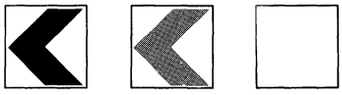

Diversity

The Big Things that Run The World — A Sequel to E. O. Wilson

Just a year ago in this space Professor E. O. Wilson extolled the importance of invertebrates to the rest of life, pointing out that perhaps 90% of the earth's biodiversity resides in this group of organisms and describing with dramatic flourish what might happen to the rest of nature should all invertebrates suddenly disappear from the scene. While I do not wish to dispute any of the points made by Professor Wilson or to belittle the essential role the "little things" play in maintaining the balance of nature, I would like to reply with a comment on the stabilizing function provided by the "big things."

Big things such as elephants, jaguars, and tapirs tend to be neglected by ecologists, for the very reason that by being big, they lack amenability to study. Aside from the problems presented by unwieldy bulk, they occur at low densities, are generally difficult to capture, mark, or observe, and present an almost insurmountable challenge in the accumulation of adequate sample sizes. Not the stuff of NSF grants. All these difficulties disappear when one studies lizards, songbirds, or salamanders, and so quite understandably, vertebrate ecologists tend to invest their energies in such lesser creatures. I suspect that for this reason the key functions provided by the big things are underappreciated.

For the past 15 years I have been privileged to spend 3 to 4 months annually at a pristine site in Amazonia where big things such as peccaries, jaguars, and spider monkeys are an everyday part of the environment. Over this period, one or another of my associates has conducted a major study of each of these species, and of a number of other large vertebrates as well. As our collective knowledge has deepened, so has my conviction that predation exerts a profound structuring influence on the ecosystem, one that extends far beyond the demographic impact on its immediate victims. If what I suspect is true, the top predators in this system — jaguar, puma, and harpy eagle — hold the key to its stability and to the maintenance of its extraordinary diversity of plants and animals. They do so through what can be called "indirect effects." This refers to the propagation of perturbations through one or more trophic levels in an ecosystem, so that consequences are felt in organisms that may seem far removed, both ecologically and taxonomically, from the subjects of the perturbation. Even some of Professor Wilson's favored ants and beetles may ultimately owe their continued existence on this earth to jaguars and other megafauna. How could this be so?

To answer this, I shall begin by reviewing some facts on predation that have been established through the work of Louise Emmons at Cocha Cashu in Amazonian Peru. The top terrestrial predators at this site are jaguar and puma. Together these two carnivores annually consume about 8% of the standing crop of terrestrial mammals weighing 1 kg or more as adults, a figure that accords well with the take of lion in the Serengeti. So much may seem unremarkable. What makes this fact interesting is that prey species appear in puma and jaguar scats in almost precisely the same proportions as their relative abundances in the environment, as determined by direct census. This unexpected finding indicates that forest felids, unlike their savannah-dwelling brethren, harvest a wide spectrum of prey species in an almost perfectly nonselective fashion. In other words, forest felids act as ideal "searchers," *sensu* MacArthur & Levins, while lions and cheetahs fill the role of "pursuers" in the open plains of Africa.

The finding of nonselective prey harvest carries another, more subtle implication growing out of the fact that the fecundity rates of the various prey species are not all the same. Some, such as peccary and capybara, may have litters of 3 or 4, while others, such as agouti, paca, and coati, normally have only 1 or 2. The productivity of the high-fecundity species, as measured in kg of consumable material per unit area per year, may thus be considerably greater than that of the low-fecundity species, especially given the fact that in this case the high-fecundity species are of larger body size. This being so, a few high-productivity prey species may largely determine the carrying capacity of the environment for large felid predators. In the presence of an elevated density of nonselective predators — elevated beyond the numbers their own intrinsic productivities could sustain — the abundances of the low-fecundity prey species could be severely depressed to levels far below what they might be in the absence of predators. Here we have an example of one type of indirect effect. When first described in the literature, it was termed "apparent competition" because the action of a predator induces the same type of reciprocal density relationship between two prey species that would be expected under classical Lotka-Volterra competition.

The obvious test of this interpretation is to remove the top predators and observe the demographic response of the prey. This test has been gratuitously performed on Barro Colorado Island, Panama. At 16 km^2, Barro Colorado is too small to support a population of pumas or jaguars, though both were known to have been in the area before the canal was built. In other respects the environment at BCI is similar to that of Cocha Cashu. The former lies at 10 degrees north and receives about 2,500 mm of rain while the latter lies at 12 degrees south and receives about 2,100 mm. If one compares the densities of terrestrial mammals in the two localities, the contrast is stunning. The numbers of several species — agouti, paca, coati — are more than 10 times greater on BCI, while those of some others — cottontail, armadillo, opossum — are from 2 to 10 times greater. Few ecologists would have predicted such dramatic effects of release from predation in large terrestrial vertebrates.

The implications of puma and jaguar predation may not end here, because three of their principal prey species — peccary, paca, and agouti — are themselves predators of a different kind — seed predators. They subsist on the fallen seeds of canopy and subcanopy trees. Just as it has been found that the removal of granivorous kangaroo rats in the Chihuahuan Desert allows certain large-seeded annual plants to increase up to 1,000 times over control densities, it is possible that major changes in the abundance of terrestrial seed predators in the tropical forest would lead ultimately to altered tree densities. One can easily imagine an interaction chain beginning with top predators, leading next to the major terrestrial seed predators, extending from these to large-seeded canopy trees, then, by way of seedling competition to small-seeded canopy and subcanopy plants, continuing to their seed predators — mice, rats, tinamous — and finally ending in the predators of these lesser seed predators — hawks, owls, and ocelots (Fig. 1). The succession of links describes the direct effects in the system, while indirect effects occur between the large and small seed predators and between large and small carnivores and across the diagonals (lines omitted for simplicity).

Testing all the functional interrelationships in this scheme would obviously require a major research program, one that has not yet been undertaken. At this stage the sole available comparison, that of Cocha Cashu with BCI, suggests that the absence of top carnivores leads to dramatic increases in the numbers of terrestrial vertebrate seed predators.

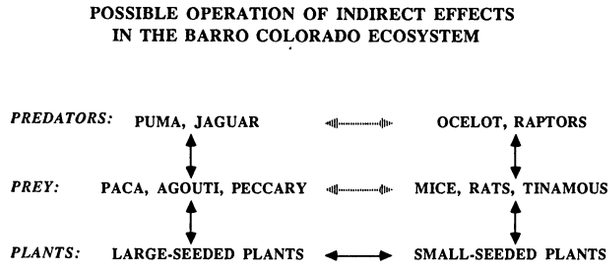

Figure 1.

The next question one would logically ask is whether the superabundance of terrestrial seed predators has affected the recruitment of large-seeded tree species on BCI. Although there are no data that speak directly to this point, there is a manuscript in press by E. Leigh, J. Wright, and J. Putz that offers a tantalizing bit of circumstantial evidence.

These authors noticed that the composition of the forest on tiny islets in Lake Gatun is quite different from that on the nearby mainland. Air photos from the 1920s show that the islets were then covered by mature forest, and so one can safely presume that they were forested when they became islands about a decade previously. The smaller ones (<2 ha) are too small to support large vertebrate seed predators. When one compares the forests of these islets with those of equivalent sites on the mainland, the contrast is dramatic: they are heavily enriched with species of *Protium, Oenocarpus, Sheelea, Astrocaryum, Dipteryx,* and other large-seeded trees. Whether it is the absence of vertebrate seed predators or some other peculiarity of the islets that has led to the contrast has not yet been established with certainty. Nevertheless, the suggestion is clear that the presence or absence of large terrestrial seed predators may have a decisive effect in determining the composition, and possibly the tree species diversity, of the neotropical forest.

While such a conclusion must remain for the time being in the realm of conjecture, its implications for the future management of isolated forest fragments are so far-reaching that it should not merely be brushed aside as premature speculation. If, in fact, jaguars and pumas do control the numbers of large terrestrial seed predators, and if these, in turn, do regulate the balance between large- and small-seeded tree species in forest regeneration, we shall confront a reality in which the perpetuation of diversity in tropical forests will require the maintenance of a more or less natural balance between predators, prey, and their plant food resources. Disrupting the balance by persecuting top carnivores, by hunting out peccaries, pacas, and agoutis, or by fragmenting the landscape into patches too small to maintain the whole interlocking system, could lead to a gradual and perhaps irreversible erosion of diversity at all levels — both plant and animal. In the end, this would work to the detriment of many of Professor Wilson's "little things." The essential point is that the big things are important too; what is worrisome in these changing times is that they are so much more vulnerable.

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