OXFORD JOURNALS
OXFORD UNIVERSITY PRESS

SOLVING THE ENIGMA OF MICROTINE "CYCLES"

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ABSTRACT.—A frequently expressed opinion is that despite massive efforts the multi-annual cycles in density exhibited by many microtine rodents remain mysterious; moreover, understanding awaits completion of one or a few clever experiments or elegant mathematical models that will discredit all but the one true hypothesis. I contend in this brief, personal essay that, on the contrary, we are actually quite close to an adequate understanding of microtine cycles. This optimistic perspective requires that we adopt a multi-factorial model of vole demography, a position that allows us to comprehend how many extrinsic and intrinsic factors act synergistically and sequentially to produce the density changes we observe. I argue that this approach is not only supported by a modern systems view of reality, but is consistent with the extensive data base accumulated over a 60 year period. A multi-factorial perspective is illustrated by data for *Microtus californicus*, a well-studied species that shows considerable geographic and temporal variation in demographic pattern. At least eight key factors (four extrinsic and four intrinsic) are required to explain the multi-annual cycles in this species. The resulting model is complex, but not chaotic or non-testable.

This paper is based on a plenary address presented at the 1987 annual meetings of the American Society of Mammalogists in Albuquerque, New Mexico. The invitation to give this address was in turn a result of my being the recipient of the Society's 1986 C. H. Merriam Award. I am indebted to the Society for honoring me with this award, and for extending to me this opportunity to reach a larger audience with my personal views on a topic that has been near and dear to me for almost three decades.

With the prospect of a captive audience for the plenary address, my social conscience dictated that I should focus on some topic of momentous importance, and this of course led me to a consideration of microtine population dynamics. This is an important topic, if for no other reason than that it has occupied the attention of many competent biologists for over 60 years. But, of course, there are other reasons as well. Microtine rodents often are abundant, sometimes economically important, and frequently are dominant or keystone members of their communities. Moreover, the topic transcends microtines in its importance, because it has contributed importantly to the development of population dynamics theory, and because it has entered into the debate on the philosophy of scientific methodology. Finally, there has evolved a certain conventional wisdom about microtines, especially as it applies to their multi-annual cycles of abundance, for which I believe the time is ripe for offering an alternative perspective. This essay, therefore, is dedicated to outlining a more optimistic, and I think realistic, approach to understanding microtine "cycles" that, while not solving all the mysteries pertaining thereto, will at least point us in more fruitful directions.

What is this conventional wisdom that I so boldly propose to oppose? It goes as follows: In spite of 60 plus years of effort and the existence of innumerable hypotheses and models, biologists have failed utterly to understand the classical multi-annual cycles exhibited by microtines. The phenomenon remains a mystery! Furthermore, what is needed is for someone clever enough to devise and conduct the correct or definitive experiment or possibly two that will solve the mystery.

225

In support of this wisdom, I offer four quotes from the literature representing a spectrum of microtine biologists of completely different traditions and views. 1) Krebs and Myers (1974:389): conclude their review by referring to "unlocking the mystery of rodent cycles," and comment that "enough is now known . . . for us to devise some simple experiments to test alternative hypotheses." 2) Stenseth (1985a:341): ". . . in spite of a century-long history of study, the causes of the microtine cycle remain a mystery." 3) Anderson (1987:454): "For more than 60 years microtine biologists have pursued an explanation of "microtine cycles" as a kind of Holy Grail. . . . Now there are signs that the age of microtine mythology may be ending." 4) Halle and Lehmann (1987:21): ". . . both the driving mechanism behind these cycles and . . . the ecological implications inherent in this strange manner of regulating density, are still under discussion."

The Problem

The first issue concerns what it is we wish to explain. In spite of some mumblings to the contrary, multi-annual cycles (2–5 years) do exist. It is indisputable that non-trivial fluctuations with peak densities at two to five year intervals occur. What does not occur, of course, are density changes that are mathematically predictable and that can be approximated by sine waves. Failure to make this distinction has led to some confusion over the term "cycle," but it is a non-issue as far as I am concerned. What is important is that there is considerable temporal and spatial variation in the existence of these multi-annual cycles, as well as variation in the shape or morphology of the cycles that do occur. Some of this variation is interspecific, that is, some species are cyclic and others are not. An additional source of variation is intra-specific geographical diversity. Numerous examples are possible; two well-documented ones will suffice. The California vole (*Microtus californicus*) shows multi-annual cycles in inland sites, annual fluctuations on Brooks Island in San Francisco Bay, and fairly stable densities in California perennial grasslands. The bank vole (*Clethrionomys glareolus*) is cyclic in northern Fennoscandia and non-cyclic further south (Bergstedt, 1965; Hansson and Henttonen, 1985; Stenseth, 1985a). Finally, there are cases of single populations that sometimes show multi-annual and sometimes annual cycles (Getz et al., 1987; Taitt and Krebs, 1985). Our appreciation for this diversity of demographic pattern within microtine rodents has sometimes been slow to be appreciated. In 1974, Krebs and Myers made the incredible statement (p. 276, 278) that "We know of no microtine data . . . which fails (sic) to show a population cycle." Later when Taitt and Krebs (1985) reviewed a substantial literature on *Microtus*, they concluded (p. 567) that "Out of 106 years of data, 59% were annual cycles."

My first important point is to express the problem before us as follows: given the widespread intraspecific and interspecific temporal and spatial variation in demographic pattern found among microtines, and even among those species exhibiting multi-annual cycles, it seems extremely unlikely that simple explanations will be found for this array of phenomena. My second important point is to offer a solution to this problem, namely that of a multi-factorial perspective. This perspective does not provide an explanation of all microtine population fluctuations, but it does offer a way to approach the problem realistically and I hope productively.

A Multi-factorial Perspective

It is my opinion that a multi-factorial perspective (MFP) is absolutely essential if we are going to understand microtine demography. Let me list several things to commend such an approach. 1) An MFP is consistent with a systems or hierarchial view of biological organization, a view most biologists accept in principle, but often ignore in their research protocols. Figure 1 schematically illustrates a subject population being influenced by a variety of environmental factors, some of which interact among themselves and all of which may vary in their impact over time. 2) A corollary of this perspective is that although simple explanations (one or two factors) are possible for microtine densities, they should not be anticipated, nor should we consider ourselves failures if we are unable to find them. 3) An MFP directs us to asking questions on an appropriate temporal and spatial scale, i.e., at least as large or long as the phenomenon we wish to understand. 4) It should also help to avoid the following logical pitfall: if A does not explain X and B does not explain X, then it follows that A and B can be omitted from any further explanation of X. This is the fallacy of multiple causation, because A *plus* B can still explain X (Hilborn and Stearns, 1982; Lidicker, 1978), and is a trap that frequently ensnares microtine biologists. 5) An MFP is also consistent with the data on microtine biology accumulated over the last 60 years.

I first proposed such an approach in a modern systems context in 1973 and more formally in 1978 (Lidicker, 1973, 1978). The basic idea was of course not novel. In fact Taitt and Krebs (1985) point out that Charles Darwin expressed such a viewpoint in 1859, and over the years a number of prominent ecologists have proffered such an approach in the context of general population dynamics theory (see Krebs, 1985a; Lidicker,
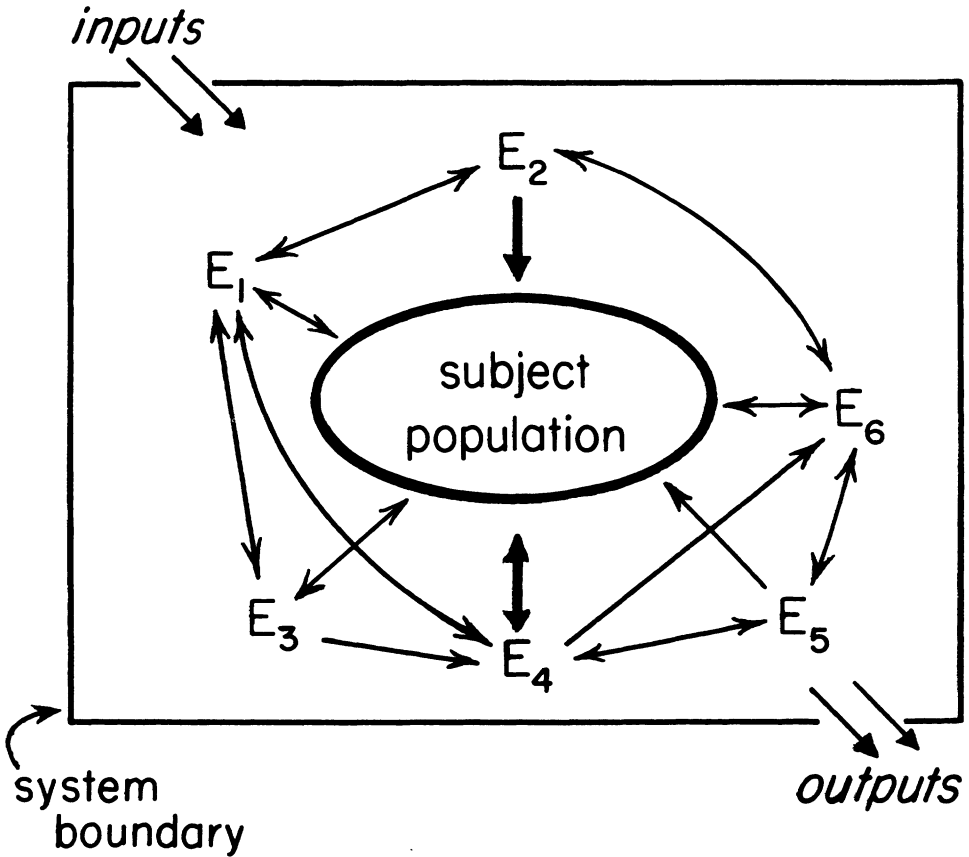
FIG. 1.—Schematic representation of the multi-factorial perspective (MFP) for population density regulation. E_i are various environmental factors, both biotic and abiotic. "Key factors" are represented by heavier interaction arrows. Reprinted from Lidicker (1978:135, fig. 4).

1978 for reviews). It also has been the prevailing wisdom in the wildlife management profession. Formal acceptability of a multifactor view in ecology, however, has depended upon progress being made in the acceptability and understanding of general systems (including hierarchy) theory. Although the intellectual climate therefore is increasingly favorable, some microtine biologists have belittled the idea. Accusations have been made that it is a chaos theory, that it is untestable, and that it is non-predictive (e.g., Conley, 1978; Krebs, 1978a, 1979a; Taitt and Krebs, 1985; Tamarin, 1978). All of which is to say that it is *not* in the realm of good science.

It is significant therefore that more recently Taitt and Krebs (1985) wrote that: "Realistic multi-factor hypotheses must be formulated" and "We are not questioning the truth of the [multi-factor] model, but rather its utility." They were quick to point out, however, that there are two classes of multi-factor hypotheses. First there is the sort exemplified by Lidicker (1978) that "are a posteriori and untestable." And then there are models such as that of Taitt (1985) that do not suffer from these afflictions. In recent years, other reviewers also have come to accept some form of multi-factor explanations for microtine cycles (e.g., Alibhai and Gipps, 1985; Flowerdew, 1985; Hanski, 1987; Hestbeck, 1986; Mihok et al., 1985; Stenseth, 1985b).

THE CASE OF THE CALIFORNIA VOLE

I would now like to take the one species of microtine that I know best (*Microtus californicus*) to illustrate both the reality and the utility of the multi-factorial approach. Clearly this can be no more than an illustrative overview. Supporting data will have to be sought in the literature cited, although in some instances unpublished data also are used. Please keep in mind that most
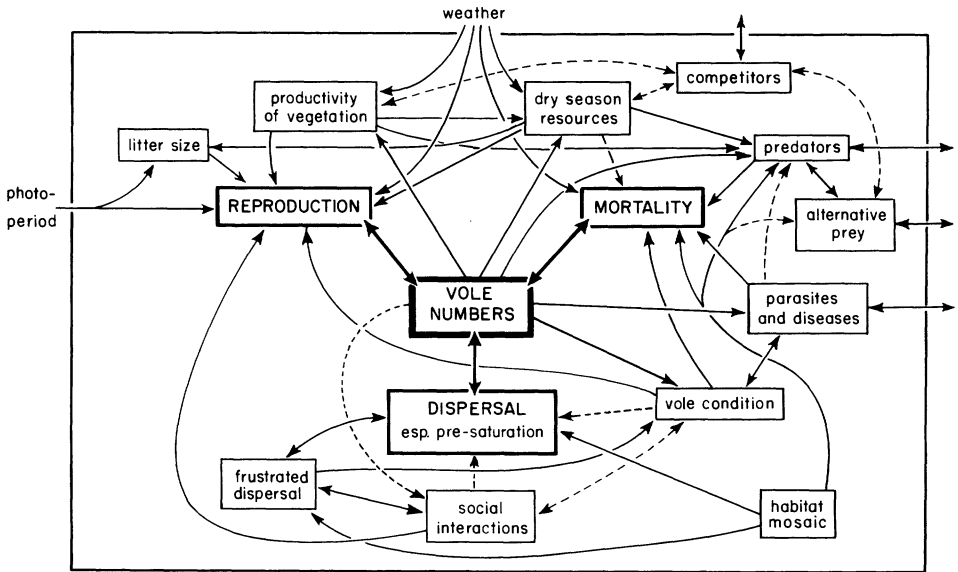
California Vole Population System

FIG. 2.—Schematic representation of factors known (solid arrows) or suspected (dashed arrows) of influencing numbers of California voles.

research on this species has been done in regions with a Mediterranean climate. This means that summers are extremely dry and represent the harsh or non-breeding season for this rodent. Breeding normally occurs after the autumn rains begin (about mid-October) and extends into June. In some years there is a mid-winter lull in breeding during the coldest and wettest periods.

Figure 2 sets the stage with a schematic representation of the factors known or suspected to affect vole densities. Not all components are present all of the time or in all populations, and in fact the relative influence of the various factors changes seasonally and with the phase of the multi-annual cycle, if there is one. In particular, in the wet season the dynamics flow primarily through the box labeled "productivity of vegetation," whereas in the dry season primary emphasis is on "dry season resources." The box called "habitat mosaic" refers to the spatial arrangement of micro-habitat patches.

Productivity of vegetation.—In California annual grasslands, considerable variation occurs in the beginning and end of the wet season and in the pattern and quantity of rainfall, all of which affects the quantity and quality of the year's vegetative growth (Evans and Young, in press; Heady, 1958). As herbivores and favorite prey for numerous predators, voles depend completely for food, shelter, and usually water on the vegetation they inhabit. They require green food for breeding and so, with rare exceptions, their breeding season is tied to the vegetation growing period (Brant, 1962; Krebs, 1966; Lidicker, 1973, 1976). The floral composition of the vegetation affects its quality for voles. Both the timing and quantity of reproduction are affected (Cockburn and Lidicker, 1983; Ostfeld and Klosterman, 1986). Mean litter sizes can vary from 2.5 to 4.7 depending in part on diet (Krohne, 1980). Also affected are survival rates, length of residency, and adult sex ratios (Cockburn and Lidicker, 1983; Heske, 1987a; Ostfeld et al., 1985; Ostfeld and Klosterman, 1986). Although undocumented, it seems likely that the stature and thickness of the vegetation also can affect predation pressures.

The dry season vegetation is equally critical if not more so, because this season is a stressful time for California voles. The ability of voles to survive the dry season is critically dependent on an interaction between the density of voles and the productivity of the vegetation during the preceding growing season (Lidicker, 1973). Figure 3A illustrates this *delayed productivity effect.*
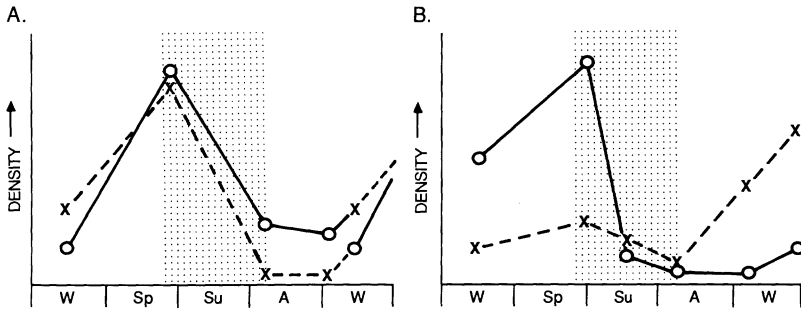
Fig. 3.—Two effects of dry season (summer) resources on densities of California voles. Shaded areas represent dry seasons. A. Delayed productivity effect. The dashed line represents a population exhibiting relatively high density in winter, and the solid line one with low winter density. B. Damaged physiology effect. The dashed line represents a population with low density at the start of the dry season, and the solid line a population beginning the harsh season at high density.

Populations going through the winter at moderately high densities negatively impact the future productivity of the vegetation (Batzli and Pitelka, 1970; Ford and Pitelka, 1984; Lidicker, in press) so that survival rates are poor through the dry season, and subsequent winter densities are low. In contrast, low winter densities result in good vegetation growth and relatively good summer survival rates, so that the following winter densities tend to be higher. The delayed response of these populations to the return of the rainy season (Fig. 3A) is explained by the *damaged physiology effect* (Fig. 3B). This is a second way in which dry season resources affect numbers. If a population enters the dry season at high density, it suffers high mortality rates and the survivors are somehow damaged physiologically so that they do not grow and reproduce for two or more months after favorable conditions return (Lidicker, 1973, 1976). This effect strongly impacts population growth by drastically reducing the length of the effective breeding season and by causing the population density to drop further before breeding commences. With very high densities in summer, even longer-term effects on the composition of the subsequent vegetation can occur (Cockburn and Lidicker, 1983; Lidicker, in press).

Dispersal.—The existence of extensive presaturation dispersal in this species affects the way the habitat mosaic fills up during population growth (Hestbeck, 1986; Lidicker and Anderson, 1962; Lidicker, 1975, 1985*a*, 1985*b*, 1985*c*). The growth rate of local populations is affected strongly by the availability of a dispersal sink (Lidicker, 1975, 1980). Peak densities occur when sinks are filled and dispersal becomes frustrated. This dispersal process seems the same as the "spacing behavior" of other authors (e.g., Krebs, 1978*b*, 1979*b*, 1985*b*; Krebs and Boonstra, 1978; Taitt, 1985; Taitt and Krebs, 1985; Watson and Moss, 1970), and clearly influences demographic patterns.

Vegetation mosaic.—This factor refers to the relative quality of habitat patches and their spatial arrangement. Considerable attention has been given recently to this landscape level of organization, and its role in microtine cycles has been recently reviewed (Lidicker, 1985*a*, 1985*b*). I postulate that a critical factor in the environment of voles is the ratio of optimal to marginal patch areas (ROMPA); see Fig. 4. If this ratio is high, multi-annual cycles are less likely because so much optimal habitat is available that harsh season populations are not reduced sufficiently to prevent complete recovery of the population during the following breeding season. At reduced ROMPA, the initial breeding season densities can be very low so that more than one year is required to repopulate the area, and multi-annual cycles occur. Of course, at very low ratios, cyclicity is again unlikely because numbers are probably maintained at chronically low levels by some other factor(s).

Predation.—It is now widely agreed that predators rarely if ever stop population growth at high microtine densities. However, there probably are situations in which generalized predators utilizing a broad prey base can keep a preferred prey species such as voles at chronically low
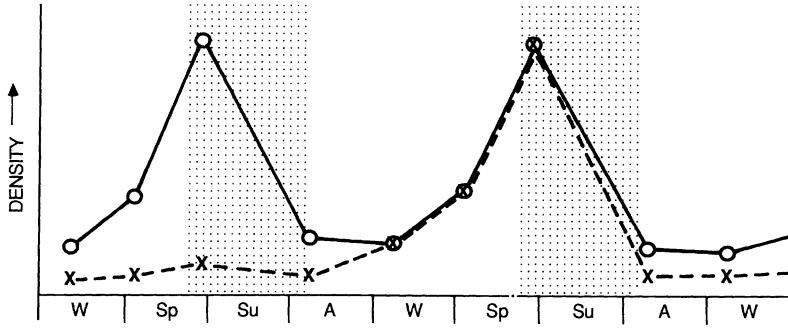
FIG. 4.—Influence of the ratio of optimal to marginal patch areas (ROMPA) on numbers of California voles. The solid line represents a population experiencing a relatively high ROMPA, that is, there is much optimal habitat relative to marginal, and the dashed line is a population inhabiting an area with low ROMPA. Shaded areas represent dry seasons.

densities (Boonstra, 1977; Erlinge et al., 1983). Such a mechanism has also been proposed by Wolff (1980) for snowshoe hare (*Lepus americanus*) populations in the Rocky Mountains.

The major effect of predators on microtine populations is that of an anti-regulating factor influencing population declines as originally suggested in 1964 by Pearson (1964, 1985). Predator–prey ratios increase dramatically as populations decline after a peak, and this forces densities to extremely low numbers. This, along with vegetation impacts, the dry season physiological damage effect, and presaturation dispersal, contributes to the inability of a population to recover promptly following crashes. Figure 5 presents some unpublished data from a 33 month study at the Russell Reservation (Contra Costa Co., California) which supports such a role for predation. Carnivore scats were collected regularly over a several hectare study area, and although there is undoubtedly some error in using numbers of scats as an index to numbers of carnivores, a positive correlation surely exists. Moreover, an effort was made to keep the search effort constant for each month. The contents of these scats are now being analyzed, but there is no doubt that voles were the major prey species. Three primary predator species were involved (feral cats, *Felis catus*; red
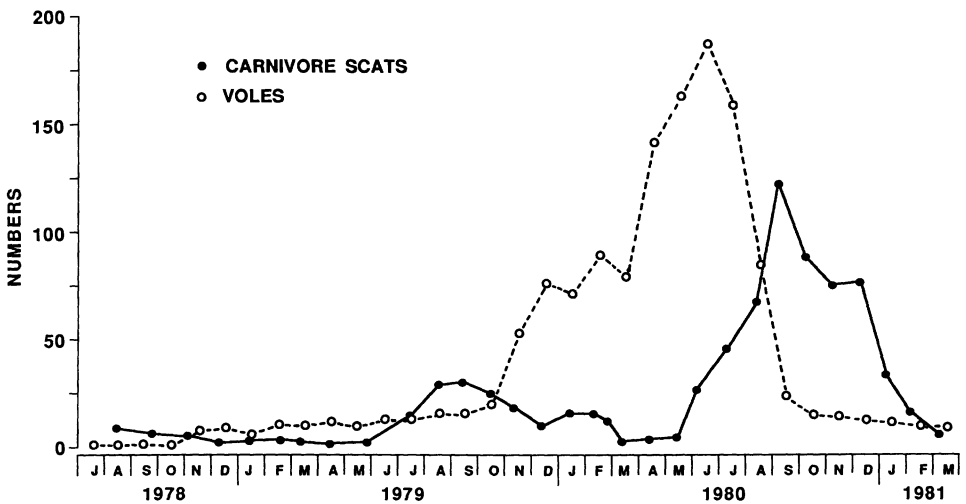

FIG. 5.—Minimum numbers of California voles known to be alive on four small grids (about ½ ha total) and the numbers of carnivore scats found (two point moving average) over a 33-month period at the Russell Reservation (Contra Costa Co., California). Vole numbers taken from Cockburn and Lidicker, 1983.

foxes, *Vulpes vulpes*; and raccoons, *Procyon lotor*) as well as three or four secondary species. The data clearly demonstrate how a high predator-prey ratio can develop through a vole decline and persist for a considerable period thereafter.

Parasites and diseases.—A little is known about seasonal changes in ectoparasite loads in California voles (Lidicker, 1973), although the frontier of endoparasites and diseases is largely unexplored (but see Krebs, 1966). I agree with Mihok et al. (1985) that such factors are likely to be important demographically. A. Dobrowolska and K. Adamczewska-Andrzejewska (in litt.) also have intriguing data on serum gamma-globulin levels relative to demography in *Microtus arvalis*, and conclude that immunological competency may be an important factor in regulating numbers of this species.

Social behavior.—Considerable effort has been expended in recent years to understand more fully the social behaviors of California voles (Heske, 1987a, 1987b; Lidicker, 1979, 1980; Ostfeld, 1985; Ostfeld et al., 1985; Rissman and Johnston, 1985). We know that territoriality has important impacts on the number of females breeding in a given area and on adult sex ratios. There are also social effects on sexual maturation, especially of males, and emigration and immigration rates are almost surely affected. In short, there is no doubt that social mores interact importantly with other factors to influence demography. Conversely, it also seems clear that social behavior alone cannot explain observed demography, as has been proposed in a number of widely acclaimed hypotheses about density regulation in voles. Arguments for this position have been summarized recently (Heske et al., in press), and need not be repeated here. Suffice it to say that there is too much variation in demographic pattern relative to variation in social behavior, and many of the assumptions on which the social regulation hypotheses are based cannot be supported by data from California voles.

The Chitty Effect.—The occurrence of extra-heavy individuals, especially males, during peak densities (Chitty Effect) has long been considered a ubiquitous feature of multi-annual cycles in microtines (Boonstra and Krebs, 1979; Chitty, 1952; Chitty and Chitty, 1962; Krebs, 1964; Krebs and Myers, 1974; Taitt and Krebs, 1985; Zimmermann, 1955). Some authors have suggested that this phenomenon is based on a genetic polymorphism for body size and that large individuals are favored by selection during population increases. It is further supposed that this polymorphism and the alternating selection regimes related to it hold the key to unraveling the mechanism of multi-annual cycles (Chitty, unpub., cited in Taitt and Krebs, 1985; Krebs, 1978a). A failure to find the necessary genetic heritabilities for the relevant life-history traits in *M. pennsylvanicus* recently was reported by Boonstra and Boag (1987).

R. S. Ostfeld and I are currently investigating the Chitty Effect in California voles. Our preliminary results suggest that large individuals occur whenever especially good food and survival conditions prevail. Moreover, the largest males tend to live in marginal habitats where there are not a lot of breeding females. It is our feeling that, while this remains an interesting phenomenon, it is not relevant to explaining density fluctuations.

DISCUSSION AND CONCLUSIONS

Table 1 summarizes the factors I believe to be major components in the density regulation machinery of the California vole. Note that eight factors are listed and that these include both extrinsic and intrinsic items. It is inherent in a MFP that these two classes of factors would be seen to be inextricably interactive. Hence questions such as "Is density regulation a result of extrinsic or intrinsic factors?" are clearly seen as unhelpful. If these factors are viewed as an interacting system in which the most influential ones can and do vary seasonally and with density, we are close to a full understanding of the density regulating machinery in the California vole. Details of the model will vary from circumstance to circumstance, but in Fig. 6 I have illustrated how the factors in Table 1 can vary in importance over the course of a multi-annual cycle. Different temporal patterns of density will require different suites of components or different values for the same components.

I suspect that this model can be extrapolated with caution to other species of microtines and

TABLE 1.—*Major components in the density regulation machinery of the California vole.*

Extrinsic factors
  Productivity of vegetation (wet season)
  Dry season resources (food and water)
  Vegetation mosaic (ROMPA)
  Predation (predator-prey ratios and availability of alternative prey)

Intrinsic factors
  Presaturation dispersal
  Components of fecundity (litter size, interval between pregnancies, breeding season lengths, percent females
    active)
  Physiological responses to dry season stresses
  Social interactions (spacing, territoriality, frustrated dispersal, constraints on sexual maturation)

in some cases beyond. A remarkably similar model applies to snowshoe hares, at least in Alberta and Alaska (Keith and Windberg, 1978; Lidicker, 1978, 1983; Wolff, 1980). In any case an MFP can certainly be applied to organisms generally, and especially to those with complex life histories.

Is this approach a chaos theory as some have proclaimed? Of course it is not! Complexity should not be equated with chaos. Is a musical symphony more chaotic than a rhythmic drum beat? Is a tropical rainforest more chaotic than an agricultural field? Complexity is more difficult than simplicity to comprehend, but to dismiss it as chaotic is to shun reality.

Does this theory lead to predictions? If not, it may be trivial even if correct. One very important prediction based on this theory is that it will be difficult in practice to predict changes in vole density very far into the future. To do so would require that each of the many significant interacting factors influencing densities must be predictable as well as their interactive effects in order to arrive at a population-level prediction. Further, if predictions of each element in the machinery carry some possible error range, uncertainty will be compounded when multiple errors are combined. A second prediction, therefore, is that, not unlike forecasting local weather, population density prediction will have to be qualified with probability statements. Many other kinds of predictions are also possible. If vole densities reach 500/ha, we can predict confidently that the population will crash over the ensuing harsh period. Or we can predict that if particular
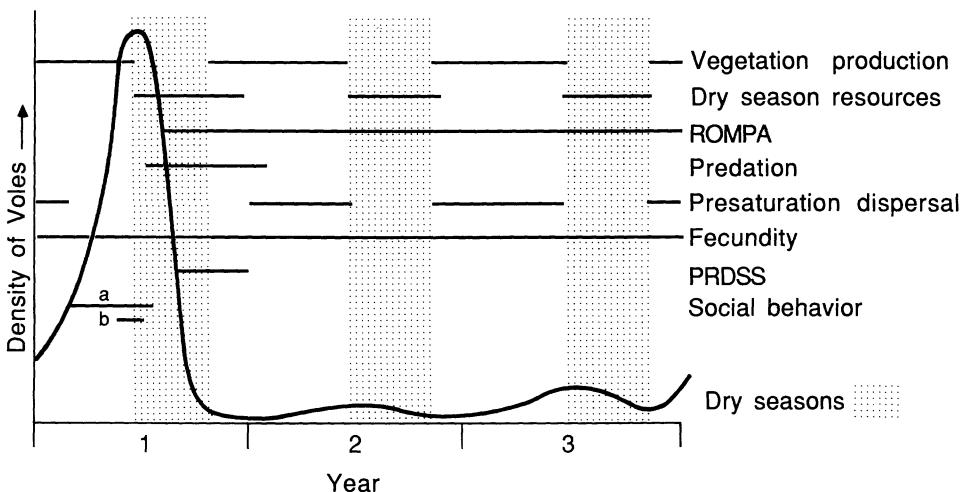
FIG. 6.—Schematic representation of a multi-annual cycle in *Microtus californicus*. The timing of major roles for various key factors are shown by the horizontal lines. See Table 1 and text for a more complete description of the 8 key components. Social behavior operates continuously, but only two short-term aspects are shown: a = frustrated dispersal; b = constraints on sexual maturation. ROMPA = ratio of optimal to marginal patch areas. PRDSS = physiological responses to dry season stresses.

combinations of conditions occur, a certain result is likely. For example, if adult female survival is excellent over the non-breeding period, and if other conditions remain favorable, a peak year will follow.

Failures to make precise predictions of future vole numbers is not caused by faulty science, but by the complexity of the system being predicted. In fact hierarchy theory specifies that the higher the level of complexity of the system being studied, the less predictable is its behavior (Allen and Starr, 1982). Basically, this is because higher level systems exist in smaller numbers and because their components often comprise "middle number systems" whose behavior is notoriously difficult to predict.

Finally, we must ask as others have, are multifactor hypotheses testable? This is a necessary criterion for scientific hypotheses, because we need to have some way of finding out if they are false. The answer is that of course these models are testable! If the hypothesis fits the evidence, it is supportable; if it does not, we need to discard or modify it. Multifactor models make clear predictions about the way density regulation works. One obvious prediction, that could in principle be wrong, is that complex processes like vole cycles will not be explicable in terms of single factors. It also predicts that demographic patterns often will vary spatially and temporally. This also could be untrue, but isn't. To test this, the same population can be compared across seasons or years under the null hypothesis that densities are explained continuously by the same single factor. Or, spatially distinct populations can be compared with the expectation that at comparable times their densities will be responding to identical factors. Moreover, the various components of the model are also testable with appropriate experimental manipulations and controls. If, for example, some factor is hypothesized to operate in a certain way at a particular cyclic phase, various experimental designs can be utilized to test both the effects of varying the intensity of the factor across cyclic phases as well as possible changes in the responsiveness of the subject population to this factor.

Good science should lead us ineluctably to a better understanding of the universe. I have tried in this essay to explain briefly, and without adequate documentation, how the way we view a complex problem can affect our ability to understand it. The microtine multi-annual cycle serves to illustrate the kind of phenomenon that demands a fresh look. If simple explanations for a phenomenon fail, complex ones may be closer to reality. In this particular case, a multifactorial model is supported by the evidence and by good sense. I am confident that it can guide us toward fruitful investigations and ultimately to powerful insights into the population dynamics of voles.

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Invited Paper, C. Hart Merriam Award, 1986. This Invited Paper was not subjected to routine editorial procedures for format and style, and it was not subjected to peer review.