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Rare Enemies and Rare Friends: Adaptations That Make Other Adaptations Maladaptive

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ABSTRACT

We show that certain adaptations can make other adaptations maladaptive. For example, one line of defence against an enemy can make an otherwise valuable, but subsequent line of defence detrimental. This can occur through indirect rare enemy effects.

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Why have certain seemingly obvious adaptations not evolved? Why, for example, do the hosts of cuckoos raise a monstrous cuckoo chick? Such hosts might simply save their efforts and fly away. This missing adaptation seems all the more strange when one takes into account the extraordinary abilities of the potential hosts of cuckoos to discriminate against cuckoo eggs [2]. One explanation for the absence of putative adaptations is that such traits would not be adaptive at all—indeed they might be maladaptations. That is, the benefits would be less than the costs. We might walk around in Faraday cages to escape potential lightning strikes, but the risk is so small—lightning strikes are so rare—that this does not pay off sufficiently to be beneficial. The evolutionary version of such a cost/benefit argument is called the rare enemy effect and can be useful to explain why certain traits have not evolved.

We suggest that even the authors who first proposed the rare enemy effect [4] have not fully understood its ramifications. For example, cuckoos are not particularly rare and cuckoo eggs are obviously more common than cuckoos. The really rare enemy is the cuckoo chick. What makes the cuckoo chick extremely rare is the hosts' first line of defence—skilful rejection of cuckoo eggs. The crucial point is that a strong first line of defence can make a normally beneficial second line of defence maladaptive. Cuckoo chicks in the nests of skilful egg-rejectors are so rare that the costs of attempting to discriminate against them are likely to outweigh the benefits. These costs may involve for example recognition errors and the consequent mistaken rejection of some of the hosts' own chicks. This deeper understanding of the causes and consequences of rarity leads to a new way to look at evolution. For the same organism, one adaptation can turn another from being beneficial to detrimental. In short, one adaptation can prevent another.

Dawkins and Krebs [5] suggested that cuckoo chicks manipulate their foster parents by producing supernormal stimuli, but this is unlikely because transplanted chicks of species other than cuckoos are reared by hosts as well [3]. Later arguments to explain the lack of chick rejection have either involved the assumption that host parents imprint on whichever chicks they first encounter in their nest [6], which seems questionable [8], or that chick rejection is not as good as egg rejection because it comes too late to save the rest of the brood [3]. Although benefits for rejecting a cuckoo chick *are* probably lower than for rejecting an egg, this misses the main point. Egg rejection reduces the abundance of the parasites and bars the emergence of chick rejection.

A recent model to study the absence of chick rejection among cuckoo hosts [7] reveals for the first time how one line of defence can prevent another through the rare enemy effect. Extending a model that combines both population dynamics and evolutionary dynamics [9], a game is played with four host types against the cuckoo, each of which has their own defence strategy combining egg and/or chick rejection. Hosts are equipped with fitness functions that depend on cuckoo density and discrimination errors for spotting parasitic eggs or chicks. The model predicts that, due to smaller benefits, chick rejectors usually cannot invade a population of egg rejectors, as suggested by Davies and Brooke [3]. However, crucially, the model also shows that hosts that reject both eggs and chicks have an intrinsic disadvantage in competition with hosts that only reject eggs.

This new insight in the working of the rare enemy effect also explains paradoxes in other parasitic systems. For example, when there is more than one level of parasitism, we can now understand why some species fail to recognize their own *friends*. Ant colonies *Myrmica schenki* are sometimes parasitised by butterfly larvae *Maculinea rebeli* [1]. In turn the butterfly larvae may be parasitised by *Ichneumon eumerus* wasps. A chemical cocktail that provokes in-fighting among the ant workers [10] allows the wasp to get access to and lay its egg in the caterpillar. Although the wasps help relieve the ants from their parasites, the ants clearly do not recognize the wasps as their allies—or why would the wasp have to cause internecine warfare to get into their nest? We suggest that the beneficial wasp is simply too rare to be recognized as a friend. The wasp is rare because the butterfly is rare: The extreme specialization within this system drives a rare friends effect.

In both cases, the actual rare enemy or rare friend is *made* rare by defences against other 'predators' in the system. Cuckoo chicks are rare because egg rejection has made them rare; wasps are rare because the butterflies are. These two parasite-host systems elucidate subtle new mechanisms in which rarity structures the evolution of organisms.

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