Ann. Zool. Fennici 25:321–333. 1988

Comments on the implication of genetic ingredients in animal population dynamics

Paavo Voipio

Voipio, P. 1988: Comments on the implication of genetic ingredients in animal population dynamics. — Ann. Zool. Fennici 25:321–333.

A survey of the literature reveals that the possibility of genetic mechanisms in population dynamics occurred to animal ecologists fairly early. The paper points out that it was chiefly animal ecologists dealing with population fluctuations who gradually became convinced of the implication of genetic ingredients in population dynamics. Although genetics offered empirical material for formulating theories of the paradigm of intrinsic regulative factors, no convincing view of population regulation on a genetic basis could be reached, for two reasons: tests of the central theory by a special genetical method failed, due to the unexpected inadequacy of the method, and the theory itself did not allow formulation of models for demonstrating its plausibility. It is concluded that the truth evidently lies in the interplay between some (perhaps rather specific) extrinsic factor(s) and intrinsic genetic factors with a large number of potential regulative functions.

P. Voipio, Dept. of Zoology, Univ. Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki, Finland.

1. Introduction

Discussion of the possibility of a genetic component in the machinery of population dynamics has been a characteristic feature of population biology for many decades. The history of population studies shows different trends in their treatment of the interaction of population dynamics and population genetics. In this paper I shall consider how the pertinent ideas in ecology, supported by the collateral development in genetics, proceeded from their first rudimentary origins to clearly formulated theories about population regulation on a genetic basis. I shall also examine why the concept of genetic factors gradually declined until their absence from population dynamics was in fact used as a null hypothesis by many of the investigators of today. The final purpose of this study is to consider to what extent the concept of intrinsic genetic factors still figures in investigations of populations with periodic fluctuations in numbers.

2. The emergence of genetical ecology

2.1. The pioneer work of Elton

Elton can be considered one of the first animal ecologists who consistently paid attention to the probable association of genetic changes with population dynamics, a circumstance not generally noted in the literature. In his classical paper Elton (1924) emphasized that the intensity, direction and quality of selection differ in different phases of the population cycle. He also pointed out that natural selection tends to be interrupted during a rapid expansion in numbers, so that "any mutation that happened to occur or be contained as a recessive at such a time of spread with no checks, would automatically spread unless it was actually very harmful" (Elton 1924:157).

This statement is connected with many of the central questions in ecological genetics as we understand it today (besides, of course, those of population ecology), and the general grasp is strikingly typical of an evolutionary ecologist. Elton (1927, 1930, 1933, 1938) repeated his suggestion about the variation of selection during population cycles in many of his later writings. It may also be noted that, contrary to what is generally stated in the literature[1], his well known book (Elton 1927) is the first in general ecology in which a separate chapter is devoted to the topic 'ecology and evolution'. His second book is the rather poorly known "Animal Ecology and Evolution" (Elton 1930), in which the phenomenon of migration (i.e. dispersal in modern terms) in association with population cycles — to mention only one of its aspects — was treated (p. 31) in terms of behavioural response as "the main key to the elasticity shown by animals in the regulation of their numbers" and in terms of genetic variation brought into contact with an increasing range of environments.

The fact that Elton was deeply convinced of the unavoidable "convergence between genetics and ecology" from the very beginning of his scientific activity is apparent from his third little book (Elton 1933), in which he emphasizes the importance of fluctuations in numbers to the theories of evolution and, further, from his paper (Elton 1938) "Animal numbers and adaptation". The latter was obviously written under the inspiring influence of the works of Haldane (1932) and Dobzhansky (1937), which are cited by him.

Elton (1938:136–137) also asked "whether moderate efficiency in certain adaptations is not in the long run more likely to preserve the species than what is usually described as 'beautiful' adaptations", and he bravely prophesied that "it may be found that ... the predator-prey or parasite-host systems with most chances of endurance are those in which efficiency is equally matched, and in which neither is too highly developed". In other words, the ecological properties of the interacting species must be considered an outcome of their joint evolutionary histories or coevolution, which is one of the key questions in current evolutionary ecology (for suggestions along the same lines, see also Elton 1927: 141).

Elton's work actually foreshadows the later development of ecology, which gradually embraced genetics and led to the adoption of the Darwinian principles in the investigations of the ecological machinery of populations. This was a slow process, taking place in scattered nuclei here and there, but all students of evolutionary ecology from the thirties to the fifties must have benefited from Elton, consciously or unconsciously.

2.2. Other early contributions

Nicholson (1927) deserves special mention, since his famous analysis of the parasite-host system led Elton to his suggestion that selection for moderate adaptation in interacting species prevents too violent oscillations, allowing mutual adjustment, i.e. their coevolution. Most remarkable, however, is Nicholson's suggestion that genetic change is a causal factor in population dynamics.

A few years later, Ford (1931), an ecology-minded population geneticist, suggested that selection determining the frequencies of the polymorphic phases may be correlated with the total abundance because "the whole ecological situation may be different when the population is at its maximum and at its minimum". Ford based his suggestion upon Elton's observations on the regular 3–4-year cycle of the Arctic Fox in North America. In fact, he adopted the idea of "the alternate selection in different directions" proposed by Elton (1924:156). In regard to population control, Ford (1931) concluded from observations on the Marsh fritillary butterfly (*Melitaea aurinia*) in England (Ford & Ford 1930) that cycles in natural populations may be generated by genetic changes. This was one of the first proposals of this kind. In his paper "Gene frequency fluctuations in relation to population cycles in the colored fox in Canada", Calhoun (1946) suggested that some correlation may exist in this species between the numbers and the polymorph ratio.

Franz (1949) tried to give a genetical explanation of the abrupt cessation of the population increase and the succeeding collapse and more or less complete local extinction of an insect pest. He based his view on indications of a general physiological weakening of the populations before and during the crash. This, he suggested, might be due to inbreeding, the ascending population having started from a small number of individuals, and to relaxation of selection during the phase of mass increase. As a consequence, the genetic constitution of the population had changed (homozygosity for deleterious genes) and the quality of the individuals deteriorated (*Degenerationstyp der*

---

[1] While some refer to Allee et al. (1949) as one of the earliest works including a section on "Ecology and Evolution", others refer to a still later book by Andrewartha & Birch (1954).

Krisenentstehung), which led to a sudden collapse. This is one of the first clearly expressed ecogenetic explanations of population control.

It had become evident that the most numerous animals are subject to considerable, regularly recurring fluctuations in abundance. This phenomenon attracted increasing attention and stimulated studies on its fundamental features, particularly the relationship between the periodic fluctuations in abundance and the genodynamics of the populations. It was suggested (Voipio 1950a), for example, that the migratory behaviour (i.e. dispersal) associated with the population cycles might be a polymorphic property.

It may be noted that until the beginning of the fifties all these considerations were theoretical in nature, mainly representing purely verbal models. Many of the ideas then presented were accepted later as working hypotheses or as aspects in the pertinent theories. An important extension of the thinking on these lines was Chitty's genetic-behaviour hypothesis, basically formulated in the early 1960s. This phase of the study is the main concern of the following chapter.

2.3. The flowering of hypotheses on intrinsic regulation in population dynamics

The latter part of the fifties was an important period in ecology. As the decade progressed, investigators increasingly focused their attention on the intrinsic factors in population dynamics and on changes in the quality of individuals during the course of the cycle. Interest increased in the genetic variation associated with periodic fluctuations in numbers and efforts were made to clarify its significance for the self-regulating mechanisms involved. It may be argued that to be of any importance in population regulation, genetic variation must persist throughout the cycle, irrespective of whether it is a causal factor or a mere side effect. This inevitably leads to the assumption that the mechanism must be genetic polymorphism, whose permanence is ensured by density-dependent selection or heterozygote superiority (or by some other genetic mechanisms; for these see, e.g., Maynard Smith 1970, Williamson 1972). Only a few of the ecologists had taken this final step, however, by the end of the fifties. One of these was Andrewartha (1959) who writes: "I would ... like to suggest that it would be reasonable to look for some form of balanced polymorphism in any population that shows territorial behaviour, or perhaps even more generally, in any population that shows ... some other form of self-regulating mechanisms".

Practical investigations were started by Chitty (1952) who — as Dawson & King (1971) express it — added two new elements to the debate on the causes of periodic fluctuation in population size: genetic variation and recurrent selection for different optima. He noted definite differences in the quality of the individuals in different generations in the cycle, but did not yet touch on their possible genetic implications. In his later investigations in the field and laboratory, however, Chitty (1957) suggested that changes in the viability of individuals during the cycle are in some way correlated (associated) with a genetic factor (possibly, as he then suggested, with that causing haemolytic anaemia), the preservation of which in the population is based on polymorphic balance, i.e. physiological polymorphism in the proper sense of the word.

Similar conclusions were reached at the same time by the entomologist Wellington (1957) in his studies on the Western tent caterpillar (Malacosoma pluvi*alis*). He pointed out the role of differences among individuals in the population dynamics, observing that the proportions of the different types within the populations changed both annually and areally with changing density "throughout the course of a whole outbreak" (Wellington 1957:316). He was not yet able to demonstrate the role of genetic factors but it seemed possible that the differences had a genetic basis; i.e. the population consisted of physiologically different types, the persistence of which depended on some kind of polymorphic balance (Wellington 1960).

However, the central role in the later development of these ideas was played by Dennis Chitty, who formulated his genetic behaviour hypothesis in the 1960s (Chitty 1960, 1967). In the following decades this hypothesis directed studies on animal population biology to the intrinsic factors of population regulation. In several of his papers, Stenseth (1977, 1981, 1985) analysed the various elements of the theory and showed the reasons for the long-lasting debate around it (see later).

Animal ecologists were evidently beginning to take account of genetic aspects in their considerations of the machinery underlying population dynamics. A milestone in the literature on this subject was the article by L. C. Birch entitled "The genetic factor in population biology", which appeared in "The American Naturalist" in 1960. It was a convincing sign of a new orientation and strongly influenced the contemporary ecological thinking. In regarding individual genetic variation not only as the outcome of population dynamics but also as a possible cause, it contributes to unite population ecology and population genetics. As expressed by Birch (1960:5) himself, "these two disciplines meet when the questions are asked, how does the kind of animal (i.e. genotype) influence the numbers and how does the number of animals influence the kind, i.e. the genetical composition of the population? These questions are as much ecological as they are genetical".

These same questions had been asked by a few individual workers since Elton's time, but the refinement of techniques in the field and laboratory work finally made it possible to reach "a synthesis which would ... address itself to questions, admittedly not newly stated, but which have newly acquired the property of being meaningful, that is to say, solvable" (Lerner 1965:489).

3. Collateral development in genetics

3.1. Polymorphism in focus

The attention of population genetics was naturally attracted fairly early by species showing clear-cut morphological differences with a relatively simple genetic basis. The earliest quantitative data on selection occurring in natural populations and covering a whole century were presented by Haldane (1942) in his study of the polymorphism of the Red Fox in North America (Labrador), based on game statistics collected by Elton (1942). Haldane (1942) also paid attention to the geographical gradient in the frequency of the silver fox in northwestern North America, suggesting that it can hardly be due to human agency but is more plausibly attributable to natural selection. In other words, he suggested selection correlated with some environmental gradient, which determines the cline of the polymorph ratio. According to this view, although the mechanism of polymorphism is genetic, it also has an ecological aspect, since the relative viability of the polymorphic forms changes with the environmental conditions.

The accumulation of experience from several polymorphic species in nature and the laboratory allowed some general conclusions. It appeared that the relative frequencies of the morphs generally change in time and space and that most of these changes are more or less distinctly correlated with the environmental conditions, reflecting geographical gradients, long-term changes in climate, seasonal variation or cyclic fluctuation in abundance. The evidence accumulated showed, first, how sensitively the genetic structure of a population reflects the ecological conditions and, second, that at least most of the seemingly neutral characteristics, thought to be drifting fortuitously, actually represent pleiotropic effects of the polymorph genes, which control cryptic (physiological) characteristics strongly influencing the survival and relative viability of their bearers. Especially important was the general observation that, in the case of polymorphism, natural selection operates with surprisingly high selection coefficients.

One of the earliest workers in this field was Ford (1931). As mentioned earlier, he suggested that the relative frequencies of the morphs may be based on selective balance determined by the different ecological conditions in different phases of the population cycle. He wrote that: "stability is preserved in that the optimum proportions [of the morphs] tend to be maintained", though these optimum proportions are not the same at different levels of abundance.

One of the earliest well-investigated cases of polymorphism is the classical study of the ladybird (*Adalia bipunctata*). Timofeeff-Ressovsky (1940) showed that in this species the different genotypes possess opposite selective values during winter and summer, and concluded that this is the reason for the maintenance of polymorphism. As is known now, this alone (i.e. without heterozygote superiority) is generally not a sufficient condition for the persistence of polymorphism (see e.g. Dempster 1955), but Timofeeff-Ressovsky's finding was important because it showed how effectively (within three generations a year) the changing ecological conditions influence the genetic constitution of populations and because it formed an important model for other investigations.

In the early forties, Dobzhansky (1943) discovered that natural populations of *Drosophila pseudoobscura* undergo seasonal changes in the relative frequencies of the chromosomal types, based on inversion. His work was paralleled by the Russian studies on population genetics, among them those of Dubinin and Tiniakov (1945, 1946), who discovered the same phenomenon in *Drosophila funebris*.

Gershenson (1945) demonstrated that seasonal changes in the polymorph ratio also occur in mammals thus showing that this phenomenon is not restricted to short-lived animals with several generations per year, such as *Drosophila* or *Adalia*. He also showed that the relative frequencies of the morphs vary with abundance.

These findings were summarized by Dobzhansky (1947) in his classic and stimulating paper in "Evolution" (the first article of the new-born journal). It had been demonstrated, first, that the polymorphic balance changes rapidly in relation to varying conditions, second, that the heterozygote superiority and polymorphic balance involved are associated with some physiological properties affecting viability or fertility and, third, that natural selection operates with very high selection coefficients.

3.2. Polymorphism as an adaptive system

As the mechanisms leading to and enhancing heterozygote superiority (evolution of overdominance, linkage with lethals, supergenes with co-adapted gene complexes involved in inversions) are known to result in systems characterized by great differences in the viability of the pertinent forms, the above findings aroused particular interest among workers investigating the survival of species with periodic fluctuations in numbers. Some of these species have very low minima every third or fourth year, others every tenth year. As was pointed out by Voipio (1948: 48; 1950b:72–74), the genetically effective population size (*N*) in cyclic populations is very small, "much closer to their number at the minimum stage than to their density in maximum years" (1950b:72). It must often reach the point at which genetic drift would obtain the upper hand, if some mechanism did not exist which protects ("buffers") the population against the loss of genetic variability necessary under widely varying ecological conditions. Collateral investigations in the laboratory (e.g. Dobzhansky 1947, 1961, da Cunha 1949) have confirmed that this mechanism is balanced physiological polymorphism operating with very high selection coefficients.

Since polymorphism (viz. the relative frequencies of the pertinent morphs) appeared to be correlated with the periodic fluctuations in numbers, the question arose whether this phenomenon could be taken as a sign of rapid genetic adjustment of the species (population) to variation occurring in the environment in the different phases of the population cycle. It appeared possible that populations with cyclic fluctuations in numbers are actually harmoniously adjusted (adapted) to their varying environment by means of balanced physiological polymorphism. Similarly, the seasonal changes in the frequencies of inversion types in *Drosophila* have been interpreted as adaptive reactions to recurrent environmental changes. It has indeed been suggested that the seasonal fluctuations in the polymorphic frequencies in *Drosophila* represent, temporally, a miniature counterpart of the set of phenomena associated, in the cyclic species, with the periodic fluctuations in numbers (Voipio 1950a:152, 163; for this comparison, see also Ford 1964:16).

The experience gained from the genetics of *natural* populations automatically led to the question of the adaptive significance of polymorphism. Dobzhansky (1947:2) in fact considered the cyclic seasonal changes in the composition of the populations of *Adalia* and *Drosophila* to be "adaptive responses to the succession of seasonal environments". And this was also the case among the Russian school mentioned earlier (p. 324). This is well seen in the interesting discussion by Dubinin (1948)[1] of the ubiquity of heterozygous systems in natural populations.

4. The rise of the ecogenetic outlook in population biology

The evolutionary studies of the sixties were characterized by an emerging synthesis of genetics and ecology. The synthetic theory of evolution, essentially neo-Darwinian, was in the process of transformation into a more comprehensive theory, which included the ecological aspects, as explanatory elements of the fundamental process of evolution. This development can be seen not only in the elucidation of the so-called multi-species systems, but also in the treatment of problems at the population level. In the following, I shall confine myself to the "lower" end of the ecogenetic spectrum, i.e., to the questions of population dynamics in single-species systems.

4.1. Genetic aspects of regulative migration

One of the questions is the significance of *emigration* associated with fluctuations in numbers. Studies of the movements of animals had revealed bimodality in the dispersal curves (more individuals move relatively short distances and relatively long distances than can be expected on the basis of chance alone), suggesting the implication of a genetic ele-

---

[1] Cited in Lerner 1954:75–77, as an English translation.

ment (Howard 1960, Johnston 1961). Johnston hypothesized that "the genetic heritage of some of the individuals probably casts them in the roles of dispersers to long distances" (1961:388) and, following A. H. Miller's suggestion, he advanced the opinion that some kind of behavioural polymorphism may be involved.

The observations made by population geneticists that the migration tendency in *Drosophila* can be controlled genetically and that genetically controlled thresholds exist (see Lidicker 1962, Sakai et al. 1958) led Lidicker to attach special importance to the balance between the advantages and disadvantages (of being a short-distance or long-distance disperser) upon which the maintenance of the migration behaviour of the population is based. In other words, emigration occurs if the migration tendency is positively responsive to the density at which individuals most sensitive to increasing numbers begin to emigrate (Lidicker 1962). It seems possible that "a genetic balance (possibly a polymorphism) would develop between the perfection of responsive emigration tendencies and the tendency to be sedentary with all its attendant selective advantages" (Lidicker 1962: 31; cf. Voipio 1950a:163).

There was an increasing tendency among the research workers in the 1960s to regard the differences in individual behaviour, determined either physiologically or genetically, as part of the machinery of density regulation (e.g. Andrzejewski 1962, Andrzejewski & Wierzbowska 1961, Christian & Davis 1964, Chitty 1967, Chitty & Phipps 1966, Krebs 1966, 1970, Krebs et al. 1969, Myers & Krebs 1971). The general conclusion was is that there are different types of behaviour in the population, which at least partly represent differences in the proneness to disperse, and that the explanation of the maintenance of this mechanism under drastically varying demographic conditions can supposedly be found in the genetics of the populations. The possibility cannot, of course, be ruled out that the same processes (genetic correlations with cycles) may have other causes than differences in the proneness of the genotypes to disperse (see, e.g., Finerty 1980).

4.2. Density-dependence, an interplay of demography and genetics

The second question is connected with density-*dependence* and concerns the relative fitnesses of the genotypes in different demographic situations. Most of the evidence of density-dependent selection stemmed from genetic laboratories. The early observations (e.g. Timofeeff-Ressovsky 1934, Dobzhansky & Spassky 1944) and also some later ones (e.g. Birch 1955, Lewontin 1955) were confirmed by several studies on the genus *Drosophila* in the sixties (see, e.g., Budnik et al. 1971). In regard to the species with cyclic fluctuations in abundance, these findings were of the utmost theoretical importance. They showed, first, that recurrent demographic situations do create conditions sufficient for alternate selection on a density-dependent basis and, second, that the genetic changes observed in fluctuating populations can be considered part of the machinery determining the periodicity or amplitude of the cycles, whether or not they are their cause. If we ask with Williamson (1972:91) whether there are any phenomena for which the interaction of genetics and ecology are thought to be essential, the answer will be here, if anywhere, yes!

4.3. Heterogeneous environment, a challenge to genetic versatility

The third and last question relates to populations living in a *heterogeneous environment,* particularly an environment which is heterogeneous in time. It concerns the strategy (Lewontin 1961, Slobodkin 1964) used by the populations to survive the vicissitudes of severe recurrent alterations in the demographic situation. It can be concluded that these vicissitudes are precisely the conditions in which polymorphism can be expected to develop as a strategy for survival in an uncertain environment. Levins (1963, 1966, 1968) has contributed much to the understanding of population phenomena in terms of strategies in which both genetical and ecological parameters are involved in a successful for outcome for the population. Levins (1968) pointed out that it would soon be impossible for population geneticists to treat a single population in time without reference to ecological parameters or for population ecologists to allow the environment to vary, while treating the species as genetically homogeneous, thus ignoring evolution. Evidence has accumulated that demographic time and evolutionary time are commensurate, so that both ecological and genetical heterogeneities are essential ingredients of population biology.

The emerging picture of the interactions between the demographic and genetic characteristics of populations determined the lines along which the study of population dynamics advanced from the beginning of the seventies.

5. New developments in the seventies

5.1. Innate capacity to regulate?

An increasing tendency thus prevailed among the research workers of the 1960s to look upon differences in individual behaviour as part of the machinery of density regulation. This regulation was either physiological, as believed by Christian's school or genetical, as maintained by Krebs' school or, perhaps more appropriately, by the Chitty/Krebs school.

The former point of view has been based on the observation that populations contain individuals responding differently to crowding, i.e., they differ in their threshold values, responding to different densities, or with different sensitivity to each density (Welch & Klopfer 1961, Klopfer 1962; see also Voipio 1950a:163). The proponents of the endocrine feedback mechanism (Christian & Davis 1964, Christian 1970) did not believe that selection could be strong enough to act rapidly for a year or two with a subsequent return to the original genetic state and they thus denied the possibility of a genetic basis for the mechanism. However, considered from the angle of homeostasis, the existence of a hereditary mechanism appears possible. The rigorous socio-psychological atmosphere implies an extremely heterogeneous intraspecific environment, exceeding the individual tolerance or homeostasis, and evidenced by fundamental changes observed in the individuals' well-being. The effect of good individual homeostasis is to reduce the effective variance of the environment and make it less likely that selection will be advantageous (Levins 1965). When homeostasis is inadequate (or fails), the possibility of selection being advantageous increases with the variance of the environment. A highly variable and autocorrelated environment generates this possibility and prepares the way for the condition in which the strategy for adaptation is based on response-to-selection polymorphism, being capable of rapid adjustment in a fluctuating but largely predictable intraspecific environment. In this reasoning lies the core of the ideas presented by the group of research workers here called the Chitty/ Krebs school.

Charles Krebs and his co-workers formed a unique group of ecologists and geneticists largely dominating the research on cyclic population fluctuation in the seventies. Their ingenious and extremely painstaking project started around the end of the 1960s. Krebs (1966) had moved from his studies on lemmings to the subject of *Microtus* population biology in the same year in which Lewontin & Hubby (1966) published their important investigations of allozymic variation. This prompted several studies along these lines, the first being that on plasma esterase polymorphism in *M. agrestis* in Scotland by Semeonoff & Robertson (1968). At the same time Tamarin, a geneticist at Indiana University, was studying the transferrin locus in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus*. The results of this study were included in the joint paper by Tamarin & Krebs (1969) which formed the start of a long series of investigation carried out by Krebs' working group.

In both of the last two studies the authors concluded that their observations tended to support Chitty's suggestion of balancing selective processes in the population dynamics of *Microtus* or, in short, his genetic-behavioural hypothesis (Chitty 1960, 1967). The findings of biochemical genetics mentioned above allowed a new approach to the problem of population regulation. It may be noted that what matters here is the study of intrinsic factors on a genetic basis.

5.2. Testing the hypothesis fails

Gaines et al. (1978) have given a short historical review of the efforts up to 1978, i.e. for a slightly more recent period than that dealt with by Krebs & Myers (1974). The focal point is the studies on the relation of allozymic variation to population regulation. As they state, the first step in testing Chitty's hypothesis was to demonstrate that changes in the genetic structure of the population were associated with fluctuating density in cyclic species. It appeared that gene frequencies were correlated with population demography at a large number of loci. It was also shown that natural selection was operating on some of these loci. But the general conclusion was that "it has been impossible to determine whether genetic changes are a cause or an effect of demographic changes". The authors support Charlesworth & Giesel's (1972) suggestion that changes in gene frequency are the effects of demographic changes, not the causes of the latter. This was also confirmed experimentally, for: "the altered allelic frequencies ...

did not produce any consistent effects on demography" (p. 737). Their concluding remark is as follows: "Allozymic variation might effect population regulation but it is difficult to disentangle cause and effect. Studies monitoring genetic changes at electrophoretic loci will not provide a conclusive test of Chitty's hypothesis, but they have shown that rapid selection in field populations is a common event" (p. 738).

This conclusion was foreshadowed in the study by LeDuc & Krebs (1975:1839), who wrote that "changes in allelic frequencies at the electrophoretic loci during numerical fluctuations would be determined [rather] by the degree of favorability of the environment" and "the polymorphism itself would have no effect on the demographic processes of the population". This was an important interim evaluation of the situation as regards the advance of this line of investigation.

5.3. Towards a better understanding of the problem

It must be emphasized that the probability of an underlying genetic mechanism controlling population cycles is by no means cancelled out by the negative results obtained so far. This is evident from some general paragraphs of the papers published from the mid-1970s onwards. As stressed by LeDuc & Krebs (1975), there is still much to study about the genetic basis or processes in population dynamics which are directly involved in numerical fluctuations. Smith et al. (1975) reintroduced the subject of heterozygosity into the discussion of population dynamics in small mammals. Using the hypothesis that concurrent changes in behaviour, genetics and density are associated with successive changes in the level of heterozygosity, they developed the theory that recurrent uncompetitive and competitive demographic situations give rise to density-dependent selection for heterozygosity. Stenseth (1977) pointed out that this is a modified version of Chitty's theory (non-aggressive phenotypes at a disadvantage in peak populations), claiming that the only theory that can be considered plausible and worth further pursuit is that of Chitty (in version II, according to which regular cycles are the result of the interaction between genetic changes *and* extrinsic factors). These thoughts have been developed further by Stenseth in his later analyses of Chitty's hypothesis (Stenseth 1981, 1985, Warkowska-Dratnal & Stenseth 1985). The gist of these considerations is:

1. Chitty's genetic-behaviour theory, based on the hypothesis of two kinds (docile and aggressive) of individuals, does not function. Using a theoretical model, Stenseth (1981) demonstrated that a population consisting of *two* genetically determined behavioural types ... is not likely to cycle in an *extrinsically stable* environment (my italics, for further discussion). In other words: behavioural-genetic polymorphism alone cannot generate the regular cycles (at least not on a *di*morphic basis).

2. If, on the other hand, some extrinsic, non-biotic factor influences the population and this influence depends on the *quality* of the individuals present in the population at that time, then the interaction between intrinsic and extrinsic factors in the causation of microtine cycles seems important and Chitty's theory becomes plausible.

3. The assumption of *poly*morphism, i.e. the existence of more than two phenotypic forms in the population, poses a problem; so far, no model has been analysed in order to see whether such a polymorphic population will cycle. As pointed out by Stenseth (1981), a three-phenotype model would be important to present studies and necessary for assessing the plausibility of Chitty's theory. The same applies to the analysis of population systems with more than three components, though the difficulties involved in such an analysis might be considerable.

It may be mentioned in this context that my ideas about the ecogenetic machinery of periodic fluctuations at one time largely followed the line of reasoning presented in items 2 and 3 above (Voipio 1950a). Regarding polymorphism I argued, then, that it is not possible for a cycling population to survive on the basis of one polymorphic system alone (i.e. with two phenotypic forms) but, regarding the several recurring ecological and demographic situations, a more elaborate polymorphic system is needed. In other words, more than one polymorphic system is constantly present in the population, the different polymorphic characteristics functioning during fixed but different phases of the cycle (cf. Stenseth 1985 upon hypotheses based on extrinsic factors). These different phases present situations in which not only the demographic parameters vary, but the extrinsic factors (abiotic or biotic) relating to weather, grazing or parasites are also at work (requiring resistance to, say, cold, hunger or disease). There cannot be any talk of an extrinsically stable environment for cycling populations (see also the short passages on p. 330 of this paper). In other words: theoretical modelling needs considerable elaboration in many new dimensions to allow assessment of the plausibility of a greater number of theories concerning regular density cycles.

In the final chapter of his paper on mathematical models for microtine cycles, Stenseth (1985) presents a number of features whose inclusion in the models would provide a better understanding of why microtine cycles occur. Apart from that relating to seasonality, these features contain elements which can fairly well be interpreted as genetic ingredients in population dynamics: organization of the population into genetic (and social) groups, assessment of the importance of dispersal in genetic restructuring of the local demes, and incorporation of genetically (or phenotypically) determined resistance towards predators or pathogens and/or grazing.

On the ground that social interactions most probably play a certain role in density regulation in microtines, Tamarin (1985) emphasizes the importance of examining the intrinsic components as a clue to the mechanisms causing the microtine decline. As he points out, there are at least three important hypotheses using genetic mechanisms to explain the decline. A common feature of all of them is the supposition that increasing aggression triggers the decline. As density increases, the aggression is brought about by selection for more aggressive individuals (Chitty 1967), or by phenotypically aggressive non-related dispersers behaving aggressively towards their neighbours (Charnov & Finerty 1980), or by outbreeding, which produces more heterozygosity and through it aggression (Smith et al. 1975, cf. above p. 328). Tamarin (1985) outlines the necessary conditions for testing these theories. Gaines et al. (1978) emphasize the importance of measuring heritability of behavioural traits over population cycles and of investigating the genetic basis of hormone thresholds associated with aggressive behaviour (p. 737).

Even Lidicker (1978), a proponent of the view of the multifactorial basis of population density regulation, while being averse to "the prevailing influence of reductionist aspect", admits the importance of the study of regular short-term shifts in gene frequencies among small mammal species. Incidentally, Haukioja et al. (1983:426) recommend simple *and* complex hypotheses to ecologists "because both kinds of hypotheses can be valuable and even complementary".

Later, however, in his article on "Dispersal", Lidicker (1985) stressed the poor general result of the investigation of electromorphs, but discussed investigation of the possibility that dispersers are genetically distinct from residents, emphasizing the need for "further careful work in the future". This observation is interesting, since Lidicker (1983:10) had stressed the superiority of the multi-factorial view to earlier attempts based on less realistic paradigms ("*más promisoria que los esfuerzos pasados, basados en paradigmas menos realisticas*").

Again, we obtain a clear picture of the central position, in the minds of population biologists, of the potential role of dispersal in population ecology and the probability of genetic ingredients in this intrinsic regulation of numbers. A remark, however, is needed in this context. Theoretical study based on mathematical models (Stenseth 1986) shows that dispersal and spacing behaviour (i.e., social factors) generally stabilize population dynamics, instead of generating instability as assumed by the Chitty/Krebbs line of investigation. It seems that there are trophic interactions (e.g. predator-prey interaction) which drive the cycle. Future study may allow derivation of specific predictions to be tested experimentally, and show the limits within which the genetic factors operate in these population processes.

5.4. The paradigm of intrinsic factors is not dead

The important book on the biology of the New World microtines edited by Tamarin (1985) offers — mainly in a couple of its papers — an excellent general review of the advances made up to the middle of the 1980s. In two articles, the authors conclude that for testing Chitty's hypothesis "changes in electromorph frequencies may no longer be necessary or sufficient" (Taitt & Krebs 1985) and that "it is an error to interpret these associations [of genetic changes with density changes] as support to Chitty's (1967) hypothesis" (Gaines 1985:875). At the same time, however, they show the reverse of the medal, i.e., the possibility of investigation of the problem in the future, which certainly does not look too dark.

Taitt & Krebs (1985) point out that agonistic and exploratory behaviours, demonstrably differing between populations changing over time, have been shown to be heritable. This means that they are subject to the operation of natural selection. The authors write that "attempts to test the genotypic-behavior hypothesis must rest on estimation of the heritability of traits of dominance and spacing behavior" and give hints for conducting suitable experiments. They also argue that consideration of the role of single factors in population fluctuation "should be left to the past", recommending "the premise that *both* extrinsic *and* intrinsic factors are involved in *Microtus* population fluctuations" (Taitt & Krebs 1985:611, italics mine). They list a number of central aspects of population dynamics whose explanation may be incomplete if it ignores the possible genetic basis of variables such as growth, reproduction, response to stress, dominance and dispersal behavior (1985:612). And Gaines (1985:875) points out that "attempts to relate genetic structure to population regulation must focus on those traits deemed ecologically relevant". According to him, attention should be directed to the effect of social dynamics on the gene*tic* structure of populations, the *inheritance* and evolution of quantitative traits and, finally, the application of new molecular techniques (more sensitive in detecting genetic variation, e.g., comparison of DNA segments observed with the use of restriction endonuclease), in order to assess *genetic variation* in natural populations. These recommendations definitely point to genetic ingredients as an essential part of population machineries.

Research workers thus have reasonable grounds for suggesting that genetic factors are important in population regulation, though they can no longer be considered the sole cause of cyclic fluctuations.

6. Two opposite views, past and present — conclusion

After this review of the development of the ideas about population regulation, it may be interesting to look at some recent conclusions about the stage of our knowledge of the intrinsic regulation of population dynamics. I shall confine myself to one of the most recent studies on microtine cycles in Finland, viz. that by Henttonen (1986). My choice is based on the amusing fact that the opinions of my fellow-countryman are in sharp opposition to the ideas set forth by me some three and half decades ago — and, to be sure, also to many of the conclusions reached by investigators today.

In the earliest part of his thesis, which consists of six separate papers on microtine cycles, Henttonen claims that during the last 20 years, "hypotheses on intrinsic regulation of populations have flourished and collapsed" (Laine & Henttonen 1983:408). And in one of his latest papers (Henttonen et al. 1986), a subheading announces that "cycles cannot be due to intrinsic mechanisms".

His ideas may be further illustrated by the following quotations:

"The changes in aggressive behavior ... that are postulated to block breeding by the hypothesis of genetic-behavior *polymorphism* do not occur" (Laine & Henttonen 1983:409; italics mine).

"Social regulation, based on genetically polymorphic behavior, seems to be *in principle* unable to create a population cycle" (Henttonen et al. 1986:4; italics mine).

These assertions have been cited out of their general context and, thus give too categorical an impression of the ideas of their author(s). My intention is to relate these, as such quite well-founded assertions to the development of ideas *before* the last 20-year period, during which the hypotheses on intrinsic regulation of populations are said to have flourished and collapsed (Laine & Henttonen 1983).

The historical development has been described in the earlier chapters of this study. Here I will only give some short passages from certain works published at the start of the 1950s. They relate to a special line of the study performed at the Finnish Game Research Institute on periodic fluctuations in numbers (Voipio 1986). Attention was primarily directed to intrinsic factors. It was thought that "the cyclic species in actual fact are capable of an elastic reaction at each stage of the periodically changing conditions (Voipio 1950), so that certain individuals ... survive better than others ... in the unfavourable conditions of minimum years ... (resistance to cold, hunger, low population density, etc.) until conditions, becoming more favourable, permit ... the origination of new ecological constellations, in which again some other properties are important from the viability point of view (resistance to diseases, high population density, etc.)" (Voipio 1950b:71).

This clearly pointed to "the intrapopulation mechanisms possibly forming the basis of the adaptability of the cyclic species living in their specific conditions ... and the importance of '*balanced physiological polymorphism*' as regards to their plasticity and the resistance required in rapidly changing conditions" (Voipio 1950b:76; italics mine).

On these grounds it was, finally, assumed that "the ability of the periodically fluctuating species to maintain their positions in the regions of mass-multiplication without losing their capacity to manifest the migratory impulse during the following peak years is possibly a *polymorphic property*, the preservation of which depends upon the heterozygotes having the greatest plasticity in so far as they represent physiologically that type in which the mass-psychotic impulse leading to migration disappears sooner (e.g.

when the population density falls below a certain threshold value) or for corresponding reasons manifests itself later" (Voipio 1950a:163–4; italics mine).

This theorizing on the genetic machinery of cyclic fluctuation in 1950 disagrees in principle with the statements made in Henttonen's papers. In the earlier chapters of this study, I have examined how these ideas about the genetic mechanism of cyclicity flourished from the 1960s onwards. But can it validly be claimed that they eventually vanished or even collapsed towards the end of the 20-year period? As can be seen from the recent literature, although the weightings have changed considerably, these ideas are still essential ingredients in the discussion of periodic fluctuation in numbers.

These hypotheses do not lose their credibility merely because of the newer data and re-analyses of the older ones presented by Hansson & Henttonen (1988) in their recent wonderfully clear and rigorous paper. The most important of the new data is the observation that most rodent populations are not cyclic and that regular cycles are restricted to certain geographical, primarily northern, areas of the species ranges. When found, the explanation of this difference in rodent populations may have a considerable influence on our ideas about the cycles. But the old problems concerning the cyclic species or populations living in their special conditions in the northern Holarctic still remain.

The second important point mentioned by Hansson and Henttonen (1988) is the shift in emphasis from nutrition as a driving factor of the cycles to predators or/and disease. But this only means a clarification of the extrinsic factors once emphasized by Voipio (1950b) and later considered theoretically by Stenseth (1985) as a trigger of cyclic fluctuations in systems in which the cycle is generated by changes in the quality of individuals (i.e. polymorphism) (see Stenseth 1981:27).

I conclude: The truth evidently lies in the interaction between a (perhaps rather specific) extrinsic factor, or factors, and intrinsic genetic factors with a large number of potential regulative functions.

Acknowledgements. I thank Kari Vepsäläinen, Olli Järvinen and Heikki Henttonen for reading the manuscript in its different stages. Especially I would like to thank Nils Chr. Stenseth for critically reviewing the manuscript. Finally, I wish to thank Ilmari Pajunen and Olli Järvinen for providing me with working facilities at the Department of Zoology.

References

Allee, W. C., Emerson, A. E., Park, C., Park, T. & Schmidt, K. F. 1949: Principles of animal ecology. — Saunders, Philadelphia and London.

Andrzejewski, R. 1962: Estimation of resident and transient part of small mammal population by the capture-recapture method. — Symp. Theriol., Brno, 1960:34–39. (Russian with English summary).

Andrzejewski, R. & Wierzbowska, T. 1961: An attempt at assessing the duration of residence of small rodents in a defined forest area and the rate of interchange between individuals. — Acta Theriol. 5:153–172.

Andrewartha, H. G. 1959: Self-regulatory mechanisms in animal populations. — Austr. J. Sci. 22:200–205.

Andrewartha, H. G. & Birch, L. C. 1954: The distribution and abundance of animals. — Univ. Chicago Press, Chicago.

Birch, L. C. 1955: Selection in Drosophila pseudoobscura in relation to crowding. — Evolution 9:389–399.

—"— 1960: The genetic factor in population ecology. — Amer. Nat. 94:5–24.

Budnik, M., Brncic, D. & Koref-Santibanez, S. 1971: The effects of crowding on chromosomal polymorphism of Drosophila pavani. — Evolution 25:410–419.

Calhoun, J. B. 1946: Gene frequency fluctuations in relation to population cycles in the colored fox in Canada. — Bull. Ecol. Soc. Amer. 27:63 (quoted from Elton 1949b).

Charlesworth, B. & Giesel, J. T. 1972: Selection in populations with overlapping generations. II. Relations between gene frequency and demographic variables. — Amer. Nat. 106:388–401.

Charnov, R. & Finerty, J. 1980: Vole population cycles: a case for kin-selection. — Oecologia 45:1–2.

Chitty, D. 1952: Mortality among voles (Microtus agrestis) at Lake Vyrnwy, Montgomeryshire in 1936-39. — Phil. Trans. R. Soc., Ser. B 236:505–552.

—"— 1957: Self-regulation of numbers through changes in viability. — Cold Spring. Harb. Symp. Quant. Biol. 22:277–280.

—"— 1960: Population processes in the vole and their relevance to general theory. — Can. J. Zool. 38:99–113.

—"— 1967: The natural selection of self-regulatory behavior in animal populations. — Proc. Ecol. Soc. Austr. 2:51–78.

Chitty, D. & Phipps, E. 1966: Seasonal changes in survival in mixed populations of two species of vole. — J. Anim. Ecol. 35:313–331.

—"— 1970: Social subordination, population density, and mammalian evolution. — Science 168:84–90.

Christian, J. J. & Davis, D. E. 1964: Endocrines, behavior, and population. — Science 146:1550–1560.

da Cunha, A. B. 1949: Genetic analysis of the polymorphism and classification in Drosophila polymorpha. — Evolution 3:239–251.

Dawson, P. S. & King, C. E. (eds.) 1971: Readings in population biology. — Prentice-Hall, New Jersey.

Dempster, E. H. 1955: Maintenance of genetic heterogeneity. — Cold Spring Harb. Symp. Quant. Biol. 20:25–32.

Dobzhansky, Th. 1937: Genetics and the origin of species. — Columbia Univ. Press, New York. 2nd Ed. 1941.

—"— 1943: Genetics of natural populations. IX. Temporal changes in the composition of populations in Drosophila pseudoobscura. — Genetics 28:162–186.

—"— 1947: Adaptive changes induced by natural selection in wild populations of Drosophila. — Evolution 1:1–16.

—"— 1948: Genetic structure of natural populations. — Carnegie Inst. Wash. Year Book 47:193–203.

—"— 1961: On the dynamics of chromosomal polymorphism in Drosophila. — In: Kennedy, J. S. (ed.), Insect polymorphism. Entomol. Soc., London, pp. 30–42.

Dobzhansky, Th. & Spassky, B. 1944: Genetics of natural populations. XI. Manifestation of genetic variations in Drosophila pseudoobscura in different environments. — Genetics 20:270–290.

Dubinin, N. P. 1948: Experimental investigations of the integration of hereditary systems in processes of evolution of populations. — Zhurn. Obsch. Biol. 9:203–244. (quoted from Lerner, I. M. 1954).

Dubinin, N. P. & Tiniakov, G. G. 1945: Seasonal cycles and the concentration of inversions in populations of Drosophila funebris. — Amer. Nat. 79:570–572.

—"— 1946: Structural chromosomal variability in urban and rural populations of Drosophila funebris. — Amer. Nat. 80:393–396.

Elton, C. 1924: Periodic fluctuations in the numbers of animals: their causes and effects. — Brit. J. Exp. Biol. 2:119–164.

—"— 1927: Animal ecology. — Sidgwick & Jackson, London.

—"— 1930: Animal ecology and evolution. — Clarendon Press, Oxford.

—"— 1933: The ecology of animals. — Methuen, London.

—"— 1938: Animal numbers and adaptation. — In: de Beer, G. R. (ed.), Essays on aspects of evolutionary biology. Clarendon Press, Oxford.

—"— 1942: Voles, mice and lemmings: problems in population dynamics. — Clarendon Press, Oxford.

—"— 1949: Movements of arctic fox population in the region of Baffin Bay and Smith Sound. — Polar Record 5:296–305.

Finerty, J. P. 1980: The population ecology of cycles in small mammals: mathematical theory and biological fact. — Yale Univ. Press, New Haven.

Ford, E. B. 1931: Mendelism and evolution. — Methuen, London.

—"— 1954: Problems in the evolution of geographical races. — In: Huxley, J., Hardy, A. C. & Ford, E. B. (eds.), Evolution as a process. Allen & Unwin, London.

—"— 1964: Ecological genetics. — Methuen, London.

Ford, H. D. & Ford, E. B. 1930: Fluctuations in numbers, and its influence on variation, in Melitaea aurinia, Rott. (Lepidoptera). — Trans. Entomol. Soc. Lond. 78:345–351.

Franz, J. 1949: Über die genetischen Grundlagen des Zusammenbruchs einer Massenvermehrung aus inneren Ursachen. — Zschr. Angew. Entomol. 31:228–260.

Gaines, M. S. 1985: Genetics. — In: Tamarin, R. H. (ed.), Biology of New World Microtus. Spec. Publ. No 8 Amer. Soc. Mammal.

Gaines, M. S., McClenaghan, L. B. & Rose, R. K. 1978: Temporal patterns of allozymic variation in fluctuating populations of Microtus ochrogaster. — Evolution 32:723–739.

Gershenson, S. 1945: Evolutionary studies on the distribution and dynamics of melanism in the hamster (Cricetus cricetus L.). — Genetics 30:207–251.

Haldane, J. B. S. 1932: The causes of evolution. — Longmans, London.

—"— 1942: The selective elimination of silver foxes in Eastern Canada. — J. Genet. 44:296–304.

Hansson, L. & Henttonen, H. 1988: Rodent dynamics as community processes. — Trends Ecol. Evol. 3:195–200.

Haukioja, E., Kapiainen, K., Niemelä, P. & Tuomi, J. 1983: Plant availability hypothesis and other explanations of herbivore cycles: complementary or exclusive alternatives? — Oikos 40:419–432.

Henttonen, H. 1986: Causes and geographic patterns of microtine cycles. — Ph. D. Thesis, Univ. Helsinki, Helsinki.

Henttonen, H., Oksanen, T., Jortikka, A. & Haukisalmi, V. 1986: How much do weasels shape microtine cycles in the northern Fennoscandian taiga? — Oikos 50:353–365.

Howard, W. E. 1960: Innate and environmental dispersal of individual vertebrates. — Amer. Mid. Nat. 63:152–161.

Johnston, R. F. 1961: Population movements of birds. — Condor 63:386–389.

Klopfer, P. H. 1962: Behavioral aspects of ecology. — Prentice-Hall, New Jersey.

Krebs, C. J. 1966: Demographic changes in fluctuating populations of Microtus californicus. — Ecol. Monogr. 35:239–273.

—"— 1970: Microtus population biology: Behavioral changes associated with the population cycle in M. ochrogaster and M. pennsylvanicus. — Ecology 51:34–52.

Krebs, C. J., Keller, B. L. & Tamarin, R. H. 1969: Microtus population biology: demographic changes in fluctuating populations of M. ochrogaster and M. pennsylvanicus. — Ecology 50:587–607.

Krebs, C. J., Myers, J. H. 1974: Population cycles in small mammals. — Adv. Ecol. Res. 8:267–399.

Laine, K. & Henttonen, H. 1983: The role of plant production in microtine cycles in northern Fennoscandia. — Oikos 40:407–418.

LeDuc, J. & Krebs, C. J. 1975: Demographic consequences of artificial selection at the LAP locus in voles (Microtus townsendii). — Can. J. Zool. 53:1825–1840.

Lerner, I. M. 1954: Genetic homeostasis. — Wiley, New York.

—"— 1965: Synthesis. — Genetics Today 2:489–494. — Proc. XI. Congr. Genet., The Hague.

Levins, R. 1963: Theory of fitness in a heterogeneous environment. II. Developmental flexibility and niche selection. — Amer. Nat. 97:75–90.

—"— 1965: Theory of fitness in a heterogeneous environment. V. Optimal genetic systems. — Genetics 52: 891–904.

—"— 1966: The strategy of model building in population biology. — Amer. Sci. 54:421–431.

—"— 1968: Evolution in changing environments. Some theoretical explorations. — Princeton Univ. Press, New Jersey.

Lewontin, R. C. 1955: The effects of population density and composition on viability in Drosophila melanogaster. — Evolution 9:27–41.

—"— 1961: Evolution and the theory of games. — J. Theor. Biol. 1:382–403.

Lewontin, R. C. & Hubby, J. L. 1966: A molecular approach to the study of genic heterozygosity in natural populations. II. Amount of variation and degree of heterozygosity in natural populations of Drosophila pseudoobscura. — Genetics 54:595–609.

Lidicker, W. Z. 1962: Emigration as a possible mechanism permitting the regulation of population density below carrying capacity. — Amer. Nat. 96:29–33.

—"— 1978: Regulation in numbers in small mammal populations — historical reflections and a synthesis. — In: Snyder, D. P. (ed.), Populations of small mammals under natural conditions. Pymatuning Laboratory of Ecology, Special Publ. 5:122–141. Univ. of Pittsburgh.

—"— 1983: Regulación poblacional de mamiferos. — Medio Ambiente 6:3–11.

—"— 1985: Dispersal. — In: Tamarin, R. H. (ed.), Biology of New World Microtus. Amer. Soc. Mammal., Spec. Publ. 8:420–454.

Maynard Smith, J. 1970: The causes of polymorphism. — Symp. Zool. Soc. Lond. 26:371–383.

Myers, J. H. & Krebs, C. J. 1971: Genetic behavioral and reproductive attributes of dispersing field voles Microtus pennsylvanicus and Microtus ochrogaster. — Ecol. Monogr. 41:52–78.

Nicholson, A. J. 1927: A new theory of mimicry in insects. — Austr. Zool. 5:10–104. (ref. only)

Sakai, K., Narise, T., Hiraizumi, Y. & Iyama, S. 1958: Studies on competition in plants and animals. IX. Experimental studies on migration in Drosophila melanogaster. — Evolution 12:93–101.

Semeonoff, R. & Robertson, F. W. 1968: A biochemical and ecological study of plasma esterase polymorphism in natural populations of the field vole, Microtus agrestis L. — Biochem. Gen. 1:205–227.

Slobodkin, L. B. 1964: The strategy of evolution. — Amer. Sci. 52:342–357.

Smith, M. H., Garten, C. T. & Ramsey, P. R. 1975: Genic heterozygosity and population dynamics in small mammals. — In: Markert, C. L. (ed.), Isozymes IV. Genetics and evolution: 85–102. Acad. Press, New York.

Stenseth, N. C. 1977: Evolutionary aspects of demographic cycles: the relevance of some models of cycles for microtine fluctuations. — Oikos 29:525–538.

—"— 1981: On Chitty's theory for fluctuating populations: the importance of genetic polymorphism in the generation of regular cycles. — J. Theor. Biol. 90:9–36.

—"— 1985: Mathematical models of microtine cycles: models and the real world. — Acta Zool. Fennica 173:7–12.

—"— 1986: On the interaction between stabilizing social factors and destabilizing trophic factors in small rodent populations. — Theor. Popul. Biol. 29:365–384.

Taitt, M. J. & Krebs, C. J. 1985: Population dynamics and cycles. — In: Tamarin, R. H. (ed.), Biology of New World Microtus. Amer. Soc. Mammal., Spec. Publ. 8:567–620.

Tamarin, R. H. (ed.) 1985: Biology of New World Microtus. — Amer. Soc. Mammal., Spec. Publ. 8. 893 p.

—"— 1985: Intrinsic mechanisms of population regulation in microtine rodents. — Acta Zool. Fennica 173:19–21.

Tamarin, R. H. & Krebs, C. J. 1969: Microtus population biology. II. Genetic changes at the transferrin locus in fluctuating populations of two vole species. — Evolution 23:183–211.

Timofeeff-Ressovsky, N. W. 1934: Über die Vitalität einiger Genmutationen und ihrer Kombinationen bei Drosophila funebris und ihre Abhängigkeit vom "genotypischen" und vom äusseren Milieu. — Zeitschr. Ind. Abst. Vererb. lehre 66:319–344.

—"— 1940: Mutations and geographical variation. — In: Huxley, J. (ed.), The new systematics: 73–136. Oxford Univ. Press, Oxford.

Voipio, P. 1948: Riistan laadun parantaminen ja sen biologiset edellytykset. (Summary: Improving the quality of the game and the biological requirement therefore.) — Suomen Riista 2:7–76.

—"— 1950a: Jaksoittainen runsaudenvaihtelu ja paikallisten eläinkantojen säilyminen. (Summary: On survival during the cycles.) — Suomen Riista 5:144–164.

—"— 1950b: Evolution at the population level with special reference to the game animals and practical game management. — Pap. Game Res. 5:1–176.

—"— 1986: Suomalaisen eläinekologian riistabiologisia linjoja vuosisatamme keskivaiheilla. (Summary: On certain lines of research in the animal ecology in Finland.) — Suomen Riista 33:97–110.

Warkowska-Dratnal, H. & Stenseth, N. C. 1985: Dispersal and the microtine cycle: comparison of two hypotheses. — Oecologia 65:468–477.

Welch, B. L. & Klopfer, P. H. 1961: Endocrine variability as a factor in the regulation of population density. — Amer. Nat. 95:256–260.

Wellington, W. G. 1957: Individual differences as a factor in population dynamics: the development of a problem. — Can. J. Zool. 35:292–323.

—"— 1960: Qualitative changes in natural populations during changes of abundance. — Can. J. Zool. 38:289–314.

Williamson, M. 1972: The analysis of biological populations. — Arnold, London.

Received 10.IX.1987, revised 20.X.1988
Printed 30.XII.1988