INTRODUCTION / INTRODUCTION

Enemies of biodiversity[1]

Douglas W. Morris

Abstract: Natural enemies, including humans, play a major role in the diversification of species and the maintenance of biodiversity. Compared with humans, most enemies faced by the rest of biodiversity are restricted in the magnitude of their effects, the spatial extent of their distribution, and the variety of species that they influence. Recognition of the similarities and differences between natural and human enemies should help us preserve and manage biodiversity.

Résumé : Les ennemis naturels, y compris les humains, jouent un rôle majeur dans la diversification des espèces et le maintien de la biodiversité. Par comparaison aux humains, la plupart des ennemis auxquels fait face le reste de la biodiversité sont limités dans l'importance de leurs effets, l'étendue spatiale de leur répartition et la gamme des espèces qu'ils influencent. L'identification des ressemblances et des différences entre les ennemis naturels et les ennemis humains devrait aider à conserver et à gérer la biodiversité.

[Traduit par la Rédaction]

One of the great commonalities that binds life together is that all species are both enemies and victims. Enemies include the obvious predators, parasites, and pathogens with their multifarious direct and indirect effects on prey and hosts. But enemies also include the not-so-obvious competitors that, in some way, either reduce or restrict access to resources. Viewed in this light, evolution by natural selection becomes a hazardous game of pursuit and escape where the winners and the losers can be one and the same. Evolution is also a ruthless game where friends are often foes and where the net effects of even the most lethal enemies may nevertheless endear them to survivors.

Thus, as Vamosi (2005) points out in this issue's contribution to the "Biodiversity Series", it is surprising that evolutionary biologists have only recently modeled the paramount roles that enemies play in the diversification of their victims. The story has numerous and delightful twists and turns driven by the inherent density and frequency dependence of enemy and victim interactions. In one scenario, disruptive selection on sympatric prey by specialized predators not only increases prey species diversity, but also causes diversification and subsequent speciation in the predators. In another, adaptive divergence yields specialized prey and generalist predators. And, in some models, all bets are off. Prey can diverge in antipredator traits, converge, or change in parallel with one another.

The theories spring to life with Vamosi's (2005) examples that span not only life forms, but the very history of life on Earth. We learn that predators may have been responsible for the origin of multicellular organisms. We learn that the diversity of Mesozoic molluscivores caused major changes in armour and habitat use by their prey. We see that predators in freshwater systems often induce character shifts among prey species. But we also discover that evidence for prey diversification is far from universal. Experiments on bacteria illustrate that divergence among allopatric populations exposed to phages is complemented by convergence within populations. Evolutionary radiations of plants with anti-herbivore adaptations are stymied when herbivores short-circuit the defenses. Diversification of mimics is constrained by the variety of models. And the species richness of aposematic species that so easily capture our attention is more than equaled by their cryptic ancestors.

We might think, nevertheless, that we have the models, both theoretical and empirical, to assess the impact of the human enemy on current and future biodiversity. When we specialize on certain age or size classes, prey populations diverge from our specialization. Examples include the rapid adaptive evolution of reduced body size and altered fecundity in commercially exploited fish species (Olsen et al. 2004) and similar reductions in body mass and horn size in bighorn sheep, *Ovis canadensis* Shaw, 1804, caused by trophy hunting (Coltman et al. 2003). The evolutionary divergence of prey, as it is for natural enemies, depends on whether we choose to consume common phenotypes (disruptive selection), or whether we attempt to harvest only the most extreme individuals (directional or stabilizing selection).

We also see tacit agreement with theory when species converge in response to human effects that influence several

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D.W. Morris. Department of Biology, Lakehead University, Thunder Bay, ON P7B 5E1, Canada (e-mail: douglas.morris@lakeheadu.ca).

[1]One of several occasional papers dealing with aspects of biodiversity published in the Journal from time to time. The first review in this series was published in vol. 78, issue 12, pp. 2061–2078.

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species simultaneously. Predation on weeds by generations of farmers has produced a variety of convergent vegetative mimics on food plants, as well as seed mimics whose sizes, shapes, and masses have converged on those of numerous cereals and other seed crops (Barrett 1983). The relative strengths of directional versus stabilizing selection on weeds depend on the shape and location of the original phenotype distribution relative to the distribution of the cultivars selected by humans. Meanwhile, untold numbers of species are adapting to human-induced mortality from pests, pesticides, and antibiotics (Morris and Heidinga 1997; Palumbi 2001).

In each case that we have explored thus far, the evolutionary dynamics are determined by soft selection where survival and future reproduction depend on the victim's phenotype. For these species, the human touch on biodiversity is indeed soft. But there are many others for whom the hard selection of humanity's iron fist gives no quarter. What phenotypic adaptations must vernal wildflowers possess if they are to bloom in a city's high-rise concrete forest? What traits will protect benthic invertebrates from the industrial fisher's bottom trawl? What kinds of species possess the range of tolerances that will enable some of their members to survive climate change and global warming?

We need not venture far to find the answer. Evolution by natural selection capitalizes on ecological opportunity. As we strip the opportunities for much of biodiversity, we create unparalleled options for others to profit by exploiting our domesticated plants and animals, by invading our modified habitats, and by taking advantage of an incredibly common resource, ourselves. The examples surround us: emerging diseases; novel competitors in our fields; new pests in our granaries, lakes, and cities; and old pests, weeds, and pathogens that are resistant to our controls.

Humans also destroy and disrupt native biodiversity by acting as agents of dispersal for alien species. Whether we introduce enemies by intention or accident, their impacts rival our own (e.g., Park 2004). Eradication of the invaders is sometimes effective, but there is no guarantee that native populations will recover their original abundance or distribution. Nor is there any guarantee that evolutionary adjustments to the aliens will be reversed. In each instance, we can learn from our own example. When faced with irrefutable evidence of human impact, such as through overharvesting, intelligent managers have often "eradicated" the human predator by closing seasons, establishing reserves, and protecting endangered species. Recovery of those populations can help us assess the potential return from control measures on alien invaders. Preliminary results are not encouraging.

I searched the Web site of the Committee On the Status of Endangered Wildlife In Canada (COSEWIC) to determine whether listed species that had been re-evaluated were considered under more or less threat than before. Presumably such species have witnessed some attempts at protection from negative human influences. As of November 2004, 292 species were listed as endangered or threatened (COSEWIC 2004). Of the subset whose status had been reassessed from 2000 through 2004, 63 species were placed in a higher risk category and only 2 were placed in a lower one. To be fair, the assaults on many species come from a variety of directions and involve numerous impacts. Some species do not have operating recovery plans (Anonymous 2004), and most plans that are in effect have been implemented only recently. The data are, nevertheless, a sobering reminder of how ineffective we have been thus far at rescuing threatened and endangered populations.

We are in a deadly race — not just to save species, to reduce our cumulative and interactive impacts, or to escape our enemies, but to find long-term solutions while we still have time to do so. We need to engage more scientists in the study of biodiversity and its conservation. There is work for everyone. We need more theory. We need definitive experiments. We need to look carefully and creatively at the few examples where we have snatched victory from our foes. We must pay attention to the mistakes and successes of others (Diamond 2005), and make better use of adaptive management (Park 2004). We can learn from Vamosi (2005). Natural enemies are multifaceted, and so too are their effects on prey. The evolutionary response of prey to their enemies depends on the direct and selective predation of certain phenotypes over others, on the indirect effects of enemies mediated through coexisting prey species, on coevolution within and across trophic levels, and on phylogenetic constraints. But here's the rub. Success is the architect of failure. Any population freed from its enemies soon becomes an enemy unto itself.

Population growth of any species cannot be sustained. Competition from too many individuals leads either to gross inequalities in resource sharing, where the powerful and lucky survive and reproduce at the expense of their miserable conspecifics, or a shared misery by all. Why, in the face of the evidence, and armed with intelligence, are we so complacent to continued growth of human populations? I suspect that we can find the answer in a well-intentioned but misunderstood interpretation of natural selection. To quote Darwin (1859):

> All that we can do, is to keep steadily in mind that each organic being is striving to increase at a geometrical ratio; that each at some period of its life, during some season of the year, during each generation or at intervals, has to struggle for life, and to suffer great destruction. When we reflect on this struggle, we may console ourselves with the full belief, that the war of nature is not incessant, that no fear is felt, that death is generally prompt, and that the vigorous, the healthy, and the happy survive and multiply.

Oh Charles, if only it was true!

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