POPULATION DYNAMICS AND CYCLES

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Abstract

WE address two questions about North American *Microtus*: 1) what type of numerical changes occur in their populations? and 2) what factors must be invoked to explain these population changes?

Historically, studies of *Microtus* population dynamics have centered around descriptions of multi-annual cycles in abundance. Examination of field data collected over the last two decades on species of *Microtus* in North America reveals three demographic patterns: annual fluctuations, multi-annual cycles, and both, in sequence. Out of a total of 106 years of data, we estimated 59% were years of annual fluctuations and 41% were cyclic. In two species exhibiting both patterns in sequence there were 9 years of annual fluctuations and three multi-annual cycles. It appears that annual fluctuations in density are more common than multi-annual cycles in some *Microtus* populations.

If we compare annual fluctuations and cycles, we find that the amplitude of numerical change is always less than five-fold for annual fluctuations and usually over 10-fold for cycles. Peak cyclic densities are typically three times greater than the maximum densities of annual fluctuations. Substantial spring declines in density are characteristic of annual fluctuations, whereas little or no spring decline (particularly in female numbers) occurs in years of cyclic peak densities.

There are still problems associated with obtaining reliable estimates of population parameters for *Microtus* species. The use of more than one trapping technique, especially in high density populations, is strongly recommended.

Microtus numbers increase when extra food is provided experimentally to field populations, but no one yet has prevented a cyclic decline by food addition. It is not yet certain whether plant secondary compounds play any role in vole cycles. Predation interacts with cover to affect vole numbers, and predators can take large numbers of voles under certain conditions. Predators may prolong the phase of low vole densities but it is not clear that they can generate cycles.

Spacing behavior operating through differential dispersal may be a key element in the adjustment of *Microtus* densities to available resources. Surplus voles exist in some populations, but we do not know what role such voles play in generating the population dynamics observed. Spacing behavior could be under both genotypic and phenotypic control, which suggests a multi-factor component in vole population dynamics. There is renewed interest in physiological responses of voles and lemmings to stress, and speculations about its effect on suppression of the immune-inflammatory system, especially at high population densities.

A brief consideration of two phenomena suggests how multi-factor explanations could be associated with population cycles in *Microtus*. Body weight may be heritable, but the expression of the trait could be modified by, for example, food conditions in the increase phase or population density at the peak. Mature female voles should perhaps be considered analogous to territorial male birds in maintaining space for production of offspring. The size of territories, and hence the number of mature females, may be determined partly by genetic predisposition and partly by behavioral adjustments to environmental conditions and to local vole density.

Future modeling and research on *Microtus* population dynamics should address the two patterns of fluctuation described. Heritability of growth, reproduction, dominance, and dispersal should be investigated in populations exhibiting both patterns of fluctuation in sequence as well as in predominantly cyclic and non-cyclic populations. Realistic multi-factor hypotheses must be formulated. These should assign factors in a hierarchy over time to predict the patterns observed and be testable by field experiments. There is still much to do.

Introduction

Population dynamics of species in the genus *Microtus* have been, with other small rodents, the subject of several reviews. Historical descriptions of outbreaks and plagues were compiled by Charles Elton (1942) in his book "Voles, Mice and Lemmings." The economic consequences of rodent population irruptions, curiosity about mechanisms of population regulation, and a desire to predict abundance have stimulated much research into rodent population dynamics since Elton's book. Most of the research done up to the early 1970s was reviewed extensively by Krebs and Myers (1974).

In the present review, we evaluate field studies that, for the most part, were conducted since the review by Krebs and Myers (1974), and are restricted to rodents of the genus *Microtus* in North America. We attempt to answer two major questions in this chapter: 1) What type of population changes occur in *Microtus* species in North America? and 2) What factors must be invoked to explain these population changes? By a critical evaluation of past work we hope to provide a paradigm for future studies on these rodents.

Methods of Study

Voles of the genus *Microtus* typically live in underground burrow systems in grasslands. Where grass cover is dense, they develop extensive surface runways. Direct observation of individual voles in the field is, therefore, virtually impossible. Most population data are collected as a result of trapping individuals.

Researchers in North America use snap-traps for census work and live-traps for continuous mark-recapture monitoring of vole populations. Most of the live-traps in use are Longworths (Chitty and Kempson, 1949), or Shermans (Morris, 1968), although pitfalls (Boonstra and Krebs, 1978; Kott, 1965) and multiple-catch traps are also used.

Live-traps are usually placed in square grids with a specific distance (often 25 ft, 7.62 m) between stations. One or two traps are put at each point on the grid, and positioned in active surface runways. In order to catch voles of some species, it is necessary to pre-bait for a period before commencing with a regular trapping program (for example, *M. townsendii* has to be pre-baited for four weeks before appreciable numbers are caught). In the pre-baiting period, food is put in each trap, which is then locked open and placed in position on the grid. Many studies over the last decade have used the field technique suggested by Krebs (1966). In this technique the traps are set with food and bedding (usually a handful of oats and cotton batting). A typical trapping session involves setting traps in the afternoon, checking them for voles the next morning, re-setting, and checking that afternoon, re-setting and checking for the last time the next morning. The traps are then locked open with a handful of oats as pre-bait over the interval until the next trapping session, normally two weeks later. In summer, the daytime trapping period is abandoned to avoid death from overheating of surface metal traps. This is not a problem with pitfall traps.

When a vole is first caught, it is individually marked for future identification. This is most often done by placing a numbered fingerling fish-tag in one ear; alternatively, a system of toe-clipping is used. On first capture within a trapping session, individuals are sexed and weighed to the nearest g. Males are classified according to the position of the testes, either abdominal or scrotal. Females are checked for vaginal perforation: open or closed (estrus or anestrus); size of nipples and amount of lactation tissue: small, medium or large (not lactating, beginning or end of lactation, mid-lactation); separation of the pubic bones: closed (immature), slightly open (previously littered), or open (has just or is about to deliver). All pregnancies and trap litters are recorded. In some studies the number of wounds is recorded; recent wounds are easily identified by blowing the fur and looking for small, usually paired, incisions which indicate the bite of another vole. Every time an individual is caught its number and grid location is recorded.

There is a large literature on the problems of estimating population size in small mammals; we do not review it here (Seber, 1982). The studies that we review are based on live-trapping with a single type of trap. There is now a suggestion in at least one species (*M. townsendii* at high density in summer when daytime trapping is not possible) that pitfall trapping is needed in addition to Longworth trapping to census adult populations (Beacham and Krebs, 1980; Boonstra and Krebs, 1978). In these two studies of peak populations, 40–45% of the adult voles were captured only in pitfall traps. We do not know if these adults could have been caught in Longworth traps if the number of Longworths had been doubled or quadrupled. Nor do we know whether this problem is specific to *M. townsendii,* but it is clear that future studies should use two different trapping techniques whenever possible. Alternatively, multiple-capture traps could be used.

Details of trapping methods might be less critical in vole population studies if we could use mark-recapture methods such as the Jolly-Seber model (Jolly, 1965; Seber, 1982). Because of early indications that *Microtus* does not respond randomly to traps (Krebs, 1966; Leslie et al., 1953) many workers have used enumeration to provide an estimate of abundance. Enumerated densities (minimum number alive) have a negative bias. Hilborn et al. (1976) estimated at least a 10–20% bias in enumerated densities of five species of *Microtus* but pointed out that if unmarked animals had very low probabilities of capture, the minimum-number-alive estimator would seriously underestimate the true number. This is another way of emphasizing the need for pitfall trapping or additional techniques for sampling voles which might not be caught in normal live-traps.

Jolly and Dickson (1983) argued for the use of Jolly-Seber estimates in populations whose individuals show unequal catchability. The Jolly-Seber estimates will have a negative bias under these conditions, but less of a bias than enumeration techniques. Carothers (1973, 1979) showed that unequal catchability has only a very small effect on Jolly-Seber estimates of numbers and survival, if the probability of capture is above 0.5 in each trapping session. These studies suggest that small mammal ecologists should use Jolly-Seber estimates to estimate numbers rather than enumeration methods, but it is important to qualify this recommendation with the reminder that no statistical method can provide accurate estimates of abundance when a large fraction of the population does not enter the traps at all.

Many factors can affect trapping success in small rodents and odors associated with traps is one possibly important factor (Boonstra and Krebs, 1976; Stoddart, 1982). In *M. townsendii,* individuals entered dirty Longworth traps more than clean traps during the breeding season. Voles also may avoid traps visited by other species. Boonstra et al. (1982) showed that *M. pennsylvanicus* was much less likely to be caught in a Longworth trap previously occupied by *Blarina, Mus, Zapus,* or *Peromyscus.* Stoddart (1982) claimed that unmarked *M. agrestis* was more readily caught in clean traps than in dirty ones, but his conclusions cannot be accepted because of faulty experimental design (no pre-baiting) and no suitable controls to measure late summer recruitment of young (cf. Chitty and Phipps, 1966:323). Further work on the effects of odor on trapping success in *Microtus* will be useful particularly if it addresses how present trapping techniques could be improved.

We assume in this chapter that population data obtained by live-trapping is a reliable index of actual changes in numbers if sampling is done at least monthly with an excess of live-traps and a probability of capture above 50% for adult animals. Attempts to sample at a lower intensity have so far proven unreliable at providing a detailed picture of population dynamics, although they may reveal large-scale trends.

Observed Population Patterns

In the last decade, field studies have been conducted on populations of *Microtus* in North America at locations shown in Fig. 1. These empirical studies tend to be short-term and are usually conducted in man-made grasslands where grass cover is dense and the number of voles can be substantial in a 2–3 year period (average workspan of a graduate student). This raises an important general question: are the population dynamics observed in these habitats typical? Bearing this in mind, and trying to allow for differences in trapping regime, sampling periods, and grid size, we ask what population patterns have been observed in the North American species of *Microtus*.

In Tables 1–6, we summarize the demographic patterns observed on control areas in studies of North American *Microtus* populations. We calculated densities of voles by adding a boundary strip one-half the inter-trap distance to each edge of the live-trapping area. In some cases authors have already presented population data as densities and we used these when given. In all cases we rounded densities to the nearest 5/ha because of the error in estimating numbers from published graphs, so the density estimates we give should be viewed as approximations only. We divided demographic patterns into two classes: 1) annual fluctuations, and 2) multi-annual cycles. Annual fluctuations generally have an autumn or winter, end-of-breeding season maximum, and a spring, or onset-of-breeding, minimum. Cycles are defined by a low-peak-decline sequence over at least two years, and by additional demographic criteria defined by Krebs and Myers (1974) when such data are available. When long-term, detailed data are available (Figs. 2, 3), the classification of annual versus cyclic patterns is usually clear. Problems arise in classifying some studies, particularly short-term ones. We think that these two patterns could be quantified by analyzing the variance of spring breeding densities, or more precisely the variance of the natural logarithms of spring densities. For an-

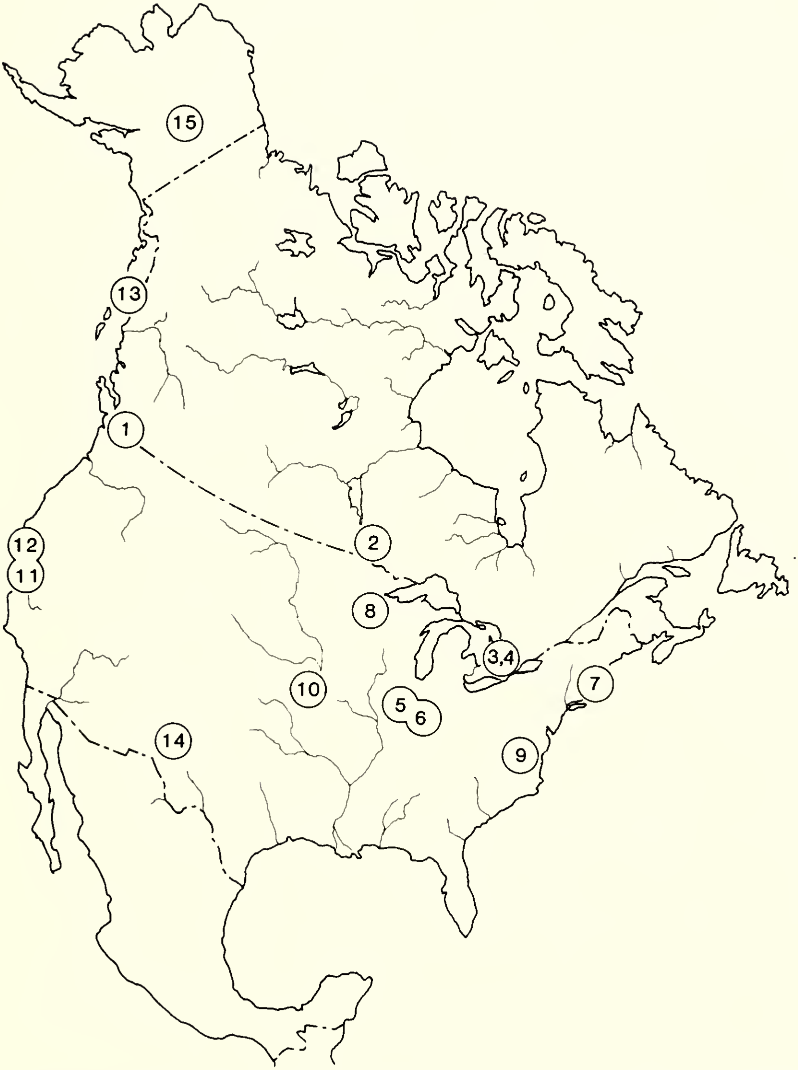

FIG. 1. Population study sites of *Microtus* in North America. Numbers refer to studies identified in Tables 1–6.

TABLE 1

POPULATION DENSITIES FROM LIVE-TRAPPING STUDIES OF *Microtus townsendii* IN BRITISH COLUMBIA

		Density/ha			Spring dynamics				
Grid	Years	High	Low	Pattern	Density[1]	Sex[2]	Notes[3]	Map location (Fig. 1)	References
I	1971–76	285	150	Annual	Low	Both	Perennial grassland; no competitors; Westham Island	1	Krebs (1979)
		385	85	Annual	Low	Both			
		385	75	Annual	Low	Both			
		625	40	Cycle	435	♂ only			
C1	1980	260	85	Annual	Low	Both	Winter–spring study	1	Taitt et al. (1981)
C2	1980	150	30	Annual	Low	Both	Winter–spring study		Taitt et al. (1981)
C1	1981	375	125	Annual	Low	Both	Winter–spring study		Taitt and Krebs (1982)
C2	1981	175	145	Annual	Low	Both	Winter–spring study		Taitt and Krebs
C	1982	345	265	Annual?	Low	Both	Winter–spring study		Taitt and Krebs (1983)
A	1976–78	800	65	Cycle	365	♂ only	Perennial grassland; no competitors; Reifel Island	1	Beacham (1979*a*)
D	1976–78	665	40	Cycle	430	♂ only			
C	1971–75	400?	50	Cycle?					
		210	150	Annual	Low	Both	Perennial grassland; no competitors; Mainland	1	Krebs (1979)
		360	115	Annual	Low	Both			
		210	150	Annual	Low	Both			
E	1971–76	50	15	Annual	Low	Both	Perennial grassland; *M. oregoni* and *Peromyscus maniculatus*; Mainland	1	Krebs (1979)
		100	65	Annual	Low	Both			
		100	85	Annual	Low	Both			
		525	150?	Cycle?	185?	♂ only			

[1] Density in number/ha at the end of the spring decline. Low means equal to the low density given in previous column.

[2] Sex indicates whether the spring decline occurred in both sexes or only in one sex primarily.

[3] Species listed here were present on the grid; they may or may not have been competitors.

nual fluctuations we expect this variance to be less than 0.5, and for cycles, greater than 1.0. Note that spring densities are critical, not autumn densities (Krebs and Myers, 1974). We do not know whether the dichotomy between annual and cyclic populations is real, or whether there is a continuum between the two extremes. In the following, we discuss demographic patterns for each species.

M. townsendii

All of the long-term population data on this species come from the Vancouver area of British Columbia. We identified (Table 1) four probable cycles in four populations of this species and 13 annual fluctuations in three populations. Figure 2 illustrates population changes on one area that was monitored for 11 years. A cyclic peak is evident in 1975 but in most years annual fluctuations occur. Cyclic peaks in this species ranged from 525 to 800/ha, averaging 697 voles/ha (Longworth-trapped population only). Annual fluctuations had average maximums of 239 voles/ha and minimums of 94 voles/ha. Most of the communities studied consisted only of this vole species. One area (grid E; see Krebs, 1979:Fig. 3) contained *Peromyscus maniculatus* and *M. oregoni* when *M. townsendii* was at low numbers, but both these potential competitors disappeared when *M. townsendii* increased above 100/ha.

M. pennsylvanicus

Studies on *M. pennsylvanicus* have been conducted over a broad geographic range (Fig. 1) and an array of demographic patterns has been described. There are large differences in average density of this species in different areas and these regional differences cannot be due simply to techniques (Table 2). In Ontario, recent work indicates that annual fluctuations are common with maximum densities averaging 410/ha and minima averaging 120/ha. Boonstra and Rodd (1983) provided 3 years of data from Toronto showing annual fluctuations at high densities. A striking population pattern was observed by Iverson, Turner and Mihok in Manitoba (Fig. 3; Mihok, in press). This population exhibited a cycle, a cyclic low density followed by another cycle, then three annual fluctuations. In Manitoba, densities were very low, averaging 90/ha at cyclic peaks and 10/ha at cyclic lows; annual fluctuations averaged 55/ha at maximum and 30/ha at minimum.

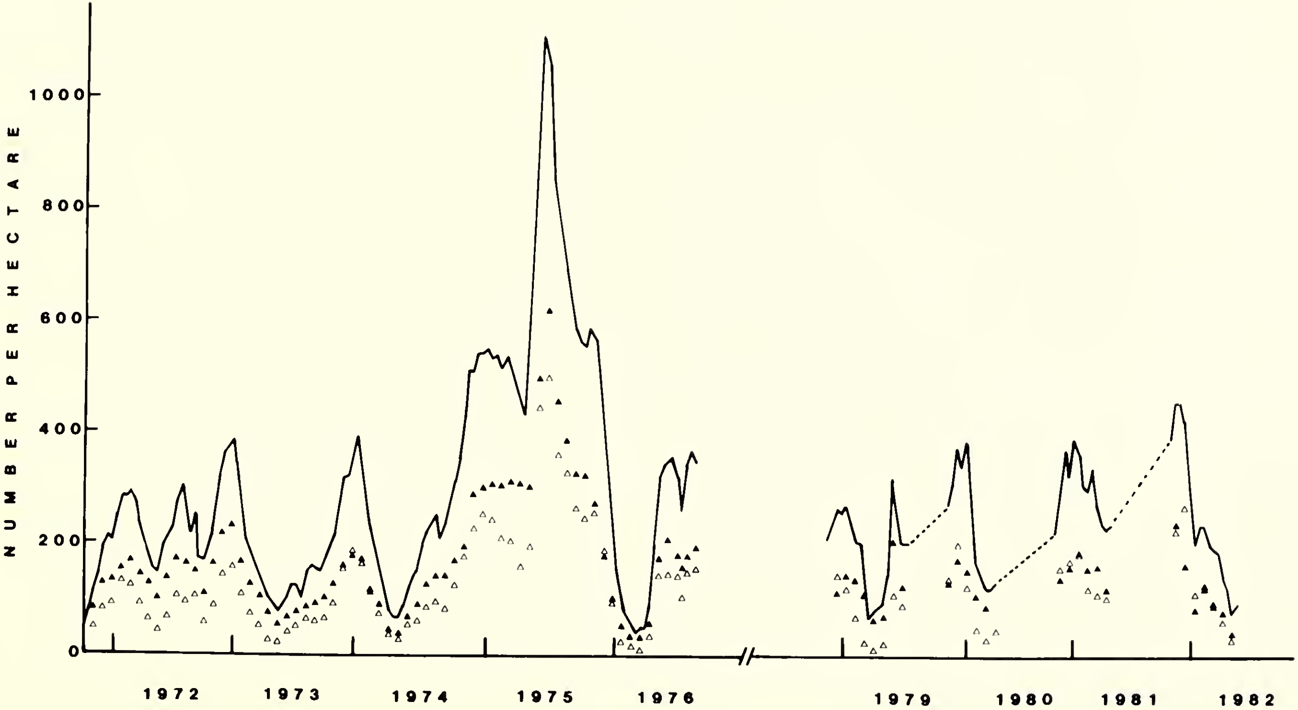

FIG. 2. Population densities of *Microtus townsendii* on control grids on Westham Island, British Columbia. Pitfall trap data are included for summers 1975, 1976, and 1979. Symbols are: △, males; ▲, females.

Indiana data on *M. pennsylvanicus* are almost intermediate between cyclic and annual fluctuations and we interpret them as 2-year cycles. The cyclic maxima averaged 180/ha and the minima averaged 40/ha. These figures are similar to those obtained by Tamarin (1977) in Massachusetts. Virginia data on this species seem to show the end of one cycle and then 2 years of annual fluctuations averaging 85/ha maximum and 35/ha minimum. In Minnesota, 2 years of annual fluctuations averaged 85/ha maximum and 10/ha minimum. In Illinois, *M. pennsylvanicus* invaded habitats formerly occupied by *M. ochrogaster*; to date, populations are sparse, with maxima averaging only 30/ha. From these studies we estimate that, for 33 years of data, 17 years showed annual fluctuations and 16 years were cyclic. There is no clear evidence of a competitive density reduction in those areas in which a second *Microtus* species occurred.

M. ochrogaster

Populations of *M. ochrogaster* have been studied extensively in Kansas, Illinois, and Indiana. Most populations studied in Illinois and Indiana showed 2–4 year cycles in numbers, averaging 130 voles/ha at the peak and often falling to local extinction during cyclic lows (average 4/ha). In Indiana and, since 1975 in Illinois, there was potential competition from *M. pennsylvanicus.* Krebs (1977) could find no clear evidence of competition between these two species in Indiana. But in Illinois the 1975 *M. ochrogaster* peak (*M. pennsylvanicus* present) was only half that of the 1972 peak when *M. pennsylvanicus* was absent (Getz et al., 1979:fig. 1). In Kansas after an initial 3-year cycle (Gaines and Rose, 1976), *M. ochrogaster* populations exhibited a series of annual fluctuations averaging 55/ha at the maximum and 15/ha at the minimum (Gaines et al., 1979). Densities in Kansas were higher in the one cyclic peak observed (120/ha), and fell to less than 5/ha in the cyclic low. Other studies in Kansas (Martin, 1956) reported an absence of cycling in *M. ochrogaster* during 4 years. For the studies that are included in Table 3 we tallied 13 years of cyclic populations out of 20 total years of data.

M. californicus

The California vole (Table 4) has a restricted geographical distribution but has been studied extensively by the research group at

TABLE 2

Population Densities from Live-trapping for *M. pennsylvanicus*. See Footnotes of Table 1

Grid	Years	Density/ha		Pattern	Spring dynamics		Notes	Map location (Fig. 1)	References
		High	Low		Density	Sex			
C	1968–78	85	5	Cycle	75				
		90	15	Cycle	40		Mainland, Manitoba; no competitors	2	Mihok (in press)
		50	30	Annual	Low				
		60	30	Annual	Low				
		55	35	Annual	Low				
	1977–78	400	80	Annual?	Low		Mainland, Ontario; no competitors	3	Webster and Brooks (1981)
SG	1974–76	265	15	Annual	Low		Mainland, Ontario; no competitors; SG, short grass; OF, old field		Baker and Brooks (1981)
OF	1974–76	200	50	Annual	Low				
C	1978–81	500	115	Annual	Low				
		415	265	Annual	Low		Mainland, Ontario; no competitors	4	Boonstra and Rudd (1983)
		665	215	Annual	Low				
A	1975–76	10	0	Annual			Mainland, Illinois; *M. ochrogaster* A, alfalfa; B, bluegrass; P, prairie colonizing	5	Getz et al. (1979)
B	1976–76	50	10	Cycle	30				
P	1975–76	15	5	Annual	Low				
		30	?	Annual					

TABLE 2
CONTINUED

Grid	Years	Density/ha		Pattern	Spring dynamics		Notes	Map location (Fig. 1)	References
		High	Low		Density	Sex			
A	1965–70	190	55	Cycle	95	♂ > ♀			
		155	30	Cycle	95	♂ > ♀	Mainland, Indiana; *M. ochrogaster*	6	Myers and Krebs (1971)
F	1967–70	75	5	Cycle	45	♂ only			
I	1967–70	210	35	Cycle	80	♂ > ♀			
D	1972–75	220	0	Cycle	135	♂ only	Mainland, Massachusetts; *P. leucopus*	7	Tamarin (1977)
F	1972–75	255	30	Cycle	75	♂ only			
WL	1973–75	80	10	Annual	Low		Mainland, Minnesota; no competitors; WL, wetland	8	Birney et al. (1976)
		95	10	Annual	Low				
1	1974–78	225	40	Cycle			Mainland, Virginia; *Peromyscus maniculatus*	9	Dueser et al. (1981)
		115	40	Annual	Low				
		115	40	Annual	Low				
		15	0	Annual	Low				
5	1976–77	90	55	Annual	Low				

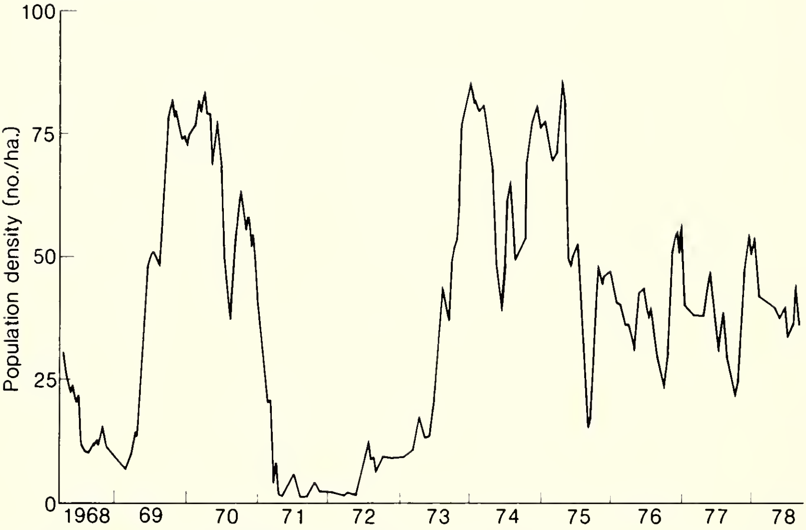

FIG. 3. Population densities of *Microtus pennsylvanicus* on a control oldfield at Pinawa, Manitoba (reproduced, with permission, from Mihok, in press).

Berkeley led by Pearson, Lidicker, and Pitelka. Unfortunately, like most vole population studies, techniques have not been standardized and we can only hope that results are comparable, as Pearson (1971) demonstrated for two studies. Lidicker (1973) reported the longest time series for this species (13 years), but we consider only the first 5 years to be sufficiently accurate for this analysis. Lidicker (1973) found annual fluctuations to be common on Brooks Island and Krebs (1966) reported cases of annual fluctuations on the mainland. Krohne (1982) recently reported annual fluctuations in perennial grasslands in northern California. Densities varied greatly in different areas. Lidicker's (1973) Brooks Island densities were 3–10 times those reported in areas on the mainland. This difference may be due to an island effect or a difference in techniques. For mainland sites, cyclic peak densities averaged 570 voles/ha, and cyclic lows average 15/ha. Annual fluctuations on the mainland reached average maxima of 85/ha and average minima of 20/ha. We do not know if *M. californicus* cycles in southern California. Blaustein (1980) reported declines that could be either cyclic or the result of an irregular annual fluctuation with frequent extinctions. For the studies summarized in Table 4, we suggest that there were 7 years

TABLE 3

Population Densities from Live-trapping for *M. ochrogaster*. See footnotes of Table 1

Grid	Years	Density/ha High	Density/ha Low	Pattern	Spring dynamics Density	Spring dynamics Sex	Notes	Map location (Fig. 1)	References
C	1975–76	90	20	Annual?			Mainland, Illinois; *M. pennsylvanicus* removed; predation—cats	5	Cole and Batzli (1978)
		70	5	Annual?					
A	1972–76	240	0	Cycle			Mainland, Illinois; A, alfalfa; no competitors *M. pennsylvanicus*; B, bluegrass	5	Getz et al. (1979)
		100	5	Cycle?	60				
B	1972–76	130	0	Cycle					
		60	5	Cycle?	10				
A	1965–70	140	0	Cycle	35	♂ only	Mainland, Indiana; *M. pennsylvanicus* spring influx	6	Myers and Krebs (1971)
		35	0	Annual?	3				
H	1967–79	135	0	Cycle?	25	Both			Krebs (1970)
A	1970–73	155	0	Cycle	Low		Mainland, Kansas; no competitors	10	Gaines and Rose (1976)
B	1970–73	120	10	Cycle	Low				
C	1970–73	125	0	Cycle?	Low				
D	1970–73	85	5	Cycle?	Low				
B	1973–76	55	10	Annual	28				
		50	0	Annual?			Mainland, Kansas; no competitors	10	Gaines et al. (1979)
D	1973–77	60	30	Annual	Low				
		60	20	Annual	Low				
		45	15	Annual	Low				
I	1975–76	65	5	Annual	Low				

TABLE 4

POPULATION DENSITIES FROM LIVE-TRAPPING FOR *M. californicus*. SEE FOOTNOTES OF TABLE 1

Grid	Years	Density/ha		Pattern	Spring dynamics		Notes	Map location (Fig. 1)	References
		High	Low		Density	Sex			
BI	1959–63	1,580	50	Cycle?	952		Brooks Island, California; *Mus musculus*, rats; annual grassland	11	Lidicker (1973)
		1,250	450	Annual?	Low				
		650	150	Annual	Low				
		1,000	?	Annual?	Low				
TC	1962–64	640	25	Cycle					
RFS3	1962–64	300	0	Cycle	60		Mainland, California; annual grassland	12	Krebs (1966)
PARR	1962–64	1,150	20	Cycle?					
RFS4	1962–64	160	10	Annual					
RFS5	1962–64	50	2	Annual					
Richmond	1966–68	395	10	Cycle	100		Mainland, California; annual grassland	12	Batzli and Pitelka (1971)
Russell	1966–68	370	?	Cycle	105				
A	1977–79	100	25	Annual	Low				
		125	35	Annual	Low		Mainland, California; perennial grasslands	12	Krohne (1982)
B	1977–79	45	25	Annual	Low				
		40	20	Annual	Low				

of cycles and 7 years of annual fluctuations reported in this species. There are no apparent competitors of *M. californicus,* which seems to dominate all other rodents in its grassland habitat (Blaustein, 1980; DeLong, 1966; Lidicker, 1966). We did not include Garsd and Howard's (1982) analysis of pit-trap data; we do not know whether their pitfall technique adequately measures vole population densities.

M. oregoni

The Oregon vole is unusual for *Microtus* species because it lives in a variety of habitats from virgin conifer forests to clearcut areas in forests and grasslands (Hawes, 1975). It has never been recorded at high densities (Table 5), so it illustrates the difficulty of trying to determine if cycles are present. There is no clear evidence for cycles except for two cases reported in Sullivan and Krebs (1981). Gashwiler (1972) reported some fluctuations in *M. oregoni* in clearcut habitats but little fluctuation in virgin timber areas. Hawes (1975) found only annual fluctuations in *M. oregoni* and showed that this species was reduced in density when it came into competition with *M. townsendii.* Petticrew and Sadleir (1974) reported a possible cycle of *M. oregoni* in a Douglas-fir plantation; Taitt (1978) found *M. oregoni* invading a forest trapping area in 1 of 3 years of study. We conclude that *M. oregoni* populations may cycle, but they most frequently have annual fluctuations that average 32/ha at maximum and 7/ha at minimum density. Cyclic populations are suggested to have peak densities 2–3 times the annual maxima (Table 5).

M. breweri

This island species was shown to have annual fluctuations on Muskeget Island (Tamarin, 1977); the average peak was 170 voles/ha and the average minimum was 68/ha (Table 6).

M. longicaudus

Few studies of *M. longicaudus* have been carried out (Table 6). In Alaska, an annual cycle at low density seemed to occur in logged areas (Van Horne, 1982). Densities averaged 33/ha at maximum and 11/ha at minimum. Conley (1976) reported a possible cyclic peak of this species at 105/ha in a New Mexico grassland. In the

TABLE 5

Population Densities from Live-trapping for *M. oregoni*. See Footnotes of Table 1

Grid	Years	Density/ha		Pattern	Spring dynamics		Notes	Map location (Fig. 1)	References
		High	Low		Density	Sex			
OF	1971–74	45	5	Annual	Low		Mainland, B.C. OF, old field	1	Sullivan and Krebs (1981)
		45	5	Annual	Low				
		70	?	Cycle?	30				
L	1971–74	90	15	Cycle?			Mainland, B.C. L, Ladner Grassland with *M. townsendii* and *Peromyscus maniculatus*	1	Sullivan and Krebs (1981)
		40	15	Annual	Low				
		40	15	Annual	Low				
		35	15	Annual	Low				
G	1972–74	35	5	Annual	Low		Mainland, B.C. G, grassland with *M. townsendii* and *P. maniculatus*	1	Sullivan and Krebs (1981)
		20	5	Annual	Low				
S	1975–80	15	0	Annual	Low		Mainland, B.C. S, shrub *P. maniculatus*	1	Sullivan and Krebs (1981)
		10	0	Annual	Low				
		35	0	Annual	Low				
		20	?	Annual?					

TABLE 6

Population Densities from Live-trapping for *M. breweri*, *M. longicaudus*, *M. mexicanus*, and *M. oeconomus*. See Footnotes of Table 1

			Density/ha			Spring dynamics				
Species	Grid	Years	High	Low	Pattern	Density	Sex	Notes	Map location (Fig. 1)	References
M. breweri	A	1972–75	125	96	Annual	Low	Both	Muskeget Island, Massachusetts; *Peromyscus leucopus*	7	Tamarin (1977)
			230	125						
			150	60						
	B	1972–75	115	40	Annual	Low	Both	Muskeget Island, Massachusetts; *P. leucopus*	7	Tamarin (1977)
			215	65	Annual	Low	Both			
			185	20	Annual					
M. longicaudus	1	1977–79	30	20	Annual	Low				
			30	5	Annual	Low				
	2	1977–79	50	20	Annual	Low		Mainland, Alaska; *P. maniculatus*, weasels; summer only	13	Van Horne (1982)
			50	30	Annual	Low				
	3	1977–79	45	5	Annual	Low				
			35	0	Annual	Low				
	4	1977–79	10	5	Annual	Low				
			15	0	Annual	Low				
M. longicaudus	C	1969–70	120	30	Cycle?	?	?	New Mexico; *M. mexicanus*	14	Conley (1976)
			30	20	Annual?	Low	Both			
M. mexicanus	C	1969–70	50	10	Annual	Low	Both	New Mexico; *M. longicaudus*		Conley (1976)
			50	15	Annual?	Low	Both			
M. oeconomus	A	1968–71	70	0	Cycle?	35		Mainland, Alaska; *Clethrionomys rutilus*	15	Whitney (1976)
	B	1968–71	80	0	Cycle?	—				
M. xanthognathus		1976	90	50	Annual	Low	Both	Mainland, Alaska	15	Wolff and Lidicker (1980)
		1977	110	60	Annual	Low	Both			

southwestern Yukon we found only one high-density population of *M. longicaudus* in 5 years of snap-trapping (Krebs, unpublished).

M. mexicanus

A single study of this interesting species by Conley (1976) suggested annual density fluctuations between a low of 15/ha and a high of 50/ha (Table 6).

M. oeconomus

This species fluctuates cyclically in Finland, and Whitney (1976) suggested one cyclic decline in central Alaska with a peak density around 70–80 voles/ha (Table 6).

M. xanthognathus

One 3-year study of this enigmatic vole by Wolff and Lidicker (1980) in central Alaska showed only annual density fluctuations and no evidence of cyclic changes.

General Conclusion

We present a synopsis of density changes in the species of *Microtus* for which the data indicate a clear population pattern in Table 7. Two major conclusions emerge from this analysis. First, annual fluctuations are common in most *Microtus* species. Of a grand total of 106 years of data on all species, 59% of the years had annual fluctuations and 41% were part of cycles. Second, both the amplitude and maximum density are higher in cyclic populations of a species than in annual fluctuations of the same species. The amplitude is always less than five-fold for annual fluctuations and usually well above 10-fold for cyclic fluctuations. The summary statistics given in Table 7 cannot be assumed to be more than general indications of the types of dynamics observed in each species. The available data show that *M. townsendii* sustains the highest average densities of any North American *Microtus,* closely followed by *M. californicus.* These trends do not apply to all populations of these species, as Krohne (1982) pointed out for *M. californicus.* We conclude that we must explain both patterns of fluctuation, especially because data for the two longest-term *Microtus* studies (Figs.

TABLE 7
SUMMARY OF POPULATION PATTERNS

Species	Pattern	Average density/ha Maximum	Average density/ha Minimum	Amplitude (max./min.)	No. years data	Proportion of years cyclic
M. townsendii	Annual	239	94	2.5	12	0.29
	Cycle	697	48	14.5	5	
M. pennsylvanicus	Annual	172	57	3.0	17	0.48
	Cycle	156	23	6.8	16	
M. ochrogaster	Annual	59	12	5.0	7	0.65
	Cycle	129	2	51.6	13	
M. californicus	Annual	167	38	4.4	7	0.50
	Cycle	427	12	35.6	7	
M. oregoni	Annual	32	7	4.6	10	<0.2?
M. breweri	Annual	170	68	2.5	3	0
M. longicaudus	Annual	33	11	3.0	2	0
M. mexicanus	Annual	50	15	3.3	2	0
M. oeconomus	Cycle	75	0	?	3	1.0
M. xanthognathus	Annual	100	55	1.8	2+	0

2, 3) show that individual populations can exhibit both patterns over time.

In the fifth column of Tables 1–6, we summarize the spring dynamics of each *Microtus* population study. The spring dynamics of *M. townsendii* show two patterns associated with the two forms of population fluctuation (Fig. 2). An annual fluctuation is preceded by a substantial spring decline. By contrast, in cyclic peak years (1975, 1977; Table 1) the spring decline is slight (Fig. 2). Taitt (in press) suggested that the form of the spring decline may indicate the type of population pattern shown by this species. A similar suggestion was made by Hansson (1971) for *M. agrestis* in south Sweden. The data for *M. townsendii* also indicate that the sexes have two patterns of spring decline: both male and female numbers decline in the spring of an annual fluctuation, but females do not decline in a cyclic peak spring (Fig. 2).

Spring densities of *M. pennsylvanicus* in Manitoba, Indiana, Massachusetts, Minnesota, and Illinois tend to be lower in years of annual fluctuation than in years of cycles (Table 2). This pattern also is seen in *M. ochrogaster* (Table 3), *M. californicus* (Table 4), and *M. breweri* (Table 6). Few of the studies in Tables 2–6 provided data on density change according to sex. But in six cases male *M. pennsylvanicus* declined more than females in the spring of cyclic years. Data for other species listed in Tables 5 and 6 are inadequate to establish whether this pattern is a general one. However, we know of no exceptions to the pattern of a strong spring decline being associated with annual fluctuations and weak spring declines being associated with cyclic peak populations.

Hypotheses to Explain Population Patterns

Since the review of Krebs and Myers (1974), there has been considerable development of hypotheses that account particularly for cyclic fluctuations in voles. We first state the hypotheses and then review the evidence in favor of each one.

Food Hypotheses

There are at least three food hypotheses now in the literature:

1) food quantity,
2) food quality,
3) secondary compounds.

The food-quantity hypothesis states that fluctuations in population size are produced by changes in the amount of available food. It was discussed by Elton (1942) and put forward by Lack (1954) as an explanation of cycles. In nutritional terms, it states that calories limit populations, and that malnutrition causes changes in birth and death rates.

The food-quality hypothesis arose in opposition to the simple world-is-green argument, and states that even though food supplies are abundant, they may be deficient in one or more nutrients that will stop reproduction and growth or accelerate mortality (Pitelka and Schultz, 1964). For example, Kalela (1962) postulated that fluctuations in boreal small rodents may be triggered by plant rhythms in production and growth. The food-quality hypothesis is now a family of hypotheses that explain population fluctuations by one or more macro- or micro-nutrients such as nitrogen, potassium, phosphorus, or sodium. For example, White (1978) argued that herbivores are limited by a relative shortage of nitrogenous food for young animals.

Plant secondary compounds can affect herbivores in three general ways. They can alter digestibility of forage and thus cause symptoms of food-quality deficiencies, they can be toxic directly and cause death, or they can inhibit (Berger et al., 1977) or stimulate (Berger et al., 1981) reproduction. Freeland (1974) was the first to suggest the toxic-compound hypothesis. General hypotheses about the role of plant secondary compounds were presented by Freeland and Janzen (1974). Haukioja and Hakala (1975) and Haukioja (1980) suggested that production of some compounds may be induced by herbivore grazing.

Predation Hypotheses

Predation on small mammals is postulated to determine the amplitude and timing of cycles (Pearson, 1971). Predation is not thought to act on increasing populations to stop their increase but rather to accelerate declines and hold numbers low. Mammalian predators are thought to be more effective than avian predators at hunting low-density populations (see Pearson, this volume).

Avian predation is one component of the effect of vegetative cover on vole populations. Birney et al. (1976) presented a two-threshold model called the "cover level hypothesis." Below the lower threshold of cover no population can exist. Non-cyclic populations with annual fluctuations are found at medium levels of cover. Cover can influence predation, available food supply, and behavioral interactions (Taitt and Krebs, 1983); it is reconsidered when we discuss multi-factor hypotheses.

Spacing-Behavior Hypotheses

The possibility that animals might limit their density by territorial behavior has been argued by ornithologists for 60 years. Wynne-Edwards (1962) elevated this idea to the general hypothesis that animals adjust their population density to available resources through social behavior. Watson and Moss (1970) provided an operational set of criteria that could be applied to field populations to determine whether breeding density is regulated by spacing behavior (Table 8).

The spacing-behavior hypothesis has been closely associated with

TABLE 8

THE CRITERIA SUGGESTED BY WATSON AND MOSS (1970) TO DETERMINE WHETHER SPACING BEHAVIOR LIMITS BREEDING DENSITY OF A POPULATION

A. A substantial part of the population does not breed; they die, are unsuccessful at breeding, are inhibited from breeding, or they breed later.
B. Such non-breeders are capable of breeding.
C. Breeding animals are not resource limited.
D. Spacing behavior is compensatory.
E. If A to D are true, and densities change according to shifts in food availability, then both spacing behavior and food limit the number of breeders.

the role of dispersal in microtine population regulation. Spacing behavior in field populations produces dispersal. Lidicker (1975) recognized pre-saturation, saturation, and frustrated dispersal (Lidicker, this volume). Abramsky and Tracy (1979) suggested that immigration was necessary to produce population cycles. Populations with emigration but no immigration showed annual density fluctuations. Gaines and McClenaghan (1980) recently reviewed dispersal in small mammals. Anderson (1980) also reviewed dispersal in microtines but did not discuss how dispersal affects population fluctuations or cycles. The exact mechanism by which spacing behavior produces population declines has not been specified.

There are two other groups of social-behavior hypotheses which we call phenotypic-behavior and genotypic-behavior hypotheses. We tentatively separate these hypotheses from spacing behavior in this review because they suggest specific mechanisms for the cyclic decline. Watson and Moss (1970) discussed the important role of "surplus" animals in their criteria (Table 8), but neither Christian (1978) nor Chitty (1967) discussed them. We suggest that the criteria of Watson and Moss (1970) will be essential to testing both of these groups of hypotheses.

Phenotypic-Behavior Hypotheses

These hypotheses state that social behavior limits breeding density and that the relevant behaviors are under phenotypic (non-heritable), physiological control. The best known is the stress hypothesis or neurobehavioral-endocrine mechanism of regulation of population growth, which was discussed in detail by Christian

(1978, 1980). This hypothesis was the first proposed to explain population fluctuations by an intrinsic mechanism (Christian, 1950). At high density a high rate of interaction results in a stress response, which leads to increased mortality and decreased reproduction and hence to population declines.

Social behavior often is mistakenly identified with aggressive behavior, but it includes any type of dominance or spacing behavior that affects an individual's chances of surviving and breeding. Thus, social structure, as discussed by Getz (1978), can affect rates of sexual maturation through pheromones or can affect familiarity among individuals and dispersal (Bekoff, 1981). The problem is that social behavior can have such varied effects on animals that we cannot determine without field experiments whether the effects of social behavior are relevant to understanding population fluctuations. For example, in peak populations of *M. pennsylvanicus,* age at sexual maturity is increased. Is this increase due to malnutrition, to maturation-retarding pheromones, or to adrenal-pituitary stress? We must do field experiments to answer specific questions of this type.

Since the early work of Frank (1957), there have been suggestions that social organization changes during population cycles. Populations exist in socially-stable configurations (individual territories) or in unstable configurations (group territories or dominance hierarchies), which produce cyclic peaks and overpopulation. Getz (1978) suggested that *M. ochrogaster* changes from a monogamous, territorial system, to a polygamous mating system in the increase phase of a cycle. One difficulty of this model is that other *Microtus* species, such as *M. pennsylvanicus,* are polygamous at all times and yet also cycle (Getz et al., 1979). Nevertheless, the general hypothesis that a variable social system underlies the differences between annual and cyclic populations is an important one that needs testing.

Hamilton (1964) discussed how kin selection could affect the evolution of social behavior. Charnov and Finerty (1980) applied these ideas to vole cycles and argued that aggression should be low among close relatives and should become high when individuals interact with many non-relatives, as they would in a population with high dispersal rates. Note that this kin-selection hypothesis is not a genotypic-behavior hypothesis but a phenotypic one, because individual voles are not genetically programmed to act any differently in increasing or declining populations. Individuals simply apply a general rule at all times: be aggressive to non-relatives and docile to relatives.

Genotypic-Behavior Hypotheses

Genotypic-behavior hypotheses are similar to phenotypic ones in assuming that changes in population size are caused by changes in social behavior, but they differ in ascribing the changes to shifts in allelic frequencies of genes that affect behavior. Genotypic hypotheses do not deny the physiological machinery behind the behavioral changes but assume that there is an array of genotypes in natural populations with differing social behaviors and that these genotypes are alternately favored or disfavored by natural selection.

The Chitty hypothesis is the best known of the genotypic-behavior hypotheses (Chitty, 1967); the hypothesis was reviewed recently by Krebs (1978*a*). A second hypothesis involving heterozygosity was suggested by Smith et al. (1975). Increasing heterozygosity in natural populations is associated with outbreeding, population growth, and increasing aggressive behavior. Smith et al. (1978) discussed predictions that follow from their model.

If the genotypic-behavior hypothesis is correct, it allows us to predict which populations will show annual fluctuations and which will show cycles. Krebs (1979) suggested that there was a positive correlation between the amount of fluctuation in population density and the heritability of spacing behavior. Populations with strong cycles should show a high additive genetic variance in spacing behavior, and this genetic variance should provide the time lag necessary to generate a cycle.

Multi-factor Hypotheses

"In the case of every species, many different checks, acting at different periods of life, and during different seasons or years, probably come into play" (Darwin, 1859). The multi-factor hypothesis is an old idea which has become popular in vole research (Batzli, in press; Christian, 1978; Getz, 1978; Lidicker, 1973, 1978; Taitt, in press; Tamarin, 1978*a*). We recognize two variants of the multi-factor hypothesis. The Lidicker model is diagrammed in Lidicker (1978:135) and is a generalized version of the multi-factor hypothesis first suggested by Darwin. We do not accept this model as being useful for further research and agree with Tamarin's (1978*b*) criticism of Lidicker's model. We are not questioning the truth of the model but rather its utility.

Another variant of the multi-factor model was presented by Taitt (in press) and is shown in Fig. 4. The value of this model is twofold. First, it integrates intrinsic and extrinsic variables through spacing behavior, and thus begins to specify a hierarchical type of systems model appropriate for explaining population changes. Second, it is experimentally oriented and suggests entry points for manipulation of populations. Thus, it avoids the major pitfall of most multi-factor models: they are a posteriori and untestable.

A general problem with many hypotheses in vole research is that they are often stated in vague terms. For example, Lidicker (1978: 135) stated that the multi-factor hypothesis can "explain densities" and population "regulation." We know of no hypothesis that can do this. Instead, we can only explain *changes* in density over time, or *differences* in density over space (Chitty, 1960).

Multi-factor approaches have been useful for recognizing the possible role of spatial heterogeneity in vole population fluctuations. Soviet ecologists have emphasized the role of spatial variation in habitat quality (for example, Naumov, 1972). A variety of terms has been used to describe habitat variations: central and marginal, optimal and suboptimal, primary and secondary, donor and receptor, survival and colonization (Anderson, 1980; Hansson, 1977; Smith et al., 1978; Wolff, 1981). The major distinction is whether the habitat is permanently occupied or not. There is no agreement about the role of chance in spatial heterogeneity, and this has led to circularity. Do we distinguish optimal habitats by their vegetation characteristics or by the fact that they always contain voles? Is it possible in a cyclic population to have empty primary habitats and occupied secondary habitats simultaneously? As Hansson (1977) recognized, only a spatially extensive mark-recapture program can answer these questions about the role of spatial variation.

Tests of Hypotheses

In the last decade, numerous experimental studies have been conducted on *Microtus* populations in an attempt to test explicitly some of the hypotheses outlined above.

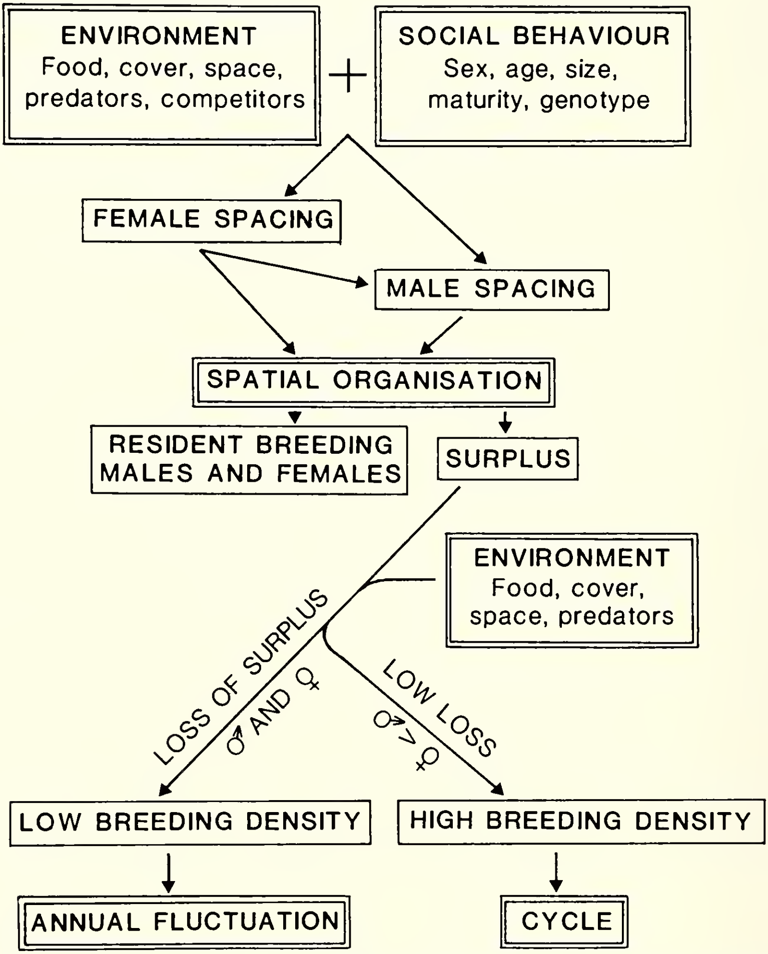

FIG. 4. General model of population dynamics for *Microtus townsendii* indicating how sex-specific spacing behavior may "decide" the potential surplus and how environmental conditions may "determine the fate" of the surplus and hence the population pattern (modified from Taitt, 1978, in press).

Food Experiments

Three food-addition experiments were conducted recently on *Microtus* populations. In spring 1973, we added two levels of food to populations of *M. townsendii* (Taitt and Krebs, 1981). The control population was fluctuating at low density, but experimental populations reached and maintained densities two (low food addition) and five times (high food addition) that of the control. An intermediate level of food the following year resulted in a doubling of density over the control, even though the control was then increasing to a cyclic peak density. Voles with extra food increased in weight and more were reproductive, and they had reduced home ranges in proportion to the level of food added. It is fairly certain (see density-controlled food experiment by Mares et al., 1982) that the reduction of resident home ranges in response to food enabled immigrants to settle on food grids and colonize new habitat in proportion to the extra food available.

A single level of extra food was supplied to *M. ochrogaster* (Cole and Batzli, 1978) and *M. pennsylvanicus* (Desy and Thompson, 1983) with similar results. But in both studies the control population cycled and, although grids with extra food reached higher densities, they declined at the same time as the controls. Cole and Batzli (1978) noted that erratic declines on their high-density food grid were associated with periodic concentrations of predators; however, they did not mention this as a cause of the severe cyclic decline. If feeding experiments are done on other cyclic species, attempts should be made to have a replicate food grid from which all predators are removed.

We conclude that these *Microtus* species do respond to an increase in food. They reach higher densities than controls because of increased growth, reproduction, and immigration. But so far extra food has not prevented cyclic declines in density.

Six 1-ha plots of shortgrass prairie were manipulated for 6 years in eastern Colorado as part of the IBP Grassland Biome study (Abramsky and Tracy, 1979; Birney et al., 1976). *M. ochrogaster* density on the control remained low (average maximum of 3.5/ha) throughout. No *Microtus* were trapped on plots receiving 50 kg/ha of ammonium nitrate. Grids treated with water had 14 *M. ochrogaster*/ha by the fourth year of treatment. Plots with both nitrogen and water added maintained the highest density (average maximum of 80/ha) of *M. ochrogaster* and had three times as much cover as the control. However, voles simply may have responded to cover and not to food quality (Birney et al., 1976).

In Fennoscandia, long-term monitoring studies indicate that peaks of plant flowering coincide with cyclic increases of rodent numbers

(Laine and Hettonen, 1983). It is not known if this correlation is a causal one or not.

The role of plant secondary compounds in vole population dynamics is difficult to assess. Although voles show food preferences (Batzli, in press), it is difficult to decide what is toxic to voles (Batzli and Pitelka, 1975; Freeland, 1974). Schlesinger (1976) challenged Freeland's (1974) first tenet, that voles must prefer non-toxic plants. But he agreed that *M. pennsylvanicus* (Thompson, 1965) and *M. californicus* (Batzli and Pitelka, 1971), both cited by Freeland, avoid toxic plants. The only other *Microtus* data considered by Schlesinger (1976) was for *M. ochrogaster,* which did not avoid toxic plants. However, Zimmerman (1965) found that *M. pennsylvanicus* avoided three toxic plant species. Problems of sample size, and the fact that seeds (which made up 66–86% of stomach contents) were not identified to species (Batzli and Pitelka, 1975) have made tests of Freeland's (1974) hypothesis inconclusive. Bergeron (1980) reported that *M. pennsylvanicus* increases its consumption of toxic plants at peak densities, as Freeland (1974) predicted, but whether these toxic food items are responsible for cyclic declines in numbers is not clear.

Details of the factors controlling reproduction and growth are discussed in other chapters (see Keller, this volume; Batzli, this volume). Since the duration of the breeding season is an important variable that can affect population changes, we need to know what factors start and stop breeding in *Microtus.* Negus and Berger (1977) reported that *M. montanus* populations given access to sprouted wheatgrass in mid-winter became reproductive in two weeks while controls remained non-reproductive. They isolated the causal chemical as 6-methoxybenzoxalinone (6-MBOA). Rose et al. (in press) fed oats impregnated with 6-MBOA to a *M. pennsylvanicus* population in January and reported 42% of females pregnant compared with 10% in a control population 5 weeks later. No field tests have been conducted on the phenolic compounds that inhibit reproduction in *M. montanus* (Berger et al., 1977).

Induction of secondary chemicals in plants eaten by *Microtus* has not been demonstrated. However, Haukioja (1980) suggested that induction of such chemicals could be ruled out if a vole population was able to increase immediately after being transferred to an area that previously had been heavily grazed. Myers and Krebs (1974) introduced *M. ochrogaster* into a fenced enclosure in which a population of this species had previously reached 5-times natural density (caused by a fence effect). The new *M. ochrogaster* population increased in 1 year to more than 10 times the density of the unenclosed control. Krebs (1966) showed that, if new voles were introduced, a population increase of *M. californicus* could be induced in an area that had just suffered a decline in density.

In summary, three *Microtus* species responded to experimental addition of food. Increases in other rodent populations were correlated with improved plant quality. Reproduction of *M. montanus* and *M. pennsylvanicus* was stimulated by the presence of 6-MBOA. Grazing-induced secondary compounds appear not to be important in two *Microtus* species. No data indicate that food is more than a necessary condition for *Microtus* population increase. Future research needs to determine whether changes in food quantity or quality are sufficient to cause cycles.

Evidence for Predation

Recent work on predation has taken into account the importance of cover as protection against predation. Reduced cover caused by cattle grazing results in low-density *Microtus* populations (Birney et al., 1976). Baker and Brooks (1981) observed high raptor densities in habitats with high numbers of *M. pennsylvanicus,* but the amount and distribution of cover affected prey availability. We experimentally increased cover by adding straw (Taitt et al., 1981), with the result that *M. townsendii* populations increased. We also reduced cover by mowing (Taitt and Krebs, 1983), and populations declined.

Avian predation is easier to quantify than mammalian predation because bird pellets tend to be localized at roosts. The most useful data on predation combine field studies of vole demography (where voles are identified by metal ear tags) and collection of as many pellets as possible in the immediate area of the vole grids. Two studies on *M. townsendii* (Beacham, 1979*b*; Boonstra, 1977*a*) indicate that avian predators take more males than females and select small voles. Still, such studies are limited because one can never find all predator pellets or scats, so the estimates of predation will always underestimate the impact of predation on tagged animals. However, Beacham (1979*b*) recorded an impressive 25% loss of *M. townsendii* to avian predation in a 1-week period of his study. Beacham found a density-dependent correlation ($r = 0.99$; $P < 0.02$) between avian predation and densities of *M. townsendii.*

Pearson (1971, this volume) argued that carnivore predation on *M. californicus* operated in an inverse density-dependent manner, so that the major effects were on low-density populations. Erlinge et al. (1983) measured both avian and mammalian predation of *M. agrestis* populations in south Sweden. They calculated that total annual predation was of the same magnitude as annual rodent production. Their result confirms Hansson's (1971) suggestion that small rodents in south Sweden are prevented from cycling by predation. Future predation studies must include both avian and mammalian species. Attempts should be made to experimentally manipulate predation, particularly at important periods during vole demographic changes (for example, at the onset of breeding; Taitt and Krebs, 1983); only then will we be able to judge the true impact of predation on vole population dynamics.

Spacing-Behavior Experiments

Krebs et al. (1976) were the first to apply the Watson and Moss (1970) criteria to determine whether spacing behavior limits the breeding density of a microtine population. They demonstrated that surplus *M. townsendii* existed that were capable of breeding (Condition A and B, Table 8) but did not do so. We now discuss briefly other recent *Microtus* studies that support the criteria of Watson and Moss (1970) in Table 8. A more detailed review recently was published by Tamarin (1983).

Condition A.—Voles occupy home ranges. If residents are removed, new voles colonize the vacant area (Baird and Birney, 1982; Krebs et al., 1976; Myers and Krebs, 1971). It is not certain whether colonizers are surplus from resident populations, but Krebs et al. (1978) found that new colonizers showed more subordinate behavior than control residents.

Condition B.—If new colonizers are allowed to remain in an area, they establish a breeding population (*M. ochrogaster* [Gaines et al. 1979]; *M. townsendii* [Krebs et al., 1978]).

Condition C.—No direct evidence has been collected for this condition in *Microtus* species. But when a vole population is fenced in, the enclosed habitat supports a much higher population than unenclosed controls (*M. pennsylvanicus* [Krebs et al., 1969]; *M. townsendii* [Boonstra and Krebs, 1977]). This suggests that food, space, and nest sites are not limiting voles directly in open control populations.

Condition D.—It is difficult to demonstrate behaviorly induced mortality in voles. If a vole ceases becoming trapped, it may have emigrated or died, or it simply may be avoiding traps. However, in a recent experiment on *M. townsendii* (Taitt and Krebs, 1983), we counted all such voles as "disappeared," and found that the number of voles that "disappeared" from five populations over the month of onset of breeding in females was correlated ($r = 0.93$; $P < 0.05$) with density of voles. Reproduction is compensatory (presumably behaviorally induced) in several species (*M. californicus* [Batzli et al., 1977]; *M. montanus, M. ochrogaster, M. pennsylvanicus* [Schaffer and Tamarin 1973]). We believe that these observations indicate that voles may show compensatory spacing behavior.

Condition E.—In one species (*M. townsendii*), we have some evidence for conditions A to D. Watson and Moss (1970) suggested that, if these populations respond to changes in food, they are regulated by both spacing behavior and food. Populations of *M. townsendii* increased to different densities in response to the amount of food added, and also colonized new habitat in response to food levels (Taitt and Krebs, 1981).

If we use the criteria in Table 8, populations of *M. townsendii* appear to be regulated by both spacing behavior and food. This, and the fact that females were more responsive to food availability, led to the formulation of the model in Fig. 4. The habitat patchiness (induced by winter rainfall) may be unique, but we feel that some of the mechanisms invoked (for example, cessation of reproduction through increased interaction as a result of winter flooding [Taitt and Krebs, 1981], and perhaps simultaneous settlement of breeding females in spring of cyclic years [Taitt and Krebs, 1983]), may be of general importance in other annual-cyclic species.

A study in Finland by Pokki (1981) on *M. agrestis* is particularly interesting because it is suggests the possible influence of dispersal on the fate of surplus animals and population fluctuations. Pokki (1981) observed that island colonization was by inter-island dispersal from small islands (isolated patches of grassland) over as much as 1 km of open water. However, dispersal on large islands was within islands between grassland and marginal habitat (woodland). Also, more inter-island dispersers colonized large islands than small ones. Pokki (1981) did not observe cycles on small islands, but *M. agrestis* appeared to be cyclic on the largest islands. This study gives a dramatic illustration of the dispersal ability of *M. agrestis,* and may provide evidence for an hypothesis about cycles (Fig. 4). If dispersers are surplus animals, can the observed population patterns be partly the result of elimination of surplus voles (on small islands), which leads to an absence of cycles, whereas survival of surplus voles (on large islands) results in cycles? Tamarin (1978*a*) suggested that the presence of a vole surplus explained the absence of cycling in *M. breweri* populations on Muskeget Island, but the two situations may not be comparable. Muskeget is isolated, and has been for 2,000–3,000 years. Experimental work is needed on island populations to test these interpretations.

Phenotypic-Behavior Experiments

A premise for both the phenotypic- and genotypic-behavior hypotheses is that the rate of interaction of individuals increases with population density. Pearson (1960) reported that *M. californicus* built more runways as numbers increased. Carroll and Getz (1976) also found that the number of active runways was correlated with population density of *M. ochrogaster.* However, it is not known if voles confine all their activities to runways. In fact, Crawford (1971) observed *M. ochrogaster* climbing low branches of trees and engaging in fighting outside burrows during a cyclic peak. In addition, interactions need not always be through direct contact, because voles probably use indirect methods such as marking (Richmond and Stehn, 1976) and vocalizations that enable them to react to increases in density.

Adrenocortical function has been evaluated indirectly in *Microtus* populations by measuring adrenal weight. But adrenal weight varies with sex, season, maturity, diet, and body weight. To and Tamarin (1977) found that adrenal weights of sexually mature *M. breweri* from non-cyclic, island populations were significantly influenced by population density. But mainland, cyclic *M. pennsylvanicus* showed no clear adrenal response to population density in their study. However, Geller and Christian (1982) found that "mean relative adrenal weight" of mature female *M. pennsylvanicus* was correlated with mean population density in spring (April to June). It is difficult to compare densities in these studies, but it appears that To and Tamarin's (1977) *M. pennsylvanicus* densities were lowest, their *M. breweri* densities were higher, and Geller and Christian's (1982) *M. pennsylvanicus* densities were highest. An interesting common trend in these studies is that, in populations where there is a relationship between adrenal weight and density, mature females showed a stronger relationship than males. Geller and Christian (1982) speculated that pregnant females, in populations at different densities, may affect fetal immune development.

Field studies on *Antechinus stuartii* in Australia indicate that males are extremely aggressive toward one another during mating (Braithwaite, 1974). This behavior is correlated with a marked increase in blood androgen (Moore, 1974). Bradley et al. (1980) showed that high free glucocorticoid concentrations in plasma result from increased total glucocorticoid and reduced plasma corticosteroid binding which, in turn, suppress the immune and inflammatory system. The consequence is that all males die after mating from gastro-intestinal hemorrhage and infection from parasites and microorganisms. No field studies on *Microtus* have demonstrated death on this scale from these causes. But such physiological responses to stress have been reported for *M. montanus* in the laboratory (Forslund, 1973). The period of spring decline is probably stressful in *M. townsendii* (coincides with a peak in male wounding and pregnancy of the first females). McDonald and Taitt (1982) found that a small sample of voles from such a population had high levels of free corticosteroids, but the highest levels were found in mature females.

Hormonal manipulation of behavior in the field has been attempted in *M. townsendii* (Gipps et al., 1981; Krebs et al., 1977; Taitt and Krebs, 1982). Pellets or silastic implants of testosterone in males had no significant effect on demography. But silastic implants of scopolamine HBr, which have been shown to reduce male aggressive behavior in *M. townsendii* (Gipps, 1982), reduced the rate of spring decline in males. Males also survived better in a population in which females were fed a synthetic steroid (mestranol), which rendered them anestrous. Female wounding is uncommon in *M. townsendii,* but females with implants of testosterone had more wounds than males, and, like males, had low survival in spring. These results suggest that male *M. townsendii* are responsive to the level of overt aggression (male or female). Normally, females may rely less on overt aggression (Caplis, 1977) and more on site-specific defensive behavior. If true, it might explain, for example, why females respond more quickly to increased food. Also, if increased vole density means more challenges to site-specific individuals, then females may be stressed more by increased population density than males.

Behavioral interactions may affect density through reproductive effects as well as through survival. The Bruce effect (pregnancy blockage) is perhaps the best known. Keller (this volume) reviewed these mechanisms and concluded that they may be important in field populations but that the evidence does not suggest a major role in generating population fluctuations. Taitt and Krebs (1981) suggested that *M. townsendii* may be driven to an annual fluctuation in most years because of winter cessation of reproduction. They hypothesized that rain causes the water table to rise to the point that voles cannot maintain deep burrows; they are forced into less space, which results in increased interaction, weight loss, and cessation of reproduction.

Social suppression of growth and reproduction may vary in different species of *Microtus* (Facemire and Batzli, 1983). Species like *M. californicus* and *M. ochrogaster,* which have a monogamous social system, show social suppression of growth when siblings are caged together. Species like *M. oeconomus* and *M. pennsylvanicus,* which are promiscuous and show no male parental care, do not exhibit social suppression of growth and reproduction. The possibility that social suppression changes over the period of a population cycle needs investigation in these species.

Future research on phenotypic behavior should concentrate more on female behavior (see section on Multi-factor Tests). Manipulations of behavior should be attempted in the field to increase or decrease stress. The consequences of such experiments may shed more light on the possibility of phenotypic maternal transfer of stressed conditions.

Genotypic-Behavior Experiments

Tests of the polymorphic behavior hypothesis typically have proceeded in two steps. First, measurable behavioral differences are demonstrated between populations changing over time. Standardized laboratory tests of agonistic or exploratory behavior are done. Second, these behaviors are shown to be heritable so that natural selection can operate on them.

Both agonistic and exploratory behavior changed with population density in *M. ochrogaster* and *M. pennsylvanicus* in Indiana (Krebs, 1970). Myers and Krebs (1971) found behavioral differences between resident and dispersing individuals of these same species. Hofmann et al. (1982) tried to repeat these observations on both species in Illinois but were unable to verify changes in behavior over a cycle. Rose and Gaines (1976) failed to find a relationship between wounding and density during a population cycle of *M. ochrogaster* in Kansas. Rasmuson et al. (1977) measured locomotory behavior in *M. agrestis* from cyclic and non-cyclic populations in Sweden and found strong differences between populations. They also demonstrated that locomotor activity was highly heritable. Anderson (1975) estimated heritability of agonistic behavior in *M. townsendii* as zero. There are no other estimates of the heritability of any component of spacing behavior in any *Microtus* species. Consequently, it is not yet possible to test the suggestions of Krebs (1979) that annual fluctuations are associated with low heritabilities of agonistic behavior and that cyclic fluctuations are associated with high heritabilities.

Several attempts have been made to test Chitty's (1967) hypothesis with electrophoretic markers in blood proteins. But because we do not understand the physiological effects associated with most electrophoretic markers or their linkage groups, changes in electrophoretic allele frequencies may no longer be necessary or sufficient to verify the hypothesis. At best, electrophoretic markers indicate the intensity of selection in field populations. LeDuc and Krebs (1975) manipulated the frequency of a leucine-aminopeptidase marker in field populations of *M. townsendii* and found no measurable effects of altered allelic frequencies on population density. We now think that experiments of this type are unlikely to be fruitful because of the difficulty of assessing linkage groups in natural vole populations.

Several attempts have been made to determine if dispersers differ in allelic frequencies from resident voles. Gaines and McClenaghan (1980) recently reviewed these studies, and concluded that electrophoretic markers are not likely to be useful in determining whether dispersal behavior is heritable. Three attempts to estimate the heritability of dispersal tendencies in *Microtus* populations produced suggestions of high heritability (Anderson, 1975; Beacham, 1979*c*; Hilborn, 1975), but the results may have been caused by maternal effects. If dispersal tendency is highly heritable and dispersal is critical for population fluctuations, we will have strong support for the polymorphic behavior hypothesis.

Chitty (in press) suggested that adult body size in *M. townsendii* is controlled by a single major gene; large voles are homozygotes (*AA*) and so are small voles (*aa*). If this simple major gene effect can be shown to underlie cyclic changes of body size in *Microtus,* it will be critical to study spacing behavior of these genotypes. Chitty (in press) suggested that the large-bodied homozygotes are in fact the hypothesized docile genotypes that dominate populations undergoing density increases. These ideas have not been confirmed for any *Microtus* species.

Attempts to test the genotypic-behavior hypothesis must rest on an estimation of the heritability of traits of dominance and spacing behavior for which few data exist at present. The most critical experimental approach would be to conduct an artificial selection experiment in a natural population, selecting for or against some form of spacing behavior and observing the demographic consequences.

Multi-factor Tests

In practice, those who invoke multi-factor hypotheses fall into two general groups. To the first group a multi-factor model comprises food and predators almost exclusively, with perhaps some climatic effects included (for example, Keith, 1974; Oksanen and Oksanen, 1981; Stenseth, 1978). In principle, there is no difficulty in testing such two-factor hypotheses experimentally, but no one seems to have done so.

To the second goup a multi-factor model involves food, predators, and social behavior. Lidicker's (1973) discussion on *M. californicus* dynamics is a good example of this approach. Social behavior can be looked at in two ways when it is part of a multi-factor hypothesis. Some authors view social behavior as a way of partitioning resources, so that it is the resources (usually food) that are critical (Lack, 1954). Others view social behavior as part of the life-history strategy in which individuals are trying to maximize their fitness.

In these situations individuals may compete for "social status," which is related only tenuously to resources (Wynne-Edwards, 1962). The central issue has become whether social behavior can regulate density below the carrying capacity dictated by food and predators (Łomnicki, 1978; Verner, 1977). Since social behaviors can be influenced by many variables (both phenotypic and genotypic), some population changes may occur in ways unrelated to resource levels.

It is difficult to test multi-factor models that include social behavior. Getz (1978) and his research group tested social-behavior hypotheses on laboratory populations of *M. ochrogaster* and are now applying them to field populations. Taitt and Krebs (1981, 1982, 1983) tried to test a complex multi-factor model on *M. townsendii* directly in field populations (Fig. 4). We do not know what factors determine the number of surplus voles in field populations or what factors determine the fate of surplus animals. We can gain insight by measuring social behavior while manipulating food and predators, and vice versa. Because dispersal is a critical element in these population systems, open populations must be the experimental units.

In what follows we consider two features associated with vole population dynamics for which multi-factor considerations may be most appropriate. The first, body weight, has a long association with the literature on small mammal cycles; the second, the role of females, has begun to receive attention over the last decade.

Body weight.—Chitty (1952) observed that peak-density populations of *M. agrestis* contained individuals of high body weight that were absent in low-density populations. All but one of the studies on *Microtus* listed as reporting cycles in abundance (Tables 1–6) found larger animals in peak populations. The exception was Gaines and Rose (1976), who reported no shift to heavier *M. ochrogaster* in a peak population. We do not know what the adaptive advantage of large size is for voles (Boonstra and Krebs, 1979); two contradictory hypotheses involving r-selection (Chitty, 1967) and α-selection (Stenseth, 1978) have been suggested.

Recent studies indicate that growth in voles is influenced by extrinsic factors. Iverson and Turner (1974) showed that mature *M. pennsylvanicus* lost weight in winter. Petterborg (1978) reported that *M. montanus* grew at a slower rate under a short photoperiod than under a long photoperiod. Beacham (1980) found that *M. townsendii* born in spring had higher growth rates than voles born in any other season. *M. townsendii* in open populations grew 20% faster than voles in enclosures (Beacham, 1979*b*); the density in the enclosures was higher than in the open populations (Beacham, 1979*a*). Finally, Batzli et al. (1977) found that growth was suppressed by social conditions in *M. californicus* and *M. ochrogaster.* These results indicate that weight cannot be correlated simply with age. However, Mallory et al. (1981) used lens weight to age *Dicrostonyx* and found that lemmings in the peak year were significantly older and heavier than lemmings in low years, suggesting that high body weights in the peak year could be the result of age.

Anderson (1975) did not find a strong genetic influence on growth rate or maximum body size in *M. townsendii.* Instead, she found that environmental effects made siblings resemble one another in growth rate, and that maximum size of offspring correlated with size of mothers. Further, female body weight is correlated positively with litter size in this species (Anderson and Boonstra, 1979).

Iverson and Turner (1974) suggested that loss of weight in old and lack of weight gain in young *M. pennsylvanicus* in winter were adaptive responses possibly cued by day length. They suggested that these were general phenomena among north temperate small rodents. But both deermice (*Peromyscus maniculatus*; Taitt, 1981) and Townsend's voles (*M. townsendii*; Taitt and Krebs, 1981) responded immediately to extra food in winter by gaining weight, suggesting that winter weight loss simply could be a proximate response to food availability. Beacham (1980) reported that "heavy" male *M. townsendii* (using ≥70 g as peak weights) in his cyclic population were animals that had gained weight throughout the preceeding ("increase") winter. Yet *M. townsendii,* given extra oats in late winter, gained weight so that mean weights of males and females were significantly higher than those on the control after only 2 weeks. In this short period, 63% of the males became "heavy" (≥70 g) compared with 23% on the control (Taitt and Krebs, 1983).

These results indicate that growth rates are highly labile. Work on *M. townsendii* indicates that animals with sufficient food can maintain positive growth rates in winter and become "heavy" animals. Because the spring decline in numbers in the peak year is slight, many of these animals may survive so that some voles in the peak population are older and heavier, whereas animals born at the peak have reduced growth rates because of high population density.

Such an explanation does not rule out a genetic basis for the morphs in peak populations (Chitty, in press). It could be that genotypes yielding potentially large body weight are not expressed phenotypically until food conditions are adequate, particularly in the winter preceeding a peak. Body weight in laboratory mice is highly heritable, but Roberts (1981) suggested that there may be a range of variation in weight over which there is little natural selection in wild populations. Also, Fulker (1970) suggested that maternal effects (behavioral and endocrine) could act as a buffering mechanism on the expression of offspring genotypes in rodents.

The phenomenon of body-weight changes in cyclic populations of *Microtus* will be understood only when both environmental and genetic influences on growth and weight are measured.

Role of females.—"Little work has been done on female aggressive behaviour . . . ." (Krebs and Myers, 1974). This situation has begun to change in the last decade, although the challenge to do so had been made much earlier. Frank (1957) made the following observations on *M. arvalis* in Germany: 1) breeding females occupied a range around their burrows from which they drove out all other voles; 2) females tolerated a strange male in their home ranges only when they were in heat; 3) males inhabited irregular large areas in which they wandered from female to female in order to mate; 4) in spring, young males without exception disappeared from their mothers' territory, but young females settled in the immediate vicinity; and 5) "great families" arose every autumn when the last two to three litters remained in the maternal home range to overwinter. In addition, Frank (1957) suggested that the social behavior of females—their tendency to remain together even if they move—might explain how peak populations arise.

One way to determine the role of females in natural populations is to alter sex ratios by removal experiments. Redfield et al. (1978) began sex-specific removal experiments on field populations of *M. townsendii* in 1972. They found that female recruitment was reduced in a population containing a majority of females and that there was an inverse relationship between the number of young voles recruited and the density of mature females (but not males). Further experiments on *M. townsendii* showed that juvenile survival was dependent on female (not male) densities (Boonstra, 1978), and that females responded before males to the addition of food (Taitt and Krebs, 1981, 1983). Also, males exhibited better survival in a population of "passive" females (Taitt and Krebs, 1982) and "passive" males (Gipps et al., 1981).

Research on other *Microtus* species also indicates that Frank's (1957) observations may apply to species other than *M. arvalis*. Radiotelemetry work by Madison (1980) showed that mature female *M. pennsylvanicus* occupy exclusive home ranges. Males, on the other hand, had large, overlapping, and more variable home ranges. Males also moved temporarily into areas occupied by estrous females. These observations were confirmed by Webster and Brooks (1981) for *M. pennsylvanicus* in Ontario. Field observations on other small mammals indicate that mature females exert control on population growth by excluding subordinates (Leuze, 1976; Viitala, 1977), or tolerating those that delay maturity (Bujalska, 1973; Jannett, 1978; Saitoh, 1981). In the laboratory, Batzli et al. (1977) found that females had more influence than males on the suppression of growth in *M. californicus* and *M. ochrogaster*. Finally, recent results on stress responses at high density also indicate that females are more responsive to stress and may subsequently affect their offspring accordingly (Geller and Christian, 1982).

Perhaps mature females in the breeding season can be considered the equivalent of territorial male birds. They secure an area for raising young (Boonstra, 1977*b*; Jannett, 1978), including ample food for lactation and space free from intraspecific intrusion. Pheromones may be the advertising currency equivalent to bird song. Male *Microtus* are forced to forage in the interstices of these female territories (Madison, 1980) and compete among themselves for estrous females (Boonstra, 1978; Krebs, 1978*b*; Madison, 1980; Webster and Brooks, 1981). Although these features suggest a polygamous mating system, the degree of polygyny could be dependent on population density (Getz, 1978).

Greenwood (1980) suggested that philopatry favors the evolution of cooperative traits between members of the sedentary sex. One such trait may be the phenomenon described by Frank (1957) in *M. arvalis* in which sisters from "great families," and sometimes their mother, remain together and breed on a common territory when conditions are optimal. Frank (1957) postulated that this "condensation potential" enabled *M. arvalis* populations to reach outbreak densities. Taitt and Krebs (1983) suggested another female behavior that might contribute to outbreaks. They argued that if conditions were favorable, all females may become reproductive simultaneously and that this might precipitate simultaneous settlement at higher than normal density, as observed in the spring of cyclic years in *M. townsendii* (Fig. 2). Large simultaneous pulses of young could be produced; the offspring, in turn, might simultaneously colonize any available habitat and so result in a spreading outbreak. Simultaneous settlement has been observed in territorial male birds by Knapton and Krebs (1974) and Tompa (1971).

Female behavior, like growth rates, appears to be influenced by extrinsic and intrinsic variables. Do Frank's (1957) observations apply to all species of *Microtus*? If so, what changes in territorial social organization precipitate a cycle in abundance? How do females respond to stress at peak density, and how does this affect survival of offspring? We suggest that answers to these questions will probably be needed before we can understand cyclic fluctuations.

Mathematical Models

In spite of the recent increase in mathematical modeling of biological populations, little work has been done on models of rodent populations. May (1981) summarized models for single-species populations. Beginning with a simple logistic model, one can add a time-lag and produce population curves that vary from stable to cyclic. The critical parameter is the time delay in the feedback mechanism that regulates population size. If the time delay is 9–12 months, the resulting populations trace cycles with a period of 3–4 years. The simple message is that for voles, which have a similar range of values for innate capacity for increase (r), we are looking for a delayed density-dependent factor that lags 9–12 months behind population density in order to establish a cyclic population. For shorter time lags an annual cycle would be produced. The problem with this simple approach is that we cannot evaluate easily any of the suggested biological mechanisms producing time delays in real vole populations.

Models of the food hypothesis were suggested by Rosenzweig and Abramsky (1980) based on a predator-prey interaction between voles and their food plants. Batzli (in press) used loop analysis to analyze the brown-lemming cycle in northern Alaska and suggested that, if vegetation quality is important in generating population cycles, it is likely to be a function of plant secondary compounds rather than delays in nutrient recycling. Stenseth et al. (1977) produced the most comprehensive and realistic model for a *Microtus* population. This model was based on the nutritional balance of individuals and how nutrition affects birth, death and dispersal. It includes some effects of predation and habitat heterogeneity, and thus begins to approach a multi-factor model. However, the model is intractable because it "is impossible to analyze in a manner providing intelligible results or predictions" (Stenseth, pers. comm.).

Models of the Chitty (1967) hypothesis have been analyzed recently by Stenseth (1981) to see if population cycles could be generated by a genetic polymorphism. Stenseth (1981) argued that intrinsic factors alone cannot generate a cycle, and that the only tenable hypothesis is that population cycles are caused by the interaction of intrinsic and extrinsic factors. Stenseth (1978) shows how this type of model can lead to cycles or annual fluctuations. The relevant extrinsic factors are not identified in his model; presumably weather, food, predators, or parasites could be involved.

The general tendency in population modeling has been to make the models more complex and include many factors. The result has not been very useful for guiding field work on *Microtus*. The most comprehensive recent effort by Finerty (1980) on population cycles includes the use of loop analysis. But almost none of these modelling studies has suggested a critical experiment, and they remain largely a posteriori analyses.

Discussion

In their review, Krebs and Myers (1974) challenged the existence of non-cycling populations of microtines. However, the pattern of fluctuations revealed in the present review indicate that field populations of *Microtus* in North America (Tables 1–6) show annual fluctuations, multi-annual cycles, and sometimes both in combination (Figs. 2, 3). We must, therefore, search for hypotheses which will allow a range of possible outcomes for density changes.

We are now more knowledgeable of the affect of temporal heterogeneity in population dynamics, but we are less well versed in understanding spatial heterogeneity. This is partly because most studies have been carried out in favorable habitats, and because it is difficult to trap in areas large enough to encompass several habitats. Habitat variation is interwoven with dispersal in population dynamics (Hansson, 1977), so it is not surprising that both these elements are poorly understood in vole populations.

The history of *Microtus* population studies is checkered by a series of arguments about the role of single factors in causing population fluctuations. We think that perhaps these arguments should be left to the past and that a new synthesis should be attempted. Perhaps this synthesis could be based on the premise that both extrinsic and intrinsic factors are involved in *Microtus* population fluctuations. A second premise could be that dominance and spacing behavior play a central role by potentially apportioning resources differentially among members of the population.

The investigation of *Microtus* population dynamics, and rodents in general, is still an expanding field of ecological research. Useful advances in the future will come largely from field experiments designed with a strong hypothesis-testing structure. Many of these tests will be difficult to formulate because they must be done on a complex system and we do not, in general, know the degree of complexity.

The present review of *Microtus* population dynamics reveals that: 1) annual fluctuations reach maximum densities typically one-third of cyclic densities; 2) the amplitude of an annual fluctuation tends to be less than five-fold, whereas that of a cycle can be more than ten-fold; and 3) substantial spring declines (of both sexes) may be characteristic of annual fluctuations, whereas reduced spring declines (sometimes confined to males) accompany cycles.

A number of specific questions has arisen from this review. Do dominance and spacing behaviors limit the breeding density of all *Microtus* populations? What restricts a population to a five-fold increase in density one year and yet allows it to reach a ten-fold increase to cyclic density in another year? If surplus voles are produced by spacing behavior, is it simply their fate at the onset of breeding that produces the two patterns of spring decline? What is the role of environmental factors on the fate of surplus animals and what bearing does this have on the population dynamics exhibited by a population? Why is body-weight distribution different in the two population patterns? Are "heavy" voles genetically different or do favorable conditions prior to peak density contribute to weight gain and longer lifespan? Are females more sensitive than males to environmental conditions such as food and cover? If so, is the spacing behavior of mature females the proximate mechanism of *Microtus* population regulation? Can maternal responses to stress be transferred to offspring? If so, what are the consequences at cyclic peak densities, and what is the time-lag of such responses?

Answers to these questions may be incomplete if they ignore the possible genetic basis of the relevant ecological variables—growth, reproduction, response to stress, dominance and dispersal behavior. Future research should emphasize the heritability of these variables in individuals from populations exhibiting both annual fluctuations and cycles in abundance (for example, see Rasmuson et al., 1977).

The paradigm suggested by this review is that future studies of *Microtus* population dynamics must address the two patterns of fluctuation. Field manipulations should be designed to test the interactions suggested, particularly between spacing behavior, food, and predation. The results should be related to the dispersal abilities of voles that enable them to exploit temporally favorable habitat, and to their potential to reach outbreak densities.

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