus did not occupy as many habitats as *Clethrionomys* and therefore occupied a relatively narrow niche.

Niche dimension has been discussed for *Clethrionomys* (p. 210) and has been measured similarly for *Microtus*:

1) Coat color is very uniform.
2) Lactic dehydrogenase variability is very low (Whitney, Lyons, and Shaughnessy, unpublished MS).
3) Tooth structure is quite specialized (Guthrie, 1965).
4) Normal body temperature of *M. oeconomus* cannot be maintained over a wide range of temperatures (Morrison, 1960) and peak metabolic rate is one-half that of *C. rutilus* (Rosenmann, pers. comm.).
5) Fat content is less variable than *C. rutilus*.
6) Food preferences are less variable than *M. oeconomus* (Grodzinski, 1971).
7) Numbers are unstable from year to year.
8) I would hypothesize that caecum and intestine morphology in *C. rutilus* is more variable than *M. oeconomus*.
9) I would predict that total genetic heterozygosity of *M. oeconomus* would be low as compared to *C. rutilus*.

The narrow niche breadth of *M. oeconomus* in addition to the more specialized dimension, indicate that *Microtus* is a highly specialized species in comparison to *Clethrionomys*. The theory developed here indicates that the cyclic pattern of population density of *Microtus* is characterized by a more highly evolved specialized population.

Zapus:

The feeding habit of _Zapus_ is apparently omnivorous. Whitaker (1963) noted that after hibernation (May), the animals consumed mostly animal material and insect larvae in particular. By June, the stomachs he analysed contained mostly seeds. There have been several references to a particular _Zapus_ feeding habit which results in an accumulation of grass stem cuttings about seven centimeters long (Bailey, 1926; Quimby, 1951). These cuttings are supposedly obtained by the animal standing up, cutting off, and pulling down on the stem until the grass stem is pulled down through the vegatative cover. When the mouse finally reached the seeds, they were eaten. Whitaker (1963) described another means of obtaining seeds which he never actually observed. I observed this procedure in August, 1970, while trapping Grid E. Ray Kendel called my attention to a _Zapus_ scrambling up a blue-joint stem. As is shown in Figure 5, this grass grew 100 to 120 cm high. Once at the top (the stem was bending toward the ground due to the mouse's weight), the _Zapus_ snipped the stem and dropped approximately 60 cm to the ground with the seed head in his mouth. He then started to eat the seeds.

Survival is a most difficult parameter to measure in _Zapus_ "for they seem to have a curious way of evacuating a field where they were plentiful and no one knows where they go" (Sheldon, 1937). Quimby (1951) and Blair (1940) also recognized this problem and Quimby noted that of the 90 known animals observed in his study, 77 per cent were found during one month only, 20 per cent for two months and two per cent for three months. This and other data indicated to Quimby that the

The overwintered adults are, for the most part, gradually replaced by the young of the year as the summer progresses. He concluded that there must be very poor survival of adults. Crosby (1971) obtained a somewhat different picture of Zapus princeps survival. Crosby's data indicates that there was a high mortality of young animals through the first hibernation after which survival is good. Brown (1967) also noted that overwinter dehydration appears to have the greatest effect on juveniles; overwintering survival in a four year study were 44 per cent for juveniles and 84 per cent for adults. Whitaker (1963) also believes that the 67 per cent winter loss was due mostly to the loss of small (young) animals.

Data presented in this thesis are equally plagued by the evacuation process described by Sheldon. The most dramatic example was observed on Grid E during the first part of July, 1970. Of the 23 Zapus captured, none were retrapped two weeks later. Only two Clethrionomys were captured in that retrapping period. One was half-eaten by a short-tailed weasel. (Zapus is a favorite food for weasels while hibernating, Northcott (1971), but Brown (1967) claims hibernating Zapus are odorless and weasels cannot locate them in a cage. Weasel predation has also been reported by Quimby (1951). Fifteen to 17 g animals were not observed making short moves (Fig. 24), hence these animals (subadults) may be largely responsible for the evacuation phenomena. During this study, overwinter survival of Zapus was excellent, especially considering the small area trapped as compared to the tendency to disperse. Of the 77 Zapus live trapped, there were 33 captured both before and after a hibernation season. The age of these animals was very difficult to determine, however using relative weight and recapture data as an index, there were 12 old, 7 young and 14 animals of questionable age. These data indicate that survival must be poor in the young animals and very good in the older animals. Live trapping indicated that four animals were at least two to three years old. Hence Zapus hudsonius data from this study does not negate Brown's (1967) hypothesis that Zapus have the lowest mortality of any North American mouse yet studied.

Home range of Zapus measured by Sheldon (1938), Blair (1940), Quimby (1951) and Crosby (1971), range in value from 0.38 to 2.70 acres. The grids used in this study are far too small for home range estimation. Evidence of one way dispersals (Table 18) indicate that home range measurements would be unstable and perhaps unsuitable for Zapus.

As Quimby (1951) noted, it is not always possible to follow the activities of a female for the entire breeding season so it was difficult to determine how many times an individual would breed per year. Quimby estimated three times, Whitaker (1963) two times and Crosby (1971) one time (Zapus princeps). Soper (1964) believes two litters in Z. princeps only occur when there was loss at parturition of the first. Fairbanks Zapus hudsonius show two peaks of breeding (see bimodal distribution of the percentage of females lactating, Fig. 16a). The appearance of young in traps also support the lactating index of two breedings per summer per overwintered females. The following litter sizes have been reported for Zapus (Table 40).

Table 40. Recorded litter sizes for Zapus.

Species	Author		Litter Size
Z. hudsonius	Quimby	(1951)	5.7
	Towsend	(1935)	4.5
	Whitaker	(1963)	5.5
	Whitney	(1973)	6.0
Z. princeps	Brown	(1967)	5.4

Since I observed only two Fairbanks Zapus with embryos, it is unlikely that the 6.0/litter indicates a significantly larger litter size in the more northern races of Z. hudsonius.

Emergence from hibernation in the field has been studied by several of the authors above (Table 40) and this study agrees with their observations that males are captured at least two weeks before females. The following data were collected to examine possible causal factors for emergence. From the three years' data (Table 41), it seems that birch phenology is not a good index of emergence, instead snow depth and disappearance of the last snow are more closely correlated. If the maximum snow depth is low, as in the 1969-70 winter (Fig. 7b), emergence

Table 41. Comparison of Zapus emergence dates with snow parameters and birch phenology.

Date of Emergence	Date of first birch leaves on Birch Hill	Max snow depth, previous winter	Date of snow disappearance
June 11, 1969	April 29, 1969	55 cm	May 7, 1969
May 20, 1970	May 15, 1970	25 cm	April 22, 1970
June 8, 1971	May 10, 1971	119 cm	May 20, 1971

will be earlier while deeper snow depth may delay emergence. The Zapus entered the traps about three to four weeks after the snow disappeared. However differential emergence did not affect the start of breeding.

Evidence for rapid preparation for hibernation is based on two types of observation. First, very few obese animals were captured. Most Zapus were last captured at weights that were six to ten g below their expected entrance weight. Body composition data for Zapus showed high fat content (Table 24c) for Zapus relative to the microtines but this was not nearly of the magnitude needed for hibernation. Hence the last push for fat deposition must be done in about two weeks. Additional evidence comes from a young animal weighing 12 g in mid-August that survived the winter. I agree with Whitaker (1963) and Morrison and Ryser (1962) that food does not cause the Zapus to hibernate nor is food limiting before October or possibly all winter. I have observed Clethrionomys with cheek pouches full of seeds in January 1969. The fact that there was an equal or greater chance of animals last caught in July surviving the winter as compared to the chances for those last captured in August or September, seems to support Quimby's (1951) observations that animals exhibiting marked weight gains early in the season entered into hibernation before those that did not. It is possible that much of the disappearance phenomena is due to early hibernators. Animals were last captured in September 1970 and August 1969. Last captures correlate well with the first freezing temperatures (Fig. 7).

Habitat preferences for Zapus seem to be quite variable over the whole range of latitudes. Wet areas have been classed as typical by

Getz (1961), Gunderson (1950), Quimby (1951) and Crosby (1971). In this study, Zapus preferred dry south facing open (often grassy) uplands (Birch Hill, Red Fox Drive). As noted by Getz (1961) and Quimby (1951), Zapus were never captured in the spruce and dense birch (north facing) or bog habitat such as found in the Fairbanks area. Population density is subject to high temporal variability due to the erratic movement patterns. Estimates in this study (Fig. 12b) reflect such instability and the maximum density of 23 animals per grid (0.48 hectare) is quite close to Whitaker's (1963) 19 per acre estimate.

A few final comments on field observations for Zapus may be helpful for future studies. The first four Zapus caught in 1969 were not ear tagged for they lept from the dumping pail in a single bound. Following these initial captures I always carried a plastic bag for removal. The Sherman trap used almost exclusively in this study is not the ideal trap for Zapus, their long tails were often pinched and broken in the spring shut door.

In summary, Zapus seems to be well adapted to life in the taiga with a specialized niche in the dry grassy areas. They exhibit very low turnover, high adult survival and uniform coat color.

Table 42. Trapping week to date conversion.

Week	Date	Week	Date
2	October 2, 1968	72	February 18, 1970
4	October 16, 1968	76	March 12, 1970
6	October 30, 1968	82	April 30, 1970
8	November 10, 1968	86	May 20, 1970
10	November 24, 1968	96	July 21, 1970
12	December 14, 1968	98	April 4, 1970
28	April 2, 1969	100	August 14, 1970
30	April 14, 1969	102	September 2, 1970
32	April 29, 1969	104	September 17, 1970
34	May 14, 1969	106	October 8, 1970
36	May 27, 1969	110	November 2, 1970
38	June 11, 1969	116	December 15, 1970
40	June 25, 1969	124	February 8, 1971
42	July 9, 1969	130	March 20, 1971
44	July 23, 1969	134	April 13, 1971
46	August 6, 1969	136	April 27, 1971
48	August 27, 1969	138	May 10, 1971
50	September 4, 1969	140	May 25, 1971
54	October 8, 1969	142	June 8, 1971
58	November 10, 1969	144	June 22, 1971
62	December 3, 1969	146	July 6, 1971
66	January 19, 1970		

SUMMARY

In the introduction to this study, emphasis was placed on the necessity to integrate the organism, population and ecosystem levels of ecology. Most studies have been primarily aimed towards one of these three levels. Throughout this study I have indicated specific phenomena that have been inadequately analyzed due to the failure of authors to integrate the ecological theory developed for the level they work in, with the theory developed for the levels just below or above. It was noted, for example, that testes inhibition, growth intensity, weight loss, length of the reproductive season, and average daily metabolic rate have in the past at least been incompletely interpreted due to lack of data on population phenomena that may override the accepted cause and effect physiological relationships. For example, weight loss has been interpreted to be either a starvation phenomena (Fuller, 1969; Klekowski and Duncan, 1973) due to limited food resource, or possibly an adaptation to cold (Dehnel, 1949). However, as the data presented in the growth and productivity section of this study indicate, the weight loss in <u>Clethrionomys</u> and <u>Microtus</u> started in late July and early August. At such an early date, the mouse populations were not likely to be subjected to starvation, since peak growth rates occurred on the same food resource six months later in mid-winter. In addition, the early date at which weight loss occurred tends to discount weight loss as a cold stress phenomena. Furthermore, growth in some individuals was initiated in mid-winter. Perhaps the most interesting feature of the weight loss phenomena in this study was the differential intensity of weight loss in various age classes. This is further indication that the animals are not starving, since in several two-week periods, some subadults were losing weight while some juveniles and adults were gaining weight. While simultaneous monitoring of population phenomena may not resolve the problems of cause of weight loss (or any of the other parameters listed), such data gives insight into optimizing physiological research efforts. In addition, these data suggest that not all individuals in a population react in a similar physiological manner. As demonstrated in the testes weight data, this physiological variability within the populations may very well be of a discontinuous nature.

At the population level of ecology, this study shows that the two species of microtines are by no means similar in their ecological niche. The Clethrionomys fluctuated in a seasonal manner reaching equal peak densities in each of the four years examined. There were interesting breeding delay phenomena and unbalanced sex ratios, yet the timing of such events indicates that this vole population was not cycling in the sense of Krebs and Myers (1973). Niche breadth and dimension were examined and the conclusion was reached that the Fairbanks Alaskan taiga Clethrionomys rutilus were quite variable in a series of morphological, physiological and ecological parameters. These animals fill the whole seed-eater niche that is more typically occupied by several species in more temperate latitudes (Baker, 1971).

In contrast, the Microtus were observed to be cycling. The criterion for cycling was not only satisfied by the appearance of two population peaks, three years apart, but also by a series of demographic parameters such as body weight distribution, unbalanced sex ratio, high juvenile mortality, etc., which all fit the cyclic syndrome. Examination of niche breadth and dimension indicates that the Fairbanks Alaskan taiga Microtus oeconomus is a very specialized population and it is proposed that future studies would indicate low heterozygosity.

While this study did not include any experiments to test the various theories of small mammal population regulation, winter trapping data gives insight into the possible role played by winter conditions. Live trap survival data in conjunction with simultaneous climatological monitoring indicate that survival during the winter is much better than survival during the summer and fall months . Correlations were made between spring thaw conditions and low nestling and adult survival. In spite of potential cause and effect relationships between thaw and survival (e.g. spring 1971), the productivity for the following summer and fall had the highest seasonal production for the three years.

Metabolism data measured on winter captured mice under simulated winter conditions produced metabolic rate values which were twice as high as those previously estimated for winter mice. The fact that the increased cost of maintenance was so much higher than expected, is another justification for complete sampling and measurement of winter populations.

Net productivity dynamics were calculated for both the Microtus and Clethrionomys population. Such a detailed analysis of small mammal productivity has heretofore only been completed for one year on an experimental island populations of Clethrionomys glareolus (Petrusewicz et al., 1968). As discussed in the text, their cohort study is not suitable for comparison to the two-week analysis of production in this study. However, comparison between years and species show interesting production rate patterns. The Clethrionomys population in this study reached equal peak production three years in a row while the Microtus population peak was twice as high as the Clethrionomys peak and amassed a seasonal total that very nearly equalled the three-year total for the Clethrionomys. Other rate variables examined indicate Clethrionomys production patterns between years may or may not be different from those of the Microtus. Zapus seasonal production of nestling and weaned animals is barely one half of the lowest year for Clethrionomys. It is signficiant that these three species had production values that far surpass what would be expected of a low diversity system (MacArthur, 1972:p. 183). A tentative explanation of such high productivity in a more northerly habitat is an extension of the ecotypic diversity theory for plants in the Kuskokwim Flats, Alaska, presented by Drury (1956). In other words, there may be fewer species in the arctic, but this does not necessarily mean that their ecotype variability does not equal or even surpass the variability among species. Theory of production in different habitats has never been adequately tested (MacArthur, 1972:p. 184). This study, an integration of physiological, population and ecosystem data, has been partially devoted to investigating relationships between production in the subarctic habitat for comparative purposes to other habitats. Based on these data, the theory developed by MacArthur does not apply to lower species diversity in the subarctic.

In conclusion, it would perhaps be appropriate to sum up my suggestions for future study of taiga small mammals. It has been encouraging to see that much of the necessary work to investigate physiological and population regulation are already underway as this study is being completed. However, taiga ecosystem ecology has been somewhat neglected. I feel that it is already apparent that communities composed of interesting populations of several species may also behave as units in natural selection and that later generations of ecologists will be working to understand evolutionary processes at that higher level (Cole, 1954). The subarctic is a marvelously unique habitat that has proven to be most useful as a benchmark reference point for many problems with which ecologists and physiologist are concerned.

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