Journal Club

Chitty cycles – at last!

Forty years ago, Dennis Chitty took a brave and pioneering step in population biology, when he proposed that the so-called ecological and evolutionary timescales might be less different than was traditionally assumed. He made this proposal in the context of linking rodent cycles to cyclic selection among different phenotypes. The core of Chitty's argument is that competition between two morphs, one a superior competitor (and inferior reproducer) and the other an inferior competitor (and superior reproducer), might generate cycles in abundance if evolution is very rapid. Two objections can been raised against the 'Chitty hypothesis' for population cycles. The first is whether selection can be strong enough to act on an ecological timescale. The second is whether there is enough heritability in such tightly fitness-linked traits as survival and fecundity. The answer to the second will clearly depend on many things. However, as for the first, evidence is mounting that evolution can be very rapid. The time might, therefore, have come for a new appreciation of this idea, in general, but in particular with respect to oscillations in the abundance of the Side-blotched Lizard (*Uta stansburiana*) of southwestern USA.

Sinervo and coworkers have just reported on a selection-induced density cycle in *U. stansburiana* from Central California[1]. Female lizards have two color morphs: a yellow-throated morph that tends to lay small clutches (with large eggs); and an orange-throated morph with large clutches (of small eggs). The authors monitored these populations in the wild for a ten-year period and documented significant cyclic variation in abundance. These lizards have a one-year life span, so the biannual fluctuations represent two-generation cycles. There is one demographic and one phenotypic cycle that parallel the oscillations in abundance: both survivorship of juveniles and frequency of the yellow morph are inversely related to density.

The reproductive traits and the throat color are linked through correlational selection on these otherwise genetically independent traits. Experimental manipulations of the allele frequencies in nature, furthermore, confirm how game theoretical dynamics cause the genetic correlation to be self reinforcing. Laboratory and field experiments further document a high degree of heritability of the various phenotypic traits, and strong inverse frequency-dependent selection on both of the color morphs. In addition, there is circumstantial evidence that the cycles are sustained both in the presence and in the absence of the chief predators of the lizard. Sinervo *et al.*'s study, thus, provides a unique example of the importance of the interplay between ecological and evolutionary dynamics. At the same time, this study elevates the Chitty cycle to the rank of 'beautiful hypotheses that were not slain by ugly facts'.

1 Sinervo, B. *et al.* (2000) Density cycles and an offspring quantity and quality game driven by natural selection. *Nature* 406, 985–988

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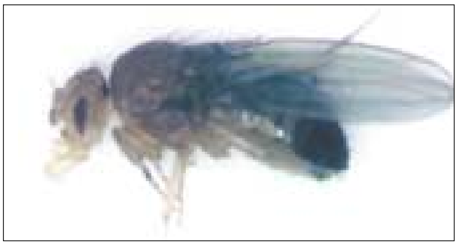
The costs of resistance in *Drosophila*: blood cells count

It is generally assumed that defence against parasites is costly to maintain, and several studies of invertebrates and their natural enemies have shown that resistance to parasites is associated with reduced fecundity, growth and/or survival. However, the proximate causes of such costs have remained elusive. In a key paper published in 1997, Lex Kraaijeveld and Charles Godfray used selection experiments to show that, under conditions of severe food shortage, the fruit fly *Drosophila melanogaster* appears to 'buy' resistance to the braconid larval parasitoid *Asobara tabida* at the expense of competitive ability. Subsequent studies showed that similar tradeoffs underlie resistance to another larval parasitoid, *Leptopilinia boulardi*, and that, in both instances, individuals from lines selected for enhanced resistance exhibited reduced feeding rates. Now, in a new study[1], Kraaijeveld and colleagues have taken a step further in identifying the proximate mechanism underlying these observations.

Studies by other workers have shown that, across *Drosophila* spp., resistance to *A. tabida* is positively correlated with the densities of circulating haemocytes (insect blood cells). It is envisaged that defense against these parasitoids is a dynamic game in which the outcome is largely determined by the rate at which the host encapsulates (engulfs with haemocytes) the parasitoid egg. If encapsulation occurs fast enough, the development of the parasitoid can be halted, but if the response is too slow, the parasitoid can hide itself within host tissues and evade the immune defenses of the host. Thus, it is believed that having a high haemocyte count is analogous to investing in a large standing army, ready to respond should an invasion occur.



To test this idea, Kraaijeveld *et al.* used the same genetic lines of *Drosophila* selected for resistance to *A. tabida* and compared their haemocyte counts with those of individuals in the respective control lines. In accord with their prediction, larvae in the four selected lines had haemocyte counts that were roughly twice those of individuals in the four control lines. Thus, it appears that *D. melanogaster* 'buys' resistance to *A. tabida* by investing in blood-cell production.

But why is an increase in haemocyte production associated with a reduction in feeding rate and competitiveness? Kraaijeveld and colleagues discuss two possibilities. One is that the selected lines differ in their energy budgets, with resistant genotypes investing in haemocyte synthesis at the expense of feeding efficiency. A second is that there is a morphogenetic switch that determines whether embryonic mesoderm differentiates into head

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musculature or into the haemopoietic tissue that makes haemocytes. Distinguishing between these, and additional hypotheses is a challenge for the future. However, by identifying haemocyte production as a constraint on immune defense in *Drosophila*, we could be one step closer to understanding the proximate basis for the cost of resistance in *D. melanogaster*. Whether this constraint is important in other insect–parasitoid interactions remains to be determined.

1 Kraaijeveld, L. *et al.* (2001) Basis of trade-off between parasitoid resistance and larval competitive ability in *Drosophila melanogaste*r. *Proc. R. Soc. London B. Biol. Sci.* 268, 1–3

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Since I have a hammer…

When equipped with a hammer, we look for nails. This relatively simple behavior threatens our ability, as scientists, to adequately describe and understand real-world patterns and processes, particularly in ecological systems that are used and managed by humans. Ecologists, on the one hand, when venturing examination of managed or utilized systems (which they do too rarely), rather consistently underestimate the ability of humans to adapt to changing conditions, or overestimate the efficacy of top-down regulation. The ecosystem is studied in all its complexity (Thank God—a nail!), and the human system is drastically simplified. On the other hand, economists or sociologists can and do examine market mechanisms or human behaviors in great detail and even design strategies to reduce environmental degradation, but they expect that the ecological systems involved will conform in a relatively predictable and straightforward manner to stated political or social goals. Under these narrowed analyses, we risk compromising our ability as scientists to understand our world and the way it works, and our ability as citizens to steer the world in favorable directions, because we are looking for nails.

Scheffer *et al.*[1] make a compelling case concerning the dangers of such an approach. They examine shallow lake systems with informed ecological, economic and political models, and show that an integrated analysis is required to capture the actual, rather than idealized, dynamics of these lakes. In particular, the authors show that, in certain ecosystems (those that respond to stress only slightly and in a smooth fashion), 'compromise' economic solutions, which allow groups of users with different goals to each derive some services from the lakes, might be most beneficial. However, 'catastrophic' ecosystems can exhibit two alternative stable states within a range of environmental conditions. Compromise solutions in these cases might be hazardous, as they tend to put the ecosystem in a state where even a slight perturbation could cause a sudden shift from the stable, desirable state to a stable, less desirable state. 'Integrative' rather than compromise solutions are called for. In either situation, differential political access by different user groups could cause a 'drift' from the socially beneficial solutions, and these forces must be considered in modeling potential real-world dynamics in these lake systems.

We need more integrated analyses of this sort if we are to push forward the frontiers of intellectual inquiry. We also need such analyses if we are to provide relevant scientific information to the public and policymakers struggling with how best to utilize and preserve the natural-resource base that sustains human welfare. We can continue using our hammers, but need to join forces with those holding other tools. This paper shows that this can be done rigorously, while yielding fundamentally new insights into the functioning of ecological systems.

1 Scheffer, M. *et al.* (2000) Socio-economic mechanisms preventing optimum use of ecosystem services: An interdisciplinary theoretical analysis. *Ecosystems* 3, 451–471

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Other mothers' ducklings – why look after them?

Not all female animals look after their own young and the attention devoted to their own offspring varies enormously among species. But even within species with well-developed female parental care, certain females might choose an alternative breeding tactic and leave their offspring in the care of others. Such brood parasitism is particularly common in ducks, where some females ('hosts') often receive eggs laid by other females ('parasites') of the same species. But why would a female accept someone else's responsibilities? After all, taking care of another female's chicks can sap the caretaker's strength and increase her exposure to predators. Several ideas have been proposed to solve this puzzle, ranging from the simple notion that females might not be able to discriminate between her own offspring and those of others, to the hypothesis that a female might actually enhance the survival of her own progeny by accepting offspring of others. An intriguing idea is that parasites and hosts could be related. As relatives share some of their genes, the costs paid by a host female might be counterbalanced by the propagation of her own genes through the offspring of her related parasite. Although the general importance of 'kin selection' was proposed by W.D. Hamilton in the 1960s, and its potential role in the evolution of brood parasitism was identified by Malte Andersson in the early 1980s, this idea still remains a matter of hot debate.

Malte Andersson and Matti Åhlund now present evidence[1,2] in favour of the kin selection hypothesis. As a part of a long-term field study on goldeneye ducks (*Bucephala clangula*), they drew albumen samples from nearly a 1000 eggs, without harming the developing chicks. As the albumen is secreted by specialized cells in the oviduct of the egg-laying female, this method is equal to sampling the female herself. Analysis of the protein contents of the albumen revealed that host and parasite were indeed often related, their average relatedness approximately that of first cousins. What is more, this relatedness did not emerge as a

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