Evolution in population dynamics

Peter Turchin

In their study of predator–prey cycles, investigators have assumed that they do not need to worry about evolution. The discovery of population cycles driven by evolutionary factors will change that view.

Ecologists studying population dynamics prefer not to bother with the possibility of evolutionary change affecting their study organisms. This is sensible, because understanding the results of interactions between, for example, populations of predators and prey is already a complicated task. Making the assumption that evolutionary processes are too slow on ecological scales greatly eases the task of modelling the commonly observed population oscillations. But an elegant study by Yoshida *et al.*[1] (page 303 of this issue) decisively demonstrates that this simplification might no longer be tenable.

The story begins at Cornell University when two members of the group — ecologist Nelson Hairston Jr and theoretician Stephen Ellner — teamed up to study the population dynamics of rotifers (Fig. 1), microscopic aquatic animals that feed on unicellular green algae. According to ecological theory, the interaction between predators (such as rotifers) and prey (algae) has an inherent propensity to oscillate[2]. Predators eat prey and multiply, causing prey numbers to crash, which in turn leads to a decline in the starving predator population, allowing prey to increase, and so on. Indeed, when the investigators placed rotifers and algae in a 'chemostat' (a laboratory set-up with continuous inflow of nutrients and outflow of waste) they observed population cycles[3]. But the phase shift between predator and prey cycles was completely 'wrong' — predators peaked when prey were at the minimum and vice versa, resulting in almost perfectly out-of-phase oscillations. This is a subtle but important point, which requires an explanation.

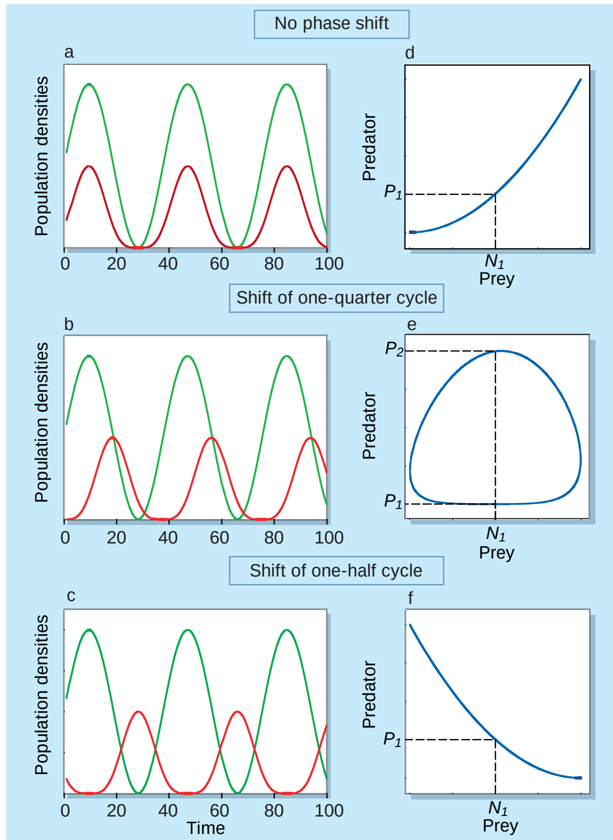

Figure 2 **Phase shifts between prey (green curve) and predators (red curve). Such shifts yield a hint about whether the oscillations are driven by the classical predator–prey mechanism. Time plots:** a, **no shift;** b, **a shift of one-quarter of a cycle;** c, **a shift of half a cycle. Phase plots corresponding to the time plots:** d, **no shift;** e, **a shift of one-quarter of a cycle;** f, **a shift of half a cycle. The rotifer–algal system studied by Yoshida *et al.*[1] exhibited the out-of-phase oscillations seen in** c **and** f**, which implies that the cycles must be driven by a factor other than the classical predator–prey interaction. The authors identify evolutionary change in the prey as that factor.**

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Figure 1 **Predator: the rotifer *Brachionus calyciflorus*[1].**

Suppose we observe three ecosystems containing predators and their prey. These three systems are in all ways identical, except in the phase shift between predators and prey: no shift (Fig. 2a), a shift of one-quarter of a cycle (Fig. 2b), and a shift of half a cycle (Fig. 2c). Clearly, there is some sort of dynamical connection between the two populations in all cases, but in which case are cycles driven by the predator–prey interaction? To answer this question we replot each trajectory in the 'phase space' — two-dimensional euclidean space in which each variable (prey and predator density) is represented with its own axis (Fig. 2d–f). When oscillations are synchronous, the trajectory goes back and forth along the same path, so that for each value of prey density (say, N_1) there is just one corresponding value of predator density (P_1). This means that if we already know the level at which prey is, knowledge of predator numbers gives us no additional information. In a differential equation describing prey dynamics we can replace all terms containing P with N by using the relationship depicted in Fig. 2d, leaving us with a single differential equation for N. But mathematical theory tells us that such single-equation models cannot generate cycles[4]. In other words, simply by noting that prey and predators oscillate in synchrony we have disproved the hypothesis that cycles are driven by the classical predator–prey mechanism described in the previous paragraph. Some other factor must be involved in producing the oscillations.

The same logic applies to the case of perfectly out-of-phase oscillations (Fig. 2c, f). However, in the case in which predators trail prey by a quarter of a cycle there are two values of P for each N (Fig. 2e). So a single equation for prey does not suffice; we must know what predators are doing. If predators are at the low point (P_1), prey will increase, but if predator numbers are high (P_2), prey numbers will crash. The full model for the system will have two equations, one for prey and one for predators, and we know that such two-dimensional models are perfectly capable of displaying cyclic behaviour.

We now see why the observation of the perfectly out-of-phase dynamics demonstrates that the rotifer–algal cycles could not be driven by the classical predator–prey mechanism. So what is the actual explanation? The path taken by the Cornell group to answer this question is an almost textbook example of how science is supposed to be done. First they advanced four competing hypotheses, suggested by various known features of algal and rotifer biology. Next they translated the hypotheses into mathematical models and contrasted model predictions with data. Only one model, based on the ability of algae to evolve rapidly in response to predation, successfully matched such features of data as period lengths and phase relationships[5]. This is a convincing result, and if we dealt with a natural system we would have to stop there because we cannot usually manipulate the genetic structure of field populations.

In the laboratory, however, such an experiment is possible, and the successful test reported by Yoshida *et al.*[1] provides the final and most decisive evidence of the rapid-evolution hypothesis. Thus, the out-of-phase cycles result from the following sequence of observed events: under intense predation, the prey population becomes dominated by clones that are resistant to predators; when most prey are resistant, the predators remain at low numbers even though prey abundance recovers; low predation pressure allows non-resistant clones to outcompete resistant ones; so predators can increase again, leading to another cycle.

The experimental demonstration that rapid evolution can drive population cycles means that ecologists will have to rethink several assumptions. To give just one example, there is a long-standing debate in population ecology on whether natural populations can exhibit chaotic dynamics. Chaos (in the mathematical sense) is irregular dynamical behaviour that looks as though it is driven by external random factors, but in fact is a result of internal workings of the system. Before the discovery of chaos, ecologists thought that all irregularities in the observed population dynamics were due to external factors such as fluctuations of climate. Now we realize that population interactions (including those between predators and prey) can also result in erratic-looking — chaotic — dynamics. Incidentally, the chaos controversy was the main reason why the Cornell group decided to study rotifer population cycles.

Some ecologists have argued that chaotic dynamics cause populations to crash to very low densities at which the probability of extinction is high, and that natural selection should therefore cause evolution away from chaos[6]. Since this argument was advanced, at least two examples of chaotic behaviour have been discovered: in the dynamics of the incidence of childhood diseases such as measles[7], and of population numbers of rodents such as voles and lemmings[8]. What is more important, however, is that the argument assumes that evolution occurs on much longer timescales than oscillations. But the results of Yoshida *et al.*[1] show that evolution can be an intrinsic part of oscillations, raising an exciting possibility that some populations might rapidly evolve both towards and away from chaos. Perhaps this is the explanation of the puzzling observation that some Finnish vole populations shift from a stable regime to oscillations, whereas others do precisely the reverse[9].

This is rank speculation, however, and will have to remain so because we cannot test it experimentally in natural systems. But in the laboratory much more is possible, as the study by Yoshida *et al.* shows. We can hope that in the near future we will see an experimental investigation of the possibility of rapid evolution to and away from chaos. ■

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Accelerator physics

In the wake of success

Robert Bingham

Particle accelerators tend to be large and expensive. But an alternative technology, which could result in more compact, cheaper machines, is proving its viability for the acceleration of subatomic particles.

Since the construction of the first particle accelerator in 1932, high-energy collisions of accelerated ions or subatomic particles (such as electrons and their antimatter counterpart, positrons) have proved a useful tool in physics research. But the escalating size and cost of future machines means that new, more compact acceleration techniques are being sought. In *Physical Review Letters*, Blue *et al.*[1] report results from a test facility at the Stanford Linear Accelerator Center (SLAC), California, that have great significance for the future of particle accelerators. Their success heralds an entirely new type of technology, the plasma wake-field accelerator.

When charged particles such as electrons or positrons pass across a gradient of electric field, they are accelerated — how much depends on the steepness of the gradient. In conventional accelerators, a radiofrequency electric field is generated inside metal (often superconductor) accelerator cavities. But the gradient can be turned up only so far before

ALAN SCHEIN/CORBIS

Figure 1 **The wake created by a boat is a familiar image, but it is also the inspiration for a new type of particle accelerator. Blue *et al.*[1] have demonstrated that waves in a hot, ionized plasma of gas can create a rippling electric field in their wake, and that this 'wake field' can accelerate subatomic particles.**