

Review



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Population cycles: generalities, exceptions and remaining mysteries

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Population cycles are one of nature's great mysteries. For almost a hundred years, innumerable studies have probed the causes of cyclic dynamics in snowshoe hares, voles and lemmings, forest Lepidoptera and grouse. Even though cyclic species have very different life histories, similarities in mechanisms related to their dynamics are apparent. In addition to high reproductive rates and density-related mortality from predators, pathogens or parasitoids, other characteristics include transgenerational reduced reproduction and dispersal with increasing-peak densities, and genetic similarity among populations. Experiments to stop cyclic dynamics and comparisons of cyclic and noncyclic populations provide some understanding but both reproduction and mortality must be considered. What determines variation in amplitude and periodicity of population outbreaks remains a mystery.

1. Introduction

If nothing in biology makes sense except in light of evolution, one could argue that nothing in ecology or evolution makes sense except in light of population dynamics. (Tom X Miller, <http://www.owl.net.rice.edu/~tm9/research.htm>).

Populations are the cornerstones of communities, ecosystems and the basic units of biodiversity because whether species are expanding or going extinct is determined by their population dynamics. To identify controlling factors, we need to determine the differences between increasing and declining populations. Thus much basic population ecology has been done with cyclic species. The dynamics of lynx, *Lynx canadensis*, and snowshoe hares, *Lepus americanus* [1] (figure 1), was the first empirical demonstration of the predator–prey cycles described in the classic models that Lotka and Volterra developed during the 1920s. In 1931, the Matamek Conference on Biological Cycles considered the potential roles of predators, parasites and food on population cycles, as well as extrinsic factors such as temperature, rain and sunspot cycles [2].

In the 87 years since the Matamek Conference, innumerable field and modelling studies have been carried out on cyclic populations. Recent comprehensive reviews have been written on cyclic population dynamics of snowshoe hares [3], voles and lemmings [4], forest Lepidoptera [5] and red grouse [6]. However, a synthesis across groups has not been made to shed light on population dynamics of cyclic species in general.

Here, I present a brief overview of these four groups of animals best known and most studied for their population cycles. This review reflects my personal interest in identifying general patterns and mechanisms that yield insights about the 'mystery' of population cycles. I consider: what causes cyclic dynamics? How do cyclic and noncyclic populations differ? Can cyclic dynamics be stopped experimentally? And what are the roles of extrinsic and intrinsic factors in driving the population fluctuations? Finally, I review several hypotheses that, although fascinating, have been rejected numerous times and should now be laid to rest. My aim is to identify the progress that has been made and to discover areas that are ripe for further study in the ecology of population cycles.

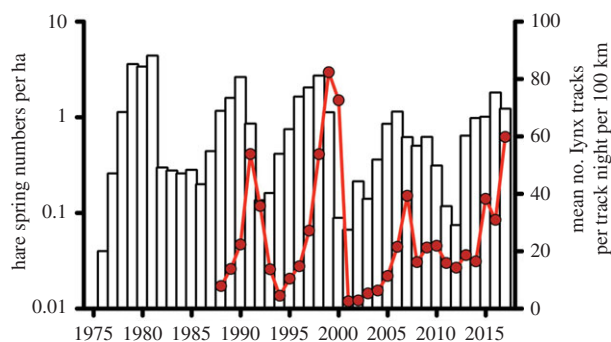


Figure 1. Population trend (bars) for snowshoe hares and lynx track index (line) in the Kluane Lake region of the Yukon Territory. Data from C.J. Krebs <http://www.zoology.ubc.ca/~krebs/kluane.html>. (Online version in colour.)

2. Causes and characteristics of population cycles

The requirements for cyclic dynamics are straightforward; a high reproductive rate to allow the population increase, density-related mortality to slow and stop the increase, and a prolonged negative condition to delay the recovery of the population [5]. Cyclic dynamics can occur if the density-dependent mortality mechanism is nonlinear [7] or over compensating [8]. If the density-dependent mortality is linear, a delayed process is required to produce cyclic dynamics [9]. This could be a carry over from reduced reproduction caused by stress or food limitation [5], deteriorating resource conditions [10], reduced quality of individuals with cross generational influences [11], or continued reduced survival from natural enemy attack into the decline such as a switch from specialist to generalist predators or parasitoids [12].

The lengths of population cycles vary from 3 to 5 years in small mammals, 6 to 9 years for red grouse, and 8 to 11 years for snowshoe hares and forest Lepidoptera. Some have speculated that the periodicity of cycles is related to the number of generations a year and have proposed that this is scaled to body size, and rate of population increase for mammals [13]. A common characteristic of cyclic dynamics is an asymmetry such that the increase phase tends to be longer than the decline phase [7,14,15]. This could result if there are constraints on the potential magnitude of the rate of increase but not on the rate of decline. Variation in the degree and lengths of the increase and decline phases causes the amplitude and periodicity of the cycles to vary. One approach to discovering the processes underlying cycles is to compare cyclic and noncyclic populations.

3. Comparing cyclic and noncyclic populations

One opportunity to compare cyclic and noncyclic populations is the North–South gradient in the amplitudes of voles and autumnal moth, *Epirrita autumnata*, cycles in Fennoscandia [12,16]. This is explained by generalist and nomadic predators being directly density dependent and stabilizing the vole populations in the south while specialist predators in northern regions such as the least weasel, *Mustela nivalis nivalis*, can respond both directly to their prey abundance and with delayed density dependence in the North. This is not a general explanation, however, as in northern England weasel predation was shown

experimentally to be insufficient to drive cyclic dynamics of the field vole, *Microtus agrestis* L. [16,17].

The 10-year cycles of the autumnal moth are also much stronger in the North where attack by the wasp parasitoid, *Cotesia jucunda*, showed delayed density dependence [12]. In southern populations, only small mammal predators of pupae caused weak density-related mortality that added to the density-independent mortality from invertebrate predators and parasitoids. According to this interpretation, variation in the type of parasitoids between northern and southern populations determines whether populations of autumnal moth are cyclic or not [12].

Cycles of some forest Lepidoptera are also more obvious in harsher environments such as inland versus coastal (autumnal moth and winter moth, *Operophtera brumata* [12]) and mountain versus lowland areas (larch budmoth, *Zeiraphera diniana* [18]). On the island of Reinøya in northern Norway densities of both autumnal moth and winter moth are lower at the coast than at higher elevations [19]. Although populations of these moths never reach defoliation densities, their dynamics are synchronous with those in continental areas of Fennoscandia driven by density-dependent egg, larval and pupal parasitoids [20] and changes in moth size [21]. On Reinøya, larval parasitism was neither density dependent nor related to the rate of population growth [19]. How these populations remain cyclic at low amplitude and without density-dependent parasitism remains unexplained although dispersal of ballooning larvae from outbreak populations on the mainland [22] could possibly populate populations and create low-density fluctuations. Alternatively, some other unstudied extrinsic or intrinsic mechanism drives the low amplitude cycles.

Red grouse, *Lagopus lagopus scotica*, population numbers, as indicated by shooting records, vary in the degree to which they show cyclic dynamics and population trends range from strongly cyclic to random [23] (figure 2). Some evidence suggests that the differences between cyclic and noncyclic populations of grouse are related to the fragmentation of the habitat; populations on fragmented habitats are noncyclic [24].

Habitat fragmentation is likely to influence variation in the cyclic dynamics of other species as well. For example, forest fragmentation was associated with reduced amplitude, synchrony and frequency of outbreaks of spruce budworm as shown by tree rings in northern USA and Canada [25]. Population outbreaks of forest tent caterpillars, *Malacosoma disstria*, persist longer in fragmented forests [26]. And fragmentation can influence dispersal of vole populations and the amplitude of fluctuations. The ROMPA hypothesis (ratio of optimal to marginal patch area) predicts that increasing fragmentation increases the amplitude of vole population fluctuations within good habitat patches as dispersal is reduced [27]. How habitat fragmentation influences the amplitude of population cycles is complex and likely influenced by dispersal potential and success of the species.

Another opportunity to compare cyclic and noncyclic populations arose when cycles of voles and some forest Lepidoptera began to collapse starting in the 1980s in Europe [28,29]. This has been attributed to warming climate. Ims *et al.* [28] reviewed eight studies of voles, grouse or hares that showed geographical or temporal reductions in cyclic dynamics and found that population trends indicated reduced or delayed density dependence for six examples.

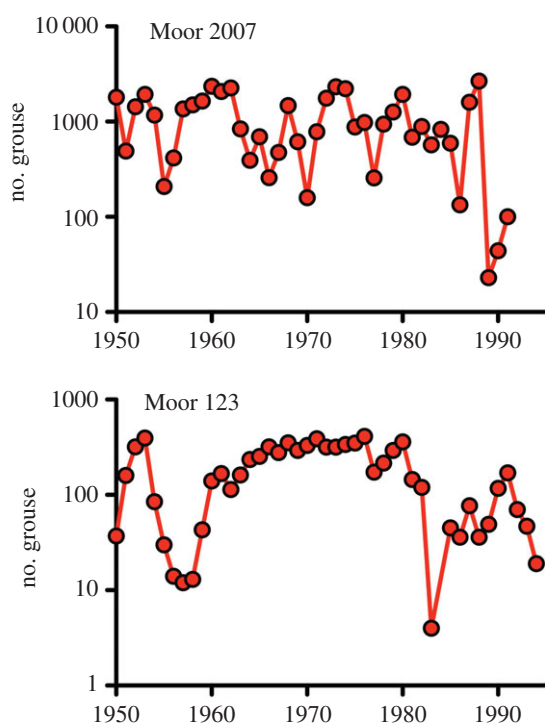


Figure 2. Red grouse bag time-series showing variation in temporal patterns among two different moors in the United Kingdom. Data from Darren Shaw and Dan Hayden, University of Glasgow. (Online version in colour.)

These changes were attributed to increases in generalist predators or decreased winter survival. However for voles, the evidence for warmer winters reducing the amplitude of the outbreaks is contradictory (see [30] and references therein). Cycles were not reduced in large areas of northern Europe, and cyclic dynamics of vole populations may be strengthening again in some more southern areas [30].

The amplitude of outbreaks of larch budmoth also declined in the late 1980s. This was attributed to a disruption of the phenology of egg hatch and leaf development ([31] and discussed in [5]) and changes in the elevation for optimal population growth [32]. In addition, prediapause temperatures in the autumn influence survival and vigour of larvae before egg hatch such that warm temperatures are detrimental. Cyclic dynamics of larch budmoth continued but at significantly lower amplitude in France (A Roques 2018, personal communication), and in Switzerland are beginning to reach higher densities again (B Wermelinger 2017, personal communication). Thus although overall warming is occurring, variation in temperatures at important times such as in the autumn and at egg hatch could still influence conditions for budmoth population growth and influence cyclic dynamics.

The return of higher amplitude cycles indicates that a simple relationship with warming climate is not a sufficient explanation for the hiatus of cyclic dynamics of some European voles and larch budmoth. Other aspects of the ecosystem change such as habitat modifications must be considered. Continued study of populations as they return to cyclic dynamics should provide the opportunity to test hypotheses about changes in predation and phenology.

4. Can cyclic dynamics be stopped?

One way to test the causes of cyclic dynamics is to remove conditions thought to be responsible. This has proven to be

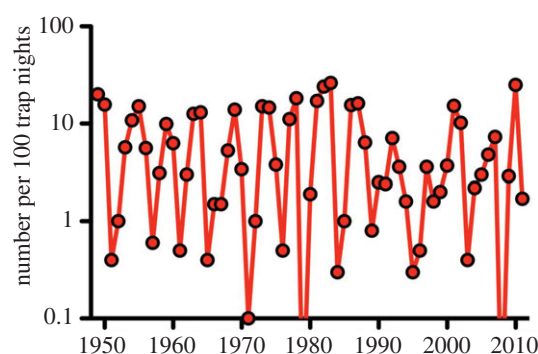


Figure 3. An example of cycles of a vole. Numbers of *Myodes rufocanus* snaptraps in the autumn in northern Finland. Data collected by Heikki Henttonen and provided by Charles Krebs. (Online version in colour.)

difficult because manipulations must be done on large scales and over long time periods. In one attempt, spraying cyclic populations of Tussock moth late in the increase phase with a nucleopolyhedrovirus, a naturally occurring pathogen, elicited an early population decline [33]. This did not prolong the cycle, however, as all populations declined the next year from natural infection [33,34]. Neither cropping populations of tent caterpillars to prevent peak densities nor introducing egg masses to new areas disrupted cyclic dynamics [35], and dispersal into treated areas likely overwhelmed the manipulations of these Lepidoptera.

To determine if adding food or excluding mammalian predators could stop the snowshoe hare cycle, Krebs *et al.* [3] carried out large-scale experiments on 1 km² plots in the Boreal Forest in the Yukon. In one plot they added rabbit chow, in another they excluded mammalian predators with an electric fence, and in a third plot they both added food and excluded predators. Only the combined treatment of food and predator exclusion improved the survival and reproductive output of hares sufficiently to maintain numbers over the period of population decline in open plots [36].

Numerous experiments have been done in attempts to delay the decline or stop the population cycles of lemmings and voles (figure 3) by feeding or excluding predators. These have had mixed results and Krebs [4] concluded that predators can 'modify' population cycles, but that predator removal cannot stop cyclic dynamics. Similarly, food addition experiments can modify vole densities but not drive cycles.

Predation is not considered to be a cause of population fluctuations of red grouse [37]. Although infection by the nematode parasite *Trichostrongylus tenuis*, is common in red grouse and reduces the production of young and can cause death [38], removing the parasite by treating with an anthelmintic in the winter was not sufficient to prevent the decline in the breeding density of grouse the next summer [39]. Population decline of red grouse was however stopped by the removal of dominant males. This increased the recruitment of young cocks and prevented the population decline for 5 years. Thus, in this species social behaviour acting through male territoriality can influence the recruitment of young and potentially cyclic population dynamics [40].

Overall, experimentally stopping or starting population cycles has proven to be largely impossible. This is perhaps an unrealistic goal for field populations where dispersal can overwhelm the influence of manipulations. It is likely

however that the density-dependent factors necessary for cyclic dynamics are not simple presence–absence mechanisms. One thing that is clear from manipulations of populations is that cycles are caused not only by changes in mortality but also by changes in reproduction [41].

5. Changes in mortality versus reproduction

Changes in reproduction, particularly continued reduced fecundity or delayed reproduction into subsequent generations following peak populations, can greatly influence population dynamics [42]. For snowshoe hares, reproductive output is lower for several years before the peak density and through the population decline [43,44] as females produce fewer than the maximum of four litters. This can reduce reproductive output by 50% (two versus four litters per year). Recent work has shown that this reduced reproduction is possibly caused by stress associated with predator avoidance [45]. This impact is carried over to subsequent generations perhaps through epigenetic changes in expression of stress regulatory genes [3]. For snowshoe hares, the length of the decline phase is related to the rate of population decline suggesting that high levels of predator risk associated with rapid population declines might cause stronger and longer lasting epigenetic influences [46].

Reproduction of voles and lemmings is also lower during the population decline [47], and the social behaviour of these small mammals influences their survival and reproduction as population density changes [48]. This has been shown mathematically to produce cyclic dynamics [49]. Dispersal is also an important element of population regulation. In 1971, we showed that dispersal of young field voles was common from increasing populations [50]. This movement to vacant suitable patches of habitat allows populations to increase regionally and is necessary for population regulation as shown by the continued increase of fenced populations from which dispersal is prevented [51].

The social scenario that characterizes cycles of voles includes high reproduction and dispersal in the increase phase, and reduced recruitment in the peak phase when the age at first reproduction is older and the breeding season is shorter [48,49]. A delay in the beginning of reproduction in the spring, perhaps associated with stress [52], has been shown mathematically to generate cycles [49]. In his review Krebs, concludes that while age at maturity and the length of the breeding season change with population density, litter size and pregnancy rate do not [4].

A recent model of vole cyclic dynamics [53] incorporates information on predation, negative density-dependent dispersal and sociality and includes the influence of dominant males on female reproductive success. This model shows that the best fit to empirical observations in terms of amplitude and periodicity of the cycles occurred when the model included all three factors. Thus, measuring predation alone is not sufficient for understanding cyclic dynamics in voles.

Cyclic populations of Western tent caterpillars in southwestern British Columbia show a pattern of a 15–20% reduction in fecundity beginning late in the population increase and into the population decline [34] (figure 4). This could be a sublethal effect of infection by a nucleopolyhedrovirus [54]. Mortality from high levels of infection in peak populations and delayed recovery of fecundity are considered

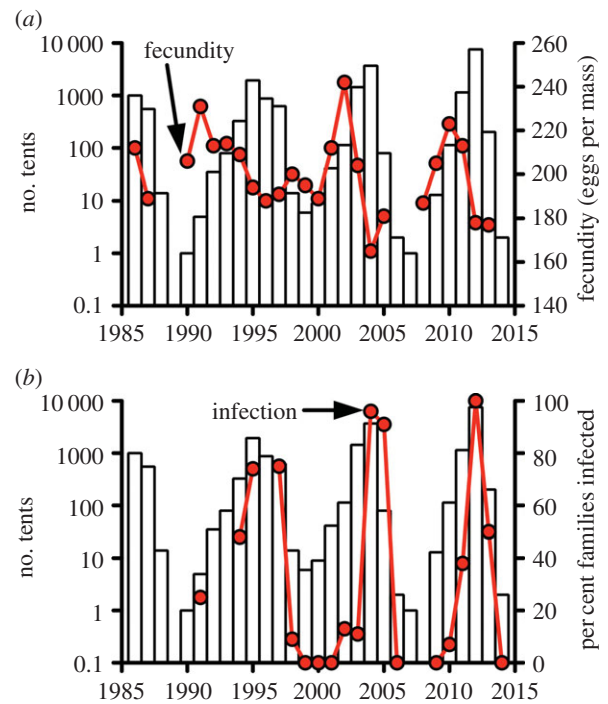


Figure 4. (a) Population and fecundity trends for a population of Western tent caterpillars on Galiano Island. (b) Population and trends in infection by nucleopolyhedrovirus for the same population (see [34] for methods). (Online version in colour.)

to be the drivers of cyclic dynamics in this species [34]. Infection by a protozoan reduced the fecundity of another cyclic Lepidoptera, the spruce needle miner, *Epirzotia tedella* [55]. Reduced fecundity or surrogates for fecundity such as moth size are characteristic of declining populations of other cyclic forest Lepidoptera [5,21]. Models can be used to show that including reduced fecundity causes the simulated dynamics to be more realistic [56,57].

For red grouse, male territorial behaviour affects the recruitment of young. During the increase and peak population phases, subordinate chicks are selected for and recruitment increases [58,59]. Alternatively, during the decline, more dominant chicks are selected for and recruitment declines. This demonstrates how variation in the aggressive behaviour of males changes with density and can influence recruitment of young and thus the cyclic dynamics.

Much work on cyclic species has focused on density-dependent mortality [60] likely reflecting the influence of the Lotka–Volterra models in population ecology. However changes in reproduction, possibly related to social stress of crowding (voles and lemmings), sublethal effects of predator avoidance (hares), or infection or food limitation following defoliation (forest Lepidoptera) are also relevant. Carryover of these influences to subsequent generations through maternal influences can provide delayed density-dependent effects and cyclic dynamics as shown in several models [42,56,57,61].

6. A lack of genetic differentiation: an indicator of dispersal in cyclic species

A lack of both genetic differentiation and isolation by distance characterize cyclic forest Lepidoptera, voles and

snowshoe hares (citations in [62]). An overview of northern cyclic species [63] concluded that density-dependent dispersal has a strong impact on the genetic structure of populations. This fits with the 'founder/flush' model with panmixia at high densities proposed to describe the genetic structure of California voles, *Microtus californicus* [64].

Even island populations can maintain genetic similarity as shown by Western tent caterpillars on the Southern Gulf Islands of British Columbia, Canada. These are separated by 30–50 km but showed, based on microsatellite markers, neither genetic isolation by distance nor genetic differentiation between cyclic peaks. A similar lack of genetic differentiation among island populations has been observed for lemmings, *Dicrostonyx groenlandicus* although more genetic differentiation occurred in *Lemmus lemmus* [65].

Similar to cyclic populations of voles and lemmings, dispersal of forest Lepidoptera among populations leads to colonization of suitable habitats and regional outbreaks. Eastern spruce budworm (*Choristoneura fumiferana* Clem.) spread from epicentres in Quebec, Canada, as populations increased and the outbreak moved from the west toward eastern Canada [66,67]. In this case, mass flights of moths have been observed [68]. Gene flow among populations is high and genetic structure low [69].

Red grouse are an exception to the lack of genetic structure of cyclic populations. Populations show both genetic differentiation and isolation at distances over 1.5 km [70,71]. This is related to the territorial behaviour of males and the tendency for sons to inherit the natal territory. Thus for grouse, panmixia does not occur from density-related dispersal as described above for other groups.

Cyclic population dynamics with periodic phases of very low density provide the opportunity for local population extinctions [5] or for genetic drift to occur but this seems not to be the case. High levels of dispersal can 'rescue' local populations [72] during regional population outbreaks of cyclic species. Determining the relative influences on cyclic population dynamics of habitat heterogeneity, dispersal success and genetic differentiation remain areas for further experimental study [27,50].

7. Amplitude and periodicity

As described above, the periodicity of cycles varies such that we talk about 3 to 5 year cycles of small mammals and 8 to 11 year cycles of forest Lepidoptera. In addition, as shown in the figures above, the amplitude of cycles varies among peaks. Predicting the density of the next peak and whether the cycle will be longer or shorter than average remains challenging. Ginzburg & Krebs [61] proposed that extrinsic factors determine the amplitude and intrinsic factors the periods of population cycles. For example, they predicted that the most recent hare outbreak in the Yukon would be very low because lynx numbers remained high between outbreaks. Figure 1 shows that the recent peak density was moderate and thus the prediction was not upheld.

If the conditions influencing the densities of predators, parasitoids or diseases vary, so might the amplitude of the peak. However, if the density at the peak influences stress or food limitation and thus the expression of intrinsic factors, such as reduced body size, fecundity or age at reproduction, the rate of decline and the cycle period should vary

accordingly. An example is shown for Western tent caterpillars in figure 4. The decline was slower and the trough less deep following the lower but more prolonged peak in 1995–1997 compared to that of 2012 from which the population had still not recovered five years later. Snowshoe hares show a similar pattern in which more severe declines were associated with longer trough periods (figure 1) [46]. High peaks should be followed by more rapid declines if stress influences the intrinsic condition of the animals. Perplexing is the continued cyclic dynamics at low density such as discussed for larch budmoth mentioned above and for voles [29].

8. Rejected hypotheses

(a) The Chitty or behavioural polymorphism hypothesis

In 1967, Dennis Chitty proposed that larger and more aggressive voles would be selected for in increasing and high densities, and smaller voles with delayed reproductive maturity in low densities [73]. The 'Chitty Hypothesis' predicted that variable selection would lead to a genetic shift over the 3 to 4 year cycle of voles. However, the genetic shifts predicted by this hypothesis have not been observed and the levels of heritability of traits required for the shift were unrealistically high [4].

Other cyclic species such as snowshoe hares and forest Lepidoptera do not have the social behaviour required for the 'Chitty Hypothesis' selection mechanism to work. In red grouse, kin selection occurs because territorial males are more accepting of recruitment of their sons [71,74]. The 'Chitty Hypothesis' however, predicted the opposite, that more subordinate individuals should be selected for at high densities [58]. The Chitty Hypothesis has not been supported in any cyclic species [4]. Rather, changes in morphological phenotypes, reproduction and behaviour that have been observed in a variety of species are likely to reflect physiological effects and environmentally determined plasticity. Epigenetic changes might be occurring as well.

(b) The induced defense hypothesis

The 'induced defense hypothesis' predicts that feeding damage causes plants to produce defensive compounds either directly or following a delay, and that these reduce the growth, reproduction or survival of the herbivore [75–78]. This hypothesis has been particularly widely studied in forest Lepidoptera and support is variable [79,80]. While much evidence demonstrates the potential negative (direct) effects of plant induction on insect performance, these are not consistently linked to fluctuations in population density in the field [75]. There is some support for this hypothesis for snowshoe hares in Alaska [81] but the hypothesis has been rejected for snowshoe hares in the Yukon [82] and for red grouse [83]. Thus, this attractive hypothesis for explaining cyclic dynamics has not been generally supported across species and locations.

(c) Sunspots and other cycles

It is tempting to connect population cycles of animals to exogenous environmental cycles of a similar length such as sunspots [84–86], or more recently to the lunar nodal phase cycle [87]. Two problems with this approach are

Table 1. Processes that influence populations and their impacts that result in cyclic dynamics of voles, lemmings, snowshoe hares, forest Lepidoptera.

cycle phase	process	result
trough and beginning of increase	high fecundity and good survival	population increase
mid-increase	dispersal to vacant habitats and among populations	regional outbreak and genetic similarity among populations
mid to late increase	crowding or predator-related stress, sublethal infection, negative social interactions	triggering of reduced reproduction and transgenerational maternal effect
late increase and peak	linear, curvilinear or threshold density-related mortality (predators, parasitoids, parasites, infection)	reduced survival and population decline
trough	reduced population density, stress, predation, parasitism and/or infection	improved survival and reproduction leading to population increase

first identifying a mechanism associated with the exogenous cycle that might influence the population dynamics of the animals, and secondly, comparing cycles of similar but slightly different lengths that may go in and out of phase over time resulting in spurious associations [88,89]. Although it would be satisfying to find a relationship between animal population cycles and cyclic environmental cues, there is no support for a consistent association over space and time.

9. The role of models in understanding cyclic dynamics

A vast literature exists in which models have been used to explore the possibility of various mechanisms to create cyclic dynamics, e.g. [90], and the examples mentioned above. Although models can potentially identify what might cause cyclic dynamics, the simulated population trends are often unrealistic. Models seldom distinguish between multiple factors, and testable predictions arising from models are rarely made.

Models can also be used to explore if population dynamics seen in long-term data fit a density-dependent structure—direct density dependence (first order [91]), delayed density dependence (second order [9]) or curvilinear or overcompensatory density dependence [8,91,92]. These models are descriptive and again do not identify or test mechanisms.

Barraquand *et al.* [93] in a recent overview of modelling cyclic dynamics, concluded that by ‘gaining better insight into the drivers of population cycles, we can begin to understand the causes of cycle gain and loss’. This throws the gauntlet back to the field ecologists. The synthesis above indicates that a great deal is known about the drivers of population cycles.

10. Conclusion and the future

The main features of cyclic population dynamics for small mammals, snowshoe hares and forest Lepidoptera are summarized in table 1. It is surprising that these commonalities exist across these very different types of animals. Red

grouse population cycles are more variable and do not fit into this general pattern as clearly (figure 2).

A lingering question is, ‘how can low amplitude cycles persist if high densities are required for the build-up of predators, parasitoids, pathogens or detrimental conditions leading to reduced reproduction?’ This points to the need to know what triggers changes in reproduction associated with outbreak density. As suggested for snowshoe hares, epigenetic changes to genes related to stress responses [46,94] or for grouse [95] and insects [96] to disease resistance, might be occurring.

For all cyclic species, the interactions that occur at low density are difficult to measure. Whether a period of low density persists (figure 1, 1981–1986 for snowshoe hares) or if change is continual as seen in figure 3 for voles or figure 4 for tent caterpillars, influences the interpretation of mechanisms involved in the population dynamics. For example, if spruce budworm populations go through a ‘predator pit’ that maintains a low-density equilibrium or if the oscillation is continual and the result of a second-order density-dependent process, remains controversial [97].

What causes the switch from decreasing to increasing populations is a difficult question to answer. Many studies implicate some aspect of appropriate weather conditions is necessary for the switch, e.g. [67]. But widespread evidence for weather conditions cueing outbreaks is lacking. Other changes could trigger the shift from decline to increase such as a reduction in the stressful conditions, a reduction in predation, parasitism or infection after several generations of low host (prey) density, or a combination of factors.

Variation in the amplitude and periodicity of population cycles also require further study and a more food web-based approach is necessary. For example, why did lynx remain at moderate density after the 2006 snowshoe hare outbreak in the Yukon (figure 1)? Recent work in Alaska suggests that weather-driven variation in primary productivity influences the amplitude of population peaks in voles and hares [98]. The influences of both bottom up and top down processes must be considered.

In conclusion, while much has been learned about the cyclic dynamics of animal populations, future work should consider the following: (1) the relative influences of mortality and reproduction in transitions from peak to trough to

increase phases, (2) the causes behind transgenerational reductions in reproduction, (3) the importance of trophic interactions in determining the variation in amplitude and periodicity shown in long-term data, and (4) how cyclic dynamics at low amplitudes persist. Crucial to future progress is the continuation of long-term and detailed monitoring of populations, their characteristics and the habitats in which they are embedded. My advice to young population ecologists is to start when you are young and live to be old to acquire good long-term population data. These long-term data are necessary to describe, understand and

test causes of cyclic dynamics and the influences of changing conditions in the future.

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