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Editorial overview: Pests and resistance: Shedding the albatross of resistance starts by embracing the ecological complexities of its evolution

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Thomas W Sappington is a Research Entomologist with USDA-ARS. He received his PhD in Systematics & Ecology at the University of Kansas. He is an insect ecologist with primary expertise in movement ecology, especially of agricultural pests in corn and cotton production systems. He combines a variety of experimental approaches to help characterize insect dispersal at different spatial scales, including mark-recapture, laboratory flight mills, and population genetics. His current research is focused on characterizing long-distance dispersal of western corn rootworm, and the drivers underlying this behavior, in the context of insect resistance evolution and management.

Ah! well a-day! what evil looks
Had I from old and young!
Instead of the cross, the Albatross
About my neck was hung.

Samuel Taylor Coleridge, 1798

In *The Rime of the Ancient Mariner*, Samuel Taylor Coleridge's great poem, a mariner tells the tale of his ship trapped in Antarctic ice. An albatross appears, the ice splits, and a south wind helps the ship escape. The sailors befriend the good-luck albatross, which follows the ship as it sails northward. One day, for no apparent reason, the mariner shoots the albatross with his crossbow. The ship's luck changes, becalmed for days in windless seas. The crew, dying of thirst, hangs the dead albatross around the mariner's neck, an inescapable reminder of the curse now laid upon them all for killing the harmless bird that had rescued them.

In some ways, evolution of resistance by insect pests to human control tactics is a curse as burdensome as an albatross hung round our necks: a reminder of our all-too-human hubris, an oppressive hindrance to our attempts to protect ourselves and our domesticated crops from the ravages wrought by pests. Of course the analogy is not fully transferable, in that pests are not exactly our innocent friends (though we may become fond of the organism we spend so many intimate hours with each day . . .). But like the curse of the albatross, resistance is difficult to avoid when we are generating strong selection pressure via the bolts of our latest crossbow, and its wrath is inescapable once it has evolved to the point of repeated field failure [1].

To escape the curse of resistance, we scientists seek to understand the molecular, biochemical, and physiological mechanisms that shield the insect from our crossbow, as well as the genes ultimately responsible for these proximate mechanisms. Such knowledge of resistance mechanisms is usually essential to designing effective countermeasures in the form of different management tactics or improved strategies of applying existing tactics. But to truly shed the albatross of pest resistance from around our necks for a given system, we must also come to grips with the evolutionary ecology behind its rise, spread, and maintenance in and among populations.

Adaptation of a species to a pest control measure, such as an insecticide, involves essentially the same evolutionary processes as adaptation to any environmental stressor [2,3]. The living insects targeted by a control tactic are the latest product of countless generations of natural selection by a

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complex history of stressors on their ancestors. New chemical insecticides, or transgenic crops using engineered DNA from *Bacillus thuringiensis* (Bt) to produce an insecticidal protein, are often deployed widely and quickly by humans, putting pest populations under intense selection pressure. Some pest species may adapt rapidly, like Colorado potato beetle (*Leptinotarsa decemlineata*) has to many insecticides [4] and like western corn rootworm (*Diabrotica virgifera virgifera*) has to Bt corn [5]. Others, such as the European corn borer (*Ostrinia nubilalis*) in corn [6] and pink bollworm (*Pectinophora gossypiella*) in U.S. cotton [7], have remained susceptible to transgenic Bt toxins for many generations.

Adaptations to environmental stressors can pre-adapt insects to either tolerate or evolve resistance to human-imposed stressors, that is, control tactics. Several of the reviews in this issue touch on the phenomenon of pre-existing resistance mechanisms, how they arise and how they are maintained. Hoffmann examines what we can learn about rapid adaptation of insect pests to climatic stresses, something of interest and increasingly researchable given the accelerating pace of climate change [3]. Research on the ability of pest populations to adapt to ongoing climate change is not only of direct importance to predicting life history responses or range expansions. In addition, they can help us understand the underlying patterns and potential of adaptive response to control measures like insecticides. Hoffmann finds that the few examples available so far suggest pests can adapt rapidly to changes in climate, but, importantly, they also reveal constraints to rapid adaptation. Understanding the nature of such adaptability and constraints will be facilitated as more pest genomes are used in comparative studies to identify markers associated with adaptive shifts.

Plants do not sit idly by, evolutionarily (and metaphorically) speaking, allowing themselves to be grazed on by every herbivorous insect that happens along. They are usually protected by a toxic cocktail of chemical compounds, which the herbivore must be adapted to detoxify or otherwise circumvent [8]. Alyokhin and Chen explore the connection between the evolution of detoxification mechanisms in insects that allow them to feed on certain host plants, and the ability to adapt to synthetic chemical insecticides by adjusting expression of pre-existing detoxification genes. Insects associated with host plants protected by abundant or novel secondary metabolic compounds tend to be primed to detoxify pesticides. In their review, French-Constant and Bass point out the common assumption that resistance to an insecticide carries a fitness cost, and that resistance allele frequencies will decline in the absence of selection by the insecticide because of those costs. However, they find that evidence for fitness costs of resistance rarely comes from experiments using genetically related strains, which is important for avoiding confounding effects of strain-specific variation. Instead, molecular studies show that pre-existing resistance alleles can be maintained in a population by sexual anatagonism and by mechanisms promoting permanent heterozygosity.

Zalucki and Furlong examine the evidence for behavioral resistance to insecticides. Though often posited as a resistance mechanism, they point out the widespread problem of confusing pre-existing behavioral mechanisms promoting avoidance of a toxic compound or toxic environment, with true behavioral resistance. The latter requires demonstration of a heritable increase in a protective behavior in a population over generations. Unambiguous evidence for true behavioral resistance is not at all common. Although Zalucki and Furlong focus on behavior as a resistance mechanism, it occurs to us that the same principle applies to all pre-existing mechanisms