

News & views

Population biology

Predator–prey cycles achieved at last

Alan Hastings

A combination of laboratory experiments and mathematical and statistical analysis provides an affirmative answer to a decades-old question – can a predator and its prey coexist indefinitely?

A key question in ecology is what allows species to persist over time – particularly when there are pairs of species in which one is an exploiter and the other its victim. A long-standing theory attempts to answer this question by explaining how relative numbers of predators and their prey can cycle continuously¹. First, prey numbers would increase, giving the predator more food. The subsequent increase in predators would lead to a decline in prey. Predator numbers would then decline owing to a lack of food, restarting the cycle. However, it has proved unexpectedly challenging to demonstrate this type of persistent predator–prey cycle in simple controlled systems in the laboratory. Writing in *Nature*, Blasius *et al.*² report just such a demonstration, succeeding where almost 90 years of experimental work has failed.

Ecological theories of persistent predator–prey cycles are supported by the apparent existence of such cycles in nature, for instance between the lynx and hare in Canada³. However, it is hard to prove that these cycles endure in the wild, because observations over many decades would be needed. But if the theories provide a complete explanation of natural cycles, then it should be possible to demonstrate persistent cyclic behaviour in the laboratory, using species that have much shorter cycle times.

The challenge posed by such a demonstration was exemplified in 1934 by the ecologist Georgii Gause⁴, who studied the dynamics of two unicellular organisms – the predator *Didinium nasutum* and its prey, *Paramecium caudatum*. Gause found that, on the one hand, if the predator was efficient, it ate up all the prey and then starved. On the other hand, if part of the environment helped to conceal the prey, the predator was less efficient – and so

starved (Fig. 1a). Coexistence and long-term cycles could be achieved only through artificial means – namely, by adding prey at regular intervals.

In 1974, work with the same system showed that, by making the predator less efficient and by providing the prey with less food, the two populations could persist for longer⁵. Even so, coexistence could be maintained for just a few predator–prey cycles. Since then, some models that allow long-term cycle persistence have focused on space, for instance incorporating metapopulation dynamics⁶. In this phenomenon, subpopulations of a species migrate around a larger region. Although a subpopulation might become extinct in one area, the species persists across the region as a whole and can migrate back into that area. However, a better understanding of whether exploiter–victim cycles can persist locally without external input is still sorely needed.

Blasius and colleagues studied the aquatic invertebrate *Brachionus calyciflorus* and its prey, the green algal species *Monoraphidium minutum*. They found that, under simple and constant environmental conditions, the two species could coexist for more than a year – that is, over 50 predator–prey cycles. This result finally demonstrates that the long-standing theory of persistent cycles can be consistent with the reality of simple ecological systems.

Next, the researchers carried out a rigorous statistical analysis of the cycle dynamics in their system. Specifically, they used wavelet analysis, which focuses on dynamics over short periods; the technique has become a standard way to study the presence of periodic behaviour in ecological time series⁷. The analysis revealed interesting dynamic phenomena. The oscillations in the relative numbers of each species showed a characteristic lag in phase, with predator numbers mostly changing in the wake of altered prey numbers. However, these oscillations would undergo sudden shifts, without any external driver. During these transient periods, both populations would oscillate out of sync with one another, before the in-phase cyclic dynamic resumed (Fig. 1b).

The authors also performed experiments in which they introduced pulses of nutrients to the species' environment. This mimics seasonal environmental changes experienced in many natural systems. The overall dynamics of the predator–prey cycle remained the same in these conditions, indicating that predator–prey interactions can govern cycle dynamics, even in a seasonally varying environment.

Although Blasius and colleagues' work

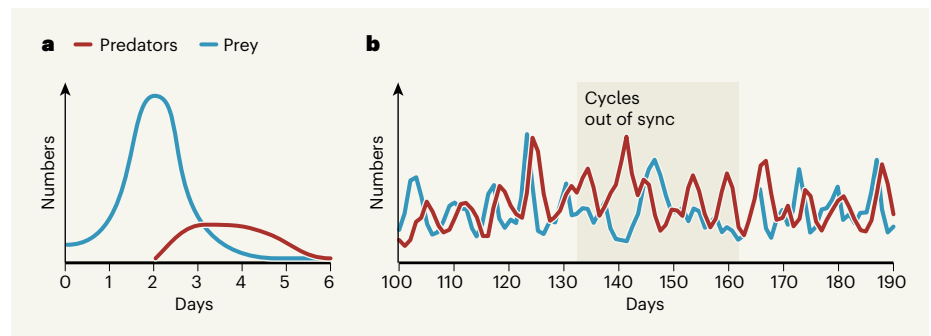


Figure 1 | A difficult balance to strike. Ecological theory predicts that the relative numbers of a predator and its prey should oscillate in persistent cycles, but demonstrating this in the laboratory has been hard. **a**, Classic experiments⁴ from the 1930s failed to achieve cycles, because predators were either too inefficient at eating prey (not shown) or too efficient, and ate them all. Either way, predator numbers dwindled. **b**, Blasius *et al.*² have succeeded in achieving persistent predator–prey cycles in the laboratory. They found that cycles were mostly in phase, with predator cycles slightly lagging behind prey cycles. However, there were transient periods in which the two – for unknown reasons – fell out of sync. (Adapted from Fig. 2b of the paper.)

answers one question, it raises others. First and foremost, why are the results so different from those of earlier experiments? It is not just a quirk of the species used, because the authors repeated the experiment using a different prey species and achieved the same result. One contributing factor could be that the researchers used a predator that has a complex life history involving transitions through several stages, from egg to adulthood. Another could be that persistence depends on the specific amplitude of oscillation in the cycle.

In support of these ideas, previous work involving a predator with a simpler life cycle demonstrated that populations of predators, prey or both went extinct if cycles reached an amplitude at which population numbers become low⁴. In addition, analysis of a different marine predator–prey combination⁸ showed that cyclic dynamics eventually gave way either to extinction or to persistence of the two populations in equilibrium. And mathematical theory¹ suggests that the small-amplitude cycles observed by Blasius and colleagues would occur only under very specific conditions. Demonstrating persistent cycles in

other systems is therefore a key challenge for the future. The life-history characteristics of the predator used by Blasius and colleagues could be a starting point in the search for systems that show similar behaviour.

Another intriguing avenue for future study is to determine the relationship between transient dynamics and switches in system behaviour. Does a sudden change in the dynamics of a cycling system reflect changing environmental conditions, or is it an intrinsic phenomenon? The existence of unexpected, transient shifts in predator–prey dynamics limits the predictability of ecological systems⁹. In the real world, sudden shifts of this nature could spur an erroneous quest to identify drivers of the change, whereas the current study indicates that there may be none. The possibility of transient dynamics could also make it more difficult to predict the effect of ecological-management strategies.

Blasius *et al.* have provided one of the clearest demonstrations so far of transient dynamics in the laboratory, where it is absolutely certain that no external influences caused the change. It will be important to bring

together this work (and another convincing experimental demonstration¹⁰) with theoretical models that are currently being developed⁹. Doing so should provide more insights into the role of transient dynamics in natural systems.

Alan Hastings is in the Department of Environmental Science and Policy, University of California, Davis, Davis, California 95616, USA, and at the Santa Fe Institute, Santa Fe, New Mexico, USA.
e-mail: amhastings@ucdavis.edu

1. Kendall, B. E. *et al.* *Ecology* **80**, 1789–1805 (1999).
2. Blasius, B., Rudolf, L., Weithoff, G., Gaedke, U. & Fussmann, G. F. *Nature* <https://doi.org/10.1038/s41586-019-1857-0> (2019).
3. Elton, C. & Nicholson, M. J. *J. Anim. Ecol.* **11**, 215–244 (1942).
4. Gause, G. F. *The Struggle for Existence* (Williams & Wilkins, 1934).
5. Luckinbill, L. *Ecology* **55**, 1142–1147 (1974).
6. Hanski, I. *Metapopulation Ecology* (Oxford Univ. Press, 1999).
7. Cazelles, B. *et al.* *Oecologia* **156**, 287–304 (2008).
8. Fussmann, G. F., Ellner, S. P., Shertzer, K. W. & Hairston, N. G. *Science* **290**, 1358–1360 (2000).
9. Hastings, A. *et al.* *Science* **361**, eaat6412 (2018).
10. Cushing, J. & Desharnais, C. J. *J. Anim. Ecol.* **67**, 298–306 (1998).