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From arctic lemmings to adaptive dynamics: Charles Elton's legacy in population ecology

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ABSTRACT

We shall examine the impact of Charles S. Elton's 1924 article on periodic fluctuations in animal populations on the development of modern population ecology. We argue that his impact has been substantial and that during the past 75 years of research on multi-annual periodic fluctuations in numbers of voles, lemmings, hares, lynx and game animals he has contributed much to the contemporary understanding of the causes and consequences of population regulation. Elton was convinced that the cause of the regular fluctuations was climatic variation. To support this conclusion, he examined long-term population data then available. Despite his firm belief in a climatic cause of the self-repeating periodic dynamics which many species display, Elton was insightful and far-sighted enough to outline many of the other hypotheses since put forward as an explanation for the enigmatic long-term dynamics of some animal populations. An interesting, but largely neglected aspect in Elton's paper is that it ends with speculation regarding the evolutionary consequences of periodic population fluctuations. The modern understanding of these issues will also be scrutinised here. In population ecology, Elton's 1924 paper has spawned a whole industry of research on populations displaying multi-annual periodicity. Despite the efforts of numerous research teams and individuals focusing on the origins of multi-annual population cycles, and despite the early availability of different explanatory hypotheses, we are still lacking rigorous tests of some of these hypotheses and, consequently, a consensus of the causes of periodic fluctuations in animal populations. Although Elton would have been happy to see so much effort spent on cyclic populations, we also argue that it is unfortunate if this focus on a special case of population dynamics should distract our attention from more general problems in population and community dynamics.

Key words: climate, cyclicity, density-dependence, ecological hypothesis, ecological theory, Elton, population dynamics, population ecology, population fluctuations, history of population ecology, trophic interactions, spatial ecology.

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I. INTRODUCTION

Ecology can be defined as the scientific endeavour to explain the distribution and abundance of species in space and time by studying the environments of individuals in natural populations. The history of modern population ecology can be dated to 1924 when Charles Sutherland Elton (Fig. 1), at the age of 24, published an article in the *British Journal of Experimental Biology* entitled 'Periodic fluctuations in the numbers of animals: their causes and effects'. After this seminal publication, ecologists not only became aware of the periodic multi-annual fluctuations of northern voles, lemmings and game animals, but it also launched an entire research programme on the causes of fluctuations in population numbers. As an indication of the influence of young Elton's visions, the research programme spawned by this essay has kept population ecologists captivated for the past 75 years.

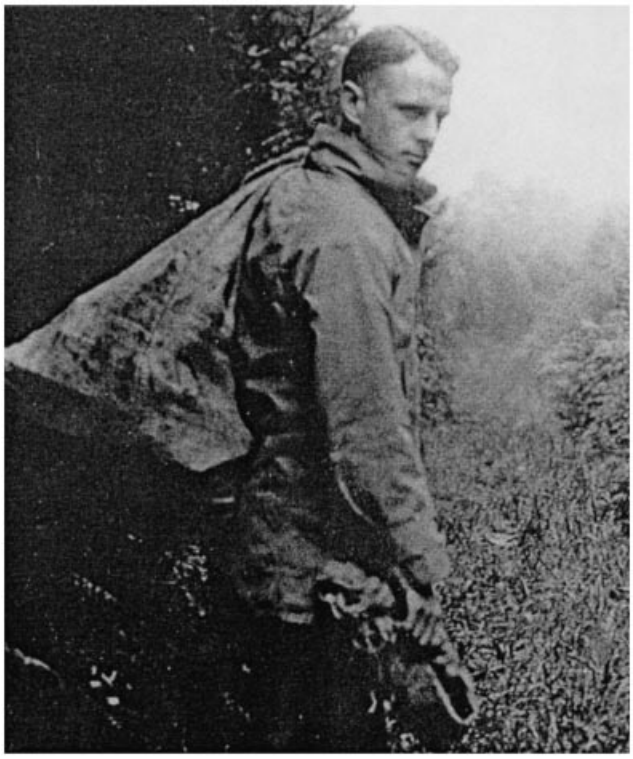

Fig. 1. Charles Elton in Wytham's Wood, Oxford in 1926 (courtesy of British Ecological Society).

Initially, it was Elton himself who took the programme most seriously. In 1932 he established and headed the Bureau of Animal Population in Oxford, and rapidly set a research programme in action (Kingsland, 1985; Crowcroft, 1991; Chitty, 1996). Together with his secretary Mary Nicholson he compiled information from the long-term records of fur returns of the Canada lynx (*Lynx canadensis*) from Hudson's Bay Company's trading posts (Elton & Nicholson, 1942). Also in 1942 he published the treatise 'Voles, Mice and Lemmings'. Moreover, Elton organised the Canada-wide 'Snowshoe Rabbit Enquiry', where data were collected in a questionnaire form on the population fluctuations of the snowshoe hare (*Lepus americanus*) in the 1930s and 1940s (Smith, 1983). Despite recent landmark

papers on multi-annual periodic fluctuations in animal numbers (e.g. Hanski, Hansson & Henttonen, 1991; Hanski *et al*. 1993; Korpimäki, 1994; Krebs *et al*., 1995; Korpimäki & Norrdahl, 1998; Stenseth *et al*., 1998*b*, *c*, 1999; Hansen, Stenseth & Henttonen, 1999; Hansen *et al*., 1999*b*), it remains the case that unravelling the causes and consequences of periodical population fluctuations will keep Elton's agenda alive for many years to come.

Thus, it is clear Elton (1924) is one of the cornerstones of contemporary ecology. However, against modern publication standards, his paper is somewhat liberally structured, and may have allowed subsequent misinterpretation. He first presents evidence for climatic cycles, because he was convinced that the observed periodic fluctuations in the numbers of species and populations 'must be due to climatic variations' (Elton, 1924, p. 119). Thereafter, he deals with the evidence for periodic fluctuations in numbers of several different species and populations from lemmings to insects. It is an impressive amalgamation of the existing population data in an era without electronic information services. Finally, Elton speculates about the possible evolutionary causes of regular population fluctuations. In this, Elton was clearly visionary; his evolutionary ideas can only now be analysed using developed techniques and tools (see Section V). He also diverged from most of his contemporaries by using evolutionary thinking as an integral part of ecological studies (Kingsland, 1985).

In this review, we will attempt to relate Elton's (1924) findings and hypotheses to current evidence and theory of multi-annual periodic fluctuations in animal populations. In doing this, we shall first scrutinise Elton's hypotheses and the data he used to support his major conclusion of a climatic origin for periodic population fluctuations. We then trace the accumulated research conducted in this area during the past three-quarters of a century, aiming at building a genealogical tree of the spread of Elton's (1924) ideas. This section will end with the most recent analyses of multi-annually fluctuating population dynamics of voles, lemmings and lynx. Current research focuses (i) on time-series analysis of the extant long-term data on cyclic population fluctuations (Stenseth, 1999), (ii) on experimental testing of some suggested causes of the periodic fluctuations (Korpimäki & Norrdahl, 1998), and (iii) on explicit theoretical modelling of this type of population behaviour (Hanski *et al*., 1993; Turchin & Hanski, 1997; Kendall *et al*., 1999). A substantial part of this review will concentrate on the evolutionary consequences of regular multi-annual fluctuations in animal populations. Finally, we shall comment upon the revival of Elton's ideas on population fluctuations in time over large regions in space. A wealth of recent literature (e.g. Bascompte & Solé, 1997; Hanski & Gilpin, 1997; Grenfell *et al*., 1998; Hanski, 1999; Ranta *et al*., 1999*a*, *b*; Ruxton & Rohani, 1999) has attempted to expand population dynamics and theories of population dynamics into the domain of spatially structured populations. Here, instead of looking at the dynamics of a single population the focus is on several population subunits, each self-sustaining, coupled by dispersing individuals or *via* sharing a common environment. Elton's (1924) ideas have also proved influential in this area.

II. ELTON'S ARGUMENT

A good climate, *like a good dinner*, *is more than the mere sum of its separate parts* (Elton, 1924, p. 125).

In Elton's time, there was a good body of data suggesting multi-annual periodic fluctuations in numbers of populations of several species. With the help of these data, Elton (1924) showed that periodic multi-annual dynamics (Fig. 2) were common to small northern herbivores (lemmings, voles, hares) and their major predators. Moreover, he found that in many species (lemmings, hare, fox) the periodic

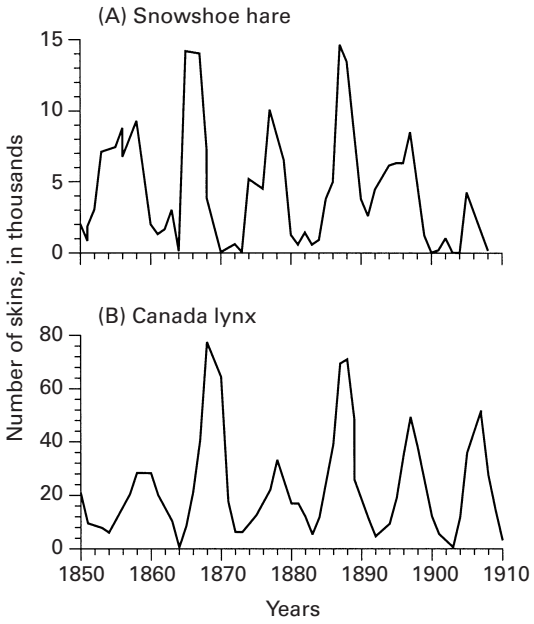

Fig. 2. Time-series showing snowshoe hare and lynx fur returns from the Hudson's Bay Company. Based on Fig. 5 in Elton (1924), as reproduced from Hewitt (1921).

fluctuations coincide temporally over large geographic areas. This synchronisation is, in fact, one of his central arguments for climatic variation being the cause of multi-annual periodic dynamics in many of the taxa he discusses.

The cycle period lengths in the dynamics of the animal populations mentioned in Elton (1924) were 2, 3, 4, 5, 10, 11, and 22 years, i.e. there is no one single period length. It could be more informative to accumulate a frequency table of all period lengths and species displaying these periods. However, this is beyond the scope of the present review and would perhaps be unproductive as even a single species may exhibit geographic variability in period length and amplitude (Lack, 1954*b*; Hansson & Henttonen, 1985; Lindström, 1994; Bjørnstad, Falck & Stenseth, 1995).

(1) Elton's candidates for the climatic factors

Elton (1924) made his argument for a climatic cause behind the documented cases of cyclic dynamics very explicit in several passages of his text. His arguments for the climate hypothesis are as follows.

Fluctuations in the numbers of certain animals must be due to climatic variation. The variation in climate might be caused by changes in the sunspot numbers (i.e. sun's activity), by some other extra-terrestrial agent (e.g. moon), or be of terrestrial origin (e.g. volcanic eruptions). Elton very carefully presents evidence against moon and volcanic eruptions being the cause of the fluctuations. In brief, volcanoes do not erupt frequently enough to coincide with the periodicity of the dynamics in many populations and species (Fig. 2). Similarly, the moon has either too short a cycle (28 days), or too long a cycle (18.4 years) to match the observed period lengths. Thus, for Elton (1924), the only agent remaining is solar variation, which must affect plants and animals through climatic changes. In fact, Elton (1924, p. 152) suggests that meteorologists and geophysicists could use known periodic fluctuations in the numbers of animals to collect data on climatic cycles.

(2) Evidence from Norwegian lemming and snowshoe hare

The best evidence that Elton (1924) gives for the presence of multi-annual periodic population fluctuations is for the Norwegian lemming (*Lemmus lemmus*) and the snowshoe hare (i.e. the varying hare or the Canadian rabbit, as it was known by Elton). It is likely (e.g. Stenseth, 1999) that Elton learnt of the fluctuations in lemming populations from Collett (1911–12). In fact, Stenseth & Ims (1993, p. 9) argue that Elton's (1924) contribution was actually a rediscovery. However, Elton (1924) certainly provided a complete synthesis of what was known at that time on the spatial and temporal population dynamics of lemmings, supplemented with factually better quality data on the snowshoe hare and Canada lynx, and with scattered notes on multi-annual periodic fluctuations in numbers of other species.

Collett (1911–12) may very well have been the source of inspiration for Elton, but Elton (1924) systematised the study of periodic fluctuations and thus made it subject to scientific research programmes. More importantly, however, he directly initiated both field work and laboratory research to address the topic (Crowcroft, 1991). Elton also attracted people to address the problem from a theoretical point of view, although this took longer (Moran, 1952, 1953*a*, *b*; Leslie, 1959).

The lemming is famous for its periodic mass-migrations ('lemming years') over much of Southern Norway and other parts of Northern Scandinavia (Stenseth & Ims, 1993). Elton (1924, p. 128) accumulated the available evidence of lemming years in South Norway, Greenland, and Canada. The data from Canada were derived by Elton from numbers of arctic fox (*Alopex lagopus*), which is a predator specialising on lemmings. Arctic fox has been a favourite target of hunters because of its valued fur, and therefore long-term population data of this species were available in the Hudson's Bay Company records. The temporal match in the occurrence of peak lemming years in Norway, Greenland and Canada is good. Elton (1924, p. 129) wrote: 'The agreement with lemming-years in Norway is seen to be remarkable. In three cases the maximum in Canada occurs a year before, and in three cases a year after that in South Norway'. This finding was influential in the development of Elton's climate hypothesis.

Population fluctuations in the snowshoe hare were well known to Elton (Preble, 1908; Seton, 1920; Hewitt, 1921). In fact, it was Hewitt (1921) who first assembled data on the population fluctuations of the snowshoe hare and the Canada lynx from the records held by the Hudson's Bay Company (Fig. 2). Snowshoe hare numbers gradually increase over a 10 year period to reach a maximum, after which the population crashes. Elton very correctly points out

three important facts from these data. First, Hewitt's (1921) numbers represent the fur totals for the whole of Canada. Second, although the population maxima do not occur at precisely the same year in all parts of this vast area, in the regional occurrence of the peak years there is only minor variation in the temporal match. Finally, the synchrony of the cyclic dynamics was evident to both Hewitt (1921) and Elton (1924). If the periodic fluctuations in the snowshoe hare and the Canada lynx populations had been phased randomly across Canada, the clear patterns plotted in Fig. 2 would not emerge. This observation formed the second cornerstone of Elton's climatic influence argument.

(3) Elton's deductions of population fluctuations

Based on the above evidence Elton concluded that the cause of population fluctuations was climatic variation. He argued that the periodic fluctuations in lemming numbers were extremely pronounced and regular, and thus that their causes must lie either with the lemmings themselves or with their environment. Such a periodic mechanism could result from the breeding system of the lemmings, causing them to increase exponentially until some critical density was reached. This increase phase would be followed by a shorter migration phase with little reproduction that would result in rapid reduction in numbers. After this crash the process would start again. However, data show temporally synchronised maxima over various mountain regions in Southern Norway, even though lemming dispersal between these regions seemed impossible. In fact, lemming years are fairly synchronous all over the arctic regions and the mountains of southern Scandinavia and often also in Northern Finland (Elton, 1924; see also Stenseth & Ims, 1993). Elton thought that such large-scale synchrony in the multi-annual periodic fluctuations made it unlikely that the cause of the lemming cycles 'lies with the lemmings themselves'. Rather, the periodicity 'must lie with the environment' (Elton, 1924, pp. 132–133). He concluded that the only conceivable factor acting similarly over large regions is climate. He did not add that it was not known how this factor acts, and whether it is direct or mediated *via* plants, or other animals.

Elton uses the same reasoning for snowshoe hare dynamics in Canada. Hewitt's (1921) data show a high degree of nationwide synchrony in hare dynamics (Fig. 2). Elton (1924, p. 136) also presents data on brood sizes and number of broods in different phases of the cycle. In peak years, there are 8–10 young per brood and 2–3 broods per season, whereas during the population lows there is only one brood with three young per season. Elton concludes that the breeding physiology of the snowshoe hare alone would not explain such an innate cycle. 'When we reflect that the rhythm would have to act in a mixed population of animals of all ages, and through several generations, and more or less simultaneously (within a few years) all over Canada, such an explanation becomes increasingly unlikely. And what is more it is quite unnecessary'. And a few lines later, 'All that can be said, and that can be said with some certainty, is that the variations in reproductive capacity, and consequently in numbers of this rabbit from year to year, are due directly or indirectly to variation in climate' (Elton, 1924, p. 136–137). He suggests that the climatic agent behind the 9–11 year periodic fluctuations is solar activity, as reflected in sunspot numbers.

(4) Other causes of population fluctuations

A careful reading of Elton (1924) reveals that he also mentioned other possible causes of cyclic population fluctuations. When discussing lemming, Elton (1924, p. 131–132) gives a list of predator species upon which the numbers of lemmings have powerful effects: a 'vast crowd of birds (owls, hawks, ravens, etc) and mammals (stoats, foxes, etc)'. These predators 'are attracted to the mountains, and their numbers increase not only by their immigration but probably by their larger and more successful broods, due to the abundance of food' (Elton, 1924, p. 132). Elton (1924, p. 140) also notes how an abundance of mice attracts large crowds of kestrels and short-eared owls, which 'only prolong the plague by keeping the numbers of mice down below the density necessary to cause the epidemic'. Thus, even though he did not directly suggest that predators might be the driving force behind population fluctuations, he does include the relevant elements of the 'predation hypothesis'. That is, specialist predators such as the arctic fox, who feed solely on lemmings in peak years, and generalist predators that are attracted to areas with a rich supply of food. Below, we use the 'predation hypothesis' to mean that predators are causing the cycle (see e.g. Henttonen *et al.*, 1987; Hanski *et al.*, 1991, 1993); note that other types of predation hypotheses have also been presented. Errington (1934), for instance, saw the role of predators as taking only the 'doomed surplus', i.e. animals that

Table 1. *Hypotheses put forward to explain small mammal cycles*

Behaviour hypotheses	Voipio (1950*a*, *b*); Chitty (1960, 1967); Krebs (1964, 1979, 1985); Charnov & Finerty (1978); Getz (1978); Abramsky & Tracy (1979); Gaines *et al.* (1979); Stenseth (1983); Hestbeck (1982); Halle & Lehmann (1987); Gliwicz (1990)
Habitat hypothesis	Bondrup-Nielsen & Ims (1988)
Predator hypotheses	Elton (1924); Shelford (1943); Pearson (1966); Erlinge *et al.* (1983); Hansson (1984); Hansson & Henttonen (1988)
Plant – herbivore hypothesis	Rosenzweig & Abramsky (1980)
Food hypotheses	Elton (1924); Lack (1954); Pitelka (1964); Schultz (1964); Freeland (1974); Haukioja (1980); Rhoades (1983); Rosenzweig & Abramsky (1980)
Disease hypothesis	Elton (1924)
Physiology hypotheses	Christian (1950, 1978); Mihok *et al.* (1985)
Multi-factor hypotheses	Elton (1924); Lidicker (1978, 1988)

would not survive anyway. According to this view, predators would not cause population cycles.

Elton also discusses the significance of epidemics (or diseases) as the cause of population crashes in the Norwegian lemming (p. 132), snowshoe hare and other species (p. 142). For example: 'About every ten years the numbers of the [Canada] rabbits increase to a maximum, just as in the shorter cycle of the lemmings, and then almost the entire population is killed off by an epidemic disease' (pp. 135–136). Indeed, Elton (1924) has been credited with supporting the 'disease hypothesis' (e.g. Batzli, 1992; Stenseth & Ims, 1993; Table 1). However, for Elton, the disease hypothesis does not explain the fluctuations in the numbers of snowshoe hare young per brood and the number of broods during the population cycle, and he therefore does not consider it further.

Although Elton (1924, p. 137) maintains that the cause behind the cyclic dynamics of hares is 'some climatic cycle', he does note that the larger number of young per brood and the number of broods in peak years might also 'be due to better food supply (climate acting through plants). The evidence on mice suggests that this is an important factor' (p. 136). Elton is here supporting the 'food hypothesis' (Fig. 3; Table 1), albeit as a part of the climate-cause hypothesis.

We are well aware, of course, that Elton raised

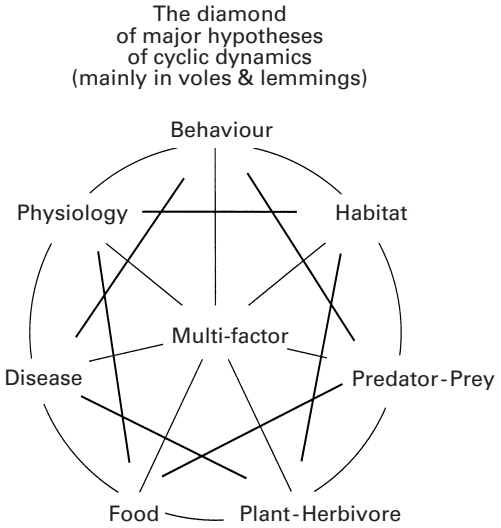

Fig. 3. The diamond of the hypotheses put forward to explain periodic fluctuations in the numbers of voles and lemmings. The graph is an aggregated version of the 23 hypotheses listed by Batzli (1992) (Had we followed him in all detail, the figure would look more like a fullerin ring).

these different arguments in a variety of contexts relating to the type of cycles and the specific animals displaying the multi-annual periodic fluctuations. The reader should judge whether Elton (1924) should be read thus in a piece-wise manner, or as a coherent whole. Our view is that Elton (1924) was

very confident that only the climatic cause could explain the observed temporal synchrony in population fluctuations over vast geographical ranges in the Norwegian lemming or the snowshoe hare in Canada. We also feel that in 1924 he had not yet fully developed his ideas regarding the causes of periodic fluctuations. For instance, in 1942 he wrote about the Canada lynx cycle, 'The long run of figures now available proves conclusively that the hypothesis put forward by Elton (1924) of control of this cycle by sunspots, acting through climatic cycles, is not true' (Elton & Nicholson, 1942, p. 242; see also Lindström, Kokko & Ranta, 1996*a*).

To end this section, we shall quote Elton (1924, p. 142): 'Now in the case of the mice there are four main factors which are thought to affect them in an important way. Firstly, mild winters favour them, and leave a larger stock to start the next season's population. Secondly, better physical conditions during the breeding season. Thirdly, abundant food supply at any time, but especially in the breeding season. This would be the effect of climate favouring plant life in some way, e.g. big crops of beech-mast or acorns. Fourthly, a favourable growing season leaves plenty of plant cover in the winter, which gives the mice protection from their enemies. There must, of course, be other factors as well. But the point is that not only are all these factors connected with climate, but the last three are all the result of the same kind of climatic complex during the breeding season'.

Given the above it seems strange that ecologists still search for a single cause for multi-annual periodic fluctuations in a high diversity of species that live in varying environments. However, as pointed out by Stenseth (1999) many 'vole ecologists' have largely ignored what others have written about the same issue [or whether the hypotheses they were putting forward, were at all water-tight enough to be called scientific hypotheses (see also Stenseth & Ims, 1993)].

(5) Concluding remarks

We believe that it is a mistake to interpret Elton (1924) as being a contribution to the study of cyclic population dynamics only. One contributory factor in this belief is that 'cyclicity' was not very strictly defined in Elton's days. For instance, in 1927 (p. 130) he wrote '… there are a number of irregular and so far unpredictable cycles, such as rainfall in England'. It seems that population fluctuations as such were considered roughly synonymous with periodic fluctuations [Andrewartha & Birch (1954) and Lack (1954*b*) share this view]. In addition, by our current standards, the first observations of fluctuating populations were ill-substantiated and often anecdotal. The best data available were the Hudson's Bay Company records of lynx and snowshoe hare pelts and these data caught Elton's primary attention. The data of Shelford (1943) and Chitty (1952) on voles and lemmings, and of Siivonen (1948) and Lack (1954*b*) on grouse could at best indicate some kind of regularity in population fluctuations.

With such a limited supply of data, it must have been very difficult to derive hypotheses regarding the mechanisms behind the cycles. Elton was, in fact, searching for the causes of both cyclicity *and* temporal synchronicity in the dynamics of periodically fluctuating populations. He concentrated primarily on the Norwegian lemming and the snowshoe hare in Canada. Both these species display characteristically periodic multi-annual fluctuations, the snowshoe hare perhaps more precisely than the lemming. A central feature in the dynamics of these two species is that within each species population fluctuations are in temporal synchrony over vast geographical areas. This is why Elton so clearly emphasises the significance of climate. Climate, of course, can be the cause of periodic fluctuations, especially with certain types of population dynamics: damped dynamics with occasional disturbances will produce population cycles (e.g. Leslie, 1959; Potts, Tapper & Hudson, 1984; Kaitala, Ranta & Lindström, 1996). It is striking that this aspect of Elton's work initially remained largely overlooked. There are but two early exceptions, the Australian statistician Patrick A. P. Moran (1953*b*), who briefly visited the Bureau in Oxford, and P. H. 'George' Leslie (1959), who was one of Elton's employees at the Bureau between 1935 and 1967 (Crowcroft, 1991).

III. ELTON TODAY

(1) Hypotheses, hypotheses and more hypotheses

The vole and lemming research inspired by Elton (1924) has resulted in a rich research field (for reviews, see Taitt & Krebs, 1985; Batzli, 1992; Stenseth & Ims, 1993; Norrdahl, 1995; Krebs, 1996; Korpimäki & Krebs, 1996; Stenseth, 1999). A characteristic feature of this field is the readiness of researchers to speculate about the causes of the observed periodic fluctuations in population num-

bers. This is well documented by Batzli (1992) who listed a total of 23 differing hypotheses published since Elton (1924). We have summarised these under eight major categories in Fig. 3 and Table 1. Bump *et al*. (1947) listed 12 different explanations for the cyclic dynamics of ruffed grouse (*Bonasa umbellus*) alone: (i) cyclic climatic change, perhaps connected with sunspots, (ii) abnormally cold winters, (iii) unusually wet springs, (iv) epidemic diseases, (v) external parasites, (vi) insufficient food in winter, (vii) natural predators, (viii) scarcity of 'buffer prey', i.e. of the common rodents which constitute the normal food of many predators, (ix) decrease in cover, (x) hunting, (xi) emigration and (xii) inbreeding. Of these, (x) will not apply to voles and lemmings. It is worth noting that (viii) is now known as the 'alternative prey hypothesis' attributed to Hagen (1952). With 12 explanations in 1947 and 23 in 1992 one can expect a new hypothesis to be raised approximately every four years. In fact, the most recent newcomer to explain multi-annual periodic oscillations in northern European vole populations is the maternal effect hypothesis (Inchausti & Ginzburg, 1998).

Thus, the fact that there is no consensus over the cause(s) of cyclic population dynamics in various taxa all over the northern hemisphere is not due to the lack of hypotheses. Surprisingly enough, as Stenseth (1999) writes, many of these hypotheses are simply put forward and never rigorously scrutinised nor tested with experiments. As Robert M. Pirsig (1974) wrote in his novel *Zen and the Art of Motorcycle Maintenance*: 'If the purpose of scientific method is to select from a multitude of hypotheses, and if the number of hypotheses grows faster than experimental method can handle, then it is clear that all hypotheses can never be tested. If all hypotheses can not be tested, then the results of any experiment are inconclusive and the entire scientific method falls short of its goal of establishing proven knowledge'. It seems that this sobering view is very close to the current situation in research seeking answers to cyclic dynamics: there are more hypotheses produced than tests carried out. Below we shall discuss some of the most recent players of the 'Eltonian game' to explain causes of cyclic population dynamics.

(2) Vole and lemming research

With only a rather superficial knowledge about the details of the biology of the study system, the most natural approach for most ecologists of Elton's time was to seek an explanation for large-scale patterns and processes among large-scale external processes such as climate. [Note the recent revival of this approach, for example, in community ecology (e.g. Polis, 1999)]. Consequently, the idea flourished that correlated weather over large geographical areas ought to be responsible for the dramatic and spatially extended phenomenon of population oscillations. Although food, predation and disease were all discussed by Elton (1924) (see Section II), they did not become as established as climate variation as plausible mechanisms early on. A multi-factorial explanation for large-scale population fluctuations was hinted at, however, very early in the history of ecology. For example, Shelford (1929) argued that ecology is '… a science of communities', suggesting that biotic interactions are the important components of an understanding of ecological patterns [this view is clearly held also by Henttonen (2000) today]. Soon, however, the hypothesis that disease might drive the cycles was developed. Nobody denied the innate capacity of populations to grow, and it was thought equally reasonable that high population densities could be followed by rather catastrophic declines due to disease.

Elton himself, by now having been engaged by the Hudson's Bay Company as a biology consultant and founder of the Bureau of Animal Population and the author of four books on animal population ecology (Elton, 1927, 1930, 1933, 1942) continued to support the climate hypothesis (Elton & Nicholson, 1942). Elton and Nicholson concluded (1942, p. 242) that 'We have at present no clue at all to the nature of the factor controlling this enormous wild-life rhythm in the northern forests, except that is seems almost certain that climatic fluctuations must play a controlling part'.

The first theoretical approach to this question came with Moran (1953*b*; see also Sections IV and VI). Theoretical and empirical developments seem to have been largely separate although Moran had close contact with Elton. David Lack (1954*b*) also mentions Moran's statistical analyses of lynx and grouse (Moran, 1949, 1952) although without actually using Moran's arguments in his analysis. But it was in the 1950s that the research into population cycles took off. The Cold Spring Harbor Symposium in 1957 attracted numerous cycle ecologists and the Journal of Wildlife Management and the Journal of Animal Ecology started to become important outlets for the different 'cycle schools' now emerging. One interesting intermezzo was provided by Cole (1954), who argued that the

observed cycles were statistical artefacts. His argument has since been shown to be wrong.

By and large, the interest in cyclic populations was concentrated where they actually occurred – in Scandinavia and North America. In Finland, the work of Lauri Siivonen (1948, 1950, 1952, 1954) and Olavi Kalela (1962) was continued by Jussi Viitala (1977, Viitala & Ylönen 1993). Finnish ecologists have played a major role in developing the study of fluctuating populations ever since. In Sweden and Norway, interest developed slightly later, perhaps best represented by Hansson (1969, 1971, 1979) and Stenseth (1977, 1978; Stenseth *et al*., 1977). Although British interest in the problem continued through the 1950s (e.g. Mackenzie, 1952; Lack, 1954*a*, *b*), it increased with studies of the red grouse (*Lagopus lagopus*) (Watson & Moss, 1979; Potts *et al*., 1984; Hudson, Dobson & Newborn, 1985). Elton's legacy was perhaps most prominently managed by the early North American school orchestrated by Dennis Chitty (e.g. 1952, 1960, 1967).

Chitty's early work focused on lemmings and the snowshoe hare, but turned soon to voles, both in Britain and the U.S. The 'Chitty hypothesis' (Chitty, 1960, 1967) concerning self-regulation through variable selection pressure on different vole morphs (aggressive and less productive individuals *versus* docile highly productive ones) was soon established, and in the 1970s several of his former graduate students had become major players in the field of vole cycle research, the most prominent of them being Charles Krebs (e.g. Krebs *et al*., 1973; Krebs & Myers, 1974; Krebs, 1978). The North American vole-cycle research has been largely devoid of formal mathematical analyses, but has focused instead on the biological details of the organisms. Dymond (1947) argued that it is the decline phase of the cycle that should be understood in order to understand the entire system, and this idea was carried on by, for example, Krebs & Myers (1974) and Taitt & Krebs (1985). The influential paper by Krebs & Myers (1974) set the stage for most population cycle research that followed. They reviewed the evidence for cycles in small mammals, as well as the proposed explanations for microtine cycles. They regarded food, predation, weather, stress, behaviour, and genetics as the most promising candidates.

George Batzli (e.g. Batzli & Pitelka, 1971; Batzli, 1985; Cole & Batzli, 1978, 1979; see also Pitelka, 1964; Schultz, 1964; Freeland, 1974) soon concentrated on the food hypothesis. It was also addressed by Finnish (e.g. Haukioja, 1980; Laine & Henttonen, 1983; Haukioja *et al*., 1983) and later by Norwegian ecologists (e.g. Seldal, Andersen & Högstedt, 1994; see also Hansson, 1971). The food hypothesis soon became embedded in the much larger realm of general plant-herbivore interactions. Here, snowshoe hare dynamics, rather than voles, seem to have received the most attention. Studies of the snowshoe hare indicated a role for plants in shaping the regular population oscillations (Keith & Surrendi, 1971; Pease, Vowles & Keith, 1979; Keith, 1983). Seminal work by John Bryant (Bryant, Clausen & Kuropat, 1985; Fox & Bryant, 1984) showed that hare browsing affected plant quality to the extent that it could negatively affect reproduction and survival in subsequent hare generations. By and large, the hare–vegetation interaction seems to have been easier to investigate than the vole–vegetation one, partly because the hares' impact on (woody) plants usually is more obvious and quantifiable than grazing and seed consumption by voles.

The predation hypothesis seems to have been more popular in Scandinavia and Finland, at least possibly as an explanation for the vole cycles. Early attempts to understand the role of predators were made by Andersson & Erlinge (1977), after which Hörnfeldt (1978) studied the synchronous fluctuations in a large number of vole and other small mammal species, grouse, fox and owl in North Sweden and came to the conclusion that predators must play a key role in sustaining cycles in the region. Sam Erlinge and co-workers (Erlinge, 1987; Erlinge *et al*., 1983, 1984, 1988) suggested that specialist predators unable to switch to alternative prey could be prime candidates for causing the vole cycles in northern Fennoscandia. This explanation has gained popularity amongst ecologists in Sweden and Finland (Hansson & Henttonen, 1985, 1988; Henttonen, 1985; Hansson, 1987; Henttonen *et al*., 1987; Hanski *et al*., 1991; Korpimäki, Norrdahl & Rinta-Jaskari, 1991; Korpimäki, 1993, 1994; Hanski & Korpimäki, 1995; Hanski & Henttonen, 1996; Klemola *et al*., 2000). Lennart Hansson, Heikki Henttonen and Erkki Korpimäki especially have played central roles in collecting long-term population data on vole dynamics in Sweden and Finland.

Although stress was dealt with at length by Krebs & Myers (1974), it has received relatively little attention during the last couple of decades, probably because it was soon realised that stress is a proximate reaction to high density, rather than a causal mechanism by itself. The most notable exception is a relatively recent suggestion by Mihok, Turner & Iverson (1985) that immunological responses could

play a role in the population dynamics of voles, an idea which has gained increasing support from theoretical predictions (e.g. Kaitala & Heino, 1996; Kaitala, Heino & Getz, 1997*a*). Despite the fact that diseases and parasites are known to be able to destabilise population dynamics (Grenfell & Dobson, 1995), the disease hypothesis first mentioned by Elton (1924) has not received the support one would have expected. Some attempts have been made to show the influence of parasites on the dynamics of voles (Haukisalmi & Henttonen, 1990; Haukisalmi, Henttonen & Tenora 1988). The host-parasite interaction in British red grouse, for example, does perhaps look more promising as a destabilising factor (Hudson *et al*., 1985; Hudson, Dobson & Newborn 1998).

The social behaviour hypotheses including the Chitty hypothesis already mentioned above are relatively recent. The 'social fence' effect was introduced by Hestbeck (1982), who suggested that if emigration is prevented by high population densities in the neighbouring areas, the resulting high population density in the focal area leads to resource exhaustion. Also Krebs (1979, 1985) among others, has argued that the potential to emigrate from over-crowded areas should be an important population regulatory mechanism, possibly preventing cycles.

This brief and sketchy review of the most popular hypotheses attempting to explain periodic fluctuations in the populations of birds and mammals is naturally far from exhaustive. We have simply attempted to indicate the wealth of approaches and to highlight the difficulties in reaching a consensus on the dominant forces involved. It is interesting to note that different taxa or systems seem to have attracted different hypotheses. Although food supply has not been investigated thoroughly in the vole system, predation has become a particularly strong candidate for the controlling mechanism in vole populations. At least initially, the food hypothesis seemed to explain well the snowshoe hare population fluctuations, whereas grouse populations in the British Isles are suggested to be driven by a host-parasite interaction. At present, it is impossible to judge whether these taxonomic/system differences are real or simply reflect different emphases by research teams on different continents. Apart from the single-factor hypotheses mentioned here, there have been attempts to synthesise several of them or to broaden their scope. Bill Lidicker (1978, 1988) suggested ways of obtaining a synthetic view of the interaction between several factors affecting the dynamics of fluctuating populations. Batzli (1992) also attempted to combine a long list of hypotheses together. A slightly different approach was taken by Lauri Oksanen and Tarja Oksanen's work on Fennoscandian small mammal dynamics. They incorporate a firm theoretical approach (the 'exploitation ecosystem hypothesis') and argue that the dominating factors behind population fluctuations vary depending on system productivity. This means for instance, that both food and predation may be important, but that their relative importance will vary across productivity gradients (e.g. Oksanen *et al*., 1987; Oksanen & Oksanen, 1992; Oksanen, Oksanen & Nordberg, 1992).

(3) Experiments

Krebs & Myers (1974) end their influential paper with a plea for experimentation. The assimilation of long-term field data was how studies in this field began in the early 1920s, and by 1974, 50 years after Elton, investigators were encouraged to probe deeper into the biological mechanisms behind the spectacular cycle phenomena then known. Some various experiments had been performed previously, but at small temporal and spatial scales. There were three particularly important approaches used.

The 'Kluane project' orchestrated by University of British Columbia, Canada (e.g. Boutin *et al*., 1995; Krebs *et al*., 1992, 1995; Turkington *et al*., 1998) includes detailed study of the vegetation, the snowshoe hare, and its predators (primarily Canada lynx and great horned owl, *Bubo virginianus*). Several-hectare blocks are used as treatments and controls; the treatments include fertilising the vegetation, adding food for the hares, excluding predators, excluding hares, and several combinations of these. In this factorial experiment, the aim is to disentangle the relative importance of some of the strongest candidates for the control of the population cycles observed in the natural system in the region. Perhaps not surprisingly, so far no one factor of the potential factors has been singled out. Since the community is a truly interactive one, the picture emerging is that food and predation act in concert to mould the fluctuating dynamics of the snowshoe hares.

Two Finnish groups of ecologists have also approached Elton's problem experimentally. Hannu Ylönen and co-workers (Ylönen, 1989, 1994; Ylönen *et al*., 1992; Ylönen & Ronkainen, 1994; Koskela & Ylönen, 1995) have shown that the presence of predators may significantly alter vole reproduction. Hence, predator-induced breeding suppression may

be an important factor shaping the population fluctuations. However, this view has not been accepted unanimously (Lambin *et al*., 1995; Kokko & Ranta, 1996; Kaitala, 1997; Kaitala *et al*., 1997*b*; Klemola, Korpimäki & Norrdahl, 1998; Klemola *et al*., 2000; Mappes, Koskela & Ylönen, 1998; Prévot-Julliard *et al*., 1999; Kokko & Ruxton, 2000).

The experiments performed by Erkki Korpimäki and his team (e.g. Korpimäki & Norrdahl, 1998; Klemola *et al*., 1998, 2000) provide a fine example of how the impact of predators on the dynamics of small mammal populations can be tested experimentally in natural conditions on a large scale. In their study area, avian predators (e.g. kestrels and owls) are the main consumers of voles. They will all use nest-boxes for breeding and it is therefore relatively easy to manipulate the density of predators e.g. by nest-box removal. The experiments (together with comparative long-term field data) show that the predators in this system may have a significant impact on the dynamics of their prey to the extent that predation could explain the multi-annual oscillations. It is worth emphasising that the experiments of Korpimäki & Norrdahl (1998) and Klemola *et al*. (1998, 2000) rendered it possible to compare the roles of intrinsic regulation and predators, and did not support a role for intrinsic regulation.

It is obviously not an easy task to carry out experiments at the temporal and spatial scale required for the investigation of multiannual fluctuations in relatively large and long-lived animals. The Kluane project and to some extent Korpimäki's predator reduction areas are the only extensive experimental programs launched so far. The alternative is to take the approach of the majority of research, i.e. to try to isolate one or a few aspects of the biology of the species of concern. In this respect, research into population cycles is no different from most population and community ecology research. There are very good theoretical and empirical reasons to believe (Sinclair *et al*., 2000) that the bird and mammal species involved in boreal and arctic population fluctuations are tightly coupled in a truly interactive food web (Henttonen, 2000). Indeed, a link between the populations of voles, predators and grouse was shown experimentally by Marcström, Kenward & Engren. (1988) on islands in the northern Baltic. The only way to understand the system is hence to treat and analyse it as a dynamic system (in the mathematical sense). This is partly taken into account in recent statistical and mechanistic modelling attempts (Kendall *et al*., 1999).

IV. MODELLING

Like most mathematicians, he [*Alfred Lotka*] *takes the hopeful biologist to the edge of the pond, points out that a good swim will help his work, and then pushes him in and leaves him to drown* (Elton, 1935).

(1) The founding fathers

Elton's influence on the study of population dynamics, in particular population cycles and fluctuations, can be seen in the variety of theories and models that his studies have spawned (Fig. 3, Table 1). However, an interest in cyclic dynamics began earlier and apparently took a route largely independent from the collection of real data for many decades. In 1907, Alfred Lotka began to publish a series of papers culminating in the book *Elements of Physical Biology* in 1925. Elton knew of the developments in theoretical ecology but, as a field biologist, found it difficult to relate the theoretical findings to his own thoughts (Kingsland, 1985). In addition, many workers were somewhat taxon orientated. Ecologists working on similar topics that with hindsight are clearly similar but on different taxa, were not aware enough of each other's work. For example, the newly discovered population cycles in birds and mammals were absent from the seminal paper by Nicholson & Bailey (1935), who gave a detailed account of both the mathematics and the biological mechanisms behind insect population cycles. Likewise, when Elton (1942) discussed population cycles, he did not cite Nicholson & Bailey (1935). The generality and importance of density-dependent feedback mechanisms in creating fluctuations was not fully understood at that time. Indeed, in spite of many efforts, the gap between 'cycle theoreticians' and field biologists is still not entirely bridged (Stenseth, 1999).

Attempts to model observed patterns in fluctuations of natural bird and mammal populations in space and time took place in the 1950s. By that time, two conflicting views competed to provide an understanding of the temporal regulation of populations. To a first approximation, the regulating factors were thought to be either intrinsic population processes (e.g. density-dependence) acting independently or tracking changes in the environmental conditions, or density-independent processes forcing populations to obey environmental changes. The main proponents of the two opposing camps were Lack (1954*b*) and Andrewartha & Birch (1954).

An unexpected but very fertile direction to the

analysis of population regulation was initiated by Pat Moran, who first enters the ecological literature with a short paper concerning the statistical analysis of sunspots and lynx population cycles (Moran, 1949). He attempted to analyse statistically the relationships between the Hudson's Bay Company's lynx fur-return time series and sunspot numbers – a topic which is still under debate (Sinclair *et al*., 1993; Lindström *et al*., 1996*a*). Moran's (1949) study arose directly from MacLulich (1937) and Elton & Nicholson (1942). Later, Moran (1953*b*) showed how synchronous dynamics between two (or more) populations following a common structure of density dependence can be caused by density-independent factors shared by the local populations.

(2) Modelling in the 1970s

A further era of theoretical work in terms of mathematical modelling of population fluctuations and cycles began in the 1970s. The use of mathematical modelling as a scientific research tool was strongly advocated, and serious attempts to model small rodent population dynamics were initiated. This development was aided by the newly emerging simulation capacities provided by computer technology. Thus, in addition to the abstract mathematical tradition of dynamic modelling begun by Lotka (1925) and Volterra (1926), more detailed models taking into account factors such as habitat utilisation and energy requirements were also presented (Maynard Smith & Slatkin, 1973; Stenseth *et al*., 1977).

Special emphasis was placed on mathematical modelling as a research tool in population dynamics at a Symposium on the population biology of the field vole (*Microtus agrestis*) held at the Tvärminne Zoological Station of the University of Helsinki in Finland in 1976. It was evident by that time that the population dynamics of the field vole, for example, show cyclic fluctuations in northern Scandinavia but lack cyclicity in southern Sweden and further south in Europe (Hansson, 1971; Hansson & Henttonen, 1985). Moreover, the periods of the cycles appeared to be more regular than their amplitudes (Stenseth, 1977, 1999). Thus, the first attempts to model periodic population fluctuations concentrated on studying the conditions under which population dynamics become unstable and population cycles can be observed (Maynard Smith & Slatkin, 1973).

In his insightful study, Nils Christian Stenseth (1977) set out to evaluate several of the then current hypotheses for population cycles. Chitty (1960, 1967) had proposed that the changes in gene frequencies in a population are a necessary driving force of population cycles. In particular, depending on the phase of the cycle, docile or aggressive forms may be more succesful. Following the modelling tradition originated by Lotka (1925) and Volterra (1926), Stenseth used a two-strategy differential equation model for the coexistence of the two competing genotypes. Thus, equations for the population dynamics process can be given in general terms as

$$\frac{dx}{dt} = f(x,y) \qquad (1a)$$

$$\frac{dy}{dt} = g(x,y), \qquad (1b)$$

where t is time, x and y denote the two different genotypes, and f and g denote the functional dependence of the population changes on the densities of each genotype. Using a logistic model for f and g, Stenseth (1977) concludes that, despite the seemingly reasonable assumptions in Chitty's (1960, 1967) hypothesis, a polymorphic population does not seem to fluctuate regularly in a stable environment.

Another possible interpretation of Chitty's (1960, 1967) hypothesis is that regular cycles result from an interaction between genetic changes and extrinsic factors. In elaborating this interpretation, Stenseth (1977) states that species whose densities are kept low by some factor (e.g. interspecific competition or predation) may be less affected by intrapopulational factors that could otherwise cause fluctuations. For example, as the aggressive strategy proposed by Chitty (1960, 1967) is supposedly more vulnerable to adverse environmental factors, extrinsic factors are likely to trigger crashes in microtine cycles only when the aggressive strategy dominates numerically. Stenseth (1977) concluded that only this latter version of Chitty's (1960, 1967) hypothesis could plausibly explain cyclicity but that empirical studies were required to test it.

In the 1970s, the significance of nonlinearities in density dependence was discovered. The work of Robert May (1976*a*) provided deep insight as well as efficient tools to develop this theme. In particular, he was able to show that very simple nonlinearities may lead to extremely complicated dynamics, such that population fluctuations in principle do not necessarily need very complicated explanations. Interestingly enough, Stenseth (1977) comments on the discrete-time population model of the form $x(t+1) = f(x(t))$, noting that it is not directly

applicable to microtine rodents, partly because discrete breeding does not occur in microtines. Furthermore, the length of microtine cycles does not agree with those produced by period doubling route to chaos, i.e. the cycle lengths of 2^n with increasing population growth rate (May 1976*a*).

Although May seldom addressed the population cycles of small rodents directly (see e.g. May, 1975, p. 92, and May, 1976*a*, p. 7), he provided a plausible alternative for discrete time population models to model them. His starting point was that time delays can destabilise population dynamics. Thus, an equation of the form

$$\frac{dx}{dt} = rx(t)\left(1-\frac{x(t-T)}{K}\right), \quad (2)$$

with r as an intrinsic growth rate, T as a delay and K as a carrying capacity, could generate the population dynamics observed in the real time series (Hutchinson, 1948; May, 1976*a*). The outcome of such modelling could be shown to match the population dynamics data of collared lemming *Dicrostonys groenlandicus* from Canada satisfactorily (May, 1976*a*). In addition to proposing an explanation to the cyclic behaviour of the populations as such, the model provided insight into the decreasing amplitude and the stabilisation of the population towards the south (Stenseth, 1977, p. 531).

(3) Recent advances

The possibility of trophic interactions cannot be ignored when analysing population cycles. Two or more directions can be identified: herbivore–plant interactions, and predator–prey (including parasite–host) interactions. Microtines are, of course, herbivores, prey, and hosts for parasites. This also suggests that small rodent population dynamics cannot be understood from the small rodent data only.

According to the current view, the annual time-series data on periodically fluctuating small rodent populations from northern regions show a two-dimensional density-dependent structure (Stenseth, 1999). This strongly hints at the presence of a direct as well as a delayed annual density dependence. Moreover, either a predator-prey type of interaction or a herbivore-plant interaction may be the underlying cause of the periodic density cycles. However, it should be emphasised that one of the interactions is expected to dominate the outcome.

Much of the recent effort in modelling population cycles has concerned log-linear autoregressive models (Bjørnstad *et al.*, 1995; Stenseth, Bjørnstad & Saitoh, 1998*a*; Stenseth *et al.* 1998*b*; Saitoh, Bjørnstad & Stenseth, 1999), exemplified by a second-order model, given as:

$$X(t) = a_0 + a_1 X(t-1) + a_2 X(t-2) + \epsilon(t), \quad (3)$$

where X_t is the population size at time t, ϵ is a noise variable, and a_0, a_1, and a_2 are constants. A deterministic version of this model cannot produce persisting periodic oscillations, but they can occur in the presence of stochasticity. Such a model corresponds to a trophic interaction model, where the interaction can occur as a specialised herbivore-plant interaction, or as a specialised predator–prey interaction, but not both (Stenseth, 1999). Thus, it has been concluded that fluctuating dynamics of voles and lemmings are regulated either from above (predators) or from below (food).

Sophisticated statistical analyses applying autoregressive models have revived ideas first studied by statisticians in the 1970s (Box, Jenkins & Reinsel, 1994). Royama (1992) used this information to show that a combination of direct and delayed density-dependence [technically an AR(2) process (Box *et al.*, 1994; Royama, 1992)] can produce the entire suite of dynamic behaviours, from sustained cycles to damped stability (Fig. 4). Note also that the dynamic processes may differ according to the phase of the cycle. That is, density dependencies, be they due to predator-prey interactions or some other mechanism, may differ depending on whether the population level is high or low. These studies have led to the use of piecewise linear models in population ecology, referred to as threshold autoregressive models (TAR) (Tong, 1990). These have been used to analyse the Canada lynx (Lin & Pourahmadi, 1998; Stenseth *et al.*, 1998*c*, 1999) and Norwegian lemming data (Stenseth *et al.*, 1998*b*).

Nordic ecologists have also developed empirically based predator–prey models for the interaction between the least weasel (*Mustela nivalis*) and the field vole (Hanski *et al.*, 1991; Hanski & Korpimäki, 1995; Hanski & Henttonen, 1996; Turchin & Hanski, 1997). These species are suspected to be the key specialist predator and prey species in the multispecies communities in the boreal forest region in Fennoscandia (Hansson, 1984). Here, predation by the least weasel is considered to be the driving force in the multiannual cycles. The importance of generalist and nomadic avian predators has also

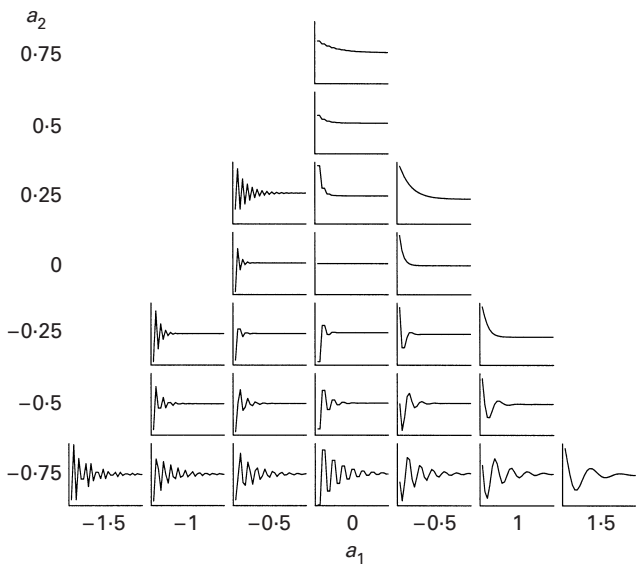

Fig. 4. Examples of the dynamics achievable with the second order autoregressive time-series model, AR(2): $X(t) = a_0 + a_1X(t-1) + a_2X(t-2)$, where $X(t)$ is the population size at time t, and a_0, a_1 and a_2 are constants. Note that cyclicity is just one kind of dynamics resulting in variation of the two parameters, a_1 and a_2. The two parameters must lie in the region described by $a_2 + a_1 < 1$, $a_2 - a_1 < 1$ and $-1 < a_2 < 1$ (see Box *et al.*, 1994 for more details and for the origin of this presentation). The application of this approach to population dynamics was introduced by Royama (1992).

been recognised. The combined effect of mammalian specialist and nomadic avian predators is also used to explain the geographic gradients in the rodent oscillations in Fennoscandia (Hanski *et al.*, 1991; Turchin & Hanski, 1997), where amplitude and cycle length decrease from north to south (Hansson & Henttonen, 1985; Bjørnstad *et al.*, 1995).

The modelling approach of Ilkka Hanski and coworkers (Hanski *et al.*, 1991; Hanski & Korpimäki, 1995; Hanski & Henttonen, 1996; Turchin & Hanski, 1997) is based on the Lotka–Volterra tradition, where the predator–prey interaction can be simplified into the form

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{cPN}{N+D}, \qquad (4a)$$

$$\frac{dP}{dt} = vP\left(1 - \frac{qP}{N}\right), \qquad (4b)$$

where N and P represent prey and predator population densities, K is the prey carrying capacity, predator carrying capacity is proportional to prey density, as indicated by parameter q, r and v are intrinsic growth rates, and c and D are parameters of the Type II functional response (Holling, 1965). The model has been modified such that a threshold prey density is included, below which predator population decreases exponentially (Hanski *et al.*, 1993; Hanski & Korpimäki, 1995). Furthermore, it is assumed that the growth rates and prey carrying capacities differ between summer and winter. With these relatively simple assumptions about model structure and with parameterisation based on empirical data, this model is capable of generating periodic dynamics reminiscent of the ones observed. Unlike the modelling attempts of the 1970s, the more recent approaches emphasise community structure and the interaction terms (such as the functional response), as well as aspects of the spatial structure of the landscape (see Section VI for details).

A recent paper by Turchin *et al.* (2000) asks whether the 'topology' of a time series can help in revealing the direction of the main trophic interactions. The idea arises from trophic-interaction models. Consumer/predator peaks are suggested to be more sharp and angular than the more blunt peaks of resource/prey. On this basis, the authors conclude that lemmings are more likely to be consumers than prey whereas vole time series clearly support the idea that voles are prey. This scenario also fits the fact that lemmings are moss-eaters and voles are folivores. Mosses recover more slowly from foraging than the food plants of voles and therefore the mosses are more likely to create a destabilizing time-lag in a trophic interaction than are vole food plants.

V. EVOLUTION IN FLUCTUATING POPULATIONS

(1) Elton's view

In his Discussion, Elton (1924, pp. 152–160) makes several points that relate to the evolution of adaptive traits in individuals that live in fluctuating populations. First, he recognises that the success of phenotypes may depend on the population size. He then proposes that during periods of unlimited growth, natural selection ceases to operate, and mutations may spread as if they were neutral. Especially when population sizes are low, this may lead to local differentiation due to a founder effect. Elton (1924, p. 158) hypothesises that species that undergo periodic population lows will be geographi-

cally more differentiated than species whose populations are more stable, and presents a two-species contrast as a possible confirmation of this rule: 'It is interesting to note that the beaver, which we have seen to lead a very regular sort of life, with no fluctuation in its numbers, has practically no geographical races, and in this is unlike the mice.'

Elton (1924, p. 159) also recognises that in addition to the above, population lows may induce genetic 'bottlenecks' (he does not use this term) that may wipe out some phenotypes that could have been equally successful. He then uses the above arguments to explain a certain degree of arbitrariness in the details of many adaptations. Some mutations, even if beneficial, could be lost in the course of a population cycle, whereas others persist if they happen to establish themselves at a favourable time (specifically, when the population is increasing and selection is weak). Thus, while very deleterious mutations will vanish from the population in the course of time, the succesful variants among several reasonably adaptive alternatives will be dictated by chance events.

(2) Fluctuating selection pressures

What is our modern view on the fate of a new mutation arising at different stages of a population cycle? Surprisingly, this question has remained without a definite answer for a long time. Very recently, Otto & Whitlock (1997) have provided a technique which is able to follow the fate of a beneficial (selection coefficient $s < 0$) or harmful ($s > 0$) mutant in a population that changes in size over time. In an exponentially growing or shrinking population, the probability of fixation turns out to approximate to $2(s+r)$, where r is the rate of population growth. Thus, population growth promotes the fixation of beneficial mutations. Interestingly, deleterious mutations become fixed more easily in shrinking populations, potentially leading to a 'mutational meltdown' of the whole population (Lynch, Conery & Bürber, 1995). The theory of Otto and Whitlock (1997) also applies to cyclic populations, where fixation probabilities can be shown to cycle with a period equal to the cycle length. Fixation probabilities peak during periods of population growth.

These results assume that the relative fitness advantage of a mutant genotype is constant, and does not depend on population size or growth rate as such. The adaptive value of a trait may, however, also depend on population density and/or growth rate: Elton's own examples (1924, p. 156) include mate searching ability and disease resistance, which may increase in importance at low or high density, respectively. Elton's general view appears to be that selection is much less intense while the population grows. However, subsequent developments in life-history theory (Fisher, 1930) formalised the idea that selection will continue to operate during periods of population growth, as long as there is genetic variability in traits that influence the intrinsic growth rate r. In stable populations, on the other hand, traits increasing carrying capacity are favoured (even though this will not happen under frequency-dependent selection). This dichotomy has become established as *r versus K*-selection (Pianka, 1970). A single trait may, of course, influence both r (the intrinsic rate of natural increase) and K (carrying capacity) of the phenotype, and the evolutionary outcome of selection of such a trait will then depend on the temporal fluctuations in population density.

Tanaka (1996) develops a model that addresses the evolution of quantitative characters under such density dependence, and shows that strong r selection is expected to occur only if populations are continuously kept below their carrying capacity due to severe and frequent disturbances. Such models could easily be extended to become more relevant to cyclic populations. Evolution under cyclic or otherwise fluctuating dynamics does not always take the classical dichotomous form of r–K selection, where logistic population growth is followed by population crashes – sudden events of 'hard selection' (Wade, 1985) that do not change gene frequencies. Evidence from Soay sheep (*Ovis aries*) (Bancroft *et al.*, 1995) and Darwin's finches (Grant & Grant, 1993, 1995) suggests that population crashes do not kill individuals randomly with respect to genotype. Thus, in cyclic populations, it is conceivable that decline phases may host important selective forces.

In addition to potential trade-offs between a trait's influence on r and K, growth and decline phases will generate interestingly conflicting selection pressures during a population cycle if the success of a trait is dependent on population growth rate (rather than population size alone). Life-history traits related to timing of reproduction are examples of such traits: Fisher's (1930) formulation of reproductive value shows that early reproduction is favoured during periods of population growth, whereas late production of young is valuable in the latter case. Clearly, a full analysis of trait evolution, e.g. age at first reproduction, through population peaks and lows requires tracking the long-term

growth rate of genotypes in density-dependent populations under a variety of temporal schedules of population growth (Rand, Wilson & McGlade, 1994; Yoshimura & Jansen, 1996; Grant, 1997). As an example of such an analysis, Benton & Grant (1999) show how temporal variability can cause marked changes in the evolutionarily stable reproductive effort and lead to the evolution of iteroparity rather than semelparity, compared to a population where vital rates are temporally stable. An interesting example of heightened reproductive effort in variable environments is provided by the arctic fox. In this species, litter sizes vary according to food availability, but inland populations living on strongly fluctuating food supplies (small rodents) produce consistently larger litters than coastal populations that rely on relatively stable resources such as seabirds and fish (Tannerfeldt & Angerbjörn, 1998). Intriguingly, a recent study on historical human populations shows the opposite pattern: the twinning rate in 18th century Finns was higher in stable food conditions than in less secure populations (Lummaa *et al*., 1998).

A further suggestion by Elton (1924) concerns genetic variation in fluctuating populations. He suggests that natural selection in fluctuating populations can choose relatively arbitrarily among several reasonably adaptive alternatives, but on the other hand fluctuations also function as a series of bottlenecks that purge populations of alternative genotypes. This would lead to populations that vary much geographically, but are locally relatively uniform. Indeed, greater diversification in bottlenecked populations has been found in species such as *Drosophila subobscura* (e.g. Balanya *et al*., 1994) and houseflies *Musca domestica* (Meffert & Bryant, 1992), chaffinches *Fringilla coelebs* (Dennison & Baker, 1991), and humans (McKusick, 1978). However, it is less clear whether the milder fluctuations that result from population dynamics, rather than colonisation events, are strong enough to provide a substantial basis for genetic divergence. Fluctuating populations have lowered effective population sizes (Falconer & Mackay, 1996), and since genetic drift operates at a rate inversely proportional to this size, levels of diversification can be predicted to increase with population fluctuations. However, this assumes no differences in generation length or degree of isolation. In reality, dispersal rates are often density dependent (Travis, Murrell & Dytham, 1999) and if fluctuations enhance dispersal at some point of the cycle, the net result in fluctuating populations may be less genetic isolation and less diversification.

In our context, the 'pruning' process as envisaged by Elton (1924) might be seen as less important for several further reasons. First, bottlenecks need to be quite severe before they significantly affect genetic variation (Falconer & Mackay, 1996). In cases where they have an effect, population bottlenecks may actually increase variation available to selection rather than decreasing it, as they may convert epistatic genetic variance to additive variance (Carson, 1990). This process, however, mainly occurs in single bottlenecks and is thus less likely to operate in cyclic populations.

While Elton's (1924) focus was on the 'pruning' effect, temporally fluctuating selection has more recently gained credibility as a potential explanation for the surprisingly high levels of heritable genetic variation that life-history and other traits are found to possess (Mousseau & Roff, 1987; Weigensberg & Roff, 1996). Instead of arbitrarily selecting one genotype, fluctuating selection might help to maintain genetic variation in populations, but to what degree it does so has caused some debate. Scepticism in this matter (Lande, 1977; Turelli, 1988; Barton & Turelli, 1989; Frank & Slatkin, 1990) has been replaced by the view that temporal variation may, when exceeding a threshold strength, indeed maintain significant levels of additive variation in a population if generations are overlapping (Ellner & Hairston, 1994; Hairston, Ellner & Kearns, 1996; Sasaki & Ellner, 1997). Insofar as population size fluctuations lead to temporally varying selection pressures, this could indeed mean heightened evolvability of populations that fluctuate rapidly. Elton's (1924) phylogenetic contrast between the mouse and the beaver uses a sample size ($N = 1$) that could be considered low by modern referees, yet we know of no modern extension of this study.

(3) Reaction norms and evolutionary optima

As discussed above, fluctuating selection pressures will lead to temporal variation in genotype frequencies, and possibly to a stable nonzero amount of genetic variation. These results assume that each genotype produces a specific phenotype. However, a genotype that could 'measure' the state of the environment, and produce the optimal phenotype in that environment, would have improved fitness in all environments (Woltereck, 1909; Schmalhausen, 1949). The relationship between the environmental cue and the trait value is called a reaction norm (e.g. Stearns, 1989). The evolution of plastic reaction norms requires that suitable environmental cues are

available, that there is genetic variability in reaction norms, that the expression of correlated characters is not limited by genetic trade-offs, and that developing a plastic response as such does not impose too high fitness costs (Via & Lande, 1985; Stearns & Koella, 1986; Scheiner & Goodnight, 1984; Reques & Tejedo, 1997).

Several studies document plastic responses to population densities, which points to the relevance of plasticity in populations that experience temporal fluctuations. Winged (dispersing) and wingless phenotypes of insects such as aphids (Kawada, 1987) and planthoppers (Matsumura, 1996) exemplify responses to crowding and/or food scarcity. Even sexually selected traits may respond to local population density: as an example, males of the moth *Plodia interpunctella* develop larger testes and produce more sperm at high larval density, but invest more in competence for migration and mate-searching if larval density is low (Gage, 1995).

As pointed out in previous sections of this paper, trophic interactions are highly relevant in shaping natality and mortality throughout the population cycle, and indeed in generating cyclic dynamics in the first place. It is therefore not surprising that the relevant cue for a density-related plastic response need not always be the species' own density. Antipredatory behaviour is an obvious example that needs to be strengthened in times of high predator density, but should be diminished at other times if its development incurs costs. Indeed, this is found to happen in several taxa: for example, the zooplankton *Daphnia pulex* develops neckteeth that function as antipredatory defence at high abundances of a chaoborid predator (Parejko & Dodson, 1991), and the acorn barnacle *Chthamalus anisopoma* switches to an alternative morphology in the presence of the predatory gastropod *Acanthina angleica* (Lively, 1986). An important group of predator-induced plastic traits are life-history characteristics such as age or size at maturity. Depending on whether predation pressure concentrates on small or large sizes, prey may mature or metamorphose at either smaller or larger size when predation pressure increases (e.g. *Daphnia magna*: Weider & Pijanowska, 1993; snails: Crowl & Covich, 1990; frogs and toads: Laurila, Kujasalo & Ranta, 1998; see also discussion on delayed maturation and breeding suppression in voles, below).

The relationship between the life-history characteristics of species X and the density of species Y is most clearly evident in cases where the life-history change in X results from direct physical contact with Y. Koella, Agnew & Michalakis (1998) review host–parasite interactions, where infected hosts may switch to an alternative life history. Such a switch may represent an adaptive response of the host, but it can also reflect manipulation by the parasite. In either case, the number of infection-induced life-history changes increases with parasite (and possibly host) density, and the host population as a whole will therefore follow a different life history depending on the prevalence of the infection.

However, as the above examples of antipredatory behaviour show, life-history traits may be sensitive to fluctuations in population densities even without such direct contact (which would, in the case of predation, be likely to result in the death of the prey before it has time to change its strategy). Generally, optimal life histories will depend on the information that is available to an individual: will it be able to measure the state of the environment (typically, the density of its own population or that of a predator or prey), or does it only 'know' that these populations obey their characteristic fluctuations? Even when no information on the phase of the cycle is available, the evolutionary information that a pattern of temporal fluctuation exists will affect the optimal life-history strategy, as is clearly shown by the work of Grant (1997) and McNamara (1997, 1998).

The primary reason why population fluctuations make a difference to optimal life histories is that fitness gains of offspring production, and hence reproductive values of the parent, vary with population size. A surviving offspring produced during an increase phase of a cycle will be especially valuable for exactly the same reason that a mutation appearing during a population increase will have favourable prospects (Otto & Whitlock, 1997). When population sizes vary, expected lifetime offspring production is not a valid fitness measure for this same reason. Consider a population with non-overlapping generations that follows a two-point cycle where it first doubles and then halves. A mutant strategy that manages to produce five offspring in the increase phase but none in the decrease phase will simply go extinct in the first instance of the decline, despite its average reproductive rate of 2.5 offspring, which clearly exceeds the 1.0 achieved by the predominant strategy. In such settings, geometric mean fitness must be used to evaluate the success of strategies (McNamara, Webb & Collins, 1995; Yoshimura & Jansen, 1996), and this equals zero for our unfortunate mutant.

Generally, dynamic optimisation techniques can be used to track the evolutionary success of life-

history strategies in a population that varies in size (McNamara *et al*., 1995). Using this kind of dynamic approach, Marrow *et al*. (1996) show that ewes of the Soay sheep make optimal reproductive decisions, when it is assumed that they have no information on the phase of the population cycle. Here, reproductive decisions (producing twins, a single lamb, or to skip reproduction) are based on mass and age of the ewe, but not on density of the population. Since the distribution of ewes in different mass and age classes varies during the cycle, this will, at a population level, lead to different reproduction in different years.

In reasonably regularly fluctuating environments such as that provided by vole cycles in boreal forests, it is also possible that individuals can measure the phase of the cycle and take this into account in their reproductive decisions. In Tengmalm's owls *Aegolius funereus* and in Ural owls *Strix uralensis*, species which both prey on voles, lifetime fitness is strongly dependent on the phase of the vole cycle in which an individual starts to breed (Korpimäki, 1992; Brommer, Pietiäinen & Kolunen, 1998). In the case of Ural owls, females that start breeding in a peak year have only half the fitness of females starting in an increase year. Survival of both breeding females and their offspring is low after a peak when vole populations crash (Korpimäki & Lagerström, 1988; Brommer, Kokko & Pietiäinen, 2000). This makes young born in peak years less valuable than those born in increase years, and one may thus expect reproductive effort to concentrate on increase years of the cycle rather than on peak years. This indeed appears to be the case both in Ural owls (Brommer *et al*., 2000) and in Tengmalm's owls (Hakkarainen, 1991; Hakkarainen & Korpimäki, 1994*a*–c). Interestingly, kestrels *Falco tinnunculus* breeding in Finland seem to be unable to adjust their breeding effort optimally, possibly because they lack site tenacity (Tolonen & Korpimäki, 1994, 1995, 1996).

Yet, it must be recognised that varying survival prospects of young are not the only factor that determines parental effort. If all other factors were equal, parental effort should increase when offspring face favourable prospects (Hirshfield & Tinkle, 1975). In a cyclic population, however, other factors do not remain constant though time: reproductive values of both parents and offspring will fluctuate according to the phase of the cycle (Brommer *et al*., 2000). Determining optimal reproductive decisions then requires considering the trade-off between the number (and quality) of offspring and the parent's own future prospects. These may also depend on whether costs of breeding are 'paid' before or after reproduction (Jönsson, Tuomi & Järemo, 1998). As an example, a delayed cost of breeding may have a much stronger effect on the survival of a parent when it has bred in a peak year and attempts to survive on the scarce food supply of the following winter, than when it has bred in an increase year and continues to overwinter with an abundant food supply. Indeed, a model of Ural owl reproduction shows that delayed costs of reproduction are necessary to explain the observed dynamics of breeding in this species (Brommer *et al*., 2000).

(4) What is the role of adaptive dynamics?

As the above sections show, fluctuations in population size have the potential to alter the outcome of selection as well as cause the evolution of complex plastic responses to population density. An interesting corollary follows when recognising that the value of any adaptation is ultimately measured as a rate of offspring production. Therefore, the evolution of adaptive traits in temporally varying populations will also lead to changes in birth and death rates, which will in turn determine the dynamics of the population. This forms a feedback loop between population dynamics and selection. Instead of simply assuming that some measure of fitness is maximised, it is increasingly recognised that adaptational analyses should ask which strategies may invade in a population that follows such a feedback loop (Metz, Nisbet & Geritz, 1992; Rand *et al*., 1994; Mylius & Diekmann, 1995). One should also note that the idea of dynamics being influenced by evolutionary processes is not new; it was discussed by Voipio early in the 1950s (Voipio, 1950*a*, *b*), although due to historical reasons (Chitty, 1996) this idea has come to be known as the 'Chitty hypothesis' after Chitty (1960, but see Voipio, 1998).

Recently, a wealth of theoretical models have been developed to explore the properties of such feedback loops, summarised under the concept of 'adaptive dynamics' (reviewed in Dieckmann, 1997; Dieckmann & Metz, in press). Several of such models are relevant for cyclic populations, as they shed light on the conditions under which behavioural or life-history evolution may shape the dynamics of species at one or more trophic levels.

Interestingly, interactions such as frequency dependence of fitness or ecological two-species interactions may hinder the evolution towards maximal fitness: evolutionarily stable fitness minima can be found in such settings (Abrams, Matsuda & Harada,

1993). Considering the dynamic consequences of such evolution, a recurring result in theoretical models is that adaptive changes in behaviour during a population cycle may reduce population fluctuations or lead to stable population dynamics. As a single-species example, adaptive habitat choice may cause cycles to disappear (Fryxell, 1997), and in a two-species model, adaptive refuge use by prey may damp Lotka-Volterra dynamics (Krivan, 1998). However, this appears not to be a general rule as opposite examples also exist. Models of predator–prey cycles indicate that the evolution of prey to become less vulnerable to predators, either alone or together with coevolving predators, may cause cycles in both the population sizes of predators and their prey and in the evolving traits (Abrams & Matsuda, 1997*a*, *b*).

Life-history characters such as maturation time or brood or clutch size form probably the clearest example where decisions taken by individuals have direct impact on population dynamics. A much debated issue in this field has been the extent to which antipredatory strategies of small mammals could influence the cyclic nature of their dynamics (Ylönen, 1994; Koskela & Ylönen, 1995). Delaying reproduction may be advantageous in the peak or decline phase of a cyclic prey population, for reasons outlined above: offspring born late are of higher value in such a setting, and current reproductive attempts may simply be too risky if predation pressure is high. This could steepen the population crash and thus possibly lead to enhanced cyclicity. This phenomenon has inspired a multitude of models, of which one thread suggests that different breeding strategies (delaying and breeding) may coexist in a single population (Kaitala, 1997; Kaitala *et al*., 1997*b*), one casts doubt on the evolutionary advantage of delaying with realistic parameter values (Kokko & Ranta, 1996), and two suggest that breeding suppression may occur but that the dynamical outcome is more likely to be a stabilisation of the dynamics rather than enhanced cyclicity (Gyllenberg *et al*., 1997; Ruxton & Lima, 1997). By relaxing the assumption of specific density-dependence functions and allowing for variable brood sizes in addition to completely abandoning breeding, Kokko & Ruxton (2000) showed that suppression may be an evolutionarily stable behaviour in either predators or prey, and that when it occurs it may either stabilise or destabilise the dynamics, depending on the shape of density-dependent functions.

Against this (rather confused!) theoretical background it is interesting to note that some of the empirical evidence for adaptive breeding suppression has recently been refuted in small rodents (e.g. Lambin *et al*., 1995; Klemola *et al*., 1998; Mappes *et al*., 1998; Prévot-Julliard *et al*., 1999). In their avian and mammalian predators, however, brood size adjustments certainly occur (reviewed in Kokko & Ruxton, 2000), but the impact this has on their population sizes and on the cyclic interaction has not been empirically verified. Studies on the effect of adaptive breeding decisions on population dynamics are undoubtedly hampered by the difficulty of designing an experiment where brood size adjustments could be prevented on a population-wide scale.

Another interesting example of the interaction between dynamics and adaptive evolution is provided by periodical *Magicicada* cicadas whose life spans are extremely long (13 or 17 years) and where the adults emerge synchronously (Beamer, 1931; Lloyd & Dybas, 1966*a*, *b*; Williams & Simon, 1995). Several models suggest that synchronous emergence could, at least under specific conditions, evolve in two-trophic interactions (Hoppenstadt & Keller, 1976; Bulmer, 1977; Godfray & Hassell, 1987). The long prime numbered generation length has been argued to be adaptive as it makes it very difficult for a shorter-lived predator to track the abundance of its prey (Lloyd & Dybas, 1966*b*; Williams & Simon, 1995). Further perfection of the periodicity could follow if there is strong interference competition between nymph age classes (Hoppenstadt & Keller, 1976; Bulmer, 1977). However, the importance of these dynamical factors relative to other explanations remains debated to this day (Heliövaara, Väisänen & Simon, 1994; Yoshimura, 1997; Cox & Carlton, 1998; Itô, 1998).

In general, evolutionary responses of populations to fluctuations of their sizes, including plastic behaviour, are undoubtedly an important component of the evolutionary process: West-Eberhard (1989) indeed suggests that phenotypic plasticity may strongly enhance diversification and speciation. Curiously, as shown above, most work on evolution in fluctuating populations is relatively recent, and Elton's (1924) ideas seem to have been seeds fallen on stony ground. The emphasis that Elton puts on population density fluctuations affecting the process of adaptation remains undoubtedly valid, even though his ideas seem to have been rediscovered independently more than half a century later. Currently, there is great interest in the theory of adaptive dynamics (Dieckmann & Metz, in press),

but empirical applications are still largely lacking. According to Elton (1924, p. 154), 'the following suggestions as to the effect of periodic fluctuations in the numbers of animals upon the method of evolution are speculative, but at the same time are mostly self-evident when once thought of'. The summary above shows that we may have pushed the frontier of knowledge further by major steps, but regarding the interplay of population dynamics and evolutionary processes, we are largely in the same position as Elton was 75 years ago: a wealth of plausible ideas is waiting to be tested. Hopefully, a new generation of research can shed more light on this issue.

VI. THE ROLE OF SPACE

(1) Elton and his contemporaries

One of our major arguments is that Elton (1924) was not solely interested in the causes of multi-annual fluctuations in animal numbers but also in the reasons behind the large-scale synchrony in the dynamics of the Norwegian lemming and the snowshoe hare. In light of the recently revived interest in spatial ecology, it becomes evident that Elton is, in fact, talking about population synchrony when he discusses climate, although this has been largely overlooked. He very explicitly discusses this synchrony with reference to the periodic population fluctuations of the Canada lynx (Elton & Nicholson, 1942, pp. 239–240): 'The [lynx] cycle covers the whole northern forest zone of Canada, from Labrador to British Columbia to Yukon.'…'The most extraordinary feature of this cycle is that it operates sufficiently in line over several million square miles of country not to get seriously out of phase in any part of it.'…'[This evidence] makes it certain that some overriding process maintains the cycle in line over the whole extent of Canada.'

Pat Moran spent from 1946 to late 1951 in Oxford at the Institute of Statistics which shared accommodation with the Bureau of Animal Population and the Edward Grey Institute of Ornithology. He was therefore able to talk directly with Charles Elton, P. H. Leslie and David Lack. This led to a series of papers on population dynamics by Moran (1949, 1950, 1952, 1953*a*, *b*). Using long-term data on British game birds (Mackenzie, 1952), Moran (1952, 1953*a*, *b*) developed tools to assess statistically the level of synchronous fluctuations between any pair of time series. Moran (1953*b*) also proposed the idea of how two (or more) populations could become synchronised due to stochastic density-independent but correlated processes. His assumption was that population regulation may be density dependent, and that populations may be divided into smaller independent subpopulations. Thus, he argued that stochastic density-independent but correlated processes may cause local populations to fluctuate synchronously.

Suppose (Moran, 1953*b*) the dynamics of two populations $X_1(t)$ and $X_2(t)$ in time t can be described as:

$$X_1(t+1) = aX_1(t) + bX_1(t-1) + \epsilon(t), \qquad (5a)$$

$$X_2(t+1) = aX_2(t) + bX_2(t-1) + \eta(t), \qquad (5b)$$

so that the a and b are identical in $X_1(t)$ and $X_2(t)$. The random elements $\epsilon(t)$ and $\eta(t)$ are different but correlated. The correlation arising between $X_1(t)$ and $X_2(t)$ will then equal the correlation between $\epsilon(t)$ and $\eta(t)$. If the density-independent series $\epsilon(t)$ and $\eta(t)$ are caused by, or just correlated with regional disturbances, there is a plausible explanation for the synchronous dynamics of the two populations $X_1(t)$ and $X_2(t)$. The density-dependent coefficients a and b do not necessarily need to be perfectly matching between the two populations. Synchronous dynamics are still achievable via external disturbances but the correlation between $X_1(t)$ and $X_2(t)$ will not equal that between $\epsilon(t)$ and $\eta(t)$. This reasoning has since become known as the Moran theorem (Royama, 1992) or the Moran effect (Ranta *et al.*, 1995, 1997*a*, 1999*b*).

George Leslie soon proposed a matrix-modelling approach to the Moran effect (Leslie, 1959). Since then, Moran's theorem was largely neglected until revived very influentially by Royama (1992). In Leslie's own example, he assumed two non-connected populations (both with four age groups) living in limited environments. These populations should be proximate enough to share in common the effect of some external random and density-independent factor. Under these conditions Leslie (1959) derived the population renewal process to be

$$\mathbf{N}_i(t+1) = \mathbf{L}\mathbf{R}^{-1}(t)\,\mathbf{N}_i(t), \qquad (6)$$

where $\mathbf{N}_i(t)$ is the column vector indicating the number of individuals in each age group of the ith population, $\mathbf{L}$ is the Leslie matrix (where the first row gives age-group-specific fecundities, and the first sub-diagonal indicates corresponding survival probabilities), while $\mathbf{R}$ is a diagonal matrix containing the density-dependent components topped with the Moran noise. Leslie showed that an iteration of such

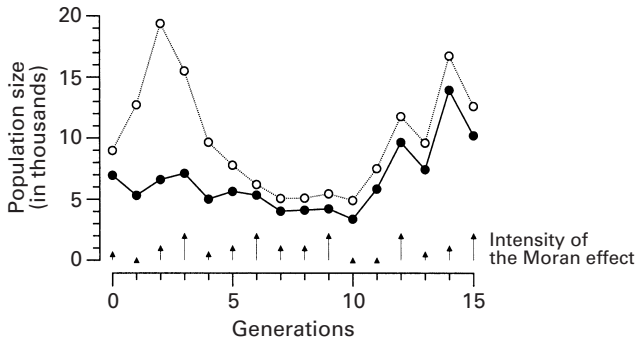

Fig. 5. Leslie's example of the Leslie-matrix approach to the synchronising effect of the Moran disturbance of dynamics of two age-structured populations. The two populations, initially out of phase, will eventually merge to fluctuate in step due to the external disturbance (the length of the arrows indicates the strength of the effect: scale 0, 0.5, 1, 1.5, 2). The data are taken from Table 2 in Leslie (1959).

a system for two populations, initially fluctuating out of phase, will rather soon (in fact on the sixth iteration step) become synchronised in their fluctuations (Fig. 5).

Huffaker (1958) developed an experimental system of oranges on a tray with mites, representing predators and prey, dispersed among the resource patches. His results, among other things, suggest that dispersal can synchronise the dynamics of local populations. A similar system was demonstrated theoretically by Andrewartha & Birch (1954) and much later in a lattice model by Maynard Smith (1974). After these pioneering steps, however, the significance of space in affecting the dynamics of populations was not examined further for many years.

(2) Spatial population dynamics now

The role of space in determining not only large-scale dynamics but also local dynamics has been studied extensively during the 1990s, and we do not attempt to provide a complete review here (for recent reviews, see e.g. Bascompte & Solé, 1997; Tilman & Kareiva, 1997; Hanski & Gilpin, 1997). Instead, we aim to show briefly how Elton's intellectual legacy is still part of the active research into spatial ecology.

The elaboration of the Moran theorem (Moran 1953*b*; Royama 1992) has recently gained increasing attention simultaneously with a shift of focus of population ecology research from single or isolated populations to populations coupled by dispersal (e.g. Bascompte & Solé, 1995, 1997; Hanski & Gilpin, 1997, Tilman & Kareiva, 1997). The current views of population ecologists emphasise the importance of the interplay of density-dependent and density-independent factors (Kaitala *et al*., 1996; Higgins *et al*., 1997; Bjørnstad *et al*., 1998; Grenfell *et al*., 1998), thus echoing Moran's (1953*b*) seminal ideas. A central finding of the current research, substantiated also by increasing evidence from long-term spatial time-series data sets from different animal taxa, suggests that populations tend to fluctuate in step over large areas and that the degree of synchrony levels off with increasing distance among the population units compared (Hanski & Woiwod, 1993; Ranta *et al*. 1995, 1997*a*, 1999*b*; Lindström, Ranta & Lindén, 1996*b*; Lambin *et al*., 1998; Bjørnstad, Ims & Lambin, 1999*a*; Bjørnstad, Stenseth & Saitoh, 1999*b*; Paradis *et al*., 1999; Kendall *et al*., 2000; Ripa, 2000).

According to one interpretation, the Moran effect (Moran, 1953*b*; Royama, 1992) can be understood as a global disturbance influencing the renewal processes similarly and simultaneously in different subpopulations or localities. We know that this kind of a Moran effect is capable of synchronising the dynamics of otherwise independent populations. However, in the exact process described by Moran's theorem, the level of synchrony will not decrease with increasing distance. This prediction does not correspond to empirical observations. Consequently, two different alternatives have been proposed to develop Moran's idea further. First, the dispersal of individuals linking population sub-units has been put forward to explain this feature (Ranta *et al*., 1995, 1997*a*, *b*,*c*; Ranta, Kaitala & Lundberg 1997*c*, 1998; Heino *et al*., 1997; Kaitala & Ranta, 1998). Second, Ranta *et al*. (1999*b*) have developed a novel modelling approach incorporating both a spatially autocorrelated Moran effect and dispersal. With several different model classes on population renewal, they show that spatially autocorrelated disturbances alone and especially together with dispersal linkage are capable of producing synchronous dynamics with synchrony levelling off with distance. Another aspect of the large-scale dynamics of populations is that at the local level, temporal changes in population density can be interpreted as 'travelling wave dynamics'. Again, vole population data have played a central role in unravelling the presence of travelling waves (Ranta & Kaitala, 1997; Kaitala & Ranta, 1998; Lambin *et al*., 1998; Bjørnstad *et al*., 1999*a*). Thus, this recent work brings us back to Elton (1924) who discussed the effects of climatic disturbances causing populations

over vast geographic ranges to become synchronised – but not perfectly – in their fluctuations.

VII. CONCLUSIONS

We have examined the impact of Charles Elton's article on 'Periodic fluctuations in the numbers of animals: their causes and effects' on the development of modern population ecology. We have examined evidence that the significance of Elton (1924) has been substantial and over the past 75 years of research on multi-annual periodic population fluctuations of voles, lemmings, hares, lynx and game animals he has contributed much to the contemporary understanding of the causes and consequences of population regulation. To summarise our review:

(1) Elton (1924), from the evidence he had available, was convinced that agent behind the regular fluctuations was climatic variation. He used the large-scale cyclic dynamics of the Norwegian lemming in Scandinavia and the snowshoe hare in Canada to illustrate this. Elton (1924), however, also outlined many of the hypotheses thus far put forward as an explanation for this enigmatic behaviour of the long-term dynamics of some populations.

(2) Elton (1924) also speculated on the evolutionary consequences of periodically fluctuating populations. This part of his paper was largely overlooked until very recently and contemporary authors seem to be largely unaware of Elton's contribution. Elton recognises several genetic consequences of fluctuating population sizes, which later have been verified to be important at least in some scenarios. Current evolutionary thinking has extended genetic and optimality approaches to take into account their ecological causes and consequences; there is necessarily a two-way interaction between the behaviour and life-history strategies of individuals and the dynamics of the population that they form.

(3) The pattern of multi-annual periodicity in fluctuations of population numbers has captivated many ecologists since Elton (1924). Researchers have devised many hypotheses to explain the causes behind the cyclic dynamics. Despite this the origins and causes of multi-annual periodic fluctuations in animal populations are not yet fully understood. Elton placed so much emphasis on the 'enigmatic' periodic population fluctuations that to some extent, this has distracted subsequent generations of ecologists away from more general problems in population and community ecology (Sandell *et al.*, 1991). The never-ending disagreements between different vole cycle 'camps' has certainly been productive but not synergistic or conclusive (Stenseth, 1999).

(4) The most promising recent developments are perhaps not the collection of new and better data, nor the confirmation or rejection of some of the classic hypotheses, but that a very powerful research programme, or methodology, is becoming firmly established in population and community ecology. There is a huge body of good theory that is now starting to be used for deriving predictions and for synthesising disparate sets of observations. New tools in pattern-oriented statistics, new methods in transforming capture-mark-recapture results to demographic models and especially the cross-fertilization of these fields are becoming fashionable and fruitful. Together, these approaches, and with the huge body of data available, make the progress in this field almost inevitable. This prediction is supported by major recent efforts in this direction (Stenseth *et al.* 1999; Kendall *et al.*, 1999). However, instead of asking why population cycles exist and which factors drive them, we raise the level of ecological problem setting by confining ourselves to how demography (and density dependence) interacts with spatial and temporal environmental variability – hoping that we will also answer the cycle question.

(5) During the past decade field data have started to accumulate on vole populations, that indicate that the characteristic cyclic periodicity is fading away, at least temporally, in vast regions of northern Finland and Sweden (Henttonen *et al.*, 1987; Hansson, 1999; Hansen *et al.*, 1999*a*). These have been the areas where the best-quality quantitative data on multi-annual periodic fluctuations in microtine population numbers have been collected since the early days of Olavi Kalela (1962; Henttonen, 1985; Hansson & Henttonen, 1988; Hanski *et al.*, 1991). It is an irony that the cyclic dynamics of Scandinavian voles seem to be disappearing just as vole ecologists have begun to understand how to begin solving the underlying mechanisms (Hanski *et al.*, 1993; Stenseth, 1999; Henttonen, 2000). Thus, it may soon be more practical to start testing the various hypotheses (Batzli, 1992; Fig. 3, Table 1) by trying to initiate cyclic dynamics in experimental enclosures in the areas where the documented cycles were known to occur between the late 1940s to the mid 1980s (Kalela, 1962; Henttonen *et al.*, 1987). As suggested by Stenseth (1999), this approach may provide the best evidence that ecologists have

properly understood density-dependent mechanisms behind population fluctuations.

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