silent males as this reduces their chances of being parasitized (~5% of females are parasitized as collateral damage), and there will then be selection on alternative ways of locating mates.

Conclusion

In an ideal world, there would be enough islands with different populations of crickets and parasites to provide replicated tests of the association between parasites and silent males, as Zuk *et al.* [1] have shown a correlated rather than causal relationship. However, it is clear that crickets on Kauai have undergone extremely rapid evolution of a trait that is fundamental to reproduction and the association with changes in parasitism rates make Zuk *et al.*'s [1] explanation persuasive. The effect of behavioural plasticity on the evolution of morphological and physiological traits is receiving increasing attention [9]. Zuk *et al.* [1] suggest that their study could be an example of behaviour leading the way in evolution [10]. However, what appears to have happened is that a morphological mutation has occurred that has spread because its negative effect of reducing mating opportunities is ameliorated by behavioural flexibility, that is, the potential for silent males to move closer to singing males. This might be better characterized as behaviour facilitating, rather than leading, evolution.

There is exciting potential for further study into whether male aggregation behaviour is genetically predetermined or facultatively deployed and into the ecology of parasites and hosts when one is evolving rapidly in response to the other. The next few years on Kauai promise to be fascinating.

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Letters

Where are the parasites in the PHA response?

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In their recent paper in *TREE* on the use of phytohaemagglutinin (PHA) response to measure immunocompetence [1], Kennedy and Nager make the point that the complex nature of the vertebrate immune system should caution researchers against using the technique to interpret detailed immune function. This underscores the weak connection between PHA data and parasite resistance. Studies of immunocompetence assume that parasites engage the immune response. Yet, an important unknown remains: how does immunocompetence relate to actual host–parasite interactions [2]?

Only a few studies show a relationship between PHA responses and parasites [3], and they reach ambiguous conclusions. Manipulative studies indicate that parasites can reduce the PHA response [4,5], which could reflect either true immunosuppression, or merely shifting defenses in a fully competent immune system. Correlative studies indicate that hosts with low responses are more often parasitized [6,7], which could reflect either inherent susceptibility, or a reaction to being parasitized that is independent of resistance. Interaction with other factors, such as the environment, or interactions among multiple parasites, can complicate things further. Moreover, the range of parasites studied (viruses [6], protozoa [7], nematodes [5] and arthropods [4,6]) encompasses interactions with the immune system that are too diverse for a 'general resistance' assay. Susceptibility and virulence vary in a host–pathogen-specific manner, and no host is resistant to all parasites [8]. In short, the use of PHA fails to identify crucial host–parasite connections. We need data that demonstrate that immune responses are elicited by, and directed against, specific parasites [3].

The technical difficulty of longitudinal studies and parasite-specific assays has spurred the popularity of this simplistic test. However, even with improved understanding

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of the PHA response [9], the complex, precise nature of host–parasite interactions can confound conclusions. For example, Bany *et al.* [10] demonstrated that *in vitro* lymphocyte responsiveness to antigen depends on time and site within the host. Cells were influenced by location and intensity of the parasite, and mitogen tests, similar to PHA, did not discriminate these important differences. Host–parasite interactions can be nuanced and flexible, defying broad characterization. Reliance on the PHA assay as a proxy for complex interactions is not likely to move the field of ecological immunology forward. If we are interested in host–parasite interactions in any context, be they fitness tradeoffs, coevolution, or virulence, greater effort to characterize specific immune responses to parasites will need to be made in parallel with efforts to improve our understanding of PHA assays.

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Alien predation and the effects of multiple levels of prey naiveté

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Cox and Lima's [1] recent *TREE* review on prey naiveté and the impacts of alien predation is a welcome addition to our understanding of why invasive species are so devastating. Overcoming prey naiveté has stimulated considerable conservation effort [2]; therefore, we believe that a system for classifying prey naiveté is needed to target management actions and to help predict the variable nature of alien impacts.

We propose three levels of naiveté to alien predators. Level 1 naiveté is for prey that show no recognition of the alien as a predation risk and adopt no anti-predator behaviour. For example, flightless birds in New Zealand, which have no native mammalian predators, show no recognition of alien stoats or rats, which have had such a catastrophic impact on local avifauna [3]. Level 2 naiveté occurs when prey recognize the predator as dangerous but adopt the wrong anti-predator response. For example, in response to approaching foxes, Australian curlews and some of the smaller wallabies adopt cryptic poses to blend into their background; this works against visually oriented avian predators, but is almost useless against scent-hunting cursorial foxes. Finally, Level 3 naiveté occurs when prey recognize the predator as dangerous, have appropriate anti-predator defences that are suited for that predator archetype, but are simply 'outgunned' by the superior hunting tactics of the alien species. For example, eastern grey kangaroos *Macropus giganteus* forage closer to cover and in larger groups in response to the presence of foxes [4], yet recruitment is still limited by fox predation [5].

These levels of naiveté apply to both terrestrial and aquatic ecosystems and refine predictions of how predator archetype influences the vulnerability of local prey. Furthermore, Level 1 prey naiveté might explain the dramatic impacts often observed soon after alien invasion, whereas Levels 2 and 3 naiveté relate more to the ongoing challenges in managing impacts of established pest predators.

The contribution of naiveté to alien predator impact can also be confused with other features of the invasion. Local enemies, which can prevent invasion, are likely to be closely related to the potential invader, representing a similar predator archetype as that defined by Cox and

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