The ailing invader

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The nature of biological invasions prompts researchers to focus on questions of great importance: How far will a nonnative species go? How fast? And what are the consequences to native species? To crops? To us? This perspective had crystallized long before Charles Elton wrote his classic treatise on the subject in 1958 (1). In it, Elton noted that scientific accounts of invasion have "a sense of urgency and scale" reflecting the uncertainties and high stakes surrounding the arrival of invaders such as brown tree snakes, Russian wheat aphids, and the West Nile virus. The resulting body of research has greatly increased our ability to estimate eventual distribution (2, 3) and the most effective modes of intervention (4). Nevertheless, the prevailing focus has left other questions virtually unasked. In this issue of PNAS, Brown *et al.* (5) take on a good one: What is the impact of invasion on the invader? Perhaps invasion biologists may be forgiven for overlooking such a question. After all, invasive species that gain our attention are highly successful in ecological terms. Despite being displaced from their native turf, they have managed not just to gain a toehold in a new environment but to thrive. Like wealthy neighbors or bright classmates, their problems may tend to escape our notice.

Arthritic Toads on a Rampage

Within the pantheon of invasive species, the cane toad, *Chaunus* [*Bufo*] *marinus* (Fig. 1), is among the more infamous. Introduced to Australia 70 years ago as a biological control agent, the cane toad failed in its assignment to control beetles on sugarcane and then overstayed its welcome. The toad has now occupied >15% of the continent and is still on the move. Its arrival in Darwin a few years ago was decades ahead of projections (6), reflecting increases in invasion speed as the toad moved across Australia's Top End (7). Recent research (8) has shown that Australian cane toads are able to move farther and faster than other amphibians (up to 1.8 km per night). Once they arrive in an area, they cause problems for native species. Lizards (9) and snakes (10) have been particularly hard hit. These predators are naïve to the toxin carried by the toads; for many, ingesting a single toad is enough to kill them. One study estimated that up to 30% of Australia's

Fig. 1. The cane toad, *Chaunus* [*Bufo*] *marinus.*

snake species may be at risk from cane toads (11). Brown *et al.* (5) initially began studying cane toads because the toads were decimating populations of the snakes on which the authors worked (10).

Now Brown *et al.* (5) report that up to 10% of adult toads within a given locality suffer from arthritis of the spine (spondylosis) severe enough to affect their movement ability. In the worst cases, vertebrae become fused. This finding is notable as the first report of spinal arthritis in an anuran. However, the critical feature of these results is the distribution of arthritis among populations. Arthritic toads are concentrated at the invasion front; arthritis has not been detected in long-established populations. The authors suggest that arthritis develops as a product of the behavior of individuals because it is absent in younger, smaller toads. They conclude that the disease is a consequence of natural selection at the invasion front. That is, impaired health is a by-product of evolution that otherwise improves the performance of the invading toads.

Invasion as an Evolving Problem

The study of invasion biology is being transformed by the relatively recent recognition that species introductions create crucibles for contemporary evolution (12). There is now broad recognition that evolutionary rates are commonly rapid enough to alter phenotypes during timescales relevant to the process of invasion (13). Studies conducted over the last 5 years or so reveal that invasive species show evidence of rapid adaptation to their introduced range (14, 15). Among the more important findings is that natural selection at the invasion front may facilitate the invasion process. Prior work by the research group that is the subject of this commentary provides one of the clearest examples of this phenomenon.

Since 1935, when the cane toad was introduced to Australia, invasion-front populations of the toad have evolved larger body size and relatively longer legs (7). These morphological changes are associated with greater capacity for movement and greater distances covered by tracked individuals. Natural selection may favor individuals at the front who are able to move faster than their peers because early arrivers can contribute disproportionately to the growth of a population. Once the toads become established, relative leg length declines, presumably because the advantage associated with rapid movement diminishes.

Prior work on cane toads, as well as the few studies of contemporary evolution in other invasive species, have emphasized the ways in which an invader improves performance as a consequence of evolutionary response to a novel environment (12). These studies offer important cautionary lessons. As one example, the traits of a species evaluated for intentional release by a government agency may not be a reliable guide to the traits that emerge once the species is released. However, these patterns also help to explain why a cost of invasion may emerge in an introduced species and why it may be confined to one part of the range.

Health Impairment and the Cost of Invasion

Few studies have estimated the costs of invasion to the invader. Nevertheless, the ecological literature is replete with examples of movement costs to noninvasive species (16), and entire fields such as metapopulation biology and metacommunity biology presume that such costs are important enough to affect the regional dynamics of a species (17). Movement, particularly long-distance movement, is hard on animals.

For cane toads, the same suite of traits that may be the subject of strong selection during invasion (longer rela-

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tive limb length, increased body size, greater propensity to move) appears to predispose them to an ailment that is otherwise rare. Brown *et al.* (5) speculate that immune function may also play a role that is as yet unstudied. Although the concept of the "ailing invader" is still new, the authors' results suggest that study of the costs of invasion, particularly as they are mediated through health, will be well worth the attention of invasion biologists.

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