

Population Cycles in Small Mammals

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I. INTRODUCTION

Vole and lemming populations undergo fluctuations which comprise one of the classic unsolved problems of animal ecology. Two facets of these fluctuations have interested ecologists: their cyclic periodicity and their amplitude. Many small rodents reach high densities every three to four years, and the word *cycle* has been used in a loose sense to describe the alternating sequence of high and low populations. The amplitude of fluctuation is great. Fields which were essentially empty one year may be scarred with microtine runways the next year. Lemmings which were hard to catch one fall may be swarming everywhere the next spring. Rodent populations thus seem to incorporate fluctuations (common in many organisms) and a cyclic rhythm longer than a year (uncommon).

Voies and lemmings have always been an enigma to population ecologists because they have never seemed to fit into the current orthodoxy. Population changes in voles and lemmings cannot be explained or predicted. We cannot apply current theories on population control to these rodents and this lack of understanding may have three explanations: (1) these small rodents are poor subjects in which to study population ecology; (2) ecologists working on these animals have been particularly inept; or (3) our current views on population control may be incomplete. Each of these explanations may be supported by a survey of the literature on this problem.

The purpose of this review is to summarize current information on population cycles in small rodents. We will look first at some general questions about cycles, then discuss the demographic machinery which drives the changes in numbers, and finally analyze the current theories which purport to explain population cycles in rodents.

II. HISTORICAL PERSPECTIVE

Outbreaks or plagues of voles and mice have been described in the Old Testament, and Charles Elton has gathered much of this historical material into his classic book "Voies, Mice and Lemmings" (1942). Elton describes (p. 3) the response of people to plagues of mice:

The affair runs always along a similar course. Voies multiply. Destruction reigns. There is dismay, followed by outcry, and demands to

Authority. Authority remembers its experts or appoints some: they ought to know. The experts advise a Cure. The Cure can be almost anything: golden mice, holy water from Mecca, a Government Commission, a culture of bacteria, poison, prayers denunciatory or tactful, a new god, a trap, a Pied Piper. The Cures have only one thing in common: with a little patience *they always work*. They have never been known entirely to fail. Likewise they have never been known to prevent the next outbreak. For the cycle of abundance and scarcity has a rhythm of its own, and the Cures are applied just when the plague of voles is going to abate through its own loss of momentum.

Although outbreaks of voles were known for thousands of years, the cyclic periodicity of high population levels was not recognized until the 1920's. Collett (1895), for example, discussed in detail the natural history of the Norwegian lemming (*Lemmus lemmus*), but in concentrating on years of very high density and the "migrations" which accompanied them, he concluded that "prolific years" recurred at irregular and unpredictable intervals. Hewitt (1921) was one of the first to quantify the popular idea of cycles in wildlife species in Canada, and he showed that lynx and red fox populations reached peaks at regular intervals of nine to ten years while the arctic fox fluctuated more rapidly with peaks at regular intervals of four years.

In 1923 Charles Elton read Collett's book and Hewitt's book and realized that the "migration years" of the Norwegian lemming might be a reflection of a regular fluctuation in populations of these small rodents. Little was known of population changes in animals in the 1920's, and the prevailing belief was that populations were stable in size and that all outbreaks of species were due to man's interference with nature (Egerton, 1968). Elton recognized that regular fluctuations in populations of rodents in arctic regions would challenge the simple "balance of nature" idea, and would open up a field of research on the causes of periodic fluctuations and their evolutionary consequences (Elton, 1924).

If periodic fluctuations in small rodents were to be understood, detailed population data would be needed. But in 1923 there was not a single census of a rodent population to show the changes from year to year, nor was there much information on birth and death rates. Elton organized at Oxford a group of biologists to study fluctuations, and this group evolved into the Bureau of Animal Population.

Interest and research on rodent populations has increased greatly since the 1930's. The importance of voles as pests of farmers and orchard growers and their role in the spread of diseases stimulated work in the U.S.S.R. and in the U.S.A., and we now turn to a review of the modern work on periodic fluctuations.

III. DEFINITION OF THE PROBLEM

The general problem of understanding cyclic fluctuations in small rodent populations can be subdivided into four specific problems:

- A. What prevents unlimited increase in the population?
- B. What causes the cyclic periodicity of three to four years?
- C. What produces synchrony of populations over large areas?
- D. What determines the amplitude of the fluctuation?

A. WHAT PREVENTS UNLIMITED INCREASE?

This is a general problem which is not specific to rodents and does not involve a necessary cyclic periodicity. For any fluctuation in a population, we can arbitrarily recognize four phases (Fig. 1). The *increase phase* is adopted as a standard of reference to which we can compare the

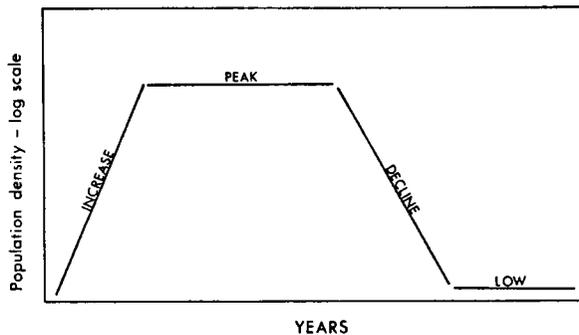


FIG. 1. Schematic diagram of the four phases of the population cycle in small rodents. The phase of low numbers may not be present in all cycles.

other phases. To determine what prevents continual population increase we look for differences between the *increase phase* and the *peak phase* which follows it. We might find, for example, a higher predation mortality in the peak than in the increase. Similarly we look for differences between the increase and decline phases, then attempt to discover if the differences described are universal to all population cycles, and to categorize differences which are universal as *necessary* or *sufficient* conditions.

necessary condition: if the population is to increase geometrically, this condition must be satisfied

sufficient condition: if this condition is satisfied, the population will enter the increase phase

For example, assume that the increase phase may occur only when disease x is not present in the population. The absence of disease x would thus be a necessary condition for population increase. However, if the disease is absent but the females are not in reproductive condition, increase will not ensue and hence the absence of disease x is not a sufficient condition for population increase. What we are actually looking for is the set of necessary conditions which together are sufficient to cause the population to increase. We thus attempt to sort out necessary factors for further analysis.

We begin by attempting to specify simple conditions but if we are unable to explain population cycles we will try to specify more complex conditions. At present no one can specify the necessary conditions for population growth in any species of vole or lemming. Why do we not abandon this approach? Can we not be more precise by recognizing the multiplicity of causes of population cycles? Since there is disagreement about the causes of population cycles, perhaps we should abandon the search for a universal explanation and be content with more restricted hypotheses for single species in particular communities.

The multiple-factor hypothesis is particularly dangerous as a methodological argument. If taken at its face value as a vague armchair theory, the multiple-factor hypothesis is certainly true. The factors which affect a lemming population in Alaska are certainly different from those affecting a vole population in Kansas. But if we adopt this hypothesis as our research strategy, we lose one of the most important checks on scientific speculation—the testability of hypotheses. Suppose that we adopt the hypothesis that the absence of disease x is a sufficient condition for population growth for *Microtus ochrogaster* in Kansas. We cannot test this hypothesis on *Microtus ochrogaster* in Nebraska because this is a different situation. Nor can we test the hypothesis on *M. pennsylvanicus* in New York. If carried to an extreme, we cannot even test the hypothesis on the next cycle of *M. ochrogaster* in Kansas because multiple factors may intervene over time as well as space.

We believe that a universal explanation must be sought for population fluctuations in voles and lemmings until we have evidence that two or more distinct explanations are required. With this approach we can test alternative hypotheses on any species in any location.

It must be pointed out that we are not interested simply in a list of factors which influence rodent populations. Abundant food and cover will certainly harbor populations capable of reaching higher densities, and predation can sometimes remove a large portion of the population. Food, weather, and predation are factors which are acting on all populations. We accept this generalization, but we wish to ask if these factors are necessary or sufficient causes of population cycles. Often a

single mechanism hypothesis is criticized simply because observations have been made in which a number of factors have been shown to influence populations. This is not a valid criticism of our search for a single underlying mechanism for microtine cycles. Many environmental factors affect the average density level of rodent populations, and we recognize this as a second problem different from the question of what prevents unlimited increase (Chitty, 1960). Other environmental factors will affect population density in a sporadic manner, and not play a necessary role in every cycle. In any single study of one species over one fluctuation, the different roles of these factors may be impossible to disentangle. The whole concept of necessary and sufficient conditions precludes generalizations from single observations.

Most of the research we will summarize here is concerned with the question of what prevents unlimited increase (although often phrased as its converse, what causes population declines).

B. WHAT CAUSES THE CYCLIC PERIODICITY?

This question is logically secondary to the first question, and yet many biologists have been concerned with the three to four year periodicity. The cause of the particular periodicity will very much depend on the driving force behind the population fluctuations. The periodicity might be imposed by the physical or biotic environment, or it might be internally generated as some function of generation time of the rodents.

C. WHAT PRODUCES SYNCHRONY?

Vole or lemming populations over thousands of square miles may reach peak numbers in the same year, and this is another aspect of population cycles that must somehow be explained. Again, this problem is logically secondary to the first problem, and only when we can explain the fluctuations will we be able to study the causes of synchrony.

D. WHAT DETERMINES THE AMPLITUDE OF THE CYCLE?

Some years of peak numbers are much higher than others, and the same is true of the low points of the cycle. Variations in amplitude have been especially noted in the Norwegian lemming in which "lemming years" occur at irregular intervals. Very few attempts have been made to determine why the amplitude is larger in some years or why it varies from one habitat to another.

IV. POPULATION DENSITY CHANGES

A. TECHNIQUES OF ESTIMATING DENSITY

Progress in defining the phenomenon of population cycles has been limited by inadequate density data. In the simplest case we recognize only two density states: "high" density and "low" density. Next we can obtain an index of density by the use of sampling with traps, surveys for runways or fecal pellets, or visual sightings. Much of the work on small rodents has utilized kill traps of various sorts to provide an index of population density. Trap catches are a function both of density and of activity patterns. If voles have large home ranges one year and small home ranges the next, a trapping index will decrease even if actual densities are the same in the two years. Individual trappers vary greatly in the ability to set traps in good locations, and this factor can add to the variance in trap catches. In general, indices of density obtained by trap sampling will show trends of density changes but cannot be interpreted quantitatively.

Absolute density estimates can also be obtained by removal trapping. This method was first developed by Leslie and Davis (1939) and independently derived by DeLury (1947). As animals are removed from an area, the catch per unit of trapping effort will fall off and reach zero at the point where the whole population has been removed. If we assume constant trappability of the whole population and no immigration, we can use linear regression techniques to estimate the size of the population being trapped. Unfortunately, two serious problems have plagued this approach (Smith *et al.*, 1971). First, the probability of capture is not constant for the whole population (Tanaka, 1960). And second, immigration occurs once the removal trapping begins. This forces one to try to measure the area depopulated by the kill traps, an area which may be several times greater than the actual area occupied by traps (Smith *et al.*, 1971). The area affected by trapping is difficult to determine in removal studies. A more basic limitation of this approach is that it destroys the population we should be trying to study, and consequently mark-and-release techniques have been utilized for long-term studies.

Mark-and-recapture techniques permit an accurate measurement of density. Since the pioneering work of Leslie *et al.* (1953), there has been available a continuously improving series of statistical techniques for this estimation problem (Cormack, 1968). The application of mark-and-recapture techniques requires an assumption of randomness of capture of marked and unmarked voles. The randomness of capture assumption has been tested on only a few vole populations, and in no

case has it been shown to be a valid assumption. Leslie *et al.* (1953) showed that *Microtus agrestis* were not sampled randomly between the marked and unmarked segments of the population. Some voles are trap-prone and others are trap-shy. The same results were obtained for *M. californicus* by Krebs (1966). Tanton (1965, 1969) showed a seasonal change in probability of capture for *Apodemus sylvaticus* and *Clethrionomys glareolus*. Tanaka (1963, 1972) has shown that the probability of capture is different for unmarked and for marked voles of *Microtus montebelli*, *Clethrionomys rufocanus*, and *C. smithi*.

One way to provide randomness of capture might be to prebait animals for several days or weeks before trapping begins. Tanaka (1970) prebaited *C. rufocanus* for three days and showed that this amount of prebaiting increased the probability of capture of unmarked voles slightly. Andrzejewski *et al.* (1971) showed that *C. glareolus* which were trap-shy were caught more readily in permanent trap sites than in random trap sites which were not prebaited. Capture was not, however, at random in either of these studies, and Krebs (1966) found that continuous prebaiting at permanent trap sites was not sufficient to provide random sampling in *Microtus californicus*. Even though prebaiting does not equalize the probability of capture over all individuals, it may still improve census estimates. We have found that *M. townsendi* cannot be live-trapped even at high densities without prebaiting (Krebs, unpublished). The same problem is found in *M. pennsylvanicus* during the summer (Krebs *et al.*, 1969).

If the assumptions of standard capture-recapture analysis cannot be met in rodent populations, two courses of action are available. First, recent techniques for mark and recapture estimation with unequal catchability can be utilized (Marten, 1970; Seber, 1970). The difficulty is that again some uniformity assumptions must be made (e.g. that an individual has a fixed probability of capture throughout its life). No one to date has used these techniques on a long-term field study. Second, one can attempt to enumerate the population by saturation live-trapping at frequent intervals and hope that the errors involved are relatively small. This approach was adopted by Chitty and Phipps (1966) and has been used by Krebs (1964a, *et seq.*). If permanent trapping stations are used, the enumeration approach seems to provide the best technique for studying population processes in small rodents.

Unfortunately, many workers on small rodent populations do not appreciate the problems of density estimation, and the literature is filled with examples of population estimates derived from the Lincoln Index with no attempt to satisfy the assumptions, examples of indices of density such as snap-trap catches being interpreted quantitatively, and sampling techniques applied with no appreciation of sampling

theory. For some purposes these faults are not critical, but when information about rates of change in density is required, the proper techniques should be used.

B. DO POPULATION CYCLES REALLY OCCUR?

There are few long-term data on vole and lemming populations and the longer the time series, the more unreliable the data. Elton (1942) summarized the bulk of the historical data on voles and lemmings. Table I gives the peak years for the Norwegian lemming in south Norway for almost 80 years. Peak years tend to recur at three- or four-year intervals. Figure 2 shows fur returns for the arctic fox

TABLE I

Peak years for the Norwegian Lemming in South Norway, 1862-1938.
(After Elton, 1942)

1862-3	1883-4	1906	1930
1866	1887-8	1909-10	1933-4
1868-9	1890-1	1918	1938
1871-2	1894-5	1920	
1875-6	1897	1922-3	
1879-80	1902-3	1926-7	

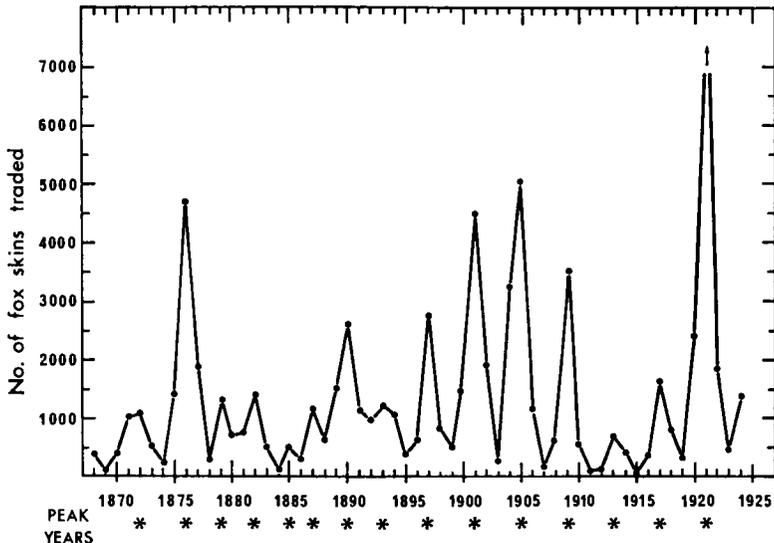


FIG. 2. Fur return statistics for the arctic fox in Ungava District, 1868-1924. (Data from Elton, 1942, pp. 415-416.)

(*Alopex lagopus*) in Ungava from 1867 to 1924. Fur returns are unreliable indicators of absolute population changes but do tend to reflect the observations of trappers and naturalists (Elton, 1942). These data show a three- or four-year cycle in arctic fox populations, which follow the abundance of lemmings.

Koshkina (1966) reports data from a standard kill-trap census of voles in the boreal forest of the Kola Peninsula (Fig. 3). Thirty years of

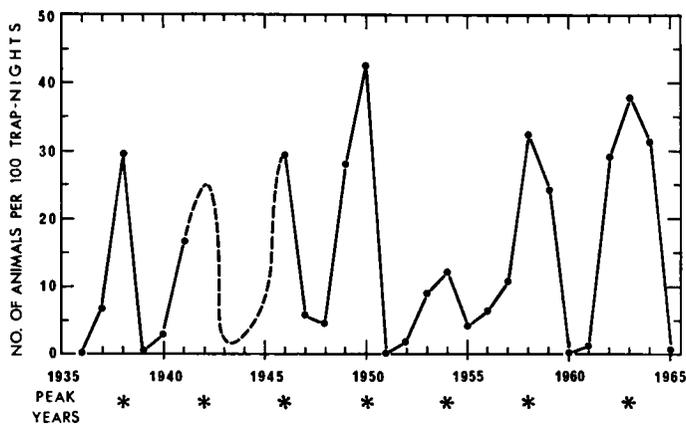


FIG. 3. Autumn population densities in the red-grey vole, *Clethrionomys rufocanus*, from the central Kola Peninsula. (After Koshkina, 1966.)

observations cover seven population cycles with a period of four or five years between peak numbers. These records comprise one of the longest runs of quantitative information on vole numbers. Chitty and Chitty (1962) report population trends in *Microtus agrestis* from Lake Vyrnwy, Wales, from 1932–1960 (Table II). Qualitative assessment of the phase of the population cycle was obtained from a mixture of snap-trapping and live-trapping studies over this 28-year period (except for World War II). Peak populations recur at intervals of four years usually, although three- and five-year cycles were found. Similar observations have been made on the brown lemming at Barrow, Alaska (Fig. 4).

Many other studies of shorter duration could be cited here. There are 18 genera and 105 species of voles and lemmings (Arata, 1967), and perhaps only one-fifth of these species has been studied in depth. We will assume here that the species studied have been representative of the group, and will draw our conclusions from an incomplete sample.

Populations of voles and lemmings thus fluctuate with a period between peaks of three to four years usually, although two-, five- and six-year cycles are not uncommon. We know of no microtine data

TABLE II

Population trends among the voles (Microtus agrestis) at Lake Vyrnwy, Wales, from 1932 to 1960. Phase of the cycle was judged from a mixture of snap-trap and live-trap samples. (After Chitty and Chitty, 1962)*

Phase of population cycle					
Increase		Peak		Decline or scarcity	
1932		1933		1934	1935
?1936		1937		1938	1939
—		—		1946	1947
1947		1948		1949	1950
1951		1952		1953	1954
1954	1955	1956	1957	1958	1959
1959	1960				

* Data for 1932–39 from Marchnant area; 1946–54 from miscellaneous areas; 1954–60 from Old Road area.

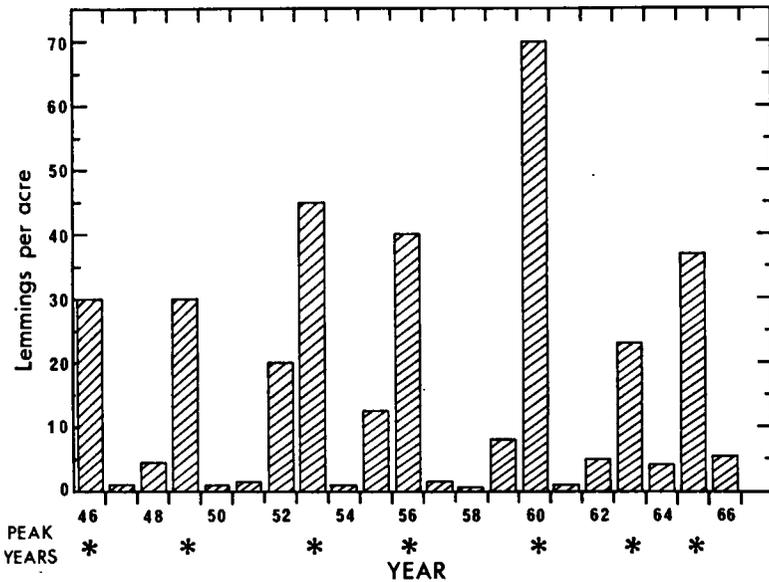


FIG. 4. Population densities in summer of brown lemming, *Lemmus trimucronatus*, at Point Barrow, Alaska. (After Schultz, 1969.)

gathered quantitatively over a three- or four-year period which fails to show a population cycle. *We conclude that microtine rodent populations normally undergo population cycles with a period of three to four years and this density pattern should be assumed to be the normal configuration.* Microtine populations that do not fluctuate cyclically are the unusual situation and if any can be located they would be exceptionally important to study. We feel that the burden of proof should be shifted to those who would claim to have a non-cyclic population.

One of the dogmas about population cycles is that they are more pronounced in arctic regions (Odum, 1971, p. 193). A corollary of this dogma is that southern populations of voles should have reduced amplitudes of cycles and ultimately reach a point of having no cyclic fluctuations at all. We have been unable to trace the origin of this dogma; perhaps it was first mentioned by Howell (1923). Dymond (1947, p. 14) also reports the dogma: "It has long been recognized that periodic fluctuations in animal populations are virtually confined to the northern part of the northern hemisphere and are especially characteristic of the Arctic, not only in America but also in Europe and Asia". Keith (1963, pp. 67-68) reports that the ten-year cycle is absent from some southern populations of snowshoe hare (*Lepus americanus*) and ruffed grouse (*Bonasa umbellus*), but the available data are poor and this conclusion uncertain. We can find no quantitative evidence that vole and lemming cycles are more pronounced in arctic regions than they are farther south. Wildhagen (1952) states that lemming fluctuations are more pronounced in northern Norway than in southern Norway, and Kalela (1962) supports this statement. But no rodent census data are available and one may be comparing the "visibility" of peak populations in northern and southern habitats rather than the cyclic amplitude.

We conclude that vole and lemming populations go through regular cycles of abundance everywhere they have been studied. We view these cycles as a special type of population fluctuation, and most of the discussion to follow is independent of whether the rodent fluctuations are regular or irregular. Even if one denies that microtine populations cycle regularly, one must still explain their fluctuations.

C. STRUCTURE OF POPULATION FLUCTUATIONS IN MICROTINES

One of the first steps toward understanding a population fluctuation is to describe it in some detail. Part of the lack of progress in explaining microtine cycles is due to the fact that emphasis has been on identifying cycles and determining relative densities. But to understand cycles we

must describe them in detail. At what season does the increase begin? How long is the peak phase? When does the decline begin and how rapid is it? We now attempt to answer some of these questions.

1. Increase phase

The increase phase is defined as a period of large increase in numbers from one spring to the next (Chitty and Chitty, 1962). There are two views on the structure of the increase phase. The increase phase might be a gradual, exponential build-up from low numbers over two or even three years. Koshkina (1966) suggests that the number of *Clethrionomys*

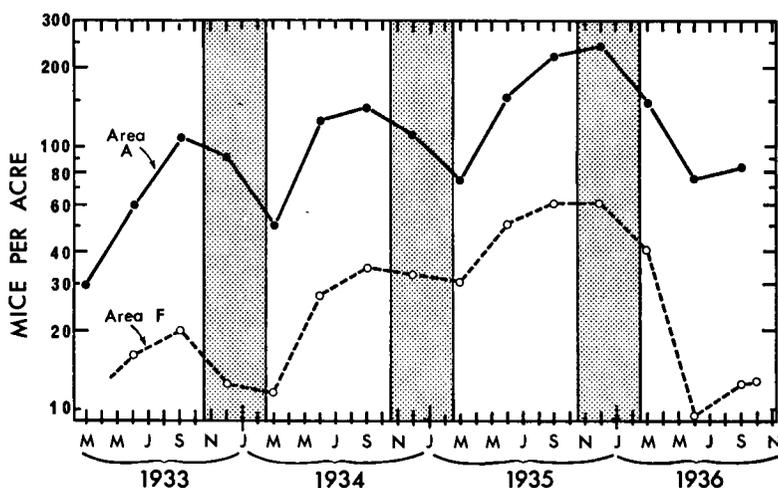


FIG. 5. A population cycle of *Microtus pennsylvanicus* on two areas near Ithaca, New York. Winter months are shaded. (After Hamilton, 1937.)

on the Kola Peninsula gradually increases over three summers to a peak. Pitelka (1958) states that brown lemming cycles in northern Alaska have two successive winters of rapid population growth so that numbers build up gradually over two years. Fuller (1969) found that *Clethrionomys gapperi* and *C. rutilus* in northern Canada increased from an extreme low in 1964 to a peak in 1966. Hamilton (1937) described a population cycle of *Microtus pennsylvanicus* in New York in which the increase occurred gradually over two years (Fig. 5). Populations increased in the summer and dropped back during the winter months, so that the net annual increase was relatively small from 1933 to 1935. Bodenheimer (1949) states that populations of *M. guentheri* in Israel increase gradually over two years to reach a peak.

An alternative view is that the increase phase is a rapid explosion

which occupies one year or less. Table II shows that a number of populations studied by Chitty and Chitty (1962) went through the increase phase in one year. Our studies of *M. ochrogaster* and *M. pennsylvanicus* in Indiana have provided several examples of rapid increases; Fig. 6 gives one example. We never found in the Indiana *Microtus* a gradual increase of the type Hamilton (1937) observed (cf. Fig. 5). Newson (1963) describes a period of increase in *Clethrionomys glareolus* near Oxford that occupied one year.

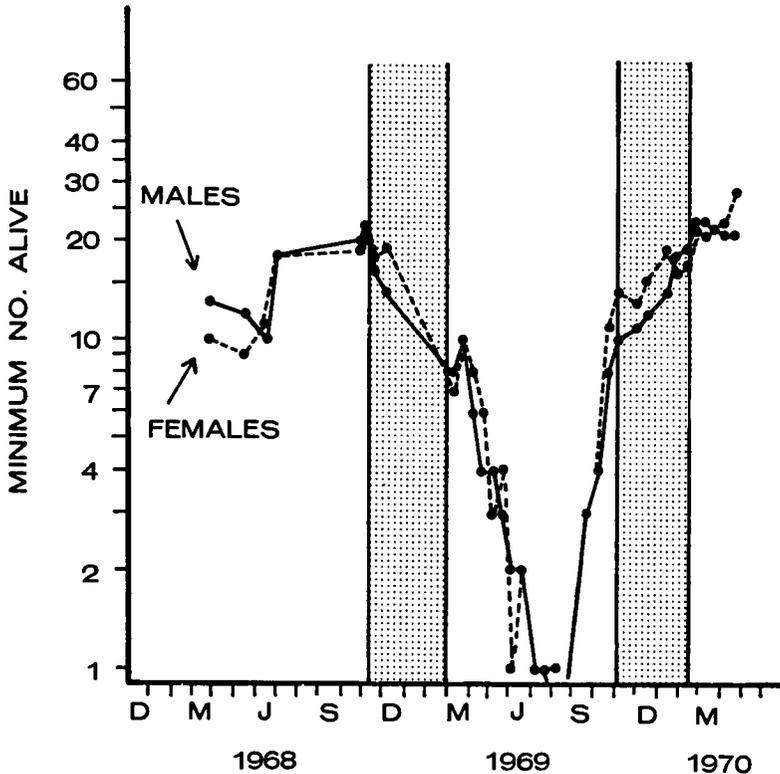


FIG. 6. A decline and subsequent increase in *Microtus ochrogaster* on the Carlson Farm area in southern Indiana. Winter months are shaded. Vertical lines delimit breeding period. (From Myers and Krebs, 1971.)

In Table III we present data on the instantaneous rate of population growth (r) for the increase phase of the population cycle. Data are presented only for populations trapped intensively at monthly intervals (or less); we include some winter estimates derived from an accurate fall sample and a spring sample. Some of the rates of increase in Table III are unusually high. The three high values for *Clethrionomys glareolus*

TABLE III

Measured rates of population growth in the increase phase of the population cycle for several vole species. Geometric increase is assumed; r is measured as instantaneous rate per week

Species	Time period	Mean r	Reference
<i>Clethrionomys glareolus</i>	March–Dec. 1958	0.074	Newson (1963)
	March 1958–Jan. 1959	0.050	Newson (1963)
	April–July 1966	0.132	Petrusewicz <i>et al.</i> (1971)
	April–July 1968	0.135	Petrusewicz <i>et al.</i> (1971)
	April–July 1970	0.129	Andrzejewski and Rajska (1972)
<i>Microtus pennsylvanicus</i>	June–Sept. 1933	0.035	Hamilton (1937)
	June–Sept. 1933	0.022	Hamilton (1937)
	March–Sept. 1933	0.051	Hamilton (1937)
	March–Sept. 1934	0.035	Hamilton (1937)
	March–Sept. 1934	0.041	Hamilton (1937)
	March–Sept. 1934	0.040	Hamilton (1937)
	June–Nov. 1965	0.100	Krebs <i>et al.</i> (1969)
	Dec. 1965–Feb. 1966	0.046	Krebs <i>et al.</i> (1969)
	Aug.–Nov. 1967	0.063	Gaines and Krebs (1971)
	Aug.–Nov. 1969	0.089	Gaines and Krebs (1971)
	Aug.–Nov. 1967	0.096	Gaines and Krebs (1971)
	Dec. 1967–Jan. 1968	0.029	Gaines and Krebs (1971)
	May–July 1967	0.059	Gaines and Krebs (1971)
	Aug.–Nov. 1967	0.134	Gaines and Krebs (1971)
	Dec. 1967–Jan. 1968	0.032	Gaines and Krebs (1971)
Aug.–Nov. 1969	0.036	Gaines and Krebs (1971)	
Dec. 1969–Feb. 1970	0.032	Myers and Krebs (1971b)	
<i>Microtus ochrogaster</i>	June–Oct. 1965	0.037	Krebs <i>et al.</i> (1969)
	Nov. 1965–March 1966	0.036	Krebs <i>et al.</i> (1969)
	Feb.–Oct. 1968	0.041	Krebs, unpublished
	June–Oct. 1967	0.031	Gaines and Krebs (1971)
	Aug.–Oct. 1969	0.231	Myers and Krebs (1971b)
	Nov. 1969–Feb. 1970	0.041	Myers and Krebs (1971b)
<i>Microtus californicus</i>	Nov. 1962–March 1963	0.088	Krebs (1966)
	Nov. 1962–July 1963	0.040	Krebs (1966)
	Jan.–April 1964	0.091	Krebs (1966)
	May–Oct. 1964	0.042	Krebs (1966)
	Aug. 1966–June 1967	0.070	Batzli and Pitelka (1971)
<i>Lemmus trimucronatus</i>	Oct. 1952–May 1953	0.051	Thompson (1955a)
	Sept. 1951–May 1952	0.115	Thompson (1955a)
	Sept. 1959–May 1960	0.083	Krebs (1964a)

TABLE III (contd.)

Species	Time period	Mean r	Reference
<i>Dicrostonyx groenlandicus</i>	Sept. 1959–May 1960	0.042	Krebs (1964a)
<i>Clethrionomys rufocanus</i>	June–Sept. 1954	0.146	Kalela (1957)

are from an island population (see later discussion). One very high r value for *Microtus ochrogaster* (0.231) was probably enhanced by immigration into the area. Table IV presents one aid to interpreting Table III; it gives doubling times for a range of r -values and the rate of growth over six months and one year.

Since Leslie and Ranson (1940) calculated that *M. agrestis* might increase ten-fold over a six-month breeding season, there have been few attempts to analyze the increase phase quantitatively. Table III indicates that for the few cases we have measured, the increase observed is more typically three-fold to six-fold over a six-month period.

TABLE IV

Table of instantaneous population growth rates, the corresponding doubling time in weeks, and the number of animals that would be present for every starting individual after six months and one year had elapsed at the indicated growth rate

Instantaneous growth rate per week	Doubling time in weeks	No. of times popln. has multiplied at the end of:	
		6 months	1 year
0.02	34.7	1.68	2.83
0.03	23.1	2.18	4.76
0.04	17.3	2.83	8.00
0.05	13.9	3.67	13.46
0.06	11.6	4.76	22.65
0.07	9.9	6.17	38.09
0.08	8.7	8.00	64.07
0.10	6.9	13.46	181.3
0.12	5.8	22.65	512.9
0.14	5.0	38.09	1451.0

2. Peak phase

The peak phase is defined as a period of little change in numbers from one spring to the next (Chitty and Chitty, 1962). The peak phase is usually obvious, since population densities are typically much higher than they are in other phases of the cycle. Some species, however, do not have a well-defined peak phase. *Microtus californicus* is one example (Fig. 7); *M. ochrogaster* is another (Krebs *et al.*, 1969). In these populations there is typically an increase phase, followed by a brief period of high numbers, and then a decline phase.

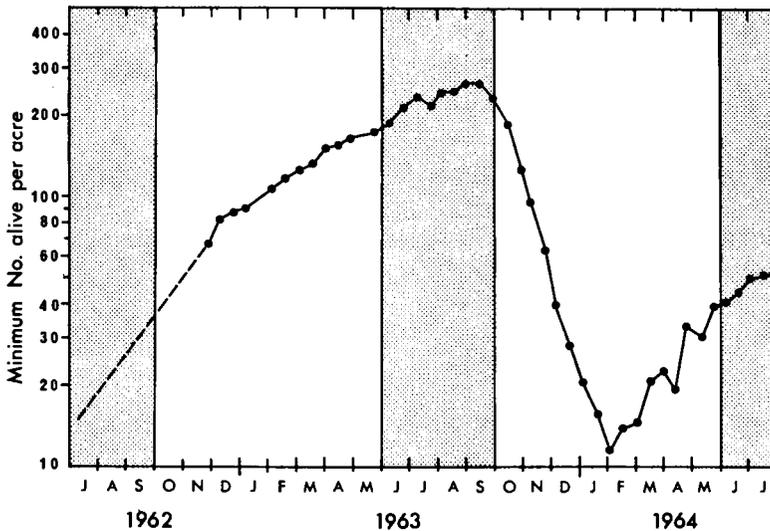


FIG. 7. A population cycle in *Microtus californicus* at Berkeley, California. (After Krebs, 1966, and Pearson, 1971.)

The peak phase in other species is well-defined and may last for a year (or rarely two years). Chitty and Chitty (1962) show that the peak year in *M. agrestis* begins with a spring decline in numbers that may come at slightly different times in the two sexes. This spring decline is followed by a more or less rapid rise in numbers so that in the fall of the peak year numbers are roughly the same as they were in the spring. Thompson (1955a) described a spring decline in the brown lemming during the peak year, and Krebs (1964a) also observed this drop in lemming populations in northern Canada. Figure 8 shows a spring decline in a peak phase of *M. pennsylvanicus* in 1968. In this particular case both males and females declined from February to early May and the population then recovered to high numbers in late summer. Half

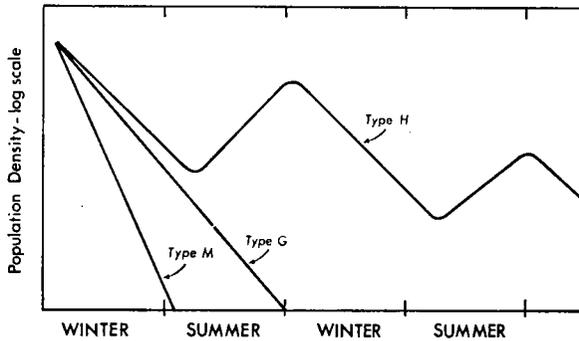


FIG. 9. Hypothetical diagram of the three types of population declines recognised by Chitty (1955).

declined through December, then dropped very rapidly and completely disappeared by mid March 1965. Krebs *et al.* (1969) monitored a population of *Microtus ochrogaster* (Fig. 10) which began declining in October 1966, fell rapidly through December, and then more gradually until completely disappearing by April 1967. A population of *M. californicus* which showed a Type M "crash" in 1963 was studied by Krebs (1966).

The Type G decline in which numbers fall continuously through a breeding season was first described by Godfrey (1955) for two populations of *M. agrestis*. A Type G decline was found in the lemmings *Lemmus trimacronatus* and *Dicrostonyx groenlandicus* in northern Canada by Krebs (1964a). Figure 6 shows a Type G decline in *Microtus ochrogaster* from Indiana. Many of the declines described by Krebs *et al.* (1969) and Gaines and Krebs (1971) for *M. pennsylvanicus* were probably Type G declines since they occurred during the breeding season, but they were followed very quickly by a return to the phase of increase.

Type H declines were first described by Hamilton (1937) for *M. pennsylvanicus*. Figure 7 shows a Type H decline in *M. californicus*. Kalela (1957) studied a population cycle of *Clethrionomys rufocanus* in Finnish Lapland; some recovery of the population was indicated after the initial decline, and hence a Type H decline occurred (Fig. 11). Koshkina (1965) presents data from two declines of *C. rutilus* in the boreal forest of the U.S.S.R.; both declines fit the Type H classification. Gaines and Krebs (1971, p. 709) show a Type H decline for *Microtus ochrogaster* in Indiana.

The recovery of the population during a Type H decline may be substantial, and this has caused much confusion about cyclic fluctuations in the literature. Chitty and Chitty (1962) observed that autumn population densities in *Microtus agrestis* could be nearly equal for

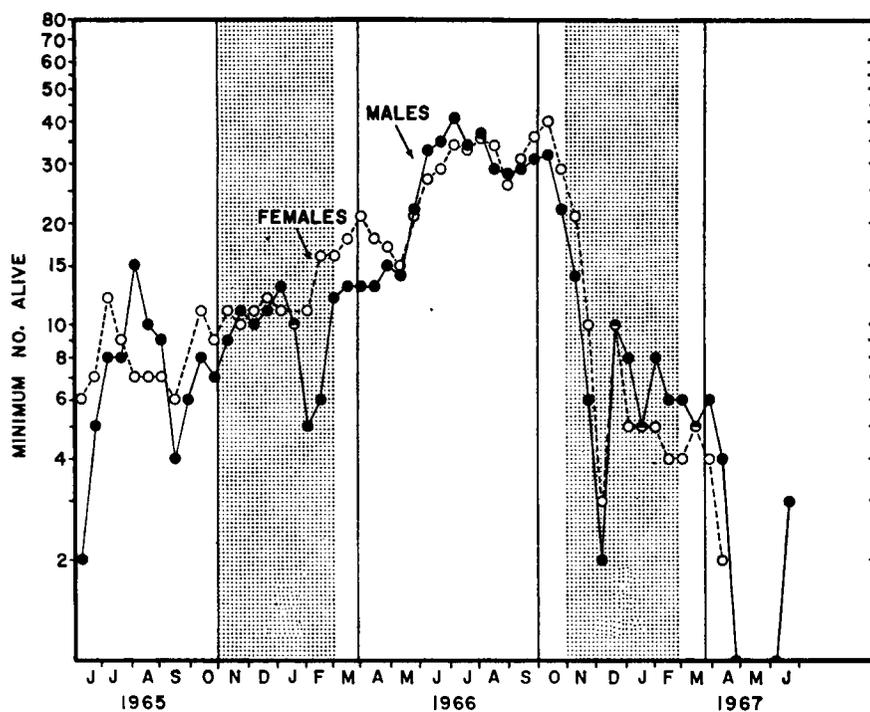


FIG. 10. A population cycle of *Microtus ochrogaster* in southern Indiana. A Type M decline occurred in the fall of 1966. (After Krebs *et al.*, 1969.)

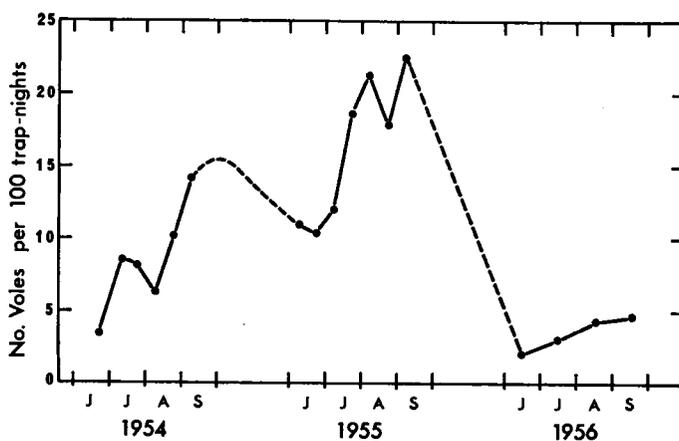


FIG. 11. A population cycle of *Clethrionomys rufocanus* in northern Finland. A Type H decline occurred in 1956. (After Kalela, 1957.)

several years in a row during the increase phase, the peak phase, and a Type H decline. Superficial observations on autumn densities thus might lead one to conclude that *M. agrestis* populations do not fluctuate in cycles.

Table V attempts to summarize the available information on rates of change in declining populations. Overwinter (or dry season) declines are separated from summer (or wet season) declines. Some of these data are only rough estimates available from kill trapping. Two points can be noted from Table V: (1) populations decline at rates which are usually

TABLE V

Measured rates of population change in the decline phase of the population cycle for several species of lemmings and voles. Geometric change is assumed; r is measured as instantaneous rate per week

Species	Time period	Type of decline	Mean r	Reference
OVERWINTER DECLINES				
<i>Clethrionomys rutilus</i>	Aug. 1963–May 1964	H ₁ *	-0.061	Koshkina (1965)
<i>Clethrionomys glareolus</i>	Dec. 1964–Feb. 1965	M	-0.275	Zejda (1967)
<i>Clethrionomys rufocanus</i>	Sept. 1955–June 1956	H ₁	-0.063	Kalela (1957)
	July 1966–April 1967	H ₁	-0.039	Petrusewicz <i>et al.</i> (1971)
	Aug. 1968–April 1969	H ₁	-0.054	Petrusewicz <i>et al.</i> (1971)
<i>Microtus pennsylvanicus</i>	Dec. 1935–June 1936	H ₁	-0.053	Hamilton (1937)
	Dec. 1935–June 1936	H ₁	-0.078	Hamilton (1937)
	Dec. 1935–June 1936	H ₁	-0.048	Hamilton (1937)
	Nov. 1966–Feb. 1967	G	-0.012	Krebs <i>et al.</i> (1969)
	Nov. 1968–Feb. 1969	G	-0.023	Gaines and Krebs (1971)
<i>Microtus ochrogaster</i>	Oct. 1966–March 1967	M	-0.065	Krebs <i>et al.</i> (1969)
	Nov. 1968–Feb. 1969	M	-0.165	Krebs, unpublished
	Nov. 1967–Feb. 1968	H ₁	-0.073	Gaines and Krebs (1971)
	Nov. 1968–Feb. 1969	H ₂	-0.183	Gaines and Krebs (1971)
	Nov. 1968–Feb. 1969	G	-0.058	Myers and Krebs (1971b)
<i>Microtus californicus</i>	Sept. 1963–Jan. 1964	H ₁	-0.156	Krebs (1966)
	Sept. 1963–Feb. 1964	H ₁	-0.084	Krebs (1966)
<i>Lemmus trimacronatus</i>	Sept. 1960–May 1961	G	-0.064	Krebs (1964a)
<i>Dicrostonyx groenlandicus</i>	Sept. 1960–May 1961	G	-0.032	Krebs (1964a)

TABLE V (contd.)

Species	Time period	Type of decline	Mean r	Reference
SUMMER DECLINES				
<i>Clethrionomys rutilus</i>	June–Aug. 1964	H ₁	+0.180†	Koshkina (1965)
<i>Clethrionomys glareolus</i>	April–Oct. 1967	H ₁	+0.042	Petrusewicz <i>et al.</i> (1971)
<i>Clethrionomys rufocanus</i>	June–Sept. 1956	H ₁	+0.062	Kalela (1957)
<i>Microtus pennsylvanicus</i>	March–July 1967	G	–0.029	Krebs <i>et al.</i> (1969)
	Feb.–July 1969	G	–0.061	Gaines and Krebs (1971)
	Feb.–July 1969	G	–0.119	Gaines and Krebs (1971)
	Feb.–July 1969	G or H ₁ ?	–0.017	Myers and Krebs (1971b)
<i>Microtus ochrogaster</i>	March–Sept. 1967	M	–0.083	Krebs <i>et al.</i> (1969)
	Feb.–Oct. 1968	H ₁	+0.023	Gaines and Krebs (1971)
	March–Aug. 1969	G	–0.142	Myers and Krebs (1971b)
<i>Microtus agrestis</i>	May–Aug. 1951	G	–0.107	Godfrey (1955)
	May–Aug. 1952	G	–0.089	Godfrey (1955)
<i>Microtus californicus</i>	Feb.–July 1964	H ₁	+0.062	Krebs (1966)
	March–July 1963	M	–0.185	Krebs (1966)
	Feb.–May 1964	H ₁	+0.076	Krebs (1966)
<i>Lemmus trimucronatus</i>	June–Aug. 1961	G	–0.124	Krebs (1964a)
<i>Dicrostonyx groenlandicus</i>	June–Aug. 1961	G	–0.131	Krebs (1964a)

* H₁ refers to the first year of a Type H decline.

† Note that populations can *increase* in the summer breeding season of the decline phase of Type H.

greater than rates at which they increase (cf. Table III). This is particularly true of Type G and M declines, and (2) during the summer breeding season of Type H declines, populations may increase at rates which equal those of the increase phase (e.g. Fig. 7). This observation is particularly important because it shows the complex nature of population cycles. Populations do not simply increase to high densities and decline to low densities. *High population density is not sufficient to produce a decline, and low density is not sufficient to stop a decline.*

4. Phase of low numbers

Populations may fall to low numbers and remain there for one to three years, but in some cycles this phase is absent and populations go directly from the decline phase to the increase phase (e.g. Fig. 6). Very little is known about the phase of low numbers in voles or lemmings. Koshkina (1966) suggested that populations of *Clethrionomys rufocanus* on the Kola Peninsula did not have a phase of low numbers but after declining began to increase gradually over two or three years. Norwegian lemming populations on the Kola Peninsula, however, did go through phases of scarcity for several years.

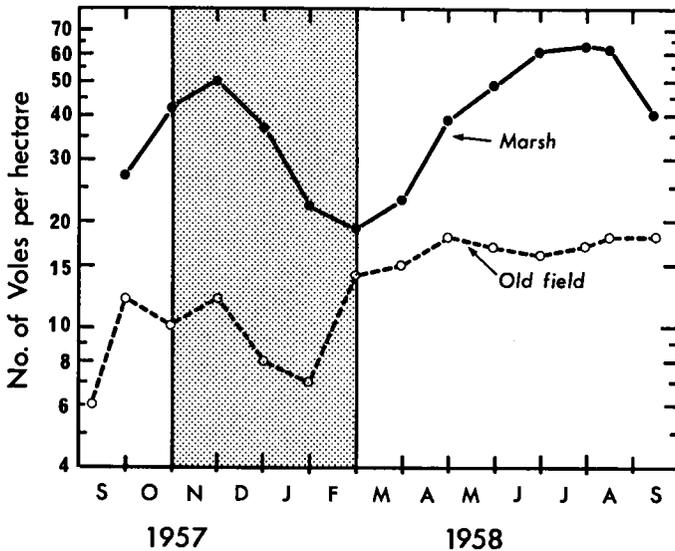


FIG. 12. Annual cycle in the phase of low numbers for *Microtus pennsylvanicus* in southern Michigan. Winter months are shaded. (After Getz, 1960.)

Getz (1960) studied a Michigan population of *Microtus pennsylvanicus* that was apparently in the phase of low numbers (Fig. 12). In both marsh and old field habitats voles showed an annual cycle with little net change in numbers. During the spring and summer increase the population grew at 7% per week, but this was not sustained. Krebs (1966) described a similar sequence in *M. californicus* in the low phase (Fig. 13); numbers rose rapidly for a short time but then fell back during the breeding season to the low density at which they started. We do not have a sufficient number of descriptions of low populations

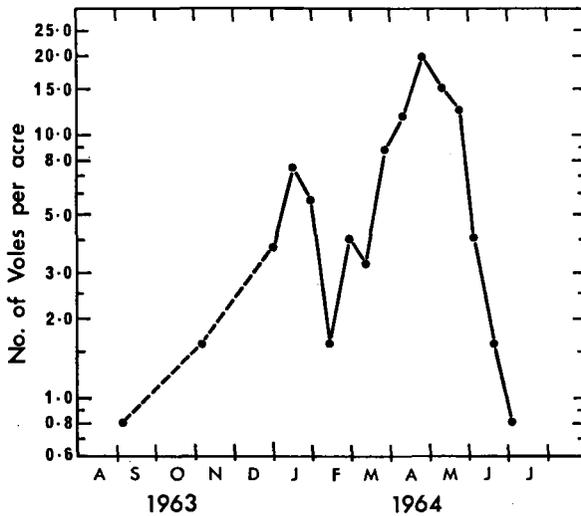


FIG. 13. Annual cycle in the phase of low numbers for *Microtus californicus* at Berkeley, California. (After Krebs, 1966.)

of any vole species to say if the patterns shown in Figs. 12 and 13 are general. Pearson (1963), for example, shows a three-year period of great scarcity in *M. californicus* but his data are not sufficient to determine whether the sequence of density change displayed in Fig. 13 applied to the three years.

Until there are more data on the phase of low numbers we will not be able to distinguish two quite different interpretations of this phase:

1. that the population declines to a level below our accuracy of measurement and then begins to grow geometrically back to the next peak; the early stages of this geometric growth we call the "phase of low numbers" but such a name reflects more our inability to measure changes in low density populations than the biological reality;
2. that the population declines and remains low for a long period; brief spurts of population growth may occur but numbers quickly fall back to a low level; this "start-stop" type of population curve persists until the phase of increase occurs, and the net population growth is zero in spite of low densities.

Biologists typically stop working on a population once it gets sparse and the critical turnaround from the low phase to the phase of increase has rarely been studied.

V. DEMOGRAPHIC MACHINERY

A. REPRODUCTION

Populations rise and fall because of changes in birth, death and dispersal rates, and we now turn to consider these three. Birth rates in polyoestrous mammals are a function of six components (Fig. 14), and we must analyze each component separately.

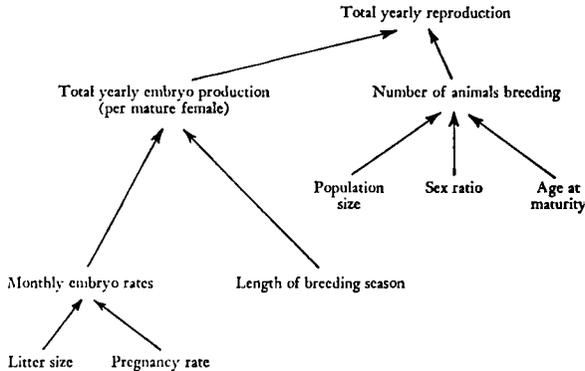


FIG. 14. Components of reproduction in polyoestrous mammals. (After Krebs, 1964.)

1. Litter size

One way in which to encourage population growth is to have larger litters, and we now enquire whether the number of embryos per pregnant female changes in relation to cyclic phase. We will not review here the statistical problems of estimating and comparing litter size in voles and lemmings (see Zejda, 1966; Keller and Krebs, 1970). Litter size may be affected by season of year, body weight of female, age and parity, and one must control for these variables if comparisons are to be valid. We have been forced to disregard a significant fraction of the data in the literature because of this problem.

Several authors have claimed that litter size does not change from phase to phase in the cycle. Kalela (1957) found no evidence that *Clethrionomys rufocanus* populations had lower litter sizes in the peak or decline phase compared with the phase of increase. Thompson (1955a) reported no change in litter size over a brown lemming cycle at Barrow, Alaska. Table VI gives average litter sizes for *C. rutilus* studied by Koshkina (1965), and illustrates the fact that litter size is unaffected by the cyclic phase. Krebs (1964a) could find no significant changes in litter size over a cycle of the lemmings *Lemmus trimucronatus*

TABLE VI

Average number of embryos in overwintered females of Clethrionomys rutilus during a cyclic fluctuation in numbers. Sample size in parentheses.
(After Koshkina, 1965)

	Year and cyclic phase		
	1962	1963	1964
	Increase	Peak	Type H decline
May	7.8 (17)	8.0 (52)	6.6 (13)
June	7.5 (43)	6.5 (42)	7.6 (39)
July	6.2 (20)	5.7 (49)	6.9 (21)
Average May to July	7.11	6.76	7.25

and *Dicrostonyx groenlandicus*. Stein (1957) could find no significant year-to-year changes in litter sizes of *Microtus arvalis* in an intensive six-year study covering two declines. Keller and Krebs (1970) could find no changes in litter size related to cyclic phase in *M. pennsylvanicus* in a three-year study. Hoffmann (1958) found no change in litter size in *M. californicus* in relation to phase of the cycle.

Several authors have claimed, to the contrary, that litter size is higher in increasing and peak populations and lower during the decline phase. Hamilton (1937) reported that litter size was higher during the increase phase of a cycle of *M. pennsylvanicus* and lower during the decline phase. His data unfortunately do not support this conclusion. The largest litter sizes were recorded in the peak year of 1935, and the increase years of 1933 and 1934 had essentially the same litter sizes as the decline year of 1936. Bodenheimer (1949) stated that *M. guentheri* had a higher average litter size in the increase phase, but no data are presented to substantiate this claim. We have been unable to find any good quantitative evidence that litter size is lower during the decline phase. Koshkina and Khalansky (1962) present data on *Lemmus lemmus* that are difficult to interpret. Litter size was highest in one year of increase and one peak year, and lowest in another peak year, and two decline years. Unfortunately data are grouped over all size classes for all months and parity classes, so it is impossible to determine if these trends are valid. If they are valid, these data would be the first to show a depressed litter size in the decline phase.

Finally, several authors have suggested that litter size is reduced in peak populations but essentially the same during the other phases of the cycle. Hoffmann (1958) reported a 10–25% drop in litter size during the peak summer for a *Microtus montanus* population. Tanaka (1964) shows a 17% drop in litter size during the peak summer for *Clethrionomys smithi* in Japan. Patric (1962) claims to have shown a 16–37% drop in litter size for *C. gapperi* populations; his estimates, however, assume no significant effects of season, weight of female, or parity on litter size. Zejda (1964) found a slight depression in litter size of *C. glareolus* in the peak summer. Keller and Krebs (1970) found that litter size was depressed 25% during the peak summer in *Microtus ochrogaster*. Koshkina (1966) states that *Clethrionomys rufocanus* has minimal litter size in the peak year, compared with the increase phase, but also minimal in the decline and low phases. Unfortunately the data presented are not sufficient to verify these claims because only mean values for the whole year are given. Reichstein (1964) shows that litter sizes of *Microtus arvalis* are reduced by 17–22% in peak years.

If the changes in litter size are to be an important driving force in the population cycle, litter size should be depressed in the decline phase and enhanced in the increase phase. We can find little evidence of these trends in the populations studied to date, and we conclude that this component of reproduction is not a critical link in the demographic machinery.

2. Pregnancy rate

We next consider the percentage of mature females which are pregnant during the breeding season. Note that we are not concerned here with the age of sexual maturity or the length of the breeding season.

Most workers seem to agree that the pregnancy rate does not vary in relation to the population cycle. Figure 15 illustrates the similar proportions of pregnant females in three years for *Clethrionomys rufocanus* in Finland. Mullen (1965) found the same result in *Lemmus trimucronatus* at Barrow, Alaska over four years. Krebs (1964a) found no cyclic variation in the percentage of females pregnant for either *Dicrostonyx groenlandicus* or *Lemmus trimucronatus* in northern Canada. Keller and Krebs (1970) found no significant differences in percentage of mature females pregnant during the summer months for *Microtus pennsylvanicus* and *M. ochrogaster*.

A few authors have suggested that the pregnancy rate goes up in the phase of increase. Hamilton (1937) measured the fraction of female *M. pennsylvanicus* in New York that were both pregnant and lactating and

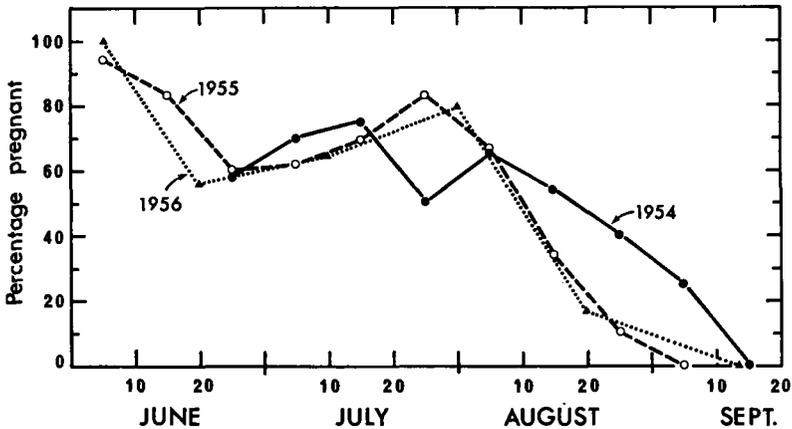


FIG. 15. Percentage of mature females pregnant in *Clethrionomys rufocanus* in northern Finland. The population increased in 1954, peaked in 1955, and declined in 1956. (After Kalela, 1957.)

claimed that the breeding rate accelerated from the beginning of the increase phase until the decline. He presents these data:

	Sample size	% pregnant and lactating
1934 (increase)	107	47.65
1935 (peak)	223	53.65
1936 (decline)	282	55.66

None of these differences are statistically significant ($\chi^2 = 2.00$, $df = 2$). Nor are any of the individual months of May to August significantly different between years. We conclude that there is no evidence of a change in the breeding rate in Hamilton's data. Bodenheimer (1949) also suggested an increased pregnancy rate in increasing populations of *Microtus guentheri*, but he presents no data to substantiate this claim.

3. Length of breeding season

The breeding season of most voles and lemmings is very elastic in length, and changes in the length of the breeding season are a major driving force in causing the population cycle.

Winter breeding is the most spectacular illustration of the reproductive abilities of microtines. Voles and lemmings can breed during some winters but not in others, and we need to know if this is related to the phase of the population cycle. Several authors have described winter breeding in lemmings. Sutton (Sutton and Hamilton, 1932) found winter breeding in both *Dicrostonyx groenlandicus* and *Lemmus*

trimucronatus in the Canadian Arctic during a period of increase. Krebs (1964a) found winter breeding in both these lemming species during a phase of increase and no winter breeding during a decline phase. Mullen (1965) shows the same result for *Lemmus* at Barrow, Alaska. Soviet workers have recognized for many years the importance of winter breeding in lemmings. Dunaeva and Kucheruk (1941) found winter breeding in both *Dicrostonyx torquatus* and *Lemmus sibiricus* during a period of increase. Nasimovich *et al.* (1948) believed that winter breeding of the Norwegian lemming was limited to the phase of increase. Koshkina and Khalansky (1962) review winter breeding in the Norwegian lemming and conclude that it plays a significant role in the rapid population growth of this species.

Winter breeding has been noted in many vole species but there is conflicting evidence of its relation to cyclic phases. After a favorable summer and autumn Khlebnikov (1970) observed winter reproduction in *Clethrionomys rutilus*. He interpreted this as being related to the increase phase. Zejda (1962) analyzed winter breeding in the bank vole, *C. glareolus*, and observed two successive winters of breeding. Neither of these episodes of winter breeding led to population growth, and he concluded that winter breeding was affected by the availability of food (principally acorns) but did not lead to an outbreak. Smyth (1966) argued that the relationship between winter breeding in voles and acorn crops is not a simple one. A good food supply, such as a heavy acorn crop, may be necessary for winter breeding but not sufficient. Newson (1963), for example, found *C. glareolus* breeding in the winter of 1958–1959 (phase of increase) but not breeding in the winters of 1957–1958 or 1959–1960. There was a good acorn crop in fall 1958, but none in 1957 or 1959. But Newson noted that voles in grassland where there were no acorns also bred during the winter of 1958–1959. Some aspect of population density may interact with the available food supply and this question awaits an experimental attack.

Winter breeding has been noted in *Microtus* by many workers, and in many cases it occurs during the increase phase of the cycle and is absent in the winter following the peak (reviewed in Keller and Krebs, 1970). This association, however, is not perfect. Chitty (personal communication) has recorded winter breeding in *Microtus agrestis* in the increase phase of the cycle, but some cycles occurred in which no winter breeding was evident.

More evidence is available on the length of the summer breeding period. In the phase of increase the summer breeding often starts early and ends late (or carries on through the winter), while in the peak year the breeding season often ends abnormally early. Koshkina and Khalansky (1962) pointed out that the Norwegian lemming stops

breeding early during the peak year, and Thompson (1955a) also observed this in the brown lemming. Krebs (1964a) observed an early stop to summer breeding in a peak year for the brown lemming and the varying lemming. Kalela (1957) found a shortened summer breeding period in both the peak year and in the decline year for *Clethrionomys rufocanus* (Fig. 15). Zejda (1967) pointed out that a very short reproductive season was a characteristic feature of the peak year. He observed a peak population of *C. glareolus* that stopped breeding in June. Koshkina (1966) states that the summer breeding season is one month shorter in the peak year for *C. rufocanus*.

In declining populations the breeding season often starts later than usual and may also end early. Godfrey (1955) observed a three-week delay in onset of summer breeding in *Microtus agrestis*. Chitty (1952) also reported a delay in the summer breeding season in declining populations of *M. agrestis*. Declining populations of *M. californicus* may delay breeding for one to two months (Krebs, 1966). A slight delay in the start of summer breeding was observed for *M. ochrogaster* and *M. pennsylvanicus* by Keller and Krebs (1970). There are few data available for northern species with respect to possible delays in the start of summer breeding. Kalela's (1957) observation on *Clethrionomys rufocanus* is one which has been noted: a declining population started breeding late in 1955 even though the spring came early. In northern species which typically begin breeding in spring when the snow melts, it may be difficult to detect any delay independent of spring weather variations. Further consideration of the interaction of weather and breeding season is discussed later.

We conclude that the phase of increase in many voles and lemmings is associated with an extended summer breeding season and possibly winter breeding. In the peak phase the summer breeding season is shortened and winter breeding is absent. The decline phase often resembles the peak phase, and may show a delay in the onset of summer reproduction.

4. Age at sexual maturity

The age at which an organism reaches sexual maturity has a critical impact on its potential for population growth (Cole, 1954). At present there are no good ways of aging living small rodents and we must rely on weight as an index of age. Several methods have been suggested for aging dead microtines. For *Clethrionomys* wear of the rooted molars can be taken as an indication of age, and Lidicker and MacLean (1969) suggest an aging method for *Microtus californicus* based on relative cranial and body measurements. However, both of these techniques are influenced by the environmental conditions to which the

individual is exposed. Therefore, slow growth during the summer causes underestimation of the age using the Lidicker and MacLean (1969) technique, and so this technique has the same biases as the use of body weight as an estimator of age. A new method for aging wild rodents based on the fractions of soluble and insoluble proteins in the eye lens is described by Otero and Dapson (1972). As the individual ages a larger portion of the lens protein becomes insoluble in water. This method is supposed to be less influenced by environmental factors than other aging techniques. If one has detailed knowledge of a population's breeding seasons and mortality rates, one can use weight as a reasonable index of age, particularly for young animals.

Natural history observations have established that age at sexual maturity is variable in microtines and that changes in the rate of sexual maturation of young voles and lemmings are a major driving force behind population cycles. Young Norwegian lemmings about 20 days old (25 g) were found pregnant in the summer of increase by Koshkina and Khalansky (1962), while almost none of the summer-born young lemmings became mature in the following year of peak density. Mullen (1965) records delayed maturation of male brown lemmings in a peak summer. Kalela (1957) in a detailed investigation of *Clethrionomys rufocanus* in Finland found that the maturation rate of the early summer young was strongly affected by population density:

	Proportion of early summer young mature	
	Males	Females
1954 (increase)	almost all	almost all
1955 (peak)	almost none	majority
1956 (decline)	majority	majority

Koshkina (1965) showed that maturation of *Clethrionomys rutilus* was inversely related to population density (Fig. 16). Note that there were always fewer males maturing than females. The same observation was made by Zejda (1967) for *C. glareolus*.

Few studies on weight at sexual maturity have utilized the quantitative techniques of Leslie *et al.* (1945) to estimate the median body weight at sexual maturity. Figure 17 shows changes in size at sexual maturity in the brown lemming over a cycle in numbers. Note that males are more strongly depressed in maturation than females. In the decline year of 1961 no young males matured, although young females did mature at about four weeks of age. Keller and Krebs (1970) show that the median weight at sexual maturity was higher in peak populations of *Microtus pennsylvanicus* and *M. ochrogaster* but equal in increasing and declining populations. This work illustrates some of the problems of using *weight* as an index of age. We know that growth

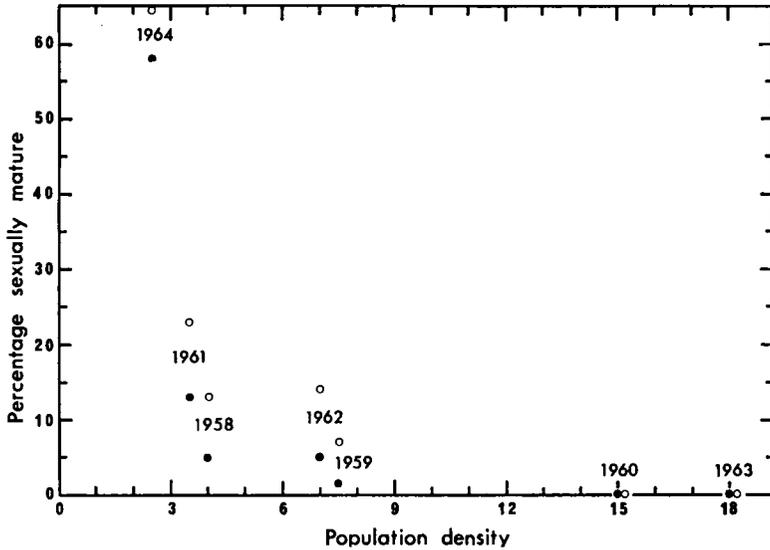


FIG. 16. Percentage of young *Clethrionomys rutilus* becoming sexually mature in their first summer in relation to the population density. Young sampled from June 15–July 31 each year; density measured by snap-trap catch per 100 trap nights in May. ○ = males; ● = females. (After Koshkina, 1965.)

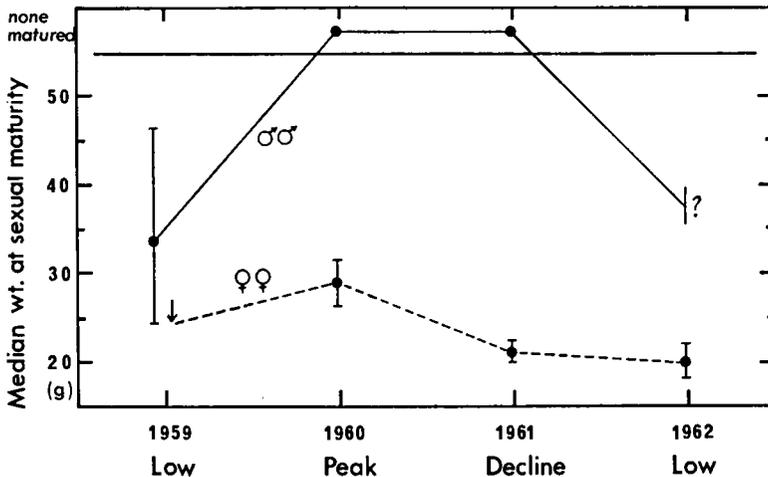


FIG. 17. Median body weight at sexual maturity for brown lemming (*Lemmus trimucronatus*) summer-born young, Baker Lake, Canada. Only the first summer litter is included. (After Krebs, 1964a.)

rates of individuals tend to be low in declining populations (Krebs *et al.*, 1969). Consequently, if *weight* at sexual maturity is equal in increasing and declining populations, *age* at sexual maturity must be greater in declining populations. If we had a reliable indicator of age in voles, we could investigate this deduction directly.

We conclude that the age of sexual maturity is an important variable in the reproductive strategy of microtine rodents. Age at sexual maturity is increased in peak populations and perhaps also in declining populations. More work is required to quantify these trends in species which can be aged.

5. Sex ratio

If the sex ratio is sufficiently disturbed from the typical 50% males two things may happen. First, if there are too few males, females might go unmated and consequently the pregnancy rate would decrease. We have not been able to find any evidence from voles or lemmings that females ever experience such limitation. Second, a shift in the population sex ratio might regulate its density. Increasing populations might have a higher percentage of females to increase the reproductive output, while peak populations might equalize the sex ratio or even favor males (Williams, 1966, p. 148). Unfortunately, natural selection does not seem to operate in such a way to maximize population fitness. Many studies on microtines have commented on sex ratios, but few have analyzed the variables which affect the observed sex ratios. Males are typically less abundant than females, but the sex ratio does not correlate with population density in *Microtus pennsylvanicus* or *M. ochrogaster* (Myers and Krebs, 1971a).

Abnormal sex ratios (20–30% males) in the wood lemming, *Myopus schisticolor*, occur in field populations because some females produce only female offspring and other females produce both sexes (Kalela and Oksala, 1966). There is as yet little information on how this abnormal sex ratio varies in relation to population density. Kalela and Oksala (1966) describe a declining population of the wood lemming in which the sex ratio increased from about 20–30% males in the peak year to about 47% males in the year of decline. Whether this change was caused by movement of animals or differential mortality is not known.

Except for the interesting case of the wood lemming, there is no indication that variations in sex ratios are associated with population fluctuations in voles and lemmings.

6. Summary

Reproductive changes are part of the machinery which drives the population cycle. Not all components of reproduction are involved,

however. Litter size does not change over the cycle, except in some species in which it is lower in the peak year. Females in declining populations have normal litter sizes. The percentage of females pregnant during the breeding season also seems to be independent of the population cycle. Length of breeding season is highly variable. Winter breeding and extended summer breeding seasons occur during the increase phase of many species. The peak year often has a shortened summer breeding season, and the decline phase may also have a restricted breeding season. Age at sexual maturity is the second component of reproduction to change during a population cycle. Animals in peak populations reach maturity at older ages and heavier weights, and young voles and lemmings may not mature at all in their first summer if born into a peak population. Age at maturity may also be delayed in declining populations. Finally, sex ratios do not seem to vary in any systematic way over the cycle in numbers.

B. MORTALITY

The reproductive changes discussed in the previous section are sufficient to generate a population cycle even if the mortality schedule were constant and independent of density. We here investigate the mortality schedules of voles and lemmings and attempt to see if there are patterns of change in mortality which reinforce or cancel the changes in reproduction.

Mark-and-recapture work is necessary for the estimation of mortality rates, and relatively little of this has been done on microtine populations throughout a cycle in numbers. Sampling problems, discussed above for the estimation of population size, plague estimation of mortality rates. Marked animals may not respond to traps in the same way. Juvenile animals are hard to catch in live traps. Animals may move off the trapping area and since disappearance is equated to death, measured mortality rates are really "loss rates".

Mortality rates are very labile in lemming and vole populations. Mortality varies with age but, given the accuracy of present methods, we recognize only three age categories: adult, juvenile and nestlings. We will now discuss each of these three age groups and then discuss prenatal mortality.

1. Adult mortality

Most of the available data on mortality rates comes from the live trapping of adult animals. Chitty (1952) estimated mortality rates in peak and declining populations of *Microtus agrestis*. Figure 18 shows some of the earliest data on survival rates in a declining population.

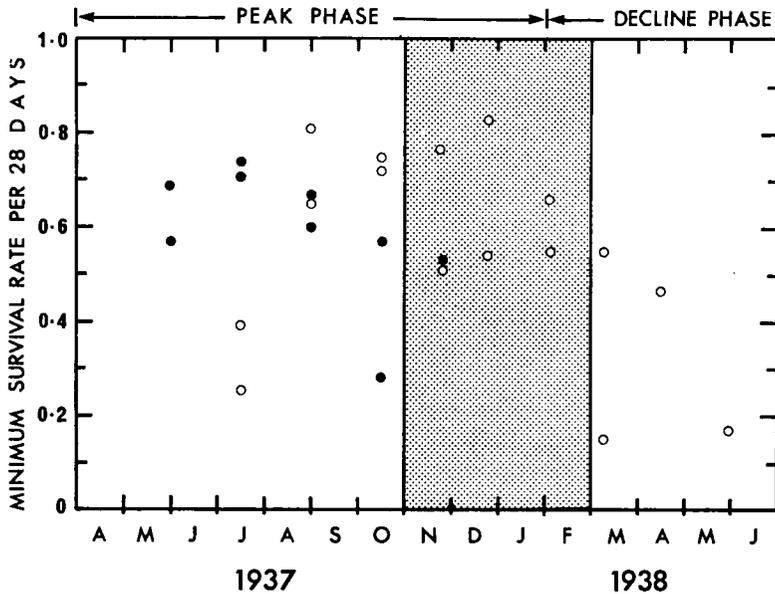


FIG. 18. Minimum survival rates per 28 days for *Microtus agrestis* during a peak and subsequent decline. Adults in 1937 gradually disappeared over the summer and the young of 1937 overwintered and declined in the spring of 1938. ● = adults of 1937, ○ = young of 1937. Two areas were live-trapped to obtain these estimates. (After Chitty, 1952.)

Adult voles in the peak year survive well (probability of survival per 28 days about 0.7) but gradually disappear through the summer to be replaced by their young. These young voles survived very poorly in the peak summer until August when survival rates improved. The young voles overwintered with good survival until January or February 1938, when survival rates dropped and the population almost disappeared. Further detailed observations were made on several declining populations of *M. agrestis* (Chitty and Chitty, 1962; Newson and Chitty, 1962). In some declines survival rates deteriorate through the winter, but in other declines survival remains good during the winter and deteriorates only in the spring. A second peculiarity of the spring deterioration in survival was noted: the two sexes may experience poor survival at different times (Chitty and Phipps, 1966). Figure 19 shows one example in which male *M. agrestis* declined about eight weeks before the females. Chitty and Phipps (1966) concluded that *M. agrestis* suffered two different types of losses: a steady drain on numbers during most of the year, and sudden severe losses, especially in spring. Spring losses occurred in peak and decline phases for *M. agrestis* and

both sexes might suffer losses at the same time or at different times (e.g. Fig. 19).

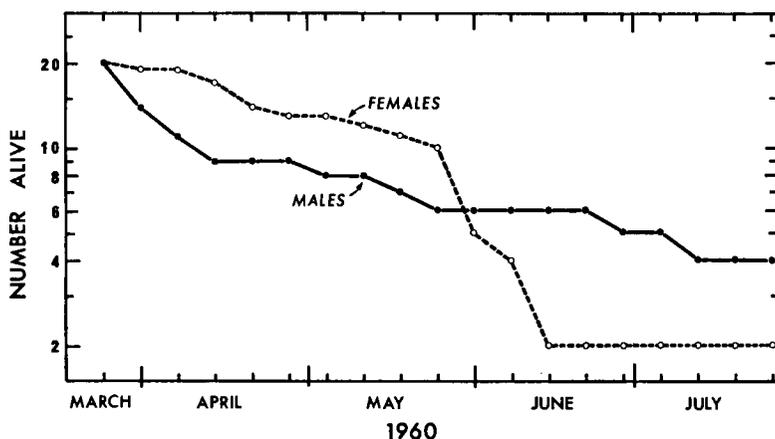


FIG. 19. Cohort survivorship curves for overwintered adults of *Microtus agrestis* in the spring of the decline phase. Note that heavy losses of males occurred at the end of March, while females survived well until the end of May. (After Chitty and Phipps, 1966.)

Adult losses are also related to cyclic phase in *Microtus californicus* (Batzli and Pitelka, 1971; Krebs, 1966). Figure 20 shows that the expectation of life is higher for voles in expanding populations. The range of average life expectation for eight populations (Krebs, 1966) was:

	Expanding populations	Declining populations
Adult males	8–12 weeks	3–6 weeks
Adult females	12–13 weeks	2–7 weeks

The poor survival characteristic of low and declining populations was manifest even in very sparse populations. For example, the RFS 5 area reached a “high” of about 20 per acre (see Fig. 13), which is about one-tenth the density of a normal peak population, but the survival rate per two weeks was only 0.45 in males and 0.36 in females. Survival rates often differed in the two sexes in *M. californicus*. The simplest interpretation of these episodes is that they are sampling artifacts from small populations, but not all episodes can be explained away so simply. Figure 21 shows a portion of the increase phase for one population of *M. californicus*. From mid March to early June 1963 males were at a plateau in numbers ($r = +0.006$ per week) while females on the same area almost doubled their numbers ($r = +0.047$). Part of the

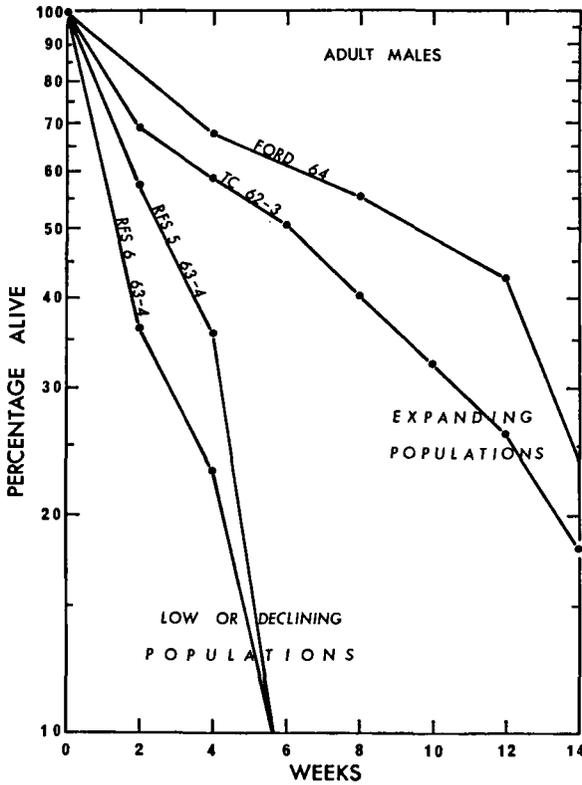


FIG. 20. Survivorship curves for *Microtus californicus* from time of first live-trap capture for animals from two expanding populations and two low or declining populations. Adult males only. (After Krebs, 1966.)

difference between the sexes was caused by lower survival rates in the males:

	Survival rates per 14 days	
	Males	Females
November 1962–March 1963	0.84	0.90
March–June 1963	0.74	0.91

Males always survive less well than females during the breeding season, but beyond this normal difference, some mortality factor affected the males but not the females in this population from March to June.

Further details of the pattern of survival changes in cyclic vole populations were obtained on *Microtus pennsylvanicus* and *M. ochrogaster* by Krebs *et al.* (1969). Figure 22 illustrates one series of survival estimates for *M. pennsylvanicus*. Survival rates differed little in

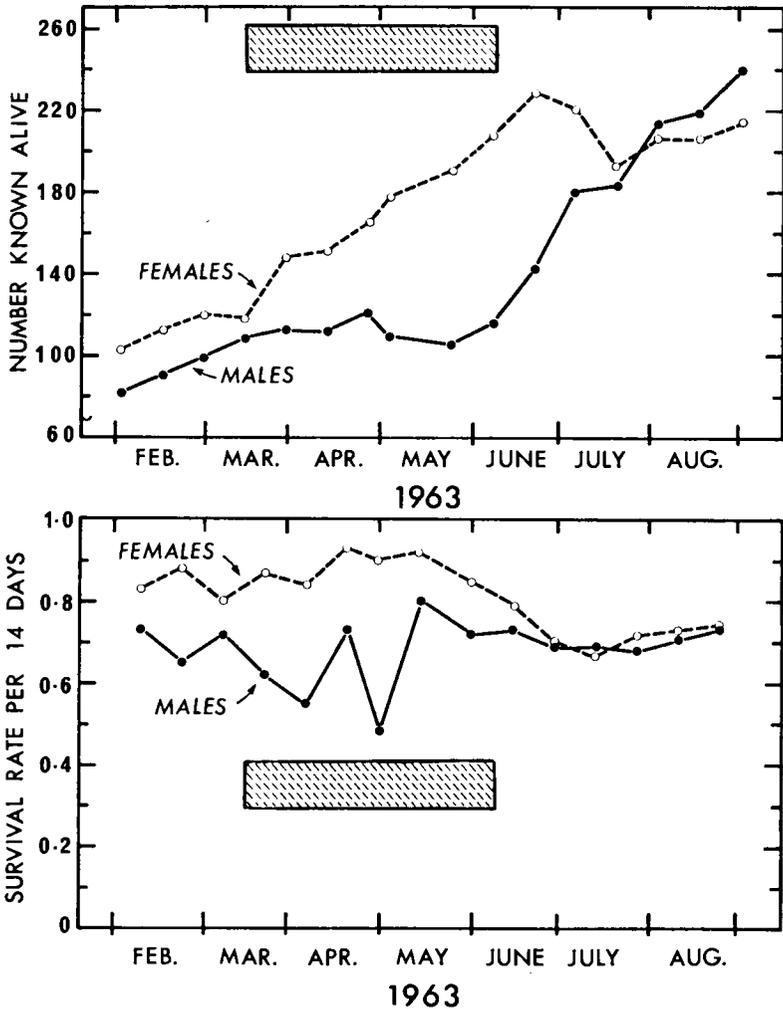


FIG. 21. An episode in the increase phase of a *Microtus californicus* population in which the two sexes behaved differently. Male survival rates were significantly below female rates for 12 weeks in a row from March to June (hatched bar). (After Krebs, 1966.)

increasing and in peak populations, but deteriorated in the decline phase, following the pattern of changes in adult survival which was described above. Survival rates do not correlate well between the two sexes on the same area, which is another way of saying that males may be surviving poorly while females survive quite well. One new observation was contributed by the study: survival rates do not correlate well

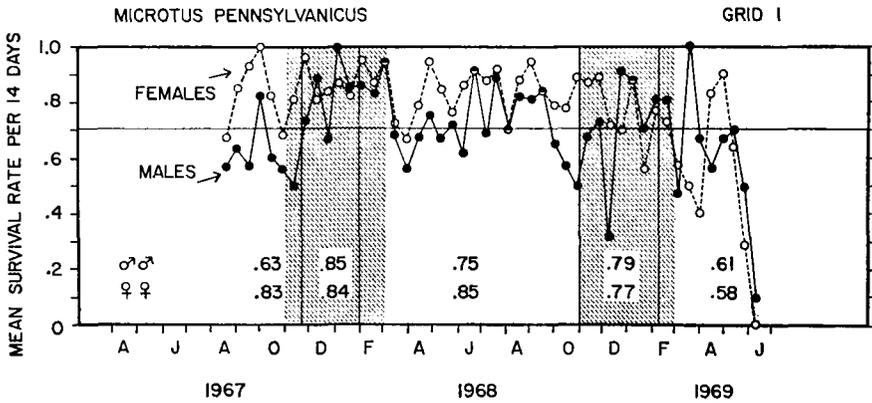


FIG. 22. Minimum survival rates obtained by bi-weekly live-trapping of a *Microtus pennsylvanicus* population in Indiana. (Density data for this population in Fig. 8.) Winter months are shaded. Mean survival rates for winter and summer periods shown at bottom. Horizontal line marks survival rate at which one half of the population disappears per month. (Krebs, unpublished data.)

between two species living together on the same area. For example, *M. ochrogaster* suffered high mortality and declined in numbers in fall, 1966, when *M. pennsylvanicus* on the same field were surviving very well (Krebs *et al.*, 1969, p. 599). Similarly Tast and Kalela (1971) report the increase of a *Lemmus lemmus* population occurring simultaneously with the decline of a *Microtus agrestis* population.

Getz (1960) estimated a mean lifespan of about eight weeks for a low population of *M. pennsylvanicus* in Michigan, and this seems to be another example of a population at low density suffering a high rate of loss. There is little information on survival rates of voles in the phase of low numbers.

There is an unfortunate shortage of quantitative data on survival changes in vole and lemming populations. The available evidence suggests that survival of adults is nearly the same in the increase and peak phases, but deteriorates in the decline phase and the phase of low numbers.

2. Juvenile mortality

Juvenile mortality rates are particularly difficult to estimate. Only a few juveniles are caught in live traps so mark-and-recapture techniques are only slightly useful for sampling this segment of the population. In most cases we can only estimate juvenile mortality indirectly by determining the number of pregnancies in the population, estimating the number of young born and then determining what fraction of these

reach the trappable population of adult voles. Sampling techniques that could catch large numbers of small juveniles would be most useful, but at present none exist (cf. Andrzejewski and Rajaska, 1972).

Chitty (1952) reported that juvenile losses in *Microtus agrestis* were high during the first half of the peak summer breeding season but were reduced in the late summer and early fall. Godfrey (1955) reported high juvenile losses in this species during the summer of two decline years. Chitty and Phipps (1966) showed that young *M. agrestis* born between March and June of a decline phase survived very poorly, while young born from July to November survived well (Fig. 23). Less than one young per pregnancy was recruited from March to June, even though mean litter size was 4.6.

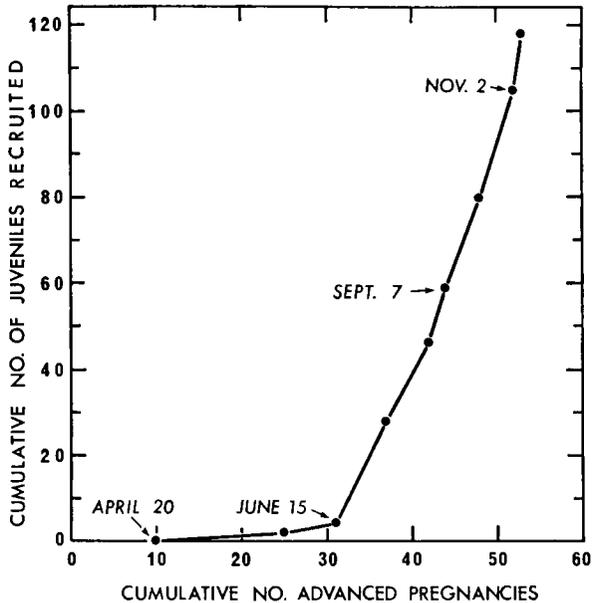


FIG. 23. Cumulative plot of number of advanced pregnancies in *Microtus agrestis* and the number of young entering the live traps four weeks later, decline phase, 1960. (After Chitty and Phipps, 1966.)

Summer mortality rates of juvenile lemmings were estimated by knowledge of litter size, number of adult females breeding on the trapping area, and subsequent number of juveniles that appeared in live traps (Krebs, 1964a). Table VII gives these data for peak and declining populations of the brown and varying lemmings in northern Canada. The results are only approximate but suggest that survival rates in the decline were only about half those in the peak.

TABLE VII

Estimated early juvenile survival rates for the brown lemming Lemmus trimucronatus and the varying lemming Dicrostonyx groenlandicus during the peak summer of 1960 and the decline summer of 1961. Juveniles were caught in live traps anywhere from two to five weeks of age; estimated survival rates are corrected for the age at first capture. (After Krebs, 1964a.)

	Brown lemming		Varying lemming	
	1960 peak summer	1961 decline summer	1960 peak summer	1961 decline summer
Total no. of litters	25	2	3	9
Calculated no. of young lemmings born	148	15	18	50
No. of juveniles later caught in traps	59	4	7	8
Estimated survival rate from birth to 14 days	0.64	0.28	0.62	0.29

By comparing the number of active mammae of female *Microtus montanus* to the number of placental scars, Hoffmann (1958) attempted to measure nestling mortality. The assumption here is that nursing young are discriminate in which nipples are suckled, so that not all nipples are developed. The frequency distribution of active mammae indicates that this may be the case since females were observed with one to seven mammae developed (median four). The inclusion of placental scars remaining after prenatal losses would increase the index of nestling mortality measured in this way. Hoffmann's data showed decreased nestling mortality in the summer of the population decline. This technique merits further testing. If Hoffmann's conclusion is correct and if juvenile losses are high in declining populations, then the major losses would have to occur after weaning.

For voles with overlapping generations Krebs and DeLong (1965) proposed an index of early juvenile survival:

$$\text{index of early juvenile survival at time } t = \frac{\text{no. of juveniles recruited at time } t}{\text{no. of lactating females at time } t-4 \text{ weeks}}$$

This index was used to investigate the association between early juvenile survival and rate of population growth in the California vole (Krebs, 1966). We wish to determine which of four independent variables—male survival rate, female survival rate, percentage of females lactating and index of early juvenile survival—are most useful for predicting the mean rate of population growth. All variables

used were mean values covering the "summer" or "winter" portions of the year (corresponding approximately to the breeding season and the non-breeding season). Table VIII gives the results of a multiple regression analysis of these five variables in the California vole. From a statistical point of view, female survival rate is the most important determinant of population growth in *Microtus californicus* and the survival rate of young juveniles is second in importance. Neither the male survival rate nor the percentage of females which are lactating are needed to predict the rate of population growth.

TABLE VIII

Multiple regression of mean rate of population growth (Y) in Microtus californicus on male survival rate (X₁), female survival rate (X₂), percentage of lactating females (X₃), and index of early juvenile survival (X₄). The best equation to describe this relationship is $Y = 0.4393 X_2 + 0.0498 X_4 - 0.3941$ which has $R = 0.88$. (Data from Krebs, 1966.)

	Multiple regression coefficient	Partial correlation coefficient	Relative importance*
Male survival rate	n.s.	0.14	—
Female survival rate	0.4393	0.86	1.0
Percentage lactating females	n.s.	0.11	—
Index of juvenile survival	0.0498	0.74	0.65

* Relative importance measured by the ratio of standardized partial regression coefficients.

A similar analysis was carried out by Krebs (1972) on a more extensive set of data on *Microtus pennsylvanicus* and *M. ochrogaster* from Indiana. For *M. ochrogaster* early juvenile survival was the most important determinant of population growth, and female survival and the percentage of lactating adults were of secondary importance. For *M. pennsylvanicus* female survival rate and the percentage of lactating adults were most important and early juvenile survival was of secondary importance. Juvenile survival was thus important in affecting population growth in both vole species.

Very few data are available concerning juvenile survival of lemmings and voles. It appears that juvenile survival is particularly low in declining populations and can also be low in peak populations, but we have no details of how this loss is distributed by age or between different litters in a population. Techniques for marking and recapturing juveniles would aid in overcoming these problems.

We can explore the relationships between population growth and

survival of adults and juveniles in a simplified life-table computation. The basic variables are the adult survival rate per 14 days and the index of early juvenile survival. The constants in the life table are the litter size at birth (4.54 in *Microtus pennsylvanicus*), the age at sexual maturity and the age at first capture. For a series of simplified calculations with *M. pennsylvanicus* we have assumed the age at first capture and the age at sexual maturity both to average five weeks. The index of early juvenile survival in association with the litter size at birth and the age at first capture determines the survival between birth and

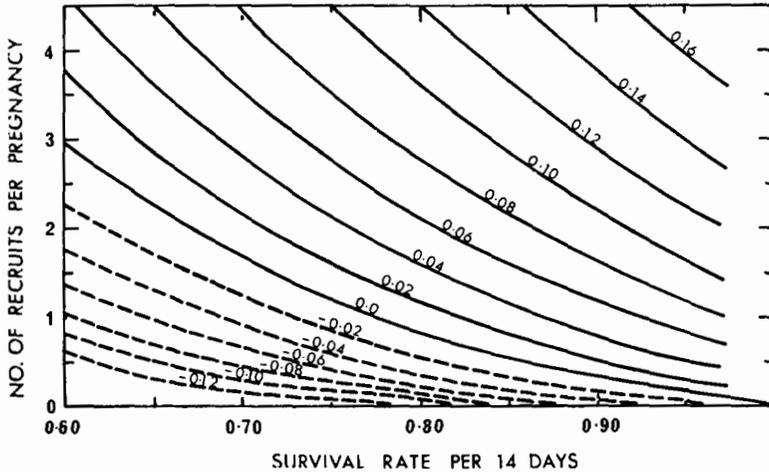


FIG. 24. Isopleths for the instantaneous rate of population growth (r) as a function of survival rate of subadult and adult voles and number of juveniles recruited into the trappable population per pregnancy. *Microtus pennsylvanicus* parameters were used in this simple life table calculation: litter size, 4.54; age at maturation, 5 weeks; age at first capture, 5 weeks.

recruitment. We assume in the simple calculations that the survival rate of adults is constant from first capture onward, and that litters are produced continually at three-week intervals throughout life. Figure 24 shows the results of this simplified life-table model for *Microtus pennsylvanicus*. In most natural populations less than two recruits are obtained from each pregnancy, and consequently the rate of population growth is very dependent on the survival rate of reproducing females. Table IX gives the average parameters of reproduction and survival for *M. pennsylvanicus* in Indiana, and illustrates the general decline in reproduction and juvenile survival from the increase phase to the peak, and the drop in subadult and adult survival from the increase and peak phases to the decline phase. Note that the survival of adult females need

TABLE IX

Demographic parameters for Microtus pennsylvanicus populations live-trapped in southern Indiana from 1965 to 1970. Early juvenile survival was measured by the number of recruits entering the trappable population per lactating female. The survival rate of adults was estimated by simple enumeration every 14 days.

	Reproduction		Survival	
	% Adults lactating	Early juvenile	Subadult and adult Males	Females
Increase phase	45	1.31	0.78	0.86
Peak phase	29	0.96	0.79	0.85
Decline phase	27	0.88	0.71	0.72

deteriorate only 0.10 to 0.15 per 14 days in order to produce a population decline. Figure 24 illustrates this also.

3. Prenatal mortality

Embryos might be lost either before implantation or after, and this mortality *in utero* could be an additional driving force behind rodent cycles. Prenatal losses are assessed by the differences in counts between corpora lutea in the ovaries, implanted foetuses in the uterus and resorbing embryos which appear in mummified form as pregnancy continues. Since most prenatal losses are small (often less than 5–10%), large sample sizes are needed to achieve statistical precision, and consequently few data are available for fluctuating populations of voles and lemmings. Kalela (1957) reported no obvious increase in prenatal mortality in a declining population of *Clethrionomys rufocanus*. Hoffmann (1958) reported only a slight change in prenatal mortality between peak and declining populations of *Microtus montanus*. Krebs (1964a) found no increase in prenatal mortality in declining populations of *Lemmus trimucronatus* and *Dicrostonyx groenlandicus* in Canada, and Mullen (1965) described the same finding for *Lemmus trimucronatus* in Alaska. Keller and Krebs (1970) found no changes in prenatal mortality over a population cycle in *Microtus ochrogaster* and *M. pennsylvanicus*. Stein (1957) reported only 3.6% resorptions in 1513 embryos of *M. arvalis*.

Thus, prenatal mortality does not seem to be related to the population cycles of small rodents. No one has yet found a population declining because of excessive prenatal losses.

4. Summary

Mortality changes are part of the syndrome of demographic events which drive population cycles in rodents. Adult mortality rates are low

in the increase and peak phases, and are high in the decline phase and also in the phase of low numbers. Juvenile losses are high in the peak phase and in the decline phase. Prenatal mortality does not seem to vary systematically during the population cycle.

C. DISPERSAL

Population densities can change because of variations in birth, death, or dispersal rates, and almost all population studies on lemmings and voles have been concerned only with births and deaths. The simplest dynamic assumption is that immigration cancels emigration and the population changes are solely a function of birth and death rates. This simple view would be adequate if there were no spatial heterogeneity in nature and no marginal habitats for small rodents (Anderson, 1970).

The importance of dispersal in population regulation of voles was first shown by studies on enclosed populations. Clarke (1955) showed that *Microtus agrestis* populations in large cement cages (67 m²) would increase to numbers far in excess of those ever found in natural areas. He obtained a population "high" at 58 individuals, which is equivalent to 3500 per acre (8657 per ha), about ten times higher than ever occurs in nature. Van Wijngaarden (1960) obtained densities of *M. arvalis* up to 7.25 voles per m² in 100 m² pens, which is equivalent to 29 300 voles per acre (72 500 per ha), approximately 100 times higher than natural. The same results were reported by Louch (1956) for *M. pennsylvanicus*, Frank (1953) for *M. arvalis*, and Houlihan (1963) for *M. californicus*.

These studies on enclosed vole populations are difficult to interpret because animals are maintained on artificial food with little or no predation, and dispersal is prevented. The next step was to study an enclosed population in a natural habitat with a normal complement of predators and natural forage. Krebs *et al.* (1969) studied populations of *Microtus pennsylvanicus* and *M. ochrogaster* enclosed in a two-acre (0.8 ha) grassland surrounded by a wire fence extending two feet above ground. These populations behaved in the same way as the confined laboratory populations—they increased to abnormally high densities and then decimated the natural forage (Fig. 25). Since severe overgrazing is rarely seen in natural grasslands, we concluded that by preventing dispersal we had destroyed the ability of the population to regulate its density at a level below that of gross starvation.

Few studies have been made of vole populations in large enclosures in the field. Gentry (1968) observed that *M. pinetorum* in a two-acre enclosure reached densities far above those in natural habitats. He

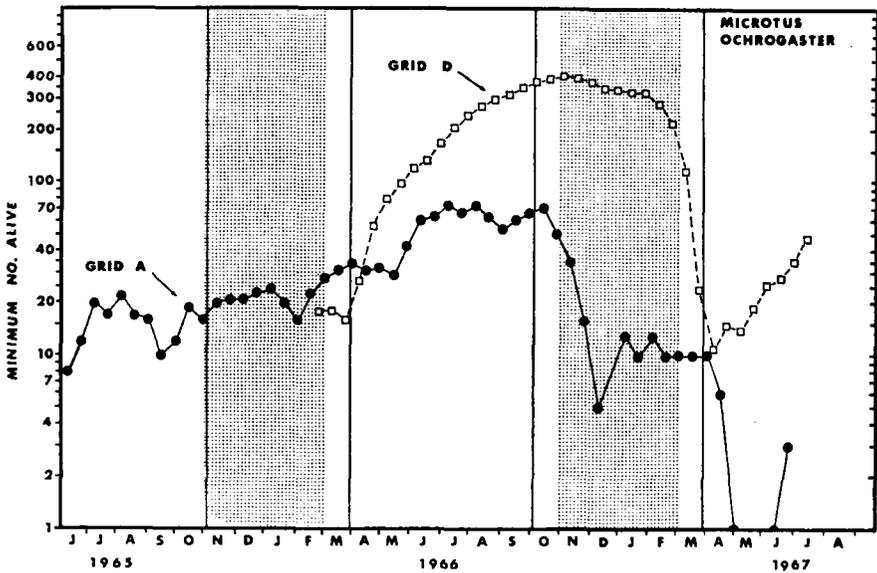


FIG. 25. "Fence-effect" in *Microtus ochrogaster*. Grid A is an unfenced control population, grid D is a two-acre fenced enclosure, which increased to a maximum of 411 voles, 5.5 times the highest control density. The habitat on grid D was destroyed by overgrazing during the winter of 1966-1967. (After Krebs *et al.*, 1969.)

attributed this "fence-effect" to a restriction of dispersal and the addition of food as trap bait.

Studies of enclosed populations suggest that dispersal may be a key factor in determining population trends in voles and lemmings. We can envisage two ways in which dispersal might be important to a population. First, dispersal may act as a safety valve for the population, and dispersing voles may normally be killed by one hazard or another. When population density becomes high more and more animals might emigrate and die, so that the decline phase might be associated with much emigration. Second, dispersal might act selectively in such a way that the quality of dispersing voles differs from the quality of residents. A number of relevant qualities might be involved: ability to avoid predators, ability to utilize certain food plants, or aggressiveness. Selective dispersal would be more important early in the population cycle and, in contrast to the first mechanism, dispersal in the increase phase might be most important for its qualitative effects. Instead of dispersers representing a random sample of the population which will be eliminated selective dispersal during the population increase could change the quality of the population resident at peak densities. In order to obtain

some information on these possible mechanisms, we must measure dispersal rates in fluctuating populations.

The measurement of dispersal rates is relatively simple in principle but few workers have tried to monitor dispersal during a population cycle. The "death rate" measured in live-trapping studies is more properly called a loss rate, since individuals which emigrate are counted in the same way as ones which die. Only one study has attempted to separate loss-by-emigration from loss-by-death *in situ*. Myers and Krebs (1971b) maintained two grassland areas free of voles for two years and measured the amount of colonization which occurred from adjacent control areas. Some voles (*Microtus pennsylvanicus* and *M. ochrogaster*) which disappeared from the control areas turned up as immigrants on the vole-free areas and hence we could obtain a minimum estimate of the proportion of the mortality given in Table IX which was

TABLE X

Percentage of losses known to be due to dispersal for two control populations of Microtus pennsylvanicus in southern Indiana. Dispersing voles were picked up as they colonized vole-free areas. Total number lost in parentheses. (After Myers and Krebs, 1971b.)

Phase of cycle	Males	Females
Increase phase	56% (32)	69% (16)
Peak phase	33% (157)	25% (127)
Decline phase	15% (53)	12% (42)

loss-by-emigration. Table X gives these results, and shows that losses-by-emigration are proportionally largest in the increase phase and smallest in the decline phase. Consequently, the high mortality rates of adult voles in the decline are associated with death *in situ* rather than with dispersal.

There are several criticisms which can be made of this single study, and more attempts must be made to measure dispersal losses before we can reach any general conclusions about the relationship between mortality and dispersal losses. First of all, in this study it was necessary for the dispersing voles to remain in the vacant habitat a sufficient length of time so that they could be caught in traps (maximum two weeks). It is possible that other dispersers existed which were not attracted to the vacant habitat and therefore could not be monitored. Thus there may have been a set of dispersers which were influenced by the peak population densities and emigrated but they were not in search of a new, less crowded, suitable habitat. These may be thought of as "pathological" dispersers most certainly to suffer high mortality

rates. In order to identify this potential type of disperser it would be necessary to catch every animal leaving a population. This could be done by monitoring egress from a semi-enclosed population. No one has done this yet.

Immigration is more difficult to measure than emigration because of the difficulties of live-trapping voles and lemmings. It is impossible to know that you have trapped and removed every single individual from an area. Thus, new individuals which appear on a live-trapping area may have been the offspring of females which had avoided being trapped. On the other hand, they may have moved in from adjacent areas. Some method of radioactive marking of pregnant females might be used to get at this problem. If it were possible to label radioactively all young being produced in surrounding areas, dispersers from these areas could be positively identified. Genetic markers might be used in a similar way. What we would like to determine is the exact source area of each immigrant. So far nothing has been done along these lines.

We expect that the results of measuring immigration would not be the converse of those for measuring emigration. Vole populations should be closed to most immigrants, at least after the increase phase is over, so that emigrants from one area will not usually be able to colonize an adjacent area, except if population densities are low or if it is a marginal habitat or is otherwise vacant for historical reasons. This discussion leads to another suggestion for studying dispersal: artificial immigration could be used to measure the ability of a population to absorb immigrants at different phases of the population cycle.

In summary, dispersal is the least studied process in the population equation for voles and lemmings. Studies on enclosed populations indicate that numbers reach abnormally high levels when dispersal is stopped. Almost no one has attempted to measure dispersal rates over a population cycle. A single study showed highest dispersal during the increase phase and almost no dispersal during the population decline. Dispersal may change a population qualitatively as well as quantitatively. This idea will be elaborated in a later section discussing the possible role of genetic changes in causing microtine cycles.

D. GROWTH

The growth of individual animals in cyclic populations is important because it is tied to the primary processes 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 can be measured in many ways but the simplest measurements are changes in weight or length. Length is a good measure of

size since it is a measure of skeletal development, while weight is a measure of robustness and a relatively poor measure of size. Weight is easy to determine for live animals in the field and it is also easily standardized among different observers. Length, by contrast, is more difficult to measure on live animals and almost impossible to standardize among observers (Jewell and Fullagar, 1966). The ideal study would consist of one observer measuring weights and lengths on all individuals, but in most cases only weight data are collected.

One of the generalized features of population cycles of rodents is that animals in peak populations are much larger than those in other phases of the cycle. This feature was first recognized by Chitty (1952) for *Microtus agrestis*. Table XI gives some representative figures for

TABLE XI

Mean body weight (± 1 standard error) of adult male voles and lemmings at the start of the breeding season in different phases of the cycle

	<i>Microtus agrestis</i> ¹ (May)	<i>Lemmus trimacronatus</i> ² (16-30 June)	<i>Microtus arvalis</i> ³ (spring)	<i>Microtus californicus</i> ⁴ (October)
Increase phase	28.3 \pm 1.0	50.2 \pm 1.8	22.6	52 \pm 2
Peak phase	34.1 \pm 1.2	79.3 \pm 2.5	24.4	64 \pm 1
Decline phase	18.9 \pm 0.9	61.6 \pm 2.1	22.4	50 \pm 1

¹ Area O, 1957-1960, from Chitty and Chitty (1962, Table 4).

² 1959-1961, from Krebs (1964a, Table 45).

³ 1951-1953, from Stein (1957, Table 10).

⁴ 1966-1968, from Batzli and Pitelka (1971, Fig. 3).

changes in mean body weight with changes in density for these microtine species, and Fig. 26 illustrates changing body weight distributions for a *M. ochrogaster* population. There are 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 juvenile 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.

We can eliminate the first explanation as a sufficient one. In *Microtus agrestis* Chitty (1952) has shown that larger voles of the peak phase are

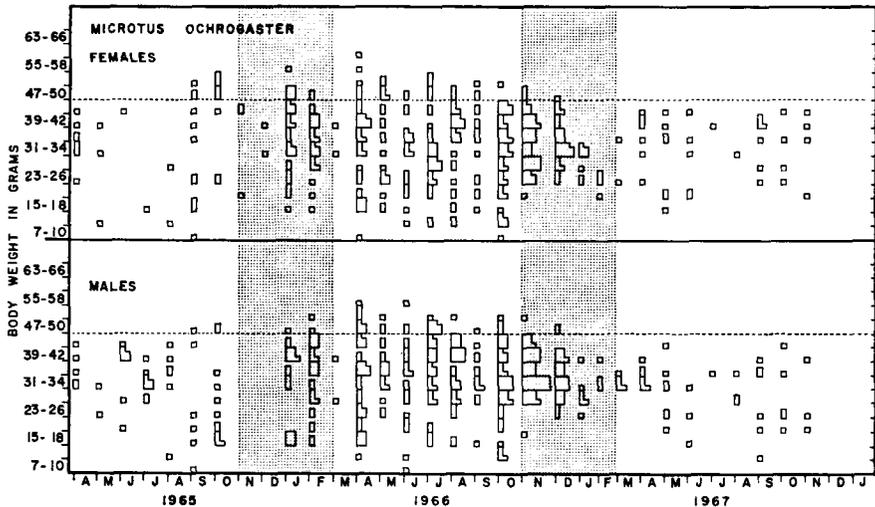


FIG. 26. Body weight distributions for snap-trapped samples of *Microtus ochrogaster* from southern Indiana. These populations increased in 1965, peaked in 1966, and declined in 1967. Winter months are shaded; one small square equals one vole. (After Keller and Krebs, 1970.)

the same ages as smaller voles of the decline phase. Zimmermann (1955) has shown that size changes in *M. arvalis* populations are not simply changes in age composition. Krebs (1964a) reported that in the lemmings *Lemmus trimucronatus* and *Dicrostonyx groenlandicus* the heavy animals of the peak year were on the average younger than the light animals of the decline phase.

The second and third explanations are difficult to separate with the available data. Growth rates are higher in increasing and peak populations of *Microtus pennsylvanicus* (Fig. 27) and *M. ochrogaster* (Krebs *et al.*, 1969), and these results support the second explanation. The same relationship was found in *M. californicus* but was confounded with seasonal and reproductive effects on growth (Krebs, 1966). Unfortunately there are no data available on growth rates for species of *Clethrionomys* or *Microtus* which do not breed during winter and yet fluctuate cyclically.

The third explanation of a variable asymptotic weight could be investigated if a sufficient number of measurements on individuals taken over time were available. Several authors have recognized that the growth curves of spring-born voles differ from those of autumn-born voles. Reichstein (1964) recognized two patterns for *Microtus arvalis*. Voles born from March to June increase rapidly in weight (to a maximum of 47 g) and become sexually mature. Voles born from

June to October increase in weight only to 15–22 g and remain all winter at these low weights. Chitty (1952) observed the same general pattern for *M. agrestis*, and Kalela (1957) reported it for *Clethrionomys rufocanus*. But while these seasonal variations have been clearly described, few have tried to relate individual growth curves to density changes.

Anderson (1970) emphasizes the distinction in growth and maturation between spring- and fall-born animals, and refers to them as nearly separate “generations”. There is little justification for such a clear-cut

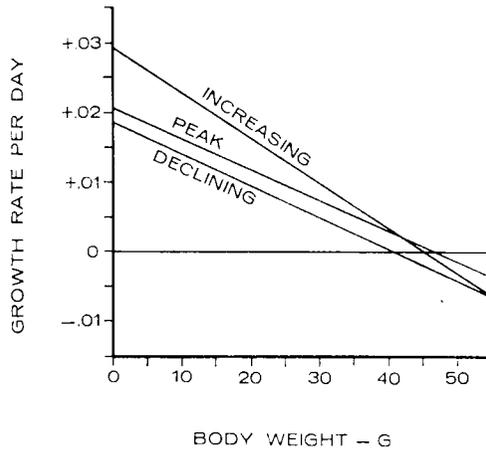


FIG. 27. Instantaneous relative growth rates of *Microtus pennsylvanicus* males from southern Indiana in relation to body weight. For increase phase, $n = 691$; for peak phase, $n = 1898$; for decline, $n = 333$. The slopes of the three regression lines are significantly different ($p < 0.01$). (After Krebs *et al.*, 1973.)

distinction between “spring and summer generations” and “autumn generations”. Clarke and Forsyth (1964), for example, document large differences in sexual activity among fall-born *Microtus agrestis* of different years. In *M. ochrogaster* and *M. pennsylvanicus* in Indiana the breeding season continues most of the year and there are several generations in the spring and summer. We do not see how the weight changes associated with population cycles can be explained by the seasonal growth patterns associated with spring-born or fall-born young. To discuss the population increase of cyclic rodents as instances of exceptional years in which the spring and summer generation survives and continues to the fall generation (Anderson, 1970) merely begs all the questions we have been trying to answer. We still have to ask why in some years the first summer generation is able to survive while in others it is not.

Differences in body weight have not been the only criterion by which one could recognize rodents from peak populations. Zimmermann (1955) found that mandible lengths in *Microtus arvalis* changed over the population cycle in the same way that body weight changed. Krebs (1964b) investigated the relationships between body size and skull size in brown and varying lemming populations from northern Canada. Lemmings were larger in peak populations, when measured by body weight, body length, or skull dimensions. But surprisingly the relationships between skull and body measurements changed systematically in relation to population density. Lemmings of a given

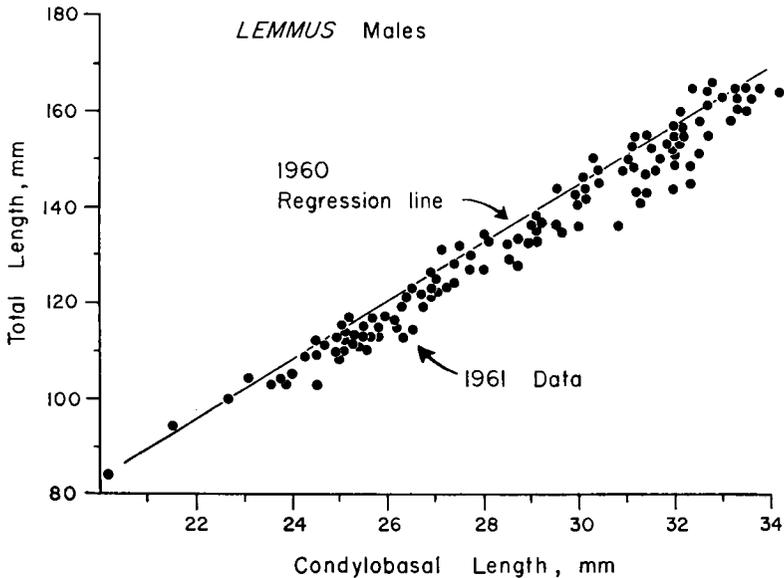


FIG. 28. Relationship between skull length and body length in male brown lemmings from northern Canada. The regression line which fits the measurements from the peak phase of summer 1960 did not fit the measurements from the decline phase of summer, 1961. The position of the regression line moves up and down the graph as the population density fluctuates. (After Krebs, 1964b.)

body size did not have the same skull size at different phases of the population cycle (Fig. 28). These changes in skull-body relationships are significant because they might be evidence for genotypic changes over the population cycle. No one has repeated these observations for any other rodent species, and we do not know how general such a pattern might be.

High body weights in the peak breeding season were considered to be characteristic of all rodent cycles by Krebs (1964a). A single exception has been found. Fuller (1969) followed a population fluctuation in

Clethrionomys rutilus and *C. gapperi* and found no change in mean body weight. Fuller presents weight data for two years only, the peak and decline summers for *C. gapperi* and two apparent peak summers for *C. rutilus*. Further data are needed for increasing and low populations, but it is puzzling that he found no differences in the declining population of *C. gapperi*. Elliott (1969) claimed that *C. gapperi* populations do not fluctuate cyclically in most of their distributional range. If high populations of *C. gapperi* represent irregular irruptions rather than regular cycles, we might use the high body weight criterion to distinguish these two classes of population fluctuations. Regardless of our classification scheme, however, it would seem important to find other microtine populations which do not behave as predicted.

Another approach to the study of growth over a rodent cycle is to compute "indices of condition". LeCren (1951) proposed a relative condition factor obtained as the ratio

$$\frac{\text{observed weight}}{\text{weight predicted from body length}}$$

Condition factors of this type have been widely used in fish population studies. We have tried to use LeCren's index of condition to investigate fluctuations of *Microtus pennsylvanicus* and *M. ochrogaster* in southern Indiana (unpublished data). Snap-trap samples were obtained over six years, and body length and weight were taken during standard autopsies (Keller and Krebs, 1970). We pooled all the data to calculate the body weight (Y)-body length (X) regression for each species, and then referred individual voles to this common regression to get the predicted weight. Figure 29 shows our results for *M. ochrogaster*, which reached peak densities in 1966 and 1969 in our study areas. It is apparent that there are large changes in "condition" of voles from year to year. We could detect no clear trends related to density, however. Condition was "poor" in increasing populations in 1965 and "average" to "good" in declining populations in 1967. There was no clear seasonal trend, and this may reflect the relatively mild winters of southern Indiana. We concluded from our analysis that there were real differences from year to year in relative condition but these differences were not related to cyclic density changes.

There is an array of more sophisticated methods for determining relative condition of rodents. Krebs (1964a) used an arbitrary fat index to judge the amount of stored fat on lemmings (*Lemmus* and *Dicrostonyx*). There was no relation between the amount of fat which lemmings had stored and population density. Batzli and Pitelka (1971) extracted the fat from *Microtus californicus* carcasses and also were not able to associate levels of stored fat with population changes.

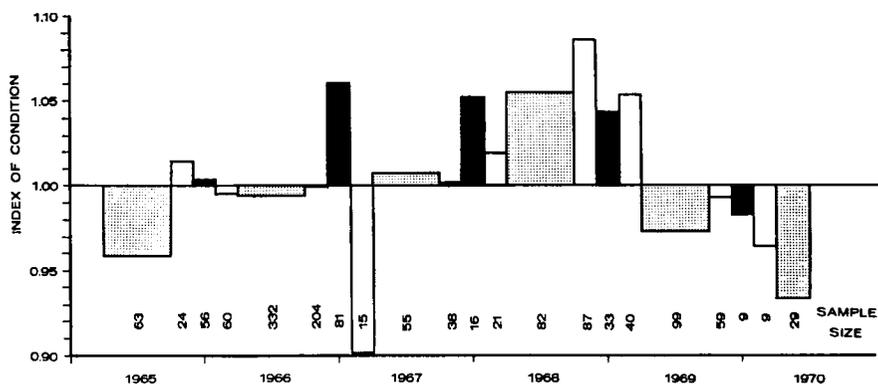


FIG. 29. Index of relative condition (observed weight/predicted weight) for *Microtus ochrogaster* in southern Indiana. Both sexes combined, snap trap samples. Populations peaked in 1966, declined in 1967, and peaked again in 1969. There is no apparent relation between relative condition and density changes. (Krebs and Myers, unpublished data.)

Therefore, the increased body weights characteristic of individuals from peak populations are not simply the result of additional stored fat.

We will not try here to review possible explanations for the growth differences described. They are part of the syndrome of changes for which any satisfactory theory must somehow account.

To summarize, high body weights have been associated with peak population densities for a variety of voles and lemmings. These large animals are not simply older animals. Growth rates are higher for individuals in increasing and peak populations for the few voles for which we have detailed data. Whether individuals from different phases of the population cycle have different asymptotic weights remains unclear. Growth differences occur not only in body size but also in skeletal proportions.

VI. HYPOTHESES TO EXPLAIN POPULATION CYCLES

We have described the demographic characteristics of microtine cycles. We will next review hypotheses which have been proposed to explain these demographic and density changes.

A. FOOD

The lemming cycle, according to Lack (1954), was due to the over-exploitation by the lemmings of their habitat with destruction of the food and cover resulting in greater exposure to predators. Thus, the

lemmings were thought to bring about their own demise by eating the vegetation which provided cover and protection while the predators acted as the agents of mortality. Pitelka (1958) reformulated the food hypothesis and suggested that the lack of food brought about by high density lemming populations led to malnutrition and reduced reproduction, and thus a population decline.

To analyze the relationship of microtines to their habitat we will consider three questions: (1) Are microtines selective in their food choices? (2) What is the effect of microtine grazing on the habitat? and (3) Does the quantity or quality of the food supply become limiting to increasing microtine populations?

1. *Selectivity of microtine food habits and habitats*

Microtines live in a variety of habitats from woodland (*Clethrionomys*) to meadows, grasslands and old fields (*Microtus*, *Synaptomys*, *Pitymys*) and to alpine meadows and tundra (*Microtus*, *Lemmus*, *Dicrostonyx*). For the grassland and tundra dwellers food and cover are provided by the same plants.

Various workers have raised the question of the selectivity of microtines in choosing food plants from their habitat. The preferred food plants of *Microtus pennsylvanicus* in Minnesota were found to be clover and dandelion, neither of which are common in the natural habitat of this animal (Thompson, 1965). Introduced grasses are readily eaten by *M. ochrogaster*, *M. pennsylvanicus* (Thompson, 1965; Zimmerman, 1965) and *M. californicus* (Batzli and Pitelka, 1971). Therefore, microtines appear to be very catholic in their food habits and they generally take what is most readily available (Martin, 1956), often introduced grass species. However, Godfrey (1953) reported that *Helicotrichon pubescens* occurred more often in fecal pellets of *Microtus agrestis* than would be predicted from its abundance in the habitat, and Batzli and Pitelka (1971) also had some evidence of food preferences of *M. californicus*. Fleharty and Olson (1969) found that, although availability of food types was an important factor, *M. ochrogaster* showed some selectivity based on the growth stage and the palatability of the food plants. Kalela and Koponen (1971) state that lemmings show preference in the types of mosses they eat, particularly favoring those of the genus *Dicranum*.

Thompson's studies of food preference of *Microtus pennsylvanicus* showed that plants from old field habitats were more acceptable than those from marshes, tall grass prairie or boreal forest, and the developmental environment of the individual *Microtus* did not influence its food preference. Also Thompson found that the quality of the soil on which a plant was grown did not influence its acceptability to *M.*

pennsylvanicus. *Poa pratensis* from gravel, clay and silt loam areas was judged by Thompson to be unfavorable, suboptimal, and optimal based on the color, vigor and succulence of the plants. Pieces of sod with grass from these three areas were presented simultaneously to *Microtus pennsylvanicus*. The percentages of the stems which were clipped by the animals were 63, 63 and 58%. This test suggests that microtines may not be very selective in choosing the quality of their food.

Microtus ochrogaster in Indiana takes a wider variety of plant species as food than does *M. pennsylvanicus*, and this is correlated with the greater diversity of plant species in habitats where *M. ochrogaster* are common (Zimmerman, 1965). Batzli and Pitelka (1971) confirmed that for *M. californicus* the species common in the habitat were also common in the diet.

If food supply is a critical influence on the dynamics of rodent cycles, we might look for differences between microtine species with different food habits. An attempt at assessing the relation of voles and their habitats to population phenomena can be made by comparing *Microtus*, which are grassland dwellers, to *Clethrionomys*, which live in scrubby or wooded areas. Comparisons of food habits of *C. rutilus* and *M. oeconomus* dwelling in a white spruce forest near College, Alaska were made by Grodzinski (1971). Berries, fruits, tree seeds, fungus and lichens were preferred by the red-backed voles (*C. rutilus*), while greens were most preferred by the tundra vole (*M. oeconomus*), although berries, fruits and seeds were also taken to a large degree. The results of laboratory preference tests agreed well with those of stomach content analyses. But all species of *Clethrionomys* are not similar in their feeding habits. Tast and Kalela (1971) state that *C. rufocanus* is a greens eater while *C. rutilus* is a seed eater. All species of *Microtus* seem to feed on greens.

That *Microtus* and *Clethrionomys* compete where sympatric has been demonstrated by observations that when only one species is present, for example on an island, it will invade the habitat usually occupied by the other species (review in Morris and Grant, 1972). Also experimental manipulations have been carried out to show that *M. pennsylvanicus* tends to exclude *C. gapperi* from grasslands and *C. gapperi* tends to exclude *M. pennsylvanicus* from wooded areas. Therefore, although their preferred habitats are different, there is some overlap in the ecological requirements of these two species.

Clethrionomys populations tend to exist at lower densities than *Microtus* populations (Table XII). Some but not all species of *Clethrionomys* seem to fluctuate in regular cycles, but whether fluctuations are related to feeding habits is not clear. One of the longest series of popula-

TABLE XII

Peak population densities in Clethrionomys

Density	Species	Author
30/acre	<i>C. rutilus</i>	Whitney (unpublished)
10/acre	<i>C. rutilus</i>	Fuller (1969)
Approx. 30/acre	<i>C. rutilus</i>	Koshkina (1965)
Approx. 30/acre	<i>C. rutilus</i>	Pruitt (1968)
10/acre	<i>C. gapperi</i>	Fuller (1969)
14/acre	<i>C. gapperi</i>	Elliott (1969)
Approx. 30/acre	<i>C. glareolus</i>	Ashby (1967)
Approx. 70/acre	<i>C. glareolus</i>	Newson (1963)
20-40/acre	<i>C. glareolus</i>	Petrusewicz <i>et al.</i> (1971)

tion data on a microtine is that of Koshkina (1966) shown in Fig. 3. These data are for *C. rufocanus* (a greens eater) and show regular population fluctuations. Density data for *C. rutilus* (a seeds eater) in the Russian taiga are included in Fig. 16, based on the data of Koshkina (1965). Of the seven years of the study (1958-1964) two years of peak abundance occurred, 1960 and 1963. Pruitt (1968) collected density data for *C. rutilus* for seven years near Fairbanks, Alaska and observed peak populations in 1954 and 1959 (Fig. 30). Others have found population fluctuations of *Clethrionomys* but with no clear cyclic pattern. For

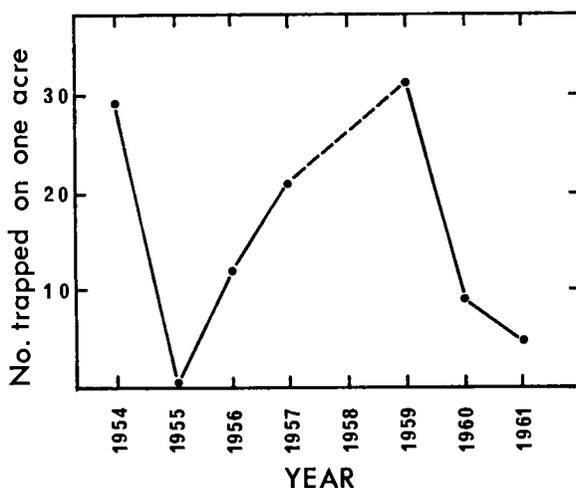
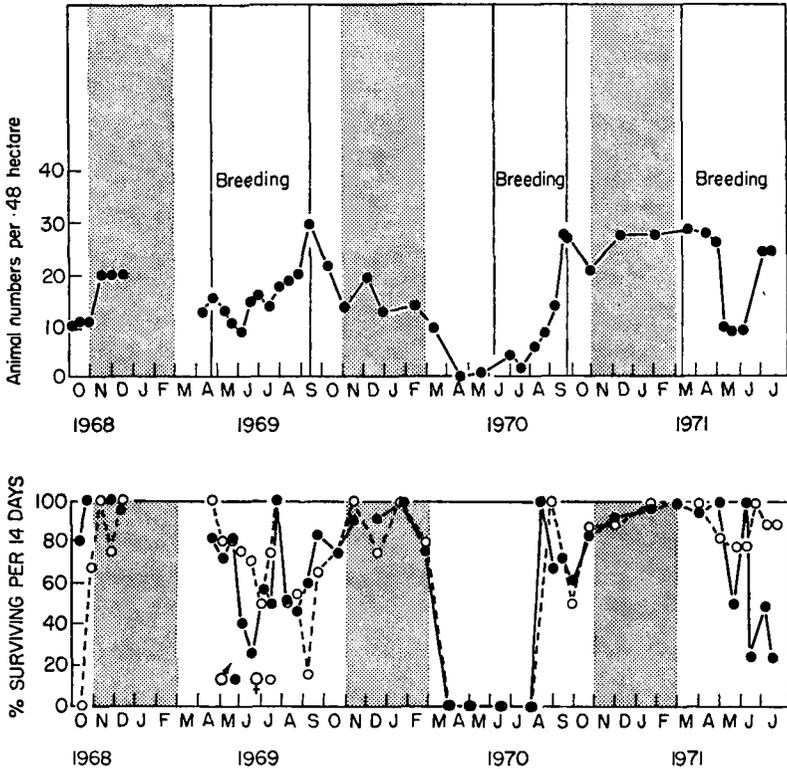


FIG. 30. The number of *Clethrionomys rutilus* trapped on a one-acre plot of taiga forest near Fairbanks, Alaska. These estimates come from a single trapping in September of each year. Data from Pruitt (1968).

example, Whitney (unpublished) (Fig. 31) had peak densities of about 20 to 30 *C. rutilus* per acre in each autumn of three years of his study, but during one summer densities were very low until late August while in other summers densities were somewhat higher. Elliott's (1969) study of *C. gapperi* showed one year in which the population maintained very low densities through the summer. An island population



All studies indicate that *Clethrionomys* reaches the annual peak late in the fall. For this reason we must be suspicious of data which are obtained from only one or two trappings a year or from field samples collected for only a short summer period.

There are only three records of winter breeding in *Clethrionomys*, and this genus would seem to differ from lemmings and *Microtus* in that winter breeding is rare. No one has investigated why *Microtus* is able to breed in some winters while *Clethrionomys* usually does not. Evernden

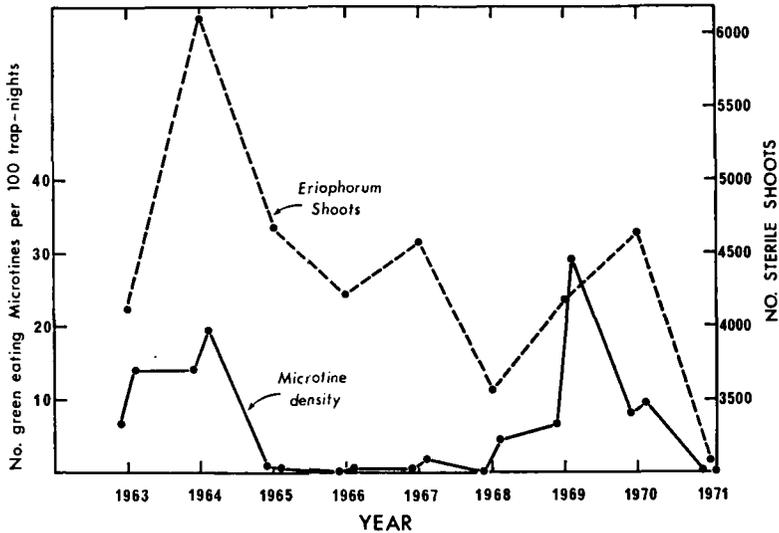


FIG. 32. The relation of microtine densities to plant production (number of *Eriophorum angustifolium* shoots per 75 sq. m) in Finnish Lapland. Data from Tast and Kalela (1971).

and Fuller (1972) have indicated that the beginning of the breeding season in *C. gapperi* is controlled by day length. Snow is a very effective light filter, and we do not know whether *C. gapperi* monitors the light levels in spring by short excursions above the snow surface. But as shown previously (p. 295), *Clethrionomys* are capable of winter breeding. In Whitney's (unpublished) study breeding began in a *C. rutilus* population in March 1971 when the snow depth was 120 cm and it was a month before the snow melted to a depth of 20 cm. Also Whitney's study showed great variability in the date of onset of the breeding season as follows: April 1969; June 1970; and March 1971.

Pinter and Negus (1965) review studies of photoperiod and reproduction on *Microtus* species. In their own work they showed that the food quality, specifically young growing shoots of oats, had a greater influence on reproduction in *M. montanus* than did photoperiod.

Data are not available for a detailed comparison of *Microtus* and *Clethrionomys*. We might predict that *Clethrionomys* with only rare winter breeding would fluctuate less than *Microtus* which can breed all year. Also *Clethrionomys* should have a lesser impact on its woodland habitat than the grassland-dwelling *Microtus*, which again might act to buffer fluctuations. There are no data available to test these simple suggestions. *Clethrionomys* show many of the demographic characteristics of fluctuating microtines (see section V). Whitney's work shows that in the same study area, *C. rutilus* reached similar densities in the autumns of the three years of the study, while *Microtus oeconomus* reached peak densities in one summer and declined to extremely low densities thereafter. Studies comparing sympatric and allopatric populations of *Microtus* and *Clethrionomys* may help us to determine more specifically those characteristics which distinguish cycling microtine populations and to determine the influence of habitat on population phenomena.

2. The effect of microtine grazing on the food supply

Do foraging activities of microtines remove a significant proportion of the food supply? Thompson (1955b) and Pitelka (1958) report extensive forage utilization preceding declines of brown lemming populations at Barrow, Alaska. However, Chitty (1960) and Krebs (1964a) reviewed studies in which neither habitat destruction nor starvation were observed to be associated with declining vole and lemming populations.

A number of studies have been carried out to measure the percentage of the available food energy which is consumed by microtines (Table XIII). With two exceptions the percentage of available energy con-

TABLE XIII

Percent of available food energy consumed per year by small mammals in a variety of habitats

Ecosystem	Principal small mammals	% Available food consumed (kcal)	Reference
Pinewood Mazury Lakeland, Poland	<i>Clethrionomys glareolus</i> <i>Apodemus flavicollis</i>	0.6-1.9	Ryszkowski (1969)
Oak-pine forest Mazury Lakeland, Poland	<i>C. glareolus</i> <i>A. flavicollis</i>	0.6-0.8	Ryszkowski (1969)
Mixed and deciduous Kompinos Forest, Poland	<i>C. glareolus</i> <i>A. flavicollis</i> <i>A. agrarius</i>	0.6	Ryszkowski (1969)

TABLE XIII (contd.)

Ecosystem	Principal small mammals	% Available food consumed (kcal)	Reference
Oak-hornbeam Cracow, Poland	<i>C. glareolus</i> <i>A. flavicollis</i>	4.6	Grodzinski (1971)
Beechwood Ojców, Poland	<i>C. glareolus</i> <i>A. flavicollis</i>	3.9	Grodzinski <i>et al.</i> (1969)
Spruce plantation Björnstorp, South Sweden	<i>Microtus agrestis</i>	1.5-2.8	Hansson (1971)
Forest plantation on peat bog Augustów Forest, Poland	<i>M. oeconomus</i>	3.1	Gebczynska (1970)
Alpine meadow Bieszczady Mountains, Poland	<i>Pitymys subterraneus</i> <i>M. agrestis</i>	1.03	Grodzinski <i>et al.</i> (1966)
Cultivated plants South-eastern Poland	<i>M. arvalis</i>	1-20	Migula <i>et al.</i> (1970)
Old field Ingels, South Finland	<i>M. agrestis</i>	3-14	Myllymäki (1969)
Cultivated fields and refuge habitats, Poland	<i>M. arvalis</i>	0.5-1.3	Trojan (1969)
Old field Alaskan Taiga Forest	<i>M. pennsylvanicus</i> <i>C. rutilus</i> , <i>M. oeconomus</i> <i>Tamiasciurus</i> <i>hudsonicus</i> , <i>Glaucomys</i> <i>sabrinus</i> , <i>Sorex</i> <i>cinereus</i>	0.4-1.6 3-47	Golley (1960) Grodzinski (1971)

sumed by the microtines has been estimated to be less than 5% of the available net primary production. The opposite side of the coin is to determine the influence of microtines on the production of the habitat. Schultz (1965) measured grass production in a tundra area from which lemmings were excluded and found that over seven years of observation, the production by vegetation in the exclosures declined (Fig. 33). Outside in grazed areas the production was almost always greater than in the exclosure although there was some variation from year to year. However, this relationship was not simple since the exclosures were actually built in 1949 and during the first four years (1950-1953) the measured production of the vegetation averaged 500 pounds per acre.

The standing crop of the tundra vegetation was measured by Schultz (1965) and these measurements showed the same variation as did the production data. While years of high lemming density seemed

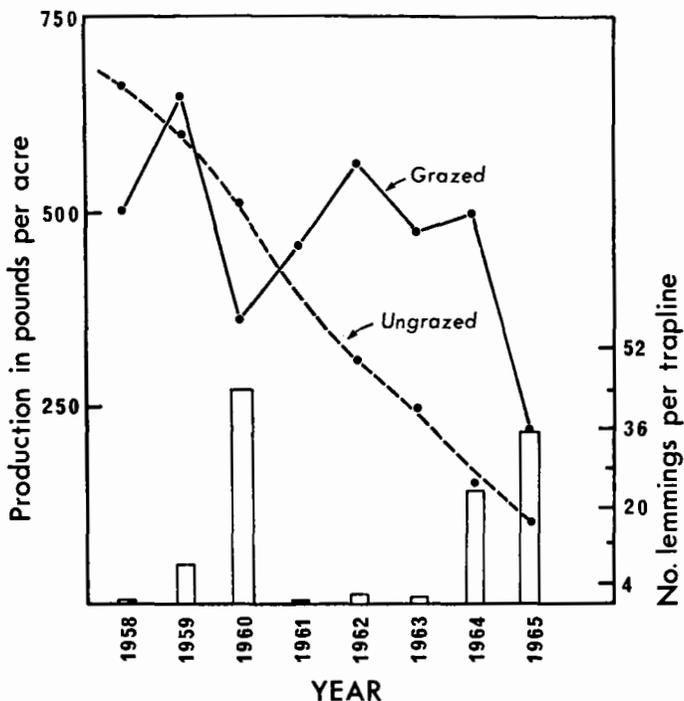


FIG. 33. Primary production in exclosures (dotted line) decreased as a result of no lemming grazing. Primary production in open tundra fluctuates and is moderately related ($r = -0.69$) to lemming density (indicated by bars). Production data from Schultz (1965) density data are maximum average number of lemmings caught per trapline of the two or three trapping periods per summer from Pitelka (1972).

to decrease the standing crop there was no significant relationship between the measured standing crop of the vegetation and the density of lemmings ($r = -0.25$, n.s.).

Estimates of the proportion of the standing crop taken by peak microtine populations have varied from low values of 15% reported by Krebs (1964a) for lemmings and 38% by Batzli and Pitelka (1970) for *Microtus californicus*, to high values of 50% by Thompson (1955b) and 50–90% by Schultz (1964) for lemmings.

Grazing by microtines has been shown to influence the plant species composition of the habitat. Summerhayes' (1941) study of *M. agrestis* showed that grazing caused reduction in the grasses and allowed flowering plants and mosses to be established. Exclosures which prevented grazing by the California vole permitted Batzli and Pitelka (1970) to observe an 85% reduction in the volume of major *M. californicus* food plants by grazing of a peak population (160 per acre),

and a 70% decrease in the seed fall of preferred grasses in grazed areas.

Kalela (1962) suggested that microtine density fluctuations were coupled to variation in plant production resulting from weather conditions. The emphasis on the climate as the underlying variable leading to microtine cycles arises from the geographically widespread synchrony observed in small mammal density fluctuations. Rodent cycles are viewed by Kalela as being the result of random oscillations of weather conditions which influence the flowering frequency of food plants and variations in their nutritional state, as well as inherent rhythms of the food plants and rodent populations. To investigate this association Tast and Kalela (1971) accumulated density data on four species of microtines (*Lemmus lemmus*, *Microtus agrestis*, *M. oeconomus*, *Clethrionomys rufocanus*) and two of their preferred food plants, narrow leaved cotton grass, *Eriophorum angustifolium*, and golden-rod, *Solidago virgaurea*.

The microtine populations, estimated by two trappings a year with snap-traps, showed peak densities in the fall of 1964 and again in the fall of 1969 (Fig. 32). While the number of shoots of the cotton grass was highest in 1964 in synchrony with the peak microtine density, in 1969, the year of the second microtine peak population, the number of cotton grass shoots was no higher than it had been during the intervening years of low microtine densities. The number of shoots of *Solidago* showed little change between 1965, when quantification of this plant began, and 1969, but the year after the microtine peak there was a small increase in the number of shoots of this plant.

Exclosures were used by Tast and Kalela to show that microtines had no influence on the number of flowering *Eriophorum* plants, and through the study there was a decrease in the number of flowering shoots of *Eriophorum* because of human disturbance. The microtines still reached peak densities in 1969 even though the number of flowering shoots of *Eriophorum* was about one-fifth that of the 1963–1964 peak. The number of flowering shoots of *Solidago* was the highest in 1966, a year of very low microtine density, and 1969, a year of peak microtine density. While Tast and Kalela (1971) report positive correlations between food conditions and rodent population fluctuations, none of the correlations were significant.

A more recent paper (Tast, 1972) has related mean winter weights of *Microtus oeconomus* to the food supply as indicated by the density of sterile shoots of *Eriophorum* (Fig. 34). A single point gives the impression that there might be a relation between these factors. The sample size on which this point is based is four animals. More data are obviously required.

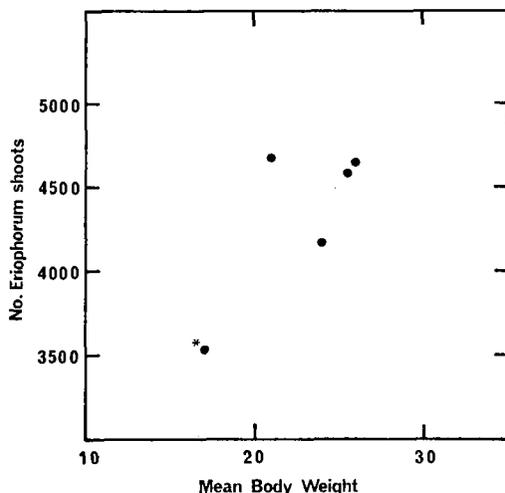


FIG. 34. The mean winter weights of *Microtus oeconomus* in relation to available food (no. of *Eriophorum* shoots the previous autumn). This apparent relationship is due to a single point (starred) for which the sample size was 4 animals. Data from Tast and Kalela (1971) and Tast (1972).

Vole and lemming populations can affect the amount of vegetation and its species composition, but they might also affect the nutrient composition of the vegetation. Relatively little work has been done on this aspect, and most of the available data is from the Barrow, Alaska studies of the brown lemming.

The levels of phosphorus, nitrogen, calcium, magnesium, potassium and sodium in the forage of lemmings in Barrow, Alaska were monitored by Pieper (1964) to elucidate the relationship between the lemmings and their habitat. Forage, clipped from ungrazed exclosures, provided controls for determining the effect of the lemmings on the nutrient levels of their habitat. Pieper found that in exclosures without lemmings there was little fluctuation from one year to the next in the nutrient levels in the forage, and that, as Schultz had found with the production of the vegetation, prevention of grazing lowered the nutrient content of the plants. Lemmings obviously stimulate the nutrient cycles on the tundra, and hence there is a correlation between lemming density and nutrient levels (Fig. 35). With the exception of magnesium, all other nutrients were at highest concentrations in the forage in the summer of the year of peak lemming density. Pieper (1964) interprets this finding as follows. In the winter preceding the summer of peak lemming density there was a rapid build-up in lemming numbers. Under the snow these lemmings were depositing quantities of fecal pellets and

urine. With the coming of the spring melt-off the nutrients contained in the excretory products were readily made available to the plants: thus the high nutrient levels. This relationship between grazing, nutrient availability, and nutrient cycling explains the synchronous cycles between lemming density and nutrient levels in Fig. 35. Lemmings clearly do influence plant nutrient composition. Whether the variation in the nutrient levels influences lemming numbers will be considered in the next section.

Unfortunately there are no comparable sets of data for voles from more temperate climates, and we do not know whether *Microtus* cycles in temperate grasslands are affecting the nutrient composition of the forage in the same way that lemmings obviously do.

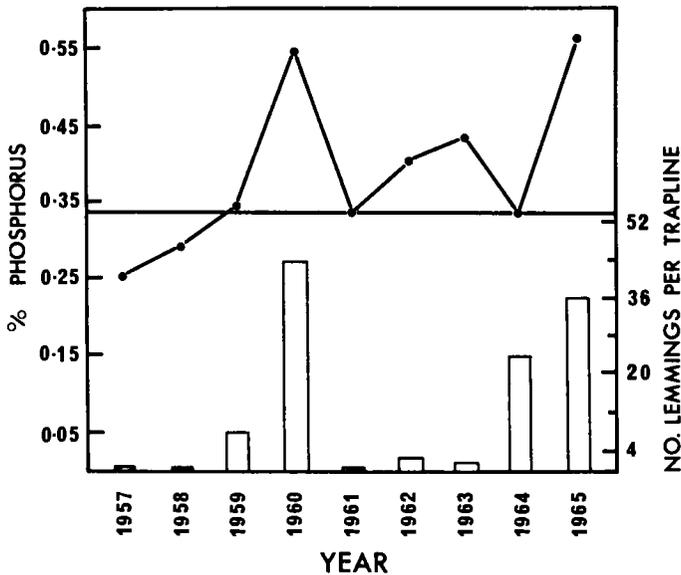


FIG. 35. Percentage phosphorus in the summer forage and brown lemming densities (bars) in Barrow, Alaska. The horizontal line indicates the similarity between phosphorus levels preceding and following years of peak population density. Data for phosphorus levels from Schultz (1969), lemming density estimates are the maximum average number of lemmings caught per trapline of the two or three trapping periods per summer from Pitelka (1972).

3. *The influence of food quality and quantity on microtine numbers*

Four experiments have now been carried out in an attempt to test the hypothesis that either the quality or the quantity of food available to microtines is a factor responsible for their population fluctuations. In the first of these Hoffmann (1958) added ammonium nitrate-phosphorus fertilizer to a meadow in the Sierra Nevada inhabited by

Microtus montanus. At the time of the fertilizer addition the *Microtus* population on the experimental area was at a lower density than the control population, but while the control population declined through the summer, the experimental population maintained its lower density and declined during the next winter. The fertilizer did not increase the amount of protein in one of the favored food plants of the voles, *Carex* sp., and there was no relation between the protein content of *Carex* and the density of voles supported, in various meadows studied by Hoffmann. Thus, no relation between quality of food and vole density could be shown and the addition of fertilizer, while possibly delaying the vole decline for a few weeks, did not prevent it.

A six-acre fertilized plot with three to four times the net primary productivity of a control plot was established in the tundra by Schultz (1969) and followed from 1961 to 1965. Protein, phosphorus and calcium levels in the vegetation were raised four to five times by this experimental treatment. Only during one winter (1963), following a year of relatively high lemming numbers, was the lemming population higher on the fertilized plot and these animals were rapidly taken by predators after the spring melt-off. A higher lemming density was not reported for the "improved" habitat in years of high lemming density and so this experiment does not provide evidence that the quantity or quality of tundra vegetation is a limiting factor to lemming populations.

Both fertilization of the grassland and supplemental feeding were tested by Krebs and DeLong (1965) as techniques for preventing the decline of *Microtus californicus*. While the animals on the experimental area demonstrated high growth rates, good recruitment, and increasing densities for the first five months of the experiment, all of these factors suddenly began to decline. The control population continued to increase to high numbers while the population with supplemental food declined to a very sparse density. This experiment was criticized by Batzli and Pitelka (1971) for the failure to take into account the quality of the natural food which was available to the voles, the nutritive quality of the supplemental food, or the possible effect of feeding stations on the social structure of the population.

Finally, biological assay of the amount of food available to populations of short-tailed voles, *Microtus agrestis* and bank voles, *Clethrionomys glareolus*, showed that just previous to the population decline there was sufficient food to maintain the populations for a year (Chitty *et al.*, 1968). A *Microtus* population given supplemental oats and carrots did not increase in density and body growth rates remained low, typical of declining vole populations. An interesting observation in this study was that it was impossible to predict either from the body weight or the condition of voles kept in 11-ft² enclosures when they had

eaten out the natural food supply and were on the brink of starvation. Three animals died without losing weight. This points out the fallacy of observations that symptoms of starvation were not observed in declining populations (Rauch, 1950, p. 176) and suggests that observations of this sort are not useful in judging the relation between an animal and its food supply.

An alternative to providing supplemental food to a microtine population is to determine if a habitat can in fact support higher microtine densities than it naturally does. Two-acre enclosures of grassland in southern Indiana supported densities of *Microtus ochrogaster* and *M. pennsylvanicus* several times greater than did a similar habitat just outside the fence. Although eventual habitat destruction resulted, immediate recovery occurred at the beginning of the next growing season, and introduced *Microtus* always responded with rapid population growth (Krebs *et al.*, 1969, 1973). These experiments showed that higher densities of voles could be supported by the Indiana habitat than normally were. Even after extensive habitat utilization there was no delay in recovery to forage vegetation sufficient for growth and reproduction of *Microtus* populations.

A further test of the influence of standing crop, amount of food available and percentage cover on microtine populations is provided by the work of Batzli and Pitelka (1970, 1971). In this study two populations of *Microtus californicus* were monitored, one in Richmond, California bordering the San Francisco Bay and the second in the Briones Hills, ten miles east of Richmond. Peak population densities of *M. californicus* in these two areas were almost the same in 1967–1968 when the study was conducted and both populations showed similar declines in the fall of 1968. However, these workers report that the standing crop, average height of vegetation and the percentage cover were all greater in the Briones study area, and the volume of *Bromus rigidus*, a major component of the food of *M. californicus*, was ten times greater at this area than in the Richmond plot. Unfortunately the study was terminated just as the *Microtus* population decline began, but it is obvious that in this case even ten times the amount of one food plant did not allow a greater peak density nor prevent the beginning of the population decline.

Field experiments have so far suggested that food limitation is not the factor stopping the increase phase of microtine populations. But we still must analyze the nutrient and lemming cycles described by Schultz (1969) in terms of what is cause and what is effect. The nutritional threshold hypothesis of Schultz is as follows: During the summer of peak lemming population the nutrients in the forage are at high concentrations, and high production and consumption

concentrates nutrients in organic material so that they are unavailable the next year to the growing plants. After the peak year, nutrient levels in the forage are low—too low to permit adequate reproduction by the lemmings. In the next two years greater amounts of nutrients are released and by the fourth year both the nutrient levels in the forage and the densities of lemmings have recovered. The building block of this hypothesis is that at some times the nutritional levels (particularly phosphorus and calcium) are below the thresholds necessary for reproduction by the lemmings.

Let us investigate this hypothesis by looking at the data on which it is based (Fig. 35). The two years of peak lemming density have corresponding peak phosphorus levels. But what is contrary to the hypothesis is that phosphorus levels are the same in the years before and after peak population densities. That is, the same levels of phosphorus give rise to increasing lemming population densities as are supposed to be limiting to the reproduction of the lemming in the year following the peak. Therefore, although data indicate synchronous cycles of nutrients and lemmings, there is no indication of nutrient levels falling below those which can give rise to increasing lemming densities.

To determine if nutrients are related to reproduction in lemmings we have plotted the proportion of females pregnant and the percentage phosphorus in the forage for July and August of the three years for which these data are available (Fig. 36). As is typical of cycling microtines (see page 296), the breeding season in the year of peak densities is shortened so that in August of 1960 when the nutrient levels are high, the proportion of pregnant females is low. There is no indication from these data that phosphorus deficiency limits reproduction in lemmings.

Calcium is another nutrient which is stressed by Schultz (1969) as being important, and in this case it is the necessity of threshold levels of calcium for adequate lactation by the lemmings which is thought to be important. Mullen (1968) in his study of lemmings at Barrow, Alaska monitored the onset and rate of mammary gland development in pregnant females. He found that in 1960, when Pieper's (1964) data show high concentrations of calcium and other nutrients in the forage, the development of the mammary glands began later and proceeded more slowly during pregnancy than in 1962 when calcium concentration was low. So there is no indication of calcium limiting lactation, at least as measured by mammary gland development.

One of the characteristics which seems almost always to be associated with increasing lemming populations is that the lemmings breed in the winter preceding the peak. From this observation one would predict

that if winter breeding were prevented in most years because of nutrient deficiency, the most important nutrient would have been strikingly higher in the autumn preceding the summer of peak lemming density (e.g. 1960). The concentration of sodium was twice as high in August of 1959 as it was in August of other years but this was the only nutrient to show this trend (Pieper, 1964). However, Schultz (1969, p. 88) dispenses with sodium as a nutrient possibly important to lemming cycles by the statement "... sodium show(s) no relationship to lemming numbers at all, nor were the data cyclic". In August,

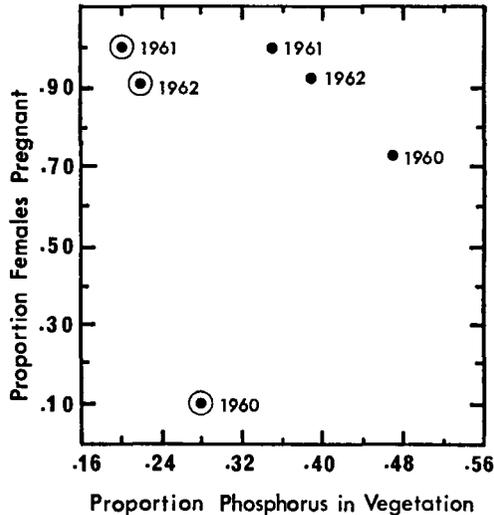


FIG. 36. The relationship between the available nutrient and reproduction in the brown lemming is shown from the proportion of females pregnant (Mullen, 1968) and the percent phosphorus in the vegetation (Pieper, 1964). July data are solid dots (●), August data (○).

1962, preceding a summer of intermediate lemming density, the sodium level of the forage was the lowest ever recorded by Pieper, suggesting that the high sodium before the 1960 peak lemming density may have been merely a chance association. And the importance of sodium to microtine cycles may be further questioned by our failure to find a correlation between soil sodium and densities of *Microtus ochrogaster* and *M. pennsylvanicus* in southern Indiana (Krebs *et al.*, 1971).

Lemmings, like other herbivores, probably select their forage, and this complicates the comparison of lemming needs and nutrient content of random forage samples. The nutrient levels reported in these studies are for all the plant parts extending above the surface of the soil. It is possible that nutrient levels in specific plant parts are

much different than those recorded for the complete plant. Whether lemmings can select plants or plant parts of high nutrient content, even when average nutrient content is low, is unknown. However, Thompson's (1965) test of the selectivity of *Microtus pennsylvanicus* indicated that they did not seem to recognize the quality of the food plant.

To summarize, we must conclude that, contrary to the statement of Schultz (1969, p. 86), the biology of the lemming is a very important element for understanding the tundra ecosystem. Evidence confirms Pieper's (1964) hypothesis that lemming grazing actually *increases* the nutrients available to plants, and that synchronous cycles between lemming density and nutrient content in plants are the result of the effect of lemming density on the availability of nutrients to the plants. Thus lemmings affect the tundra plants but the plants do not seem to determine lemming density changes. Data published thus far seem to contradict the nutritional threshold hypothesis.

What other experiments might be done to test the food hypothesis? Schultz (1969) has begun experiments by fertilizing six-acre plots in the tundra. There are two problems with this experimental design. As well as changing the quality and quantity of food, the amount of cover is also altered dramatically by fertilization. This confounds any interpretations unless cover can be changed on other areas without changing the food supply. Secondly, six acres is a very small part of the tundra. Immigration to the optimal habitat may be great, thereby complicating the understanding of the demography of lemmings in the fertilized area.

Studies using islands or enclosed populations could be very revealing. Can the tundra, like a southern Indiana grassland, support more animals than it presently does? Can an increasing lemming population be established on habitat from which a peak population has just been removed? One thing is clear: measuring lemming density alone is not sufficient. We must have detailed information about birth, death, and growth rates, or any environmental measurements are useless.

Furthermore, we need a greater understanding of how the microtine actually interacts with its environment. We still have little idea of what the nutrient requirements of microtines are, or how selective they are in choosing the quality of their food. The nutrient levels reported thus far are values for complete plants and the nutrients have only been measured during the summer.

Nutrient cycling in the tundra is exaggerated by the thin layer of soil above the permafrost and the slow rates of decomposition. Therefore, the interactions between the lemmings and their environment are likely to be quite different from those of the *Microtus* in

grasslands in California, England or New York (Haynes and Thompson, 1965). If we are seeking generalities of microtine cycles, as pointed out earlier in this article, we must not overlook the uniqueness of the tundra and we must avoid overemphasis of characteristics specific to this situation.

To summarize, microtine rodents take only a small fraction of the net primary production. Microtine grazing affects the plant species composition of the habitat, and at least in tundra ecosystems also affects the nutrient composition of the forage. No one seems to suggest that voles or lemmings are limited by the amount of food available, and attention has turned to the quality of the food available. The nutrient threshold hypothesis has been suggested as an explanation for lemming cycles, but we can find no evidence that nutrient levels cause any of the characteristic features of cyclic lemming populations.

B. PREDATION

"Foxes also hunt them, and the wild ferrets in particular destroy them; but they make no way against the prolific qualities of the animal and the rapidity of its breeding." These are the words of Aristotle quoted by Elton (1942, p. 3) and the animal to which he was referring was the field mouse. However, even though this opinion was expressed in the early stages of the history of small mammal cycles, the question whether predation might be the driving force behind population fluctuations was by no means put to rest.

Two aspects must be separated in discussing predator-prey questions: (1) How do the predators respond to variations in prey abundance? and (2) Are these responses sufficient to explain population changes in the prey? As with the food hypothesis, one of these two elements may be present without the other.

Early writers were most taken by the correspondence between fluctuations in populations of herbivores such as lemmings, voles and rabbits, and of carnivores, such as foxes, weasels and raptors. Data revealing oscillations of predators and their cycling prey was reviewed by Elton (1942) and Lack (1954, pp. 204-226). Shelford (1943) considered the cycle of the varying lemming as being typical of predator-prey oscillations described by Lotka and Volterra. The prey species increases in density providing more food for the predator, which responds with increased reproduction and a build-up in its own population to a level larger than can be supported by the prey population. A decline in the prey population ensues, followed by a fall in the predator population through death or emigration.

An extensive literature exists documenting the numerical response

of predators to microtine populations. Gross (1947) summarizes the history of snowy owl migrations from the Arctic into New England. These migrations followed years of high lemming population densities. The subsequent movement southward was triggered as food became scarce when the lemming population declined.

Avian predators can be categorized as *restricted feeders* which depend predominantly on one prey species, and *general feeders* which take a variety of prey species (Craighead and Craighead, 1969, p. 182). Restricted feeders travel about looking for high prey densities, and during a year of high *Microtus* numbers a great influx of restricted feeders into the Craigheads' study area occurred, while populations of general feeders remained about constant. Other reports of predator movements in response to fluctuating vole and lemming populations were made by Honer (1963) for the barn owl, Maher (1970) and Pitelka *et al.* (1955) for the jaeger and snowy owl, Mysterud (1970) for the boreal owl, and Stendell (1972) for the white-tailed kite. Some raptors are only able to breed when the population of their prey is relatively high (jaegers and snowy owls, Maher (1970) and Pitelka *et al.* (1955); rough-legged hawk, Hagen (1969); and the white-tailed kite, Stendell (1972)).

But given that predator species can respond to high densities of voles and lemmings by increasing their own numbers, is mortality caused by predation sufficient to regulate vole and lemming populations? Opinions are divided on this question. Some studies claim that predators took a high proportion of the prey population and therefore are a necessary factor in preventing population increase. Others claim that predators had very little influence on the prey population (Table XIV).

A modified version of the predator hypothesis was suggested by Lack (1954). Lack concluded that predators are too scarce in proportion to the prey at the time of lemming or vole peak densities, and hence predators cannot stop the increase of breeding prey populations. Therefore, it was necessary for another factor, such as food limitation or intraspecific competition, to stop the microtine increase by shutting off reproduction before the predators could catch up and exert any influence on prey population density.

The first serious attempt to quantify the influence of predation on a population of *Microtus* was made in 1951 by Brant (1962). This was done by analyzing raccoon scats which were deposited on his study area. Brant surprisingly found that twice as many *M. californicus* were taken by predators than he had estimated to be present on the study area. The source of error could be either poor estimation techniques for *Microtus* or the concentration of predator scats from a larger

TABLE XIV

The influence of predators on fluctuating populations of microtines. The accounts vary from impressions of the influence of the predators to attempts to quantify the percentage of the vole population actually taken. The values given for the predator influence are minimum values since generally a worker was concerned with only one type of predator. The studies of aerial predation generally do not consider terrestrial predation and vice versa

Prey species	Predator species	Predator influence	Author
<i>Lemmus trimucronatus</i>	Snowy owl, Pomerine jaeger	Extensive	Pitelka <i>et al.</i> (1955)
	Snowy owl, Pomerine jaeger	Varying	Pitelka (1958)
	Snowy owl, Pomarine jaeger, Least weasel	Density prey > 35/acre. No influence Density prey < 25/acre. Depressing influence	Maher (1970)
	Snowy owl, Pomerine jaeger, Least weasel	Important during decline. Weasel influence during period of low numbers	Thompson (1955b)
	Snowy owl	Ate 8-20% spring popln Ate 20-31% summer popln	Watson (1957)
	Weasels and raptors	Little effect	Krebs (1964a)
	<i>Microtus californicus</i>	Raccoons	Caused decline
Feral cats, raccoons		Ate 88, 25 and 33% declining popln	Pearson (1964, 1966, 1971)
Kites and short-eared owls		Ate 28% declining popln	Stendell (unpublished)
<i>Microtus montanus</i>	Weasels and ermine	Ate 40% decline 21-57% low numbers 8% increasing (winter poplms)	Fitzgerald (1972)
<i>Microtus agrestis</i>	Raptors	Little effect	Chitty (1952) Elton (1942, p. 192)
<i>Microtus pennsylvanicus</i>	Raptors	Ate 26% high density Ate 22% low density	Craighead and Craighead (1969, p. 321)
<i>Microtus</i>	Short-eared owl	Ate 8-51% declining popln No influence on breeding popln	Lockie (1955)

hunting area to Brant's study area. If the latter were the case, more *Microtus* remains would be deposited on the area than were removed from the area.

The most intensive work on predation has been done on *Microtus californicus* by Pearson (1964, 1966, 1971). The technique of scat analysis was used by Pearson to measure the impact of terrestrial predators on *M. californicus* populations for parts of three population fluctuations. An assumption underlying this technique is that predator droppings are not concentrated on the study area. The best estimates of the proportion of the *Microtus* population taken by predators was obtained during the population decline, when reproduction by the *Microtus* population was reduced or had ceased altogether. The vole population can be estimated at the end of the breeding season and the number of individuals taken from this "standing crop" by the predators determined. As indicated in Table XIV, the percentage of the *Microtus* population which was taken by terrestrial predators during the population decline was 88, 25 and 33% for the three cycles studied by Pearson. Why was the predation pressure during the first *Microtus* cycle so much greater than that of the next two cycles? One possible explanation is that a program of feral cat eradication was carried out in the study area after the first period of decline. Therefore, the predator population was smaller during the last two population cycles (Table XV). The rate of decrease of the vole population was very similar regardless of the proportion of the population taken by predators.

The relation of predation to microtine populations proposed by Pearson (1971) contains the following points. First, avian predators are not sufficiently intensive to determine population trends in rodents since they leave the area when prey abundance is low. Mammalian predators are the important agents of mortality because they are less mobile, and therefore, when microtines are at low densities, they

TABLE XV

Comparative predation pressure by terrestrial predators (mostly feral cats) on declining Microtus californicus populations for three periods of population decline. Data from Pearson (1966, 1971).

	1961		1963		1965	
	<i>Microtus</i> / carnivore	No. carnivores	<i>Microtus</i> / carnivore	No. carnivores	<i>Microtus</i> / carnivore	No. carnivores
Mid-decline	130	8	800	3.5	600	2
Greatest predation pressure	72	10	500	4.5	224	2.3
% Loss to predation	88		25		33	

supplement their diets with other species but remain on the area exerting predation pressure. Secondly, predators do not stop the increase of a breeding microtine population. Pearson proposes that predators can be responsible for the amplitude of microtine cycles by their ability to decrease the populations to very low levels through continued predation pressure when the microtine populations are low. Predators can also influence the periodicity of the cycle by prolonging the period of low numbers. Note that according to Pearson's ideas, the critical period to study predation on microtine rodents is during the late decline and the phase of low numbers. Unfortunately almost no one seems to do this.

The influence of predation by ermine and weasel on a *Microtus montanus* population was studied by Fitzgerald (1972) at the University of California research station on Sagehen Creek in the Sierra Nevada. Vole populations and winter predation by weasels and ermine were estimated by counting the number of winter nests made by voles (an estimate of the vole population). The number of *Microtus* nests which had been invaded by ermine and weasels as well as the remains of *Microtus* left near these nests were counted as an indication of the predators' activities. A crucial assumption of this study is that one vole nest found by Fitzgerald in the spring, indicates the presence of one vole in the overwintering populations. However, more direct estimates made by Fitzgerald in a live-trapping study, indicated a possible ratio of one to three voles per nest. This ratio varied among years. The formation in the autumn of "great families", a living unit composed of parents and several litters in a single nest, is discussed by Frank (1957) for *M. arvalis*. This also suggests that one vole per winter nest may not always be valid.

However, if we assume that one winter nest indicates at least one overwintering vole, the maximum percentages of *M. montanus* taken for the four years of the study are shown in Table XVI. In addition to the 40% of the *Microtus* population which were calculated to have been taken by predators during the winter of the population decline, 9% of the population were found dead in their nests the next spring. In many cases more than one dead *Microtus* was found in a nest, which suggests that the population estimate based on the number of nests may be an underestimate. There is no way to determine how many of the deaths in the decline would have occurred if predators had been absent.

Another study recently completed (Stendell, unpublished) quantifies the predation by raptors, particularly the white-tailed kite, *Elanus leucurus*, on *Microtus californicus* populations. In this case populations of *M. californicus* on Grizzly Island, Solano Co., California were

TABLE XVI

Data from Fitzgerald (1972) measuring winter predation on Microtus montanus populations by ermine and weasels. The number of nests is considered to be equivalent to the number of voles in the autumn and the percent eaten is calculated from the number of Microtus nests occupied by weasels and ermine and counts of remains of eaten Microtus. Only in 1968-69 did Fitzgerald find evidence for vole mortality other than by ermine and weasel predation. In this year 9% of the autumn vole population was found dead in their nests from unexplained causes.

	Winters			
	1965-66	1966-67	1967-68	1968-69
No. vole nests/34 acres	191	292	783	793
Population phase	Low	Low	Increase	Decline
% voles eaten	21.2	56.6	7.8	39.7
No. ermine	?	4?	1	4

estimated by live-trapping, snap-trapping and runway transect analysis. The populations of aerial predators were counted, and pellets containing identifiable remains of prey were analyzed to estimate the proportion of the prey eaten. During the eight months of vole population decline avian predators took approximately 28% of the prey population. However, during the first three months of the population decline only 8% of the original *Microtus* population were taken by the kites and owls (Fig. 37). As the *Microtus* population declined the predation pressure increased, as Pearson suggested. But this predation pressure was not continued because the dense kite population left the island in February, eight months after the beginning of the vole decline.

Another study of *Microtus californicus* on Grizzly Island documents the predation by terrestrial predators during a time when aerial predation was light (Myers, unpublished). On a study plot of approximately four acres the California vole population increased abruptly from May to July and then decreased between July and August (Table XVII). If we make the assumption that the number of *Microtus* remains in scats deposited on the study area equals the number of *Microtus* removed by predators, we find that during the population increase (May to June) twice as many remains of *Microtus* occurred in scats as were trapped in the area. The next month predation also remained high with the number of *Microtus* remains in scats equal to half the population trapped in June. Thirty-five percent of the loss during the first month of the decline could be accounted for by predators, as was 43% of the loss during the next month (August). House mice, which are not preyed upon to the same extent, also declined at this time, indicating that a mortality factor other than

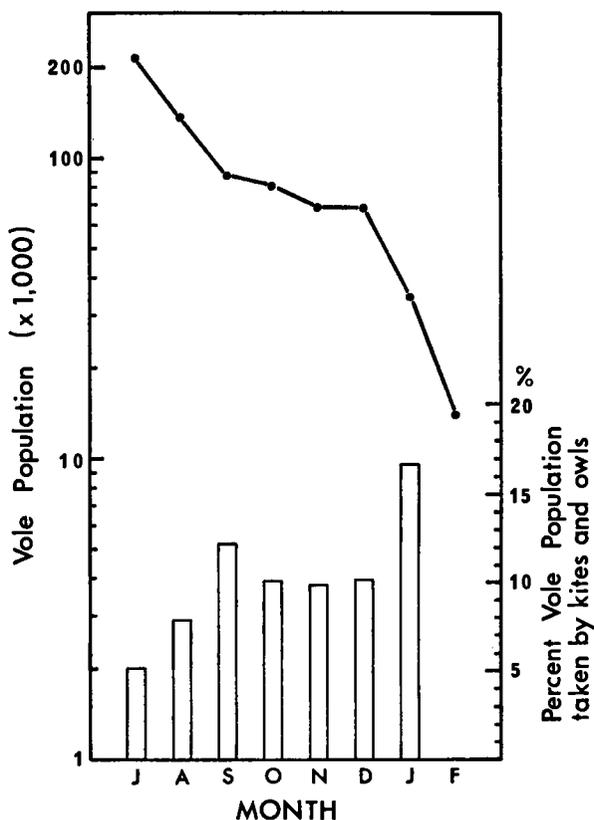


FIG. 37. As the population of *Microtus californicus* decreased from the peak of 214 200 voles in the 2380 acres of suitable habitat on Grizzly Island, the percentage of the vole population which was taken each month by the white-tailed kite, short-eared owl and the barn owl increased. Data from Stendell (unpublished).

predation was working (Table XVII). For 11 months (September to July) no *Microtus* were trapped but scats deposited on the study area still contained *Microtus* remains. This shows that terrestrial predators, in this case primarily feral cats, were able to find *Microtus* even when their numbers were low and their distribution patchy. What we need to know is whether predation pressure is strong enough to prevent the build-up of *Microtus* populations when they are at low numbers. For the present it must be concluded that feral cats are more persistent at searching for *Microtus* when they are at low numbers than are students of small mammal populations. These observations are consistent with Pearson's hypothesis.

TABLE XVII

*Predation pressure by terrestrial predators on increasing and declining *Microtus californicus* population compared to predation pressure on a sympatric house mouse population. Estimates are conservative since the densities of the small mammals are taken to be the number trapped in 600–900 trap nights on an area of approximately 4 acres (1.6 hectares). Data from Myers (unpublished).*

	<i>Microtus californicus</i>			<i>Mus musculus</i>		
	No. captured	No. in scats	% Loss due to predation	No. captured	No. in scats	% Loss due to predation
May 1971	19			120		
		40	—		3	—
June 1971	46			180		
		23	—		1	—
July 1971	155			197		
		45	35%		4	5%
Aug. 1971	28			111		
		12	43%		1	1%
Sept. 1971	0			37		
Sept. 1971– July 1972	0	27		720	41	

The trapping area in this study was very small (four acres) and so any conclusions are subject to errors from edge effects. However, there are several points which can be made. As predicted by Pearson, heavy predation did not stop the increase of the *Microtus* population; however, when the prey population was very low the terrestrial predators were still able to find them. The distribution of *Microtus* during the phase of low numbers might be very patchy. If this is the case, large areas of the habitat would have no *Microtus*, while in limited areas voles would exist. The probability of a predator dropping a scat on some section of the large area lacking *Microtus* would be greater than that of his dropping scats on the restricted areas of *Microtus* habitation. This situation would bias the data towards the appearance of high predation pressure during periods of low prey population densities in a trapping study of the sort described.

There is similarity among many studies of predation on microtine populations in regard to the proportion of the prey population taken by predators, with values usually ranging from 25 to 40%. The estimate of 88% of declining *M. californicus* population removed by terrestrial predators (Pearson, 1964) is outstandingly high. However, all estimates are conservative since usually only one type of predator, either aerial or terrestrial, is considered in an individual study (Table XIV).

Whether or not aerial and terrestrial predators compete for the same prey has not been investigated. In the *M. californicus* declines studied by Stendell (1972) and Myers (unpublished) and the *M. montanus* decline studied by Fitzgerald (1972), predation, while possibly accentuating the decline, was not sufficient to cause it. A prerequisite is the cessation of reproduction and the presence of other mortality factors which as yet are not identified.

Two important questions remain: (1) what is the predation pressure during the period of low numbers, and (2) how much loss can a breeding microtine population sustain? Unfortunately data regarding the first question are limited. Maher (1970) claims that in Point Barrow, Alaska the lemming population is free of avian predation for the first 1.75 to 2.75 years after the decline. While no *M. californicus* were trapped on the Grizzly Island study area for over 11 months, cat scats found on the study area during this time still contained vole remains. Most of the aerial predators left Grizzly Island following the vole decline, but kites and marsh hawks still hunted in some parts of the island (Stendell, 1972; Myers, personal observations).

What experiments can we devise to test the suggestion of Pearson that predation in the phase of low numbers delays the start of the next cycle? One experiment which should be done is to add predators to a population to test whether the periodicity of the cycle is lengthened, or to remove predators to determine if the cycle is shortened. Since the reduction of cats on the Pearson study area, the *M. californicus* have been exhibiting a two-year cycle (Pearson, 1971) and the populations have shown type H declines with a slight build-up of the population after the initial decline. Several replicates of this experiment will be necessary before conclusive results can be obtained. It has previously been stated that a population of *M. californicus* on Brooks Island in the San Francisco Bay, where there are no terrestrial predators, did not cycle (Pearson, 1966) but Lidicker (1973) has found evidence of a two-year cycle. However, densities of voles on this island are almost almost higher than on the mainland. The addition of a terrestrial predator to this island might be used to test the influence of predation on the amplitude and timing of a microtine cycle.

How much loss can small mammal populations sustain? No one has applied the techniques of optimum yield analysis originally developed for fisheries (Krebs, 1972, Ch. 16) to microtine rodent populations. We know that at some loss rate, a population must be driven to extinction, and that populations of different species vary enormously in their ability to withstand sustained cropping. A few experiments have been done on rodents.

In a recent study with house mice, *Mus musculus*, Adamczyk and

Walkowa (1971) removed 32% of the population every month and were not successful in decreasing the size of the population. They in fact raised the standing crop. This increase was not due to immigration but was the result of increased survival of young born into the population and longer residency of mice not removed by "artificial predation". House mice have a larger litter size and higher reproductive potential than microtines, but these experiments show that moderate mortality does not always cause a decline in a small mammal population.

Krebs (1966) removed all *Microtus californicus* weighing more than 40 g, in many cases removing more than half the number of animals trapped on the study area every two weeks, but still was not able to prevent the population from increasing. However, there was considerable immigration of animals from surrounding areas into this population. Krebs *et al.* (1969) cropped from fenced populations of *M. ochrogaster* and *M. pennsylvanicus* one-third of the adult population every two weeks and found that these populations still maintained higher instantaneous rates of population increase than unfenced control populations. This suggests that a predation rate of approximately 2% per day will not stop the increase of a breeding *Microtus* population. A population of *M. californicus* in a 120 ft² outdoor pen had to be cropped at a rate of over 50% a month to maintain a maximum population of 40 individuals (Houlihan, 1963).

If predation is an important mortality agent in rodent populations, we should be able to correlate demographic events with predation pressure. One important aspect of the mortality which occurs during a microtine decline is that it can be very selective. While two species of microtines often cycle in phase (Krebs, 1964a; Tast and Kalela, 1971), sometimes the population decline of one species will precede that of the other by several months (Krebs *et al.*, 1969; Tast and Kalela, 1971). Survival of male microtines frequently decreases before that of the females during the population decline or the mortality on the two sexes can vary sporadically (Krebs, 1966; Krebs *et al.*, 1969, 1973). If predators are causing these changes in mortality, they must be highly selective in their action. We find no support for such selectivity in the literature. Stendell (unpublished) found that kites took age categories and sexes in proportion to what was available in the trappable population of *Microtus californicus*.

To summarize, the role of predation in microtine cycles is limited to the mortality component of the demographic machinery, and consequently other factors must be invoked to explain reproductive and growth changes. No one seems to believe that predation can stop a breeding population in the increase phase, and the major function of predation is postulated to be in reducing the peak population to low

numbers and then holding numbers low so as to delay the next cyclic build-up. In some declines only a small fraction of the loss can be attributed to predation, and the evidence suggests that predation is not necessary to cause the decline phase. Predation may contribute to the rate of decline of a population, and this seems to be its major role in many populations. Whether predators hold prey numbers down in the phase of low numbers is an interesting question on which few data can be cited. Experiments manipulating predator numbers will be necessary to answer this question.

C. WEATHER AND SYNCHRONY

Weather can affect microtine populations, and Fuller (1967, 1969) has suggested that weather effects are one explanation of microtine cycles. Because Fuller's work has been concerned with high latitude microtines, he was particularly interested in winter weather conditions, the critical periods being at the time of the fall freeze and the spring thaw (Fuller, 1967). A study of *Clethrionomys gapperi*, *C. rutilus* and the cricetine *Peromyscus maniculatus* in the vicinity of Great Slave Lake, N.W.T. was undertaken by Fuller (1969) to compare the demographic characteristics of these three species living in the same habitat and under the same general weather conditions. Populations of all three rodent species were high in the summer of 1966. The spring of 1967 was the coldest and wettest, and was followed by low summer population densities of *C. gapperi* and *P. maniculatus*. Because data were not collected during the winter we do not know exactly when the populations declined. However, *C. rutilus* was undaunted by the severe winter and late spring in 1967 and remained at peak densities during the summer of 1967. Fuller proposed that the difference in the reaction of the three species to the "hard" winter of 1966-1967 was due to greater cold-tolerance of *C. rutilus*.

Another study of *Clethrionomys gapperi* was undertaken by Elliott (1969) in the vicinity of Edmonton, Alberta. This study covered the years 1965-1968. The winter of 1967-1968 was judged most severe by Elliott because of its thin and unstable snow cover and the greatest amounts of rain during weeks with freezing temperatures. *C. gapperi* densities were the lowest observed in the spring of 1968 for any of the four years of the study and there was almost no recovery of the population during the summer of 1968. Thus a severe winter was clearly associated with a population decline.

Fuller and Elliott could only conjecture what was happening to the voles during the winter because their data consisted only of density estimates in fall and in spring, and survival estimates from animals marked in the

fall and recaptured in the spring. However, Whitney (unpublished) collected survival data for *Clethrionomys rutilus* and *Microtus oeconomus* during three years, at the same time that he was monitoring winter climatological features. Two winters were classified by Whitney as poor for voles even though the conditions were quite dissimilar. The winter of 1969–1970 began with a rapid freeze but temperatures were higher than average and ten times during the winter there were thaws. Snow conditions were poor which resulted in colder than normal ground temperatures. This would probably be judged by Fuller to be a harsh winter for voles. There were two periods of loss in numbers for the *C. rutilus* population (Fig. 31). The first of these was from September to November. Survival of females was particularly low in September; this was approximately six weeks before the winter freeze and the first snows. For the remainder of the winter the percentage of voles surviving every two weeks ranged from 70 to 90%. The second period of poor survival was between February and March, over a month before the little snow present melted. In general, winter survival by *C. rutilus* was superior to summer survival. The period of poor survival at the start of the breeding season in the spring is typical of microtine populations (see p. 283) and could not be tied to specific weather factors.

Whitney reported a similar picture in a sympatric population of *Microtus oeconomus*. The survival of males was better during the winter than in the summer. The deterioration of survival in the spring occurred a month earlier in this species than in *Clethrionomys rutilus* on the same study area.

Summer survival of *C. rutilus* was low in 1970 (Fig. 31); however, it improved in August and except for a short period in September continued to be extremely high during the winter. This winter was not judged by Whitney to be good for voles either. The fall freeze was gradual, the snow fall heavy and the subnivean space was not developed until late in the winter.

Whitney's study is extremely important because it shows the necessity of obtaining detailed demographic data in judging the influence of extrinsic factors on the population. We do not yet know what characteristics of winters are most stressful for voles. But Whitney's data, in agreement with that reviewed earlier, indicates that the crucial period is really in the fall, with a period of poor survival often preceding freezing weather and snow, and in the spring, in association with the beginning of the breeding season. No simple association could be made between winter conditions and survival of *Clethrionomys rutilus* and *Microtus oeconomus*.

The spring melt-off might be a time period which is critical to

arctic microtines. There is great variation from year to year in the timing of the snow melt, and this might affect summer population growth. Without winter sampling it is difficult to judge accurately the beginning of the summer breeding season of arctic microtines. However, Mullen (1968) attempted to do this by looking for signs of recent reproduction in female brown lemmings taken in June. From this analysis he proposed that the date of beginning of the summer breeding season is crucial to the demographic performance of the population that summer. His data are presented in Table XVIII. We only have a verbal description of the demographic changes available from Mullen's work and these descriptions do not always agree with trapping data from the same vicinity given in Pitelka (1972). However, there are

TABLE XVIII

The data for the beginning of the summer breeding season and the subsequent change in the population density are recorded for five years by Mullen (1968)

Year	Beginning of breeding	Popln density and summer popln change
1960	17 June	June peak—declined ¹
1961	27 May	Low—no change
1962	7 June	Low—no change
1963	Late May	Moderate—declined ²
1965	Late June	High—declined ³

¹ Population remained constant according to Pitelka (1972).

² Population low and remained constant according to Pitelka (1972).

³ Population change from Pitelka (1972).

three summers of declining density. In two of these the breeding season began late and in the other it started quite early. Both the breeding seasons of 1961 and 1962 began relatively early and neither resulted in increasing lemming populations. We can find no evidence in these data or in the data of Krebs (1964a) that the timing of the snow melt strongly affects subsequent population trends in lemmings.

Climatic factors and the abundance of *Microtus arvalis* were investigated by Straka and Gerasimov (1971) in Bulgaria. In this case summer drought was the stressful weather condition under consideration. In the areas of Bulgaria where rain was not limiting and conditions were optimal for *M. arvalis* the populations demonstrated three cycles during the nine years of the study, and there were no correlations with temperature or rainfall variations. Similarly, at the southern edge of the species range, while densities were generally low and fluctuations erratic, there were no correlations with rainfall or temperature. However,

in northern Bulgaria, an area subject to periodic summer droughts, *M. arvalis* populations sometimes reached high densities. The determining factor seemed to be the amount of rain during the second half of the summer. Good rains and associated forage growth permitted breeding by the voles into the autumn, and therefore dense overwintering populations.

The area near Berkeley, California is characterized by summer droughts of varying lengths. The study of Batzli and Pitelka (1971) of *M. californicus* included two years in which rainfall was below normal. In one of these years the voles were at low densities and in the other at peak density. Thus summer drought does not appear to determine population trends in the California vole.

As part of a study of *M. pennsylvanicus* and *M. ochrogaster* in southern Indiana solar radiation, rainfall, soil temperature, and humidity were recorded for the five years of the study (Krebs, unpublished). No correlations could be found between these weather characteristics and *Microtus* population fluctuations. Furthermore, the two species living under the same weather regime did not always fluctuate in synchrony. Weather appears to exert little limitation on vole populations in Indiana, where extremes of drought or cold do not occur.

While it is impossible to vary winter weather experimentally and thus to test its influence on microtine cycles, populations which are out-of-phase could be used for this test. This experiment requires an increasing population contiguous with a peak or declining population. One means for accomplishing this is to introduce microtines to enclosures, where they respond by increasing in numbers. The influence of a particular winter on an enclosed and an adjacent free-living population could then be observed. The relation of drought to population phenomena of southern microtines could be tested by observing populations in irrigated areas. For example, we could ask whether irrigation abolishes the cycling of *M. californicus* populations.

One of the conceptual difficulties in recognizing the role of weather in microtine cycles is the diversity of populations in which cycles occur. Voles from arctic to temperate areas seem to go through population cycles which have many demographic attributes in common. If we explain a fluctuation in *M. oeconomus* by winter snow conditions, must we seek another explanation for *M. pennsylvanicus* in areas where snow is rare?

We recognize that weather has received too little attention from students of microtine rodents. We need to look both at the destructive aspects of weather on survival rates and at the permissive aspects of weather in allowing reproduction. Because many of these effects can

be transmitted indirectly via the food supply or cover available, the role of weather may be most difficult to untangle in natural populations, even with field experimentation.

Regular fluctuations in populations presumably require a regular stimulus, and few would claim that weather variables change in a regular three- to four-year pattern. However, the imagination is pressed to conceive of any factor other than widespread weather conditions which might act as the cue for synchronizing fluctuations of microtines over broad geographic areas. There are numerous accounts of populations of microtines which are out of phase, but synchrony seems to be the usual case. Chitty (1952, 1960) and Chitty and Chitty (1962) record asynchronous populations of *Microtus agrestis*. In southern Indiana, Krebs *et al.* (1969) found some sympatric populations of *M. ochrogaster* and *M. pennsylvanicus* which fluctuated in synchrony, but other asynchronous populations were also monitored (Keller and Krebs, 1970). Pitelka (1961) reports asynchronous brown lemming populations in northern Alaska, while Watson (1956) and Krebs (1964a) found sympatric populations of *Lemmus* and *Dicrostonyx* to fluctuate in phase. Both Mullen (1968) and Krebs (1964a) report peak brown lemming populations in the summer of 1960. Mullen's study was done in Barrow, Alaska and Krebs' in Baker Lake, N.W.T. over 2000 miles away. The microtines of Finnish Lapland appear generally to fluctuate in synchrony, but cases of asynchrony have also been observed here (Tast and Kalela, 1971).

For weather to act as a synchronizing factor it must be postulated that similar weather conditions can have contrary effects on populations in different phases of the population fluctuation (Frank, 1957). Chitty (1967, 1969) considers this to be quite possible if the quality of microtine populations varies with the density. Therefore peak populations might be severely influenced by a bout of poor weather while an expanding population would be hardly affected (Fig. 38).

Leslie (1959) proposes a model which describes how an external random factor (such as weather) acting on populations which are geographically isolated brings the oscillations of the population densities into phase. So we have some reassurance that, theoretically, weather could be a synchronizing element, but we still lack the biological understanding to determine if it is acting in this way.

A factor which has some bearing on this topic is the degree of geographical isolation of populations. In the tundra there are vast areas of suitable lemming habitat. However, in the temperate zone, *Microtus* habitat is largely a relic of farming practices. Fields in different stages of succession provide habitats of changing suitability. For this reason we might expect more out-of-phase populations in areas

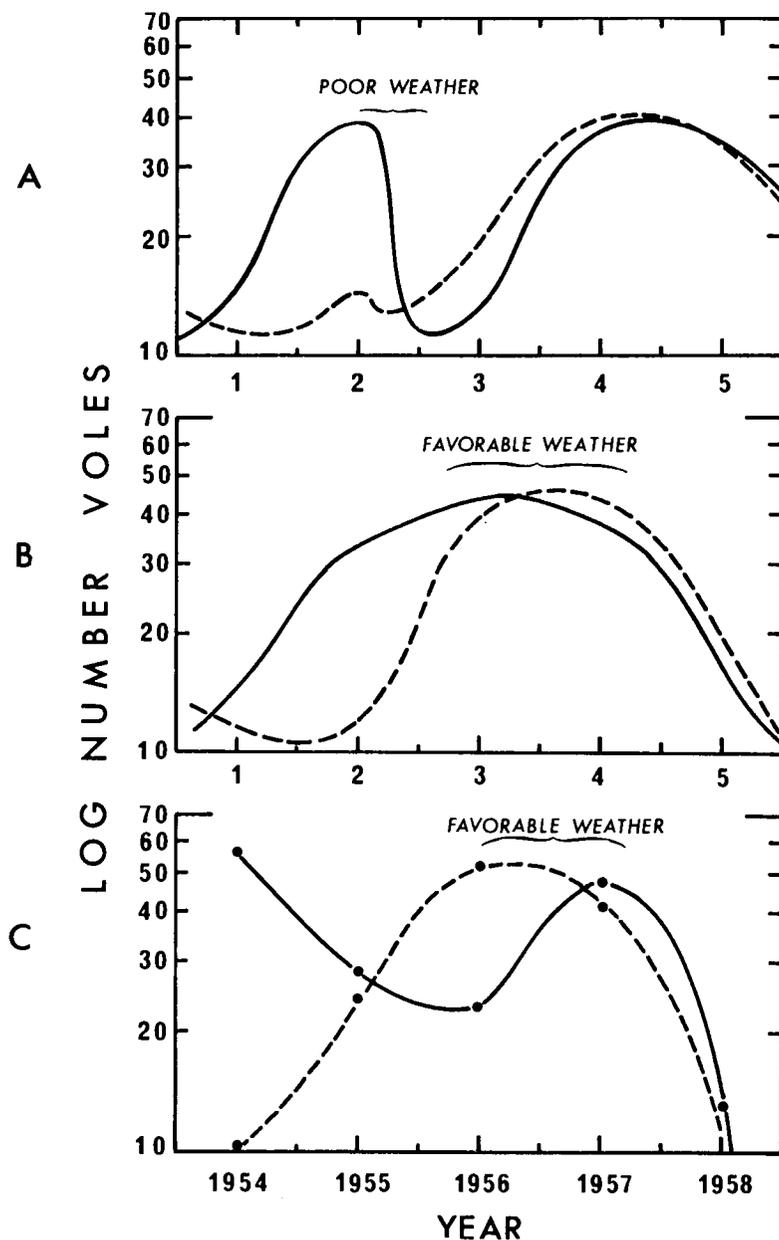


FIG. 38. Parts A and B demonstrate possible situations in which weather might act to bring two asynchronous vole populations into synchrony. In A poor weather conditions have a strong influence on a peak population while having little influence on a population in the phase of increase. In B favorable weather extends the duration of peak population density in one population and accelerates

of patchy habitat than in the tundra. Whether this is the case we do not know. It is not possible to sample lightly from a number of areas to determine if populations are fluctuating together. Each population must be studied over time. Pruitt (1968) sampled populations across the North American Arctic and while he could not verify synchronous cycles in small mammal population densities, he claimed to find a cycle in the small mammal biomass. The sizes of most samples were quite small. Haynes and Thompson (1965) found positive relationships in the amount of vole activity among areas within 20 miles of each other, but it is not possible from these data to determine whether asynchronous populations were observed.

Out-of-phase populations are hard to locate and hence rarely studied. Until we know what weather conditions are most important to microtines, we shall be unable to determine how synchrony is brought about between scattered rodent populations.

In summary, weather must be important to microtine populations if synchrony occurs. We do not know how weather acts to synchronize cycles. Few studies have been made of arctic microtines during the winter, and we have found no simple associations between weather and population events. Weather effects do not seem to explain vole and lemming cycles, and the main driving forces must be sought elsewhere.

D. STRESS HYPOTHESIS

High animal densities increase the probability that individuals will interact. If these interactions are disturbing to the animals, "social stress" may be expected to rise with increasing population densities. The stress hypothesis of Christian (1950) is probably one of the most widely known theories of population regulation, even reaching the every-day world of analogies with human populations.

The stress hypothesis is an outcrop of the work of Selye (1946) on the response of the pituitary and adrenal to stress. In the extreme case the increased activities of the pituitary and adrenals cause exhaustion, low resistance and general susceptibility of the individual to a variety of potential mortality factors. In addition a corresponding inhibition of the pituitary-gonadal function can decrease reproduction (Christian

the rate of increase in an expanding population. Part C plots data taken from Chitty and Chitty (1962) and shows the number of *Microtus agrestis* trapped per hundred trap nights. Because of favorable weather in the winter of 1956-57 one population remained at peak densities while the other increased to peak densities. The two populations declined in synchrony. The two curves represent two different populations. See discussion in Chitty (1967).

et al., 1965). Aggressive behavior of individuals is an intimate part of this theory, with stress and aggressiveness increasing in a spiral. We will consider behavioral characteristics of cycling rodents in another section of this article, but here we want to consider evidence which has been gathered relevant to the search for characteristics of physiological stress associated with high microtine densities.

First let us reiterate the characteristics of cycling microtines which must be explained if we wish to support the stress hypothesis. The impairment of reproduction occurs at peak density in the form of a shortened reproductive season, but other factors of natality such as litter size and prenatal loss do not consistently vary with microtine density. Therefore, we might expect stress to shorten the reproduction season but not to cause increased prenatal deaths. Mortality is higher during the population decline and is particularly severe in very young animals. Males and females may suffer poor survival at different times. From this we might predict that the social climate of males and females and of young animals is different.

One of the first steps toward testing the stress hypothesis is to look for evidence of hyperactivity of the adrenals among rodents of high density populations. Secondly, we would look for poor physiological conditions among animals from declining populations. Christian *et al.* (1965) cite a number of examples of rodents under abnormally high densities in the laboratory which show characteristics consistent with what would be predicted from the stress hypothesis. An extensive review of work using caged laboratory animals to elucidate the effects of isolation and grouping on brain chemistry and the functioning of the endocrine glands is available in the review by Brain (1971a) and will not be dealt with here.

For years adrenal function has been assayed by the weight of the adrenal glands. Several attempts at finding relations between adrenal weights and microtine population densities have failed (Christian, 1961; H. Chitty, 1961; Krebs, 1964a). A primary drawback has been the analysis of adrenal weight data. The adrenal weight changes with the body weight but it also varies with reproductive condition, age and sex of the individuals and season of the year. Furthermore, the relation between adrenal weight and body weight is most likely not linear (Krebs, 1964a), and it is not valid to compare adrenal weights by using values which are given in mg adrenal wt/gm body wt. Chitty (1961) and Krebs (1964a) used the technique of standardized means (Hill, 1959) to correct for body weight so that comparisons of adrenal weights could be made independent of body weight.

While adrenal weight may not be a good measure of adrenal activity (Christian and Davis, 1964; Andrews and Strohhahn, 1971), this was

the technique used by Christian and Davis (1966) in their most recent investigation. Since these authors conclude a "marked parallelism" between adrenal weights and population density for *Microtus pennsylvanicus*, this paper deserves further consideration. Overlooking previous discussions of appropriate methods for analysis of adrenal-body weight relations (Chitty, 1961; Krebs, 1964a), Christian and Davis used mg adrenal wt/100 gm body wt for their comparative index. By doing this they are assuming a relationship between adrenal weight and body weight which is linear with a slope of 1, an unlikely situation. The population index was the number of voles caught/1000 trap nights in one 24-hour period. This technique of population estimation is not reliable. Population density declined from its highest point in September 1960 until March 1961. The values are as follows:

Date	voles/1000 trap nights
24 September 1960	100
2 December 1960	28
20 January 1961	103
2 March 1961	21

As pointed out by Christian and Davis, the low value for December must underestimate the population density since it occurred during the non-breeding season and the population could not have increased to such an extent between December and January as indicated by the data. While Christian and Davis (1966) claim "a striking degree of positive correlation" between adrenal weight and the index of population size (voles/1000 trap nights) this correlation was not significant ($r = 0.59$; $0.10 > P > 0.05$).

The relationship between adrenal weight and population density (Christian and Davis, 1966) was found only among mature females. However, as reviewed earlier it is the younger animals which seem to suffer the heaviest mortality during the population peak and decline. This high mortality among the young would not be explained by social stress based on Christian and Davis' results. Later work of Christian (1971b) indicates that social stress as measured by wounding is strongest among mature male *Microtus pennsylvanicus*. Combining the results from Christian's two studies leads to the conclusion that there is no correspondence between endocrinological stress measured by adrenal weight and aggressiveness shown by wounding in mature male voles.

New approaches to the assay of adrenal activity have been used by Andrews (1968, 1970) and Andrews and Stohbehn (1971). Corticosteroid secretion rates can be measured on adrenals maintained in tissue culture.

In addition, respiratory rates of cultured adrenals are indicators of adrenal activity and the response of adrenal glands to ACTH is another measure of the state of the glands.

Andrews (1968) studied adrenal activity in brown lemmings from Barrow, Alaska. His first observation was that cultured adrenals display a circadian fluctuation in secretory activity. Therefore, comparisons among groups of individuals must be made over standard lengths of time, and during the same time of the day. The whole process is complicated by the fact that Andrews (1968) stored animals for varying lengths of time in the laboratory and this changed the timing of the circadian secretory rhythm of the adrenals. Comparison among groups in this study is most difficult.

A second complicating factor in the interpretation of Andrew's data is that his three measures of adrenal activity are not correlated. The highest respiratory rates, and secretory rates measured by the conversion of C^{14} acetate into corticosteroids, occurred in a sample of lemmings collected from a peak population in July and killed for analysis three weeks later in early August. However, the highest rate of corticosteroid secretion measured, using fluorometric determination of ethylacetate extractable steroids, occurred in a sample of lemmings also collected from a peak density population in July but maintained in the laboratory until February when they were analyzed. These results indicate that different biochemical pathways for the production of corticosteroids are being used under varying conditions. The biological significance of these results was not interpreted by Andrews (1968).

There are few statistics used in Andrews' (1968) study and so it is difficult to make comparisons between samples. However, all of his lemming samples were collected in July 1965, a year of peak lemming density at Barrow, Alaska (Pitelka, 1972). The factor which varied among samples was the length of time the lemmings were maintained in the laboratory. Therefore, when Andrews (1968, p. 91) talks about "glands obtained during summer 1965 and winter 1966, following a lemming population crisis", in fact he has collected animals from the same peak population and merely analyzed the adrenals after varying lengths of time. It is doubtful whether there is any correspondence between the physiological state of peak density lemmings maintained in the laboratory for seven months, and lemmings which remain in the natural population after the population decline. The only conclusion that can be drawn is that maintaining lemmings in the laboratory seems to change the secretion of adrenosteroids, but we have not advanced in understanding the biology of lemmings.

The respiration rate of adrenals of lemmings collected during the summer of population increase (1964) and the summer of the peak (1965)

are not significantly different. However, the respiratory rate of adrenals from animals captured in July 1965 and analyzed approximately one month later was significantly less than those of lemmings caught in July 1965 and analyzed in February 1966, seven months after capture. While ACTH stimulated steroid production in adrenals of lemmings maintained in the laboratory for seven months, it decreased steroid production of adrenals from lemmings collected and analyzed during the summer of 1965. This is interpreted as an indication that adrenals of animals collected from populations of peak densities were secreting at the maximum rate.

According to Andrews' description, the second year of his work (1969) was one of low lemming density. Sample sizes were quite small but the following trends were observed during the summer: (1) The content of ACTH in male pituitaries remained high through the summer but decreased in female pituitaries from early July through August. (2) The responsiveness of adrenals to exogenous ACTH measured as corticosteroid production was similar between males and females and seemed to increase in the August sample. (3) Andrews and Strohbehm claim a decreased sex ratio at the end of the summer, but there are no statistics to verify this and the sex ratio is 60% females ($N = 13$). This does not indicate strong differential mortality between males and females as stated by these authors, and leaves in doubt their conclusion that higher male mortality is associated with higher male adrenocortical and pituitary function.

Comparisons of data from the 1969 study of low population density to earlier data on peak populations were not made by Andrews and Strohbehm (1971). However, adrenals from low-density populations were stimulated by ACTH while those from a peak-density population were not.

Analyses of adrenal activity obtained by Andrews using the more elaborate methods are going to be even more complicated than were analyses which utilized adrenal weight. Along with the variations associated with body weight, sex, reproductive condition, and season of the year (similar to those observed in earlier studies of adrenal weights), there are circadian rhythms of adrenal secretion and respiration, and complex pictures which result from measuring steroid production with several techniques.

For any progress to be made in determining the role of the adrenal in affecting population processes, it will be necessary for proper demographic, physiological, and statistical procedures to be employed. The behavior of microtines is most certainly mediated through the endocrine system. So far no progress has been made toward correlating endocrinological changes to the early termination of the breeding

season during periods of peak lemming densities, or to high mortality in the decline.

It is possible that the adrenal steroid levels could be experimentally increased in a wild population by the injection of hormones into microtines. However, we understand so little of how these hormones work that analysis of the results of such an experiment could be too complicated to reveal any insight. The alternative might be to use sedatives to decrease social stress, but again manipulations of body chemistry can have undesirable side-effects.

In addition to all this work on the adrenal gland, various other physiological indices of condition have been studied by some workers. Hematological characteristics might be used as indicators of the physiological condition of animals. Newson and Chitty (1962) searched for an association between reticulocytosis and anemia and population decline in *Microtus agrestis*. While they found seasonal variation in hemoglobin levels of voles, the animals were not anemic during the population decline and they failed to find a physiological abnormality which might explain the decline.

An extensive investigation of the blood of brown lemmings was undertaken by Mullen (1965) in a search for physiological changes which might be associated with density. Blood glucose levels were measured to test for hypoglycemia. Hypoglycemia (low blood sugar) has had a part in the history of small mammal cycles since the report by Green and Larson (1938) that snowshoe hares in Minnesota suffered a decline because of "shock disease" characterized by low blood sugar, degeneration of the liver, and failure to store glycogen. Chitty (1959) refuted this work and recorded his own failure to find "shock disease" in *Microtus agrestis*. Also Chitty (1959) found that low glycogen reserves occurring in experimental laboratory populations of *M. agrestis* did not increase mortality. Houlihan (1963) found that blood sugar of an enclosed population of *M. californicus* decreased when the food supply was low but during a period of sharp decline (37% lost in two weeks) the blood sugar level of individuals in this population was the same as in a control population of moderate density which did not decline. Similarly, while Mullen (1965) found variation in the blood sugar level of brown lemmings, he was not able to associate this variation with population density or density changes.

It has been suggested that there is a negative relationship between the number of circulating eosinophils and adrenocortical activity in rodents (Speirs and Meyer, 1949). If this is so, determination of eosinophil levels can be used as a means of assaying adrenal activity. Houlihan (1963) studied eosinophil levels in two enclosed (120 ft² outdoor pens) populations of *Microtus californicus*. The density of one

population was maintained at approximately 40 individuals while the other population increased, with provision of additional food, to a peak density of 158 individuals. After maintaining high densities for several months the uncropped population declined. Houlihan (1963) compared eosinophil levels between these two populations. In the months before and after the decline of the uncropped population, eosinophil counts were higher than those of individuals from the moderate density control population. This indicates increased adrenal activity if eosinophil is a valid measure. However, in the month of the decline of the high density population, the eosinophil counts were significantly higher than in the other two months. Therefore, it was not possible to interpret these results in a simple manner, and Houlihan concluded that eosinophil levels should not be used as an indication of adrenal stress.

Mullen (1965) comes to the same negative conclusion as Houlihan in regard to the use of eosinophil levels as a measure of adrenal activity. Rather than using the number of eosinophils as his index, Mullen determined the percent of total leucocytes represented by eosinophils. Therefore, although there is a trend for the eosinophil level to be low in individuals taken from the 1960 peak population, this was found to be the result of a greater number of leucocytes all together, which lowers the percent of eosinophils, although the absolute number of eosinophils was actually higher in 1960 than in other years. Crowding lemmings in the laboratory did not influence eosinophil levels.

Determination of non-protein nitrogen in the blood is another physiological index in microtines. Houlihan (1963) used this measure on his artificial high and low density *Microtus* populations. The trends in this measure were the same in both populations. Houlihan did find several indications of physiological derangement in his declining population. These were: (1) a 30% decrease in thyroid activity, (2) an increase in the time required for blood clotting and a change in the quality of the blood clots, and (3) an increased susceptibility to the blood sampling procedures resulting in more deaths, particularly among males. At the time of the decline there was severe fighting and wounding. Although these enclosed populations were maintained outdoors, they were artificial in that additional food had to be added for the high density (equivalent to 4770/acre) to be reached. The degree of similarity of this microtine decline to a natural decline still remains a question.

Other physiological assays performed by Mullen (1965) on brown lemmings were leucocyte, erythrocyte and reticulocyte counts, and hematocrit values. Two factors complicate the interpretation of these data. First, experiments in which these characteristics were determined for lemmings kept under crowded conditions and kept singly in the

laboratory, showed that none of these hematological factors seemed to vary with artificially imposed density levels. Secondly, the densities of field populations given by Mullen (1965) do not agree with the trapping data of Pitelka (1972) for the same vicinity at Barrow, Alaska. Mullen refers to the summer of 1963 as a peak year while Pitelka's data indicate that it was a year of low numbers. This conflict might be explained by the fact that Mullen trapped periodically during the winter of 1962–1963. Therefore, numbers may have been high and declined before

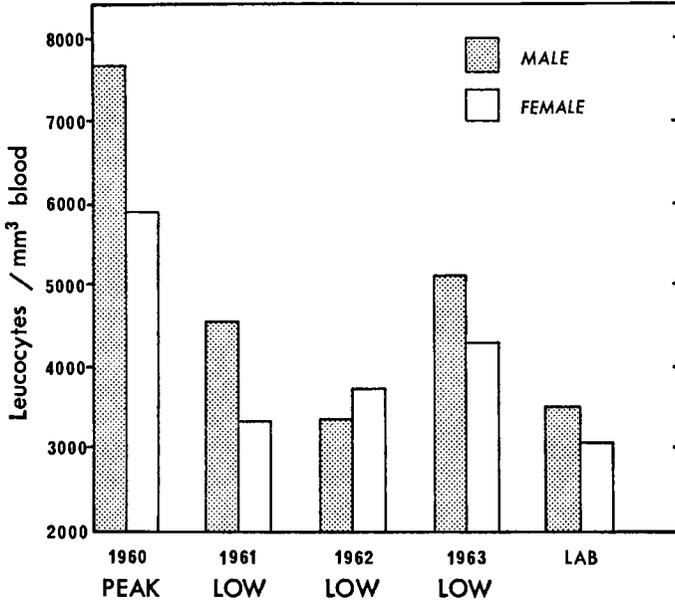


FIG. 39. Leucocyte levels of lemmings collected in the field compared to those maintained in the laboratory. The leucocyte counts for both males and females in 1960 are significantly higher than in other years. Data from Mullen (1965). While Mullen regards 1963 as a year of peak lemming density, Pitelka's trapping data for the same vicinity indicates that this was a year of low density (Pitelka, 1972).

Pitelka's June trapping period. Without adequate demographic data it is impossible to judge what phase of the population fluctuation was represented in 1963. However, there is general agreement that 1960 was a year of peak density and we can use these data to indicate the condition of lemmings from peak population densities.

The number of circulating leucocytes was significantly higher among both males and females during the peak year of 1960 (Fig. 39). High leucocyte levels are often an indication of infection or disease, but Mullen (1965) had no data on possible pathologies associated with these

elevated leucocyte levels. The number of circulating leucocytes declined in animals brought into the laboratory from the 1960 peak population.

While there was no variation in the number of circulating erythrocytes in brown lemmings during the summers of 1961 to 1963 the number of reticulocytes was higher in lemmings collected in June 1960 (peak density) and June 1963 than were those of lemmings from the intervening years of 1961 and 1962. This may indicate that during the early summer of years of high population density the production of red blood cells is greater. However, if the total number of red blood cells does not change it must also mean that the survival time of red blood cells is higher. The decline in the lemming population at Barrow did not occur until autumn or winter, 1960. Late summer reticulocyte levels were not significantly different in 1960 than in other years. It is interesting that lemmings with high levels of circulating reticular erythrocytes

TABLE XIX

Percent circulating reticular erythrocytes in the blood of lemmings collected from the field and those collected from the field and maintained in the laboratory for two to three months. Data from Mullen (1965).

Year	% Reticulocytes—Laboratory	% Reticulocytes—Field
1960	—	2.48 ± 0.15
1961	1.91 ± 0.27	2.06 ± 0.55
1962	2.25 ± 0.17	1.59 ± 0.26
1963	3.37 ± 0.35*	4.32 ± 0.46*

* Significantly higher than other years, $P < 0.01$.

from the June 1963 population, maintained these high levels after two to three months in the laboratory (Table XIX). In the natural population the level of reticulocytes declined during the summer, indicating that there was selective mortality against individuals with high reticulocyte levels. Again artificially imposed high densities did not influence the number of circulating reticular erythrocytes.

Hematocrit values did not show meaningful variation among lemmings for the years 1961–1963. The volume of blood cells remained constant although the composition of types changed.

We are left with a contradiction after an analysis of physiological indicators of stress. The strength of the stress hypothesis has been the results of experimental crowding of small mammal populations in the laboratory. Mullen (1965) has reported two hematological variations which seem to be associated with density of natural lemming populations, and yet he was not able to mimic these changes in crowded laboratory populations. Mullen's conclusion was that his data do not

support the social stress theory for population control but that they do suggest that disease or metabolic disorder may be associated with the population decline. The question remains as to whether the susceptibility to disease of individuals in high-density populations is greater. Further investigation of the comparative survival of individuals with high and low leucocyte counts and reticulocyte counts should be done. After the decline, the levels of these two blood parameters returned to normal (Mullen, 1965). Did individuals with high leucocyte and reticulocyte levels have higher mortality or did the physiology of surviving individuals change? Studies of this sort could be done by taking blood samples from individuals at intervals in the field.

Hematological tests of adrenal activity have been unsuccessful and the search for hypoglycemia associated with declining microtine populations seems to have been futile. However, the use of blood cell counts as physiological indicators deserves further consideration.

The extent of ectoparasitism in populations of *Microtus californicus* was found to vary with population density (Batzli and Pitelka, 1971). More animals were infested by fleas, lice and mites in the autumn following the peak population density than in the previous autumn of population increase. Ectoparasitism may be a useful characteristic for assay of the general condition of voles. Because there is most likely a relationship between the condition of the animals and the ectoparasite load this approach to the investigation of stress and population density deserves further consideration.

While dead animals are rarely found following a decline in microtine populations, Fitzgerald (1972) reports finding dead *M. montanus* in nests the spring after a winter decline. Dead and dying *M. californicus* were observed on Grizzly Island, California during the decline in population during the late summer of 1971 (Myers, personal observation), and Rauch (1950) observed dying lemmings during the 1949 decline in Alaska. Voles from declining populations which are brought into the laboratory seem usually to survive well (Newson and Chitty, 1962; Krebs, 1966; Andrews and Strohbehn, 1971). Because we know almost nothing of the characteristics of dying microtines or if, in fact, the animals are dying *in situ* during the decline, we cannot judge the relation of the stress theory to mortality in natural populations of cycling rodents.

There is one set of observations which remains difficult to explain with the "stress hypothesis": that enclosed populations are able to reach much higher densities than are observed in natural populations. Microtines can both live and reproduce at densities much higher than occur naturally. Proponents of the stress hypothesis argue that social stress is not a simple function of population density, and consequently

the "stress" level of a natural population at 100 per acre could be equal to the stress level of an artificial population at a caged density of 10 000 per acre. Whether or not one accepts this argument, the point we wish to make is that more attention should be paid to the behavioral interactions which must cause social stress. Excessive preoccupation with physiological measurements may have sidetracked us from more relevant behavioral aspects of social stress.

In summary, the stress hypothesis suggests that microtine populations peak and decline because of physiological deterioration of adrenal functions. Although this theory is popular even in the communications media, we can find no evidence from natural populations to support it. Few studies have discovered any apparent relationships between adrenal functions and population changes, and none of the characteristic features of reproduction, mortality, dispersal, or growth which we discussed previously have been associated with physiological measurements of adrenal changes.

E. BEHAVIOR

The behavior hypothesis suggests that interactions between individual animals are critical in causing population fluctuations in small rodents. The behavior hypothesis is an intrinsic hypothesis since it states that a necessary factor preventing unlimited increase is a change in the behavior of individuals in the population. We will consider this theory separately from the stress hypothesis and the genetic hypothesis because no mechanisms of behavioral change or inheritance are specified. We inquire, as a first approximation, only whether behavioral interactions change during a population cycle.

The primary behavior which might be involved in population events is spacing behavior. There has never been any doubt that voles and lemmings show hostility toward one another, and space themselves over the habitat; people differ greatly in how to interpret such a fact. Watson and Moss (1970) have carefully reviewed how population limitation can be achieved by means of aggression in vertebrates, and they cite three conditions which are necessary to show that aggressive behavior limits the density of breeding animals:

1. there must be a substantial "surplus" population which does not breed;
2. these surplus animals must be capable of breeding if the more dominant animals are removed;
3. the breeding animals must not be completely depleting some resource, such as food or nesting sites.

How can one demonstrate that a surplus population of microtines exists? The best way to do this is to crop a resident population of breeding animals, and to see if new animals take up the positions vacated by removals. This experiment was first done by Smyth (1968) on *Clethrionomys glareolus* at Oxford, and he found that extensive immigration offset his removals. Krebs (1966) cropped a two-acre grassland of 1758 *Microtus californicus* over one year and yet found little difference in density between the cropped population and its control. Myers and Krebs (1971b) described a substantial influx of *M. pennsylvanicus* into cropped areas in Indiana. Watts (1970) cropped a population of *Clethrionomys gapperi* of adult males during a phase of increasing density, and found little difference in the rate of growth of the control and experimental populations. Elliott (1969) removed males from another population of *C. gapperi* and found that they were replaced by other adult males. He concluded that spacing behavior was important in determining breeding densities. Dahl (1967) did the converse experiment of adding *M. pennsylvanicus* to a resident population and found that he could not increase density by adding voles.

These cropping experiments can be criticized because the "surplus" voles moving into the experimental areas might be the resident breeding animals from surrounding areas. Hence the breeding density of the whole area might be depressed by filling in the evacuated habitat, and no truly "surplus" voles might exist. This did not appear to be the case in the Krebs (1966) experiment, since not a single marked individual was drawn from the control area to the removal area 300 ft away.

Surplus animals in rodent populations presumably disperse and are largely lost to various agents of mortality. Consequently the study of dispersal in vole and lemming populations is also a study of the movements of "surplus" animals. Because of the general habits of rodents, we are not able to study their social organization in the same way we can for territorial birds. Hence the demonstration of surplus voles or lemmings will probably never be as elegant in experimental terms as similar experiments on birds.

The surplus population of microtine rodents always seems to be capable of breeding, thus satisfying condition (2) above. The immigrants of *Microtus californicus* which colonized the removal area were active breeders (Krebs, 1966), and the same was generally true in the study by Myers and Krebs (1971b), although some young animals not yet sexually mature also dispersed. Cyclic rodents seem to have adopted the general strategy of decreasing the population of breeding individuals as they go from the increase phase to the peak phase. Reproductive changes, such as increase in the age at sexual maturity, all seem to force more of the population into a "surplus", non-breeding category.

The third criterion of Watson and Moss (1970) is that the breeding animals are not completely depleting some resource, such as food. This particular criterion brings together most of the controversy over microtine cycles. We have argued above that the present evidence does not indicate that populations of cyclic rodents are completely using some resource such as food. But it is possible to argue that we do not yet appreciate what a "resource" is to a vole, and consequently we should consider other types of evidence.

If hostility is part of the mechanism for generating population cycles in rodents, we must expect that the aggressive behavior of individuals changes with density. Two types of data are available on this question. First, relatively crude data can be obtained from observing skin

TABLE XX

Proportion of skins of male brown lemmings (Lemmus trimucronatus) showing wounds on inner surface during a population cycle in northern Canada. Overwintered adults are all sexually mature; summer-born young are all sexually immature. Sample size in parentheses. After Krebs (1964a).

	Overwintered adults			Summer-born young
	June	July	August	
Increase phase (1959)	0.29 (7)	0.20 (5)	0.71 (7)	0.09 (11)
Peak phase (1960)	0.52 (99)	0.69 (39)	0.36 (14)	0.33 (255)
Decline phase (1961)	0.18 (33)	0.65 (26)	—	0.24 (45)

wounds on animals from different phases of the cycle. Krebs (1964a) scored wounds from flat skins of brown and varying lemmings, and found that wounding was more severe in peak populations than in increasing ones, but that wounding remained severe in the decline phase even though density had fallen (Table XX). Summer-born young lemmings had some wounds even though most of them were sexually immature. Some suggestion of increased wounding associated with sexual activity of summer-born lemmings was obtained from one sample in the increase phase in which one of eleven immature males was wounded compared with six of eight mature males (Krebs, 1964a, p. 49). Young females did not show this effect, and almost none of them showed wounds.

Christian (1971a) made similar observations on a peak and declining population of *Microtus pennsylvanicus*. Mature males showed more wounding in spring of the peak year than in the spring of the decline

year. He found that wounding was confined almost entirely to adult males; females had few signs of wounds on the skin. Immature young males were not subject to wounding either. Christian suggested that when the age at sexual maturity is low, fighting will be more prevalent because a larger proportion of the male population will be mature. He therefore predicts more fighting at low densities because of early maturation, but thinks that the influence of the larger portion of belligerent males is offset by the lower density.

Wounding was not greater in higher density populations of *M. californicus* (Batzli and Pitelka, 1971). Again the amount of wounding observed in males was greater than that in females.

Aggression, fighting and wounding may be greater in *Clethrionomys* than in *Microtus*. In a year of low abundance of *C. rutilus* Koshkina (1965) observed badly wounded individuals, particularly among those who were sexually mature. She judged that the wounding was sufficient to kill the animals, and badly injured voles were not often recaptured.

There are two difficulties in interpreting data on skin wounds. First, the amount of wounding can only be a very crude behavioral index of aggressiveness. Many of the techniques by which animals space themselves do not involve physical aggression (Lorenz, 1963). Second, wounding indices confound the two variables of population density and aggressiveness. We cannot decide from wounding data whether (1) the average level of individual aggressiveness is constant and independent of the cycle, and all the changes in wounding are a result of changes in density and therefore more numerous interactions, or (2) whether the behavior of individuals also changes in relation to density.

We know little of the factors affecting contact rates of individual voles or lemmings in the field. Pearson's (1960) elegant photographic work on runway usage should caution us that contact rates may not be a simple function of population density. There are indications that the area traversed by individuals is smaller when population densities are high (Krebs, 1964a, 1966, and unpublished; Koshkina, 1965). By restricting its area of activity as the population density increases, a vole may be successful at maintaining an almost constant rate of intraspecific interaction regardless of population density. Because we cannot be certain of the social climate in field populations we need to obtain behavioral measurements on individual animals, and to look at some of the details of social organization in microtine rodents.

Techniques for measuring aggressiveness on live rodents have been used in psychological research for a long time, but few attempts have been made to apply these techniques to voles and lemmings. The simplest procedure is to observe two individuals in a fighting arena.

The arena may be a neutral arena or a home cage of the animals. Often only males have been tested, in the possibly mistaken belief that important aspects of spacing behavior were restricted to males (the bird analogy), and because reproductive cycles of females complicate the analysis of their behavior.

The first attempt to see if aggressiveness varied with density was made by Tamura (1966), working with *Microtus californicus*. She ran bouts between 167 adult males brought in from a fluctuating population and tested in home cages in the laboratory. Thirty-three behavioral variables were recorded from these male-male interactions, and over the two years of study Tamura could detect no significant patterns of change in the aggressive components of behavior.

A second attempt to see if male aggressiveness varied with density was made by Krebs (1970), working with *M. ochrogaster* and *M. pennsylvanicus*. Two classes of behavioral measurements were made. Exploratory activity was measured in an open field, and aggressiveness was measured in paired encounters in a neutral arena. These measurements were made on field animals brought into the laboratory for two days and then returned to the field. Exploratory activity showed some relationship to population changes, particularly in *M. ochrogaster*, but the exploratory behavior scores of individuals were not useful in predicting either the duration of life or the home range size of the individual males. We would expect that, if we could measure behavior accurately and if the measured type of behavior is related to the demographic machinery of density changes, we could predict individual attributes such as length of life from the behavioral data. Aggressiveness scores changed significantly in both species such that voles in peak populations were most aggressive. Aggressive behavior profiles were obtained for voles from increasing, peak, and declining populations. Figure 40 illustrates profiles for *M. pennsylvanicus*. These profiles were obtained from data collected from 1965 to 1967, and we used them to predict population changes from 1967 to 1970 (Krebs, 1971). The attempt to predict population parameters from aggressive behavior data was only partly successful, and the relations between demography and aggressive behavior were weak. Krebs (1971) suggested that there might be three reasons for this: (1) aggressive behavior of female voles might be more important than male aggressiveness; (2) the set of behaviors measured might be a poor index of the important spacing behaviors in social groups in nature; or (3) aggressive behavior may not be an important factor in causing population changes in voles.

There has been relatively little work on the techniques of measuring aggressive behavior in wild rodents. We are inclined to think that our present techniques do measure something which is important in

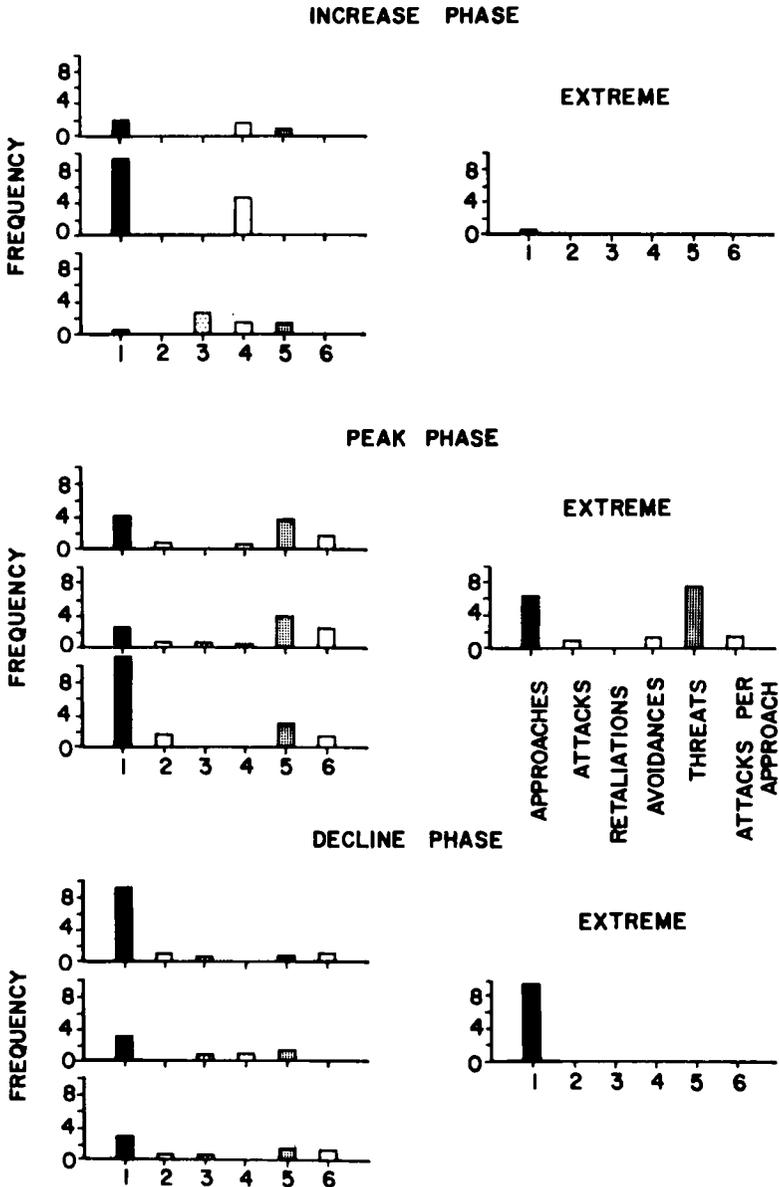


FIG. 40. Sample aggressive behavior profiles for 12 *Microtus pennsylvanicus* males showing behavior typical of increase, peak, and decline phases, with extreme cases shown at right. Frequency recorded in 10 min bouts. (After Krebs, 1970.)

nature. For example, Fig. 41 shows the trends in aggressive and avoidance behavior of *M. ochrogaster* through a population decline and subsequent increase. There was a marked change as the population finished the decline and then began to increase, but we cannot explain these changes in behavior because they are largely statistical effects. When we can obtain accurate measurements on single individuals, it

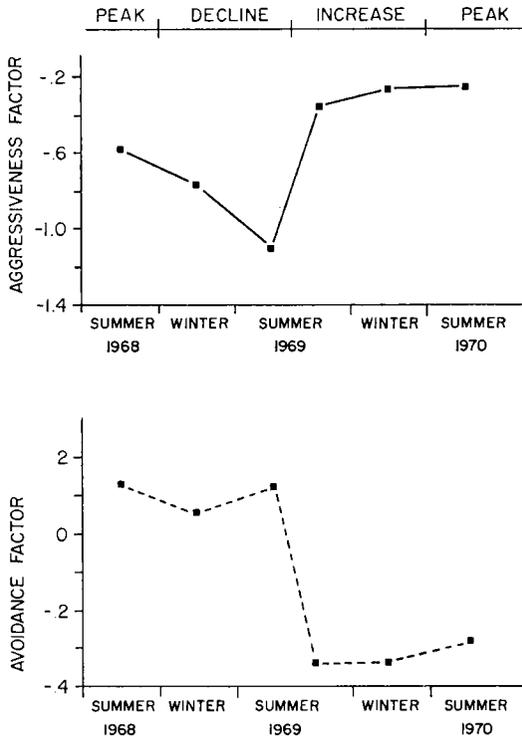


FIG. 41. Changes in the aggressiveness factor score and the avoidance factor score (defined in Krebs, 1971) for *Microtus ochrogaster* through a population cycle from 1968 to 1970 in southern Indiana. (Krebs and Myers, unpublished data.)

may be possible to determine the dynamics of the changes which seem to occur in the different phases of the cycle.

Turner (1971) has made a detailed study of the annual cycle of aggression in male *M. pennsylvanicus* from Manitoba. Aggressive acts increased in frequency at the onset of reproduction and decreased at the end of the breeding season. Turner was able to show that an individual vole's aggressive score was positively correlated with his chances of surviving and negatively correlated with home range size.

Heavier voles were usually more dominant in aggressive encounters. It is tempting to interpret these data in terms of population fluctuations. Two characteristics of peak populations are smaller home ranges and larger-sized animals. Both these characteristics were found by Turner (1971) to be related to aggressiveness in male voles. Turner's study is a model of the type of careful analysis of aggressive behavior that must be done if we are to understand the role of intraspecific strife in affecting numbers. He is presently continuing observations to determine whether aggressiveness is related to population density.

Conley (1971) measured aggressive behavior of male and female *M. longicaudus* during a peak summer and a decline summer in the mountains of New Mexico. He found that voles from a peak population were more aggressive toward each other than were voles from a declining population. Conley also studied a sympatric population of *M. mexicanus* which was at low density during the two years. This population showed no difference in aggressiveness between years. Aggressive reactions of male and female voles were the same.

Social antagonism was analyzed by Getz (1972) by the use of multiple-capture live-traps for *M. pennsylvanicus*. Getz showed that many multiple captures of two adult males occurred during his five-month study, and he could see no evidence of great antagonism between males in his declining population. However, the number of double captures of adult females was significantly less than expected, which might suggest some antagonism among females.

The movements of Norwegian lemmings, which are associated with high densities, may be triggered by the aggressiveness of both male and female residents (Clough, 1968). Unfortunately, no detailed studies have been made on changes in agonistic behavior through a population fluctuation of this legendary lemming.

Frank (1957) has argued that behavioral mechanisms are critical in determining population changes in *M. arvalis*. He refers to these behavioral mechanisms collectively as the "condensation potential". There are three major elements in the condensation potential. First, home ranges can be reduced to small sizes. Both males and females are territorial, and females drive off their male offspring and allow the young females to settle in or near their home range. Second, females can form mother-families and even "great families" at the end of the breeding season, so that groups of immature animals can overwinter together. These great families break up once breeding begins in the spring. In some cases related females remain together on a common territory and bring up their litters in a common nest. Third, males of *M. arvalis* show spacing behavior at all times when they are breeding, and consequently many more females than males occur in

peak populations. Male mortality is thus much greater than female mortality, and males fight vigorously for territories and show more wounding.

The pattern of changes described by Frank (1957) for *M. arvalis* should be evident in a changing sex ratio over a population fluctuation. There has been no evidence from any of the studies on *M. agrestis* (Chitty, 1952), *M. ochrogaster* and *M. pennsylvanicus* (Myers and Krebs, 1971a) and *M. californicus* (Krebs, 1966) that sex ratios change systematically over the population cycle. There is often a surplus of females in the trappable population, but this seems to be a constant feature of all the phases of the cycle. The absence of any sex ratio change may mean that *M. arvalis* has a different pattern of social structure to these other *Microtus* species.

More detailed studies are needed of the social structure of vole and lemming populations. Some aspects of social behavior can be studied in enclosed pens, but we badly need ways of studying field populations *in situ*. Perhaps the simplest approach we can take at this stage is to study male-male, male-female and adult-young interactions in a laboratory system, and then to use these observations as a basis for designing field experiments. For example, we might manipulate social organization by artificially changing the sex ratio in natural populations. Alternatively, by cropping one sex and age group in a population we might gain some insight on how social organization influences population density.

An alternative series of experiments might involve the modification of behavior with drugs. Implants of testosterone, for example, might be used to make selected males aggressive. Nothing has been done so far on vole and lemming populations to alter behavior with drugs.

We have said little so far about the possibility that behavioral interactions can cause the mortality associated with declining populations. Except for the observations of Koshkina on *Clethrionomys rutilus*, there is no evidence that behavioral interactions between voles or lemmings are lethal, and it seems highly unlikely that adult animals often die as a direct result of fighting. Some fraction of the loss of small juveniles might be due to aggressive interactions with adults, and more evidence is needed on this point. But we have studied fenced populations of *Microtus ochrogaster* and *M. pennsylvanicus* at very high densities and not found any significant mortality of subadult and adult voles (Krebs *et al.*, 1969). If behavioral interactions are important causes of population declines, they must act by forcing individuals to succumb to other agents of destruction. A model for this suggestion can be found in the muskrat (Errington, 1967) and the red grouse (Jenkins *et al.*, 1964). Socially inferior voles (non-aggressive animals)

might be more subject to loss by predation, bad weather, or stress diseases. Note that only a small mortality change is necessary to cause a population decline (cf. Fig. 24). A 10–15% drop in the probability of surviving per month would be sufficient to account for most of the losses in declining populations. We are thus looking for a steady mortality factor of small magnitude rather than a catastrophic mortality factor of large magnitude.

We have shown previously that there seems to be little dispersal during the decline phase, and most of the losses seem to be deaths *in situ*. This result, if it is a general one, is difficult to reconcile with the results of behavioral studies. The muskrat and red grouse models would suggest that social intolerance should produce considerable dispersal, and these dispersing animals (or those pushed into marginal habitats) should suffer high mortality. But with voles we must, at present, postulate that social intolerances in the decline phase somehow lead to mortality but without much dispersal movement.

We cannot specify now what the behavioral attributes of dispersing voles and lemmings should be. Most of the studies cited above suggest that animals in peak populations are the most aggressive. We might guess that more aggressive populations would produce more dispersal, but this is not the case since dispersal rate is highest during the phase of increase. Myers and Krebs (1971b) compared the aggressive behavior profiles of male *Microtus pennsylvanicus* which had dispersed with those of resident males, but found no clear and consistent differences in the types of variables scored by Krebs (1970). Overall the dispersing males tended to show characteristics of aggressiveness, and in one case the "increase" behavior type (Krebs, 1970) was over-represented in dispersing *M. ochrogaster*. We feel there must be some behavioral reason why some individuals disperse and others remain as residents. Perhaps the important traits which we would like to measure are so transitory they disappear after dispersal has occurred. More work is clearly required on these behavioral problems.

Behavioral interactions between individual rodents have been shown to have strong effects on reproduction and growth in confined populations (review by Christian, 1971b). The physiological and endocrinological mechanisms involved in the suppression of reproduction and growth have been particularly well studied in rodents by Christian and his co-workers. The main gap at present is the specific application of these findings to the details of changes found in field populations. For example, we need to know whether there is a certain behavioral milieu which permits winter breeding in some years and another milieu which stops the breeding season early.

If behavioral changes are important in population cycles, we must

determine the mechanisms behind the behavioral shifts. On the one hand, behavioral changes can be caused by physiological shifts in brain chemistry or hormonal balances caused by isolation or grouping (reviewed by Brain, 1971a, b). These changes are usually considered as phenotypic and are often tied in with the stress hypothesis. On the other hand, behavioral changes could have a genetic basis and be tied in with the genetic hypothesis of Chitty (1967). Obviously behavioral changes will still have physiological and endocrinological mechanisms even if they are genetically influenced. No one knows whether the behavioral changes described above are phenotypic or genotypic, and we suggest that these questions should be tackled in the logical order: (1) does spacing behavior change over the population cycle? (2) can the behavioral changes be shown to be heritable by the standard techniques of quantitative genetics? and (3) what are the physiological pathways by which the relevant spacing behaviors are influenced? At present most effort is being expended on question (3), even though we have little data on question (1) and no data at all on question (2).

In summary, the behavior hypothesis seems to hold the best possibility for explaining the changes in reproduction, mortality, dispersal, and growth which drive the population cycle. Spacing behavior, or hostility, seems to produce a "surplus" population of animals which move into vacant areas. If spacing behavior causes the population fluctuations, the aggressive behavior of individuals must change with density. This hypothesis has been verified both by examining skin wounds and by paired-encounters of males in arenas. Male voles and lemmings are most aggressive in peak populations. Little work has been done on female aggressive behavior, and some workers suggest that females may be even more aggressive than males. It is not clear how behavioral interactions can account for the mortality changes found in declining populations, since fighting itself rarely leads to deaths. No one knows whether the behavioral changes that have been found in microtine rodents are phenotypic or genotypic, and the behavioral hypothesis could be subsumed under either the stress hypothesis or the genetic hypothesis once this is known.

F. GENETICS

When Chitty (1958, 1960) first proposed his hypothesis that the quality of microtines changed with density as a result of selection on genetically determined behavioral types, two immediate objections arose. The first of these was that the hypothesis was overly complex. As stated by Pitelka (1958), "it may be a strain on Occam's razor to

suggest genetical hypotheses regarding fluctuations as long as more directly ecological explanations can be invoked and tested". The second criticism was that selection could not be sufficiently strong to bring about such dramatic genetic change over several generations as to account for population fluctuations (Christian and Davis, 1964). Both of these criticisms are examples of how only a short time ago, it was the rule for the population ecologist to view populations largely as genetically homogenous aggregates of individuals. While R.A. Fisher (1930) considered that selective advantages of approximately 1% per generation were acting on natural populations, Ford (1964) reviews cases demonstrating selective advantages of 20–30% per generation. Ford concluded in his summary of "Ecological Genetics" that "unexpectedly great selective forces are normally operating" (p. 296). If strong selection is possible in natural populations, we cannot automatically disregard the role of selection in population regulation.

Chitty's genetic behavioral hypothesis to explain the cycling of rodents began from a negative basis. All of the "simple" hypotheses proposed to explain microtine cycles had been unsatisfactory (Chitty, 1960). The positive basis for the behavioral-genetic polymorphism idea was the observation that at the time of the population decline, *Microtus agrestis* populations are composed of some individuals with high growth potentials and others with low growth rates (Newson and Chitty, 1962). Therefore, the population is a composite of individuals of different phenotypes. The presence of large voles in peak populations suggests that the composition of the population at the peak is different than that during the decline. Krebs (1964b) observed a change in the relationship of skull measurements with body measurements associated with density changes in brown and varying lemmings (see Fig. 28). This again suggests the possibility of selection varying the phenotypic composition of microtine populations during different phases of the population cycle. Whether the basis for the phenotypic change is genetic could only be suggested.

A starting point for investigation of the genetic-behavioral hypothesis is to inquire if genetic changes do occur as a microtine population undergoes fluctuations in density. Gershenson (1945) and Voipio (1969) have suggested that shifts in genetically controlled coat-color morph frequencies occur in association with density changes in rodents, but in microtines individuals with coat-color variations are scarce (Semeonoff, 1972). Another technique for elucidating genetic systems is to monitor changes in the frequency of alleles at polymorphic loci, coding proteins with differing structure (Semeonoff and Robertson, 1968; Canham, 1969; Tamarin and Krebs, 1969; Gaines and Krebs, 1971). The technique of electrophoresis enables one to demonstrate

structurally-varying proteins. Genetic polymorphisms in albumins and transferrins (both serum proteins) and esterases and leucine aminopeptidase (both enzymes occurring in serum) have now been investigated in microtines.

The first study of this type was that of Semeonoff and Robertson (1968) who discovered a change in the gene frequency of an esterase locus during a population decline of *Microtus agrestis* in Scotland. Canham (1969) monitored albumins and transferrins in *Clethrionomys rutilus* and *C. gapperi* populations in the Northwest Territories and Alberta and found a correlation between density and heterozygote fitness. The studies of Tamarin and Krebs (1969) and Gaines and Krebs (1971) covered five years' observation of gene frequencies of *Microtus ochrogaster* and *M. pennsylvanicus*. Periods of very strong selection occurred on the two loci under study, leucine aminopeptidase and transferrin (Fig. 42). Therefore, dramatic genetic changes can occur in association with density changes; but how repeatable are these observations? Many of the findings of Tamarin and Krebs (1969) were verified in the continuing study of Gaines and Krebs (1971), which included more populations over another population cycle. In both studies of *M. ochrogaster* there was a positive correlation between the frequency of the Tf^E allele and changes in population density (Fig. 43). This relationship was found to be largely the result of better survival of the heterozygote (Tf^E/Tf^F) during the population decline (Table XXI). In the six populations studied, male *M. ochrogaster* heterozygous at the transferrin locus had either better or equal survival than the Tf^E/Tf^E homozygote.

In *M. pennsylvanicus*, Tamarin and Krebs (1969) observed a negative correlation between density and frequency of the Tf^E allele in females, while Gaines and Krebs (1971) found this relationship for males (Table XXII). As shown in Table XXIII, the survival differences among genotypes in the two studies are not always consistent but tend to show the same trends. Certainly the relationship between gene frequency and density change is not a perfect one (Fig. 43) but there is a definite statistical trend.

Not all local populations are genetically similar, however. One population studied by Gaines and Krebs (1971) (Grid I) had frequencies of the Tf^E allele which were much lower than the other populations. It was most common for gene frequencies for the Tf^E allele to range between 0.40 and 0.60, but in this one population the frequencies rarely exceeded 0.40 and were most often between 0.20 and 0.40. Unlike the other populations in which the Tf^E/Tf^E homozygote and the Tf^C/Tf^E heterozygote had superior survival rates, in this population the Tf^C/Tf^C homozygote had a survival advantage. However, this population still

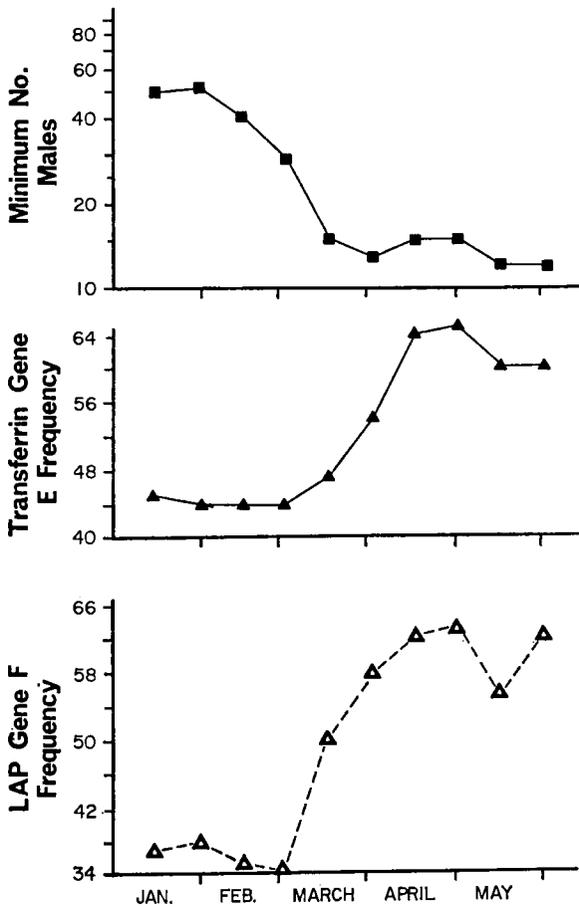


FIG. 42. Genetic changes in association with density changes for *Microtus pennsylvanicus* males on one area during the spring of 1969. (After Gaines and Krebs, 1971.)

demonstrated a population fluctuation and was not demographically distinctive from other populations.

Is this inconsistency contradictory to the genetic-behavioral hypothesis? To answer this question we must consider what we are doing by monitoring genetic changes using marker alleles. When this study began the question was simply "do genetic changes occur?" To answer this we needed a genetic trait which was easily scored for individuals without having to remove them from the populations. Electrophoretic variants were the obvious tool. We did not predict that the arbitrarily picked genetic trait would be the driving force behind

	Density decreasing	Density increasing
Tf ^E frequency decreasing	78 (56.5)	43 (64.5)
Tf ^E frequency increasing	35 (56.5)	86 (64.5)

$$\chi^2=30.70$$

$$p<0.005$$

FIG. 43. Gene frequency changes and density changes for *Microtus ochrogaster* in southern Indiana were scored for every bi-weekly trapping period. There is an apparent relationship between increasing frequency of the Tf^E allele and increasing density in *Microtus ochrogaster* (Gaines and Krebs, unpublished data).

cycles. But we did hope that, if strong selection were associated with fluctuating density, it would change gene frequencies in the marker alleles as part of the total genome. We can only guess that in a population such as that on Grid I, which had the "abnormally" low Tf^E frequency, the transferrin locus is associated in a slightly different linkage group so that selection in that population had different results than in the other populations. This population was not geographically isolated from other populations, and we would expect these differences to be smoothed out over time.

If the marker alleles can be used as indicators of the genetic types which change in frequency over the cycle, then we might be able to use these genetic types further to investigate the demographic characteristics of cycling microtines. For example, we observed that in *Microtus ochrogaster* the Tf^F allele is maintained at a very low frequency, but that selection favors heterozygotes during the population decline (Table XXI). With the beginning of the increase phase the Tf^E/Tf^E genotype regains its selective advantage and the frequency of the Tf^E allele rises. We predicted therefore that beginning with a low-density population, Tf^E/Tf^E animals should respond with a greater rate of increase than Tf^E/Tf^F individuals. The other homozygote Tf^F/Tf^F rarely occurs in nature and we predict that a population composed of all individuals of this genotype should also do poorly.

TABLE XXI

Comparison of the survival rates per 14 days for the transferrin genotypes of *Microtus ochrogaster* males in six populations studied. A¹ includes data collected during the first population cycle on area A, and A² is from the second cycle on the same area. Underlined values are the higher for that set of data.

Population change	Genotype	Area					
		F	H	I	A ¹	A ²	C
Increase	EE	0.74	0.81	—	<u>0.84</u>	<u>0.85</u>	<u>0.85</u>
	EF	<u>0.87</u>	<u>0.89</u>	—	<u>0.76</u>	<u>0.79</u>	<u>0.70</u>
Decrease	EE	<u>0.65</u>	<u>0.69</u>	0.64	0.59	0.68	0.75
	EF	<u>0.78</u>	<u>0.81</u>	<u>0.84</u>	<u>0.75</u>	0.68	0.75

TABLE XXII

Comparison of the relation between the frequency of the transferrin Tf^E allele and density in *Microtus pennsylvanicus* in the studies of Tamarin and Krebs (1969) and Gaines and Krebs (1971).

	Correlation coefficients	
	Tamarin ¹	Gaines ²
Males	0.06	-0.18*
Females	-0.67**	0.03

¹ Relationship of Tf^E frequency and density (based on one population).

² Relationship between change in Tf^E frequency and change in density (based on four populations).

* P < .05

** P < .01

TABLE XXIII

Comparison of the survival rates per 14 days for the transferrin genotypes of *Microtus pennsylvanicus* revealed in the studies of Tamarin and Krebs (1969) and Gaines and Krebs (1971). Underlined values are the highest for that set of data.

Genotype	Tamarin		Gaines	
	Increasing	Decreasing	Increasing	Decreasing
Tf ^C /Tf ^C	0.82	0.76	0.84	0.66
Tf ^C /Tf ^E	<u>0.95</u>	0.77	0.84	<u>0.75</u>
Tf ^E /Tf ^E	<u>0.90</u>	<u>0.78</u>	<u>0.94</u>	<u>0.75</u>

To test these predictions, field populations of *M. ochrogaster* were established in two-acre enclosures in Indiana with three founder populations of 20 individuals all of one genotype (Gaines *et al.*, 1971). Three such introductions were made in one year so that by the end of the experiment we had data for three populations of each of the three transferrin genotypes. The surprising result was that we could find no statistical differences between populations established with different genotypes. Populations of each of the genotypes were capable of rapid population increase. In all three populations started with heterozygotes there was an increase in the frequency of the T^F allele by the end of the experiment, which covered four months and included two generations. Because of this we suggest that when the T^F/T^F genotypes are free from competition with the other genotypes they are able to do well, but in mixed populations they are at a disadvantage.

The failure to verify predictions about the effect of selection of *M. ochrogaster* transferrin genotypes might be explained by the fact that the enclosures, which prevented dispersal, disrupted the normal demographic machinery. We suggest that perturbations of field populations may be more meaningful (Gaines *et al.*, 1971; Krebs, 1971). This could be accomplished by switching homozygotes of two types between populations and observing the demographic response.

Genetic markers can be used as the basis for classification of microtines into increase, peak or decline categories, but there will be considerable noise in the classification system. On the basis of this work with transferrin in *M. ochrogaster* and *M. pennsylvanicus*, Tamarin, Gaines and Krebs were able to distinguish increase and decline types based on the comparative success of the genotypes during these population phases. We would like to be able more directly to distinguish increase, peak and decline individuals based on those attributes which give them the advantage during these population phases. A pertinent question is: Is there a rapid growth genotype which is favoured during the increase phase or is there a genotype which is capable of withstanding crowded conditions of peak populations but is less resistant to mortality factors? The problem is to devise a system in which the heritability of the factors can be scored.

Heritability studies of ecologically important attributes would seem to offer a promising area for future work. For example, heritability of growth could be determined for microtine rodents. Few studies have attempted to determine the growth potential of animals in cycling populations. Newson and Chitty (1962) found animals of high and low growth potentials in declining populations. Krebs (1966) showed that some voles from a declining population of *M. californicus* would grow to large sizes if they were removed to the laboratory, although little

growth was found in field animals. Myers and Krebs (1971b) with a very small sample showed that male *M. ochrogaster* dispersing from an increasing population had a low growth potential. No one has monitored, under standard conditions in the laboratory, growth of microtines taken from various phases of the population fluctuation.

If specific behavior patterns which were measurable in the laboratory could be found to be associated with changes in population density, these might serve as more meaningful genetic markers. We were largely unsuccessful in our attempts to find a laboratory measurement which would distinguish dispersing and non-dispersing *M. ochrogaster* and *M. pennsylvanicus* (Myers and Krebs, 1971b). Although there is evidence for genetically determined behavioral types in house mice (Van Oortmerssen, 1970), no work has begun to determine the genetic component of behavior in microtines.

There may be ways to obtain individuals of different types if we let the field situation act as the selection process. As discussed earlier, dispersal is a particularly important process during the phase of population increase. A possible explanation for the higher density of enclosed populations is that the prevention of dispersal has forced individuals which would normally have left to stay in the population. Consequently, the quality of individuals of high populations in enclosures should be different from that of natural peak populations. Our data on dispersal in *M. pennsylvanicus* (Myers and Krebs, 1971b) indicated that those individuals with the highest reproductive potential were dispersing. These were young females which had just become sexually mature (Fig. 44). Using marker alleles at the transferrin locus we found that there was a genetic component to dispersal among females during the phase of population increase.

We suggest that instead of comparing the reproductive potential of transferrin genotypes, we should look at the reproduction potential of dispersers and non-dispersers, of animals from peak populations and declining populations, of animals from high-density populations in enclosures (those which have not been selected by dispersal) and from high-density natural populations. If we are to test the Chitty hypothesis, we must be concerned with demographically pertinent genotypes rather than marker loci which may be variously linked with loci under density selection.

In summary, data collected on the genetics of cycling vole populations by the use of electrophoretic variants as genetic markers demonstrate dramatic genetic changes associated with density changes. In some cases (*M. ochrogaster* and *M. pennsylvanicus*) there are significant correlations between changes in gene frequency and changes in density, and these changes show some consistency over two population cycles

and among different local populations. Furthermore, characteristics of fitness such as survival and growth show generally consistent patterns, although there is some variation.

While there is now general agreement that populations are composites of organisms with considerable genetic variation, and that the genetic make up of populations can change in association with density

MICROTUS PENNSYLVANICUS

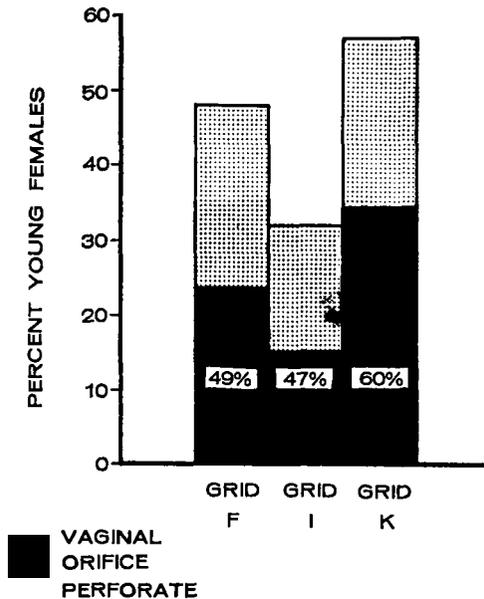


FIG. 44. Grids I and F are control populations of resident animals and Grid K represents a dispersal population which moved into an area of vacant habitat. The proportion of young females in the dispersal population is greater than that in either of the control populations and the proportion of these females which are sexually mature (vaginal orifice perforate) is also greater among the young dispersing females. (Myers and Krebs, unpublished.)

fluctuations, the question still remains as to whether genetic changes are the driving force behind demographic changes or whether density fluctuations and variation in natality and mortality associated with them cause the fluctuations in gene frequencies. This problem has been discussed in depth elsewhere (Gaines and Krebs, 1971; Krebs, 1971; Krebs *et al.*, 1973) but we will reiterate it here.

There is no simple way to separate cause and effect in this situation. If genetic changes were the driving force, it might be expected that

there would be a lag between the gene frequency change and the density change as occurs in the age-specific selection model of King and Anderson (1971). This does not seem to be the case (Fig. 42). However, if there are genotypes which grow faster and reproduce earlier during the phase of population increase as suggested by the work of Gaines and Krebs (1971), the population increase will result in a higher proportion of this genotype unless mortality compensates for the greater reproductive potential.

Charlesworth and Giesel (1972) propose a model which considers the influence of demographic structures, particularly the age structure, on changes in gene frequency of polymorphic systems. The basis of the model is that if a genotype produces early in its life, there will be little advantage if the population is primarily composed of older individuals which are already reproducing. However, if the age structure favors growing animals, those individuals which are able to reproduce early will have a greater advantage. Therefore, if there is a change in the age structure of the population, a fluctuation in gene frequency follows. While these authors claim that their model produces a population cycle and gene-frequency change which resembles the observations of Tamarin and Krebs (1969), we see some differences. First, the gene-frequency changes produced by the model were only in the order of 6–9% while observed changes in *Microtus* populations are more often in the vicinity of 20% (Fig. 42).

Furthermore, if it is assumed that a cycle of the model is equal to the period of time for an individual to reproduce (about three weeks for microtines), the rate of the gene-frequency change is very slow as compared with those of field studies. With the model a 9% gene-frequency change required 40 cycles. This would be the equivalent of over two years on a microtine time scale which clearly doesn't apply to field observations.

One of the observations arising from the field data is that gene frequencies in males and females are often quite different and it is not clear that the model would allow this result. The Charlesworth–Giesel model showed changing death rates to have little influence on gene frequencies. We have found that differential survival particularly during the decline is a major factor in gene-frequency changes.

Finally we find it impossible to interpret the correspondence between simulated population declines caused by decreasing $m(x)$ functions and declines of field populations which arise both from decreased natality and from increased mortality. We feel that the responsibility lies with the authors of theoretical models to interpret the biological consequences of assumptions made in their models, for without them statements such as "The resultant population cycle resembles vaguely the pattern

observed in oscillating vole populations" (Charlesworth and Giesel, 1972) are very misleading.

One of the criticisms made by Charlesworth and Giesel (1972) of the results showing genetic changes in fluctuating populations is that the several systems arbitrarily chosen as genetic markers have all shown a relation to population density. This criticism is not a serious one if in fact periods of dramatic density changes are associated with strong selection. In this case the whole genome would be expected to be under selection, and a large proportion of individual loci would most likely change in frequency. The females of both *Microtus ochrogaster* and *M. pennsylvanicus* demonstrated significant correlations between change in gene frequency and change in density for one of the two systems studied by Gaines and Krebs (1971) but not for the other. Significant correlations between gene frequency and density occurred for both loci in males of the two species. We interpret the general trend for all genetic systems which have been studied to show a relation between genetic change and density change, to indicate strong selection occurring with population fluctuations. However, we cannot explain the exceptions which occurred in female *M. ochrogaster* and *M. pennsylvanicus* which failed to show a relationship for one of the two loci studied (Gaines and Krebs, 1971).

In conclusion, data have not yet contradicted the Chitty genetic-behavioral hypothesis of microtine cycles, but we have only accomplished the preliminary steps in testing the hypothesis. Genetic changes seem to be a part of population fluctuations in microtines, and this aspect of genetic heterogeneity will have to be taken into consideration in future studies of microtine cycles. Our studies have indicated that dispersal, particularly during the phase of increase, is more important than originally thought by Chitty. We propose a modified version of the Chitty Hypothesis in Fig. 45. Two variations are included in this version which were not included in the model diagrammed by Krebs (1964a). The first of these is the loop which allows for emigration and the colonization of new habitats and the possible establishment of refuge populations. The second change is that rather than emphasizing aggressive behavior, we feel that other forms of spacing behavior could work in a similar way. For example, very docile individuals might be at a selective advantage as the population increases. Selection for aggressive behavior could also lead to susceptibility to other selective factors. Originally, it was thought that aggressive behavior among individuals might be the direct cause of the population decline. However, until we know the nature of the mortality factors acting during the decline we will not be able to interpret this aspect of the hypothesis.

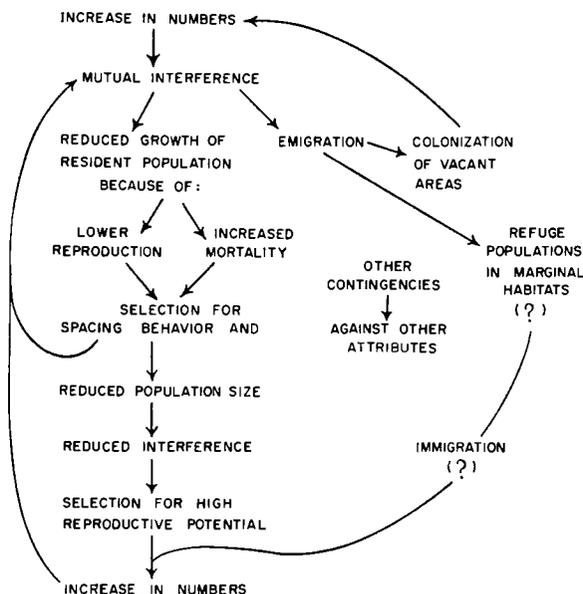


FIG. 45. Modified version of the Chitty behavioral-genetic hypothesis to explain microtine cycles. Dispersal is viewed as being a more important aspect than originally proposed by Chitty. Central to the hypothesis is selection acting through behavioral interactions and changing the genetic composition of the population with fluctuating densities.

VII. EVOLUTION OF MICROTINE CYCLES

Are microtine cycles an adaptation? This question has been mentioned only peripherally in the literature. We should note that if we support the extrinsic factor hypotheses—weather, food shortage, predation, or disease—this question is relatively meaningless, since in these cases population fluctuations are in effect forced on the population by outside agents. However, if we support the intrinsic factor hypotheses—stress, behavior, genetics—this question is important because populations must have evolved a mechanism of self-regulation to arrest population growth below the limits set by starvation. We therefore continue this discussion on the assumption that some mechanism of self-regulation occurs in voles and lemmings.

We might imagine the following scenario in the evolution of microtine rodents. These small animals are subject to an array of hazards, from bad weather to predators and diseases. If they had only bad weather to cope with, they could no doubt survive by having a good reproductive potential and behavioral adaptations for tunneling and nest

building. To cope with predators was perhaps a more serious challenge, particularly with ground predators such as weasels, and we might imagine that even higher reproductive potentials would be necessary to keep from going extinct. Those rodent species which could overcome these limitations now found themselves up against another problem. Excessive reproductive capacity carries with it the seeds of habitat destruction and starvation, particularly in areas where predators are less common. From this challenge rodent species must have evolved some form of self-regulation. This could have been achieved by individual selection or by group selection. There are obvious advantages to a group of rodents from not destroying the habitat, and we can easily see that group selection would favor the evolution of self-regulation. The more difficult question is whether individual selection would lead in the same direction.

Spacing behavior can evolve readily on the basis of individual selection. A vole which begins to drive away his neighbours by physical aggression would be at a selective advantage when crowding became serious. Brown (1964) has discussed the evolution of territoriality in birds, and has pointed out that aggressiveness is primarily a behavioral response to competition for resources which are in short supply. Since food for voles and lemmings cannot be defended readily, we would suggest that breeding space is probably the resource in short supply as density rises.

Once spacing behavior begins to evolve, the next problem is to set the upper limits to such behavior. If some aggressiveness is good in high-density populations, is not more aggressiveness even better? There are some obvious limits to excessive aggressiveness. Very aggressive rodents might find it impossible to mate, or they might destroy their own offspring. There are at least some vague upper limits to aggressiveness. But why does the population not stabilize at some intermediate level of aggressiveness? In order to fluctuate periodically, a microtine population must continually be overshooting the "optimum" level of aggressiveness.

The solution to this dilemma may lie in the fluctuating seasonal environments in which microtines live. Two extreme end-points can be selected toward. At the low density end of the scale there is no premium on aggressive behavior, and the selective premium falls on genotypes capable of breeding late into the fall and winter, maturing early, and growing rapidly. At the high density end of the scale, there is a great premium on aggressive behavior, and reproductive behavior is shifted toward deferring maturity until a later date when density has fallen. Schaffer and Tamarin (1973) have analyzed how reproductive effort should be expended in fluctuating populations in order to

maximize individual fitness. They concluded that the observed patterns of reproductive changes in cyclic rodents were consistent with the hypothesis that individuals attempt to maximize fitness in all phases of the cycle.

We can thus see how a polymorphism in spacing behavior might be maintained in a population by means of time lags in adjusting to density changes. This, however, leads us to a further question of whether the behavioral and reproductive changes need be genetically determined or could be the plastic properties of a flexible phenotype. We do not know the relative advantages and disadvantages of adopting a phenotypic self-regulating mechanism or a genotypic mechanism. We see no way of determining *a priori* which way evolution should move within the general scope of self-regulatory mechanisms.

Why does natural selection not damp out population fluctuations in rodents? There are some genetic advantages to population fluctuations that might answer this question. Carson (1968) has discussed the genetic consequences of the "population flush" in insects. The low density after the decline allows both the testing of new genotypes and the possibility of rapid spread of new genetic combinations because of founder effects. If this is true, we would predict a more rapid rate of evolutionary change in species of voles and lemmings than in species of rodents which maintain stable numbers. If we can postulate that there are genetic advantages to population fluctuations, we could then see why evolutionary changes have reinforced the fluctuations rather than damping them away.

In summary, population regulation mechanisms must be under some evolutionary control, if self-regulatory hypotheses are correct. Periodic fluctuations in microtine rodents could be generated by individual selection toward two extreme morphs: a low-density, docile, reproductive form; and a high-density, aggressive, less reproductive form. Time-lags in responding to density changes could generate a cycle. Such a self-regulatory system would be preserved by natural selection if there are some genetic advantages to population fluctuations.

VIII. SUMMARY

Population cycles in voles and lemmings are accompanied by a series of changes which we summarize here in point form:

1. The increase phase is the least variable phase and may be over very quickly.
2. The decline phase is the most variable phase; it may be very rapid or may be slow and prolonged over two years. "Crash" declines over one or two weeks are not typical.

3. The periodicity is variable, three to four years is typical, but some cycles may be two or five years in length.
4. Some populations may not fluctuate, but none of this type has been studied carefully.
5. Fluctuations occur in a variety of genera and species from arctic to temperate areas, from Mediterranean to continental climates, from snowy areas to snow-free areas.
6. Fluctuations sometimes occur in synchrony over large geographical areas (thousands of square miles). Synchrony is seldom absolute, however, and local out-of-phase populations occur. Synchrony is not continental or world-wide.
7. The amplitude of these fluctuations is *not* necessarily larger in more northern populations.
8. Populations living in a wide variety of plant communities in a small geographic area all fluctuate in the same way, often in phase.
9. Reproductive rate is highest in the increase phase, owing to (1) longer breeding season, including winter breeding in some species, and (2) lower age at sexual maturity. In the peak and decline phases reproductive rate is reduced.
10. There is no systematic difference between increasing populations and declining populations in (1) litter size, (2) percentage of adult females pregnant during the breeding season, or (3) sex ratios.
11. Mortality rates in all sex and age groups are lowest in the increase phase.
12. Adult and subadult mortality rates are low during the peak, and high in the decline phase.
13. Juvenile mortality may be high in the peak summer and may remain high until the end of the peak breeding season, when it is suddenly reduced. Juvenile losses are very high in the decline phase.
14. Survival of adult males fluctuates independently of that of adult females, when viewed on a weekly time scale. Males may suffer heavy losses in the decline for a few weeks when females are surviving very well, and vice versa.

15. Prenatal mortality may vary slightly over the cycle but is not a serious loss even in declining populations.
16. Dispersal is most frequent from increasing populations, and relatively infrequent from declining populations.
17. Two closely related species may live in the same habitat and reach peak numbers in the same year, but declines in one species may occur while the other species in the same area remains at high numbers for several months.
18. Voles brought into the laboratory from field populations which are declining will live for a very long time as isolated pairs or individuals.
19. Populations kept in small cages in the laboratory or room-sized cages outdoors increase to unnaturally high densities, several to many times that found in nature, and do not cycle.
20. Populations in two-acre enclosures in the field increase to unusually high numbers and may reach the limit of their food supply and starve.
21. Adult animals in peak populations are typically larger (by 20–50%) than those at other times in the cycle. This increase in body size is reflected in changed skeletal proportions. These large animals may occur in the late increase phase and early in the decline phase when the decline is very gradual.
22. Changes in gene frequency at marker loci occur in association with density fluctuations.
23. Aggressiveness of male and female microtines increases and home range size decreases with increasing population density.

We have attempted throughout this article to point out experiments which might be done to test various hypotheses and elucidate certain aspects of microtine cycles. Two of the most important questions which remain to be answered are: (1) what permits longer reproductive seasons in some years? and (2) what is the nature of the mortality occurring during the decline? Studies of either of these questions should not overlook the quality of the individuals in the population. While it may be possible to show what nutritional factors permit microtines to reproduce, the crucial aspect to relate nutrition to population cycles might be to demonstrate that individuals in increasing populations have lower nutritional thresholds or are more efficient in their use of nutritional factors. Similarly, there might be a number of causes of mortality

during the population decline, with the important variable being that the overall resistance of individuals from peak populations is lower than that of individuals at low or increasing densities. We emphasize that we should be concerned with the variability demonstrated by individuals composing populations.

We think that enough is now known about the natural history of microtine fluctuations for us to be able to devise some simple experiments to test alternative hypotheses. Field experiments in ecology are particularly difficult to replicate properly, and part of our effort must be geared to replicating experiments over several populations of several species. If we spend more effort on devising, executing and interpreting experiments, we may find less time devoted to specific schools defending one hypothesis at all costs. We would discourage simple descriptive studies of microtine populations, even of species yet unstudied, unless they are coupled with some experimental analysis.

Finally, we cannot resist making a prediction about the future. We feel that studies of the heritability of reproductive capabilities, growth potentials, and behavior of microtines will be the key to unlocking the mystery of rodent cycles.

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