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The Plight of Large Animals in Tropical Forests and the Consequences for Plant Regeneration

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ABSTRACT

We introduce a special section that addresses the bushmeat or wild meat crisis, its direct impact on game species, and its indirect impact on plants in tropical forests.

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Key words: bushmeat; hunting; mammals; poaching; plant diversity; seed dispersal; seed predation; seed survival; seedling survival.

TROPICAL FORESTS HARBOR AN UNMATCHED DIVERSITY OF LARGE, CHARISMATIC ANIMALS. These include birds of paradise, currasows, eagles, fruit pigeons, hornbills, parrots, tinamous, toucans and trumpeters among birds and anteaters, cats, civets, deer, elephants, flying foxes, giant armadillos, okapis, olingos, pangolins, peccaries, primates, sloths, and tapirs among mammals. These and many other large animals have inhabited tropical forests for millions of years, and their ecological interactions with one another, with smaller animals, and with plants help to shape those forests. Today, a wide range of human activities threatens many of these large, charismatic species, but hunters who seek out large species for their meat and charismatic species for their hides, ornaments, and supposed medicinal value pose a particularly acute problem. Many persecuted species have been extirpated or persist only at greatly reduced abundances in otherwise intact tropical forests, where their ecological roles either go unfilled or are taken over by smaller species. In this special section, we address both the plight of large, charismatic animals in tropical forests and the consequences for the structure, dynamics, and species composition of tropical forest plant communities.

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THE PLIGHT OF LARGE ANIMALS IN TROPICAL FORESTS

Several factors contribute to the overexploitation of large, tropical forest animals (Millner-Guland *et al.* 2003). The weak economies of many tropical countries fail to provide sufficient jobs for their growing populations while land-use change, improved infrastructure, and new technology facilitate commercial hunting. Land-use change brings hunters and their markets closer to previously remote forests. Improved infrastructure provides access to forest interiors over roads opened for timber and mineral extraction as well as access to distant urban markets. The new technologies include guns, wire snares, battery-powered lights, and motorized transport and have largely replaced traditional hunting technologies even among indigenous peoples. Collectively, land-use change, improved infrastructure, and new technologies increase the return for time spent hunting and make it possible for hunters to deplete their prey to lower levels. These factors combine to create the pantropical 'wild meat' or 'bushmeat' crisis today.

The impact of hunting varies among tropical continents. Not surprisingly given the immense population pressure in Southeast Asia, piecemeal reports for specific taxa and countries have long suggested that the large, charismatic animals of this region face the direst threat. In this special section, Corlett (2007) provides the first taxonomically comprehensive review of the impacts of hunting

for Southeast Asia and concludes that a mass extinction of large animals threatens the region. The situation is marginally better in Africa, where 60 percent of 57 large forest mammal taxa are being harvested at unsustainable levels that threaten their extirpation from the Congo Basin (Fa & Peres 2001). In contrast, no large mammal taxon faces extirpation throughout the Amazon Basin (Fa *et al*. 2002); however, this finding integrates large spatial variation in hunting intensity. In this special section, Peres and Palacios (2007) provide the first systematic estimates of the impact of hunting on the abundances of a taxonomically comprehensive set of 30 large reptile, bird, and mammal species for 101 sites scattered widely throughout the Amazon Basin and Guiana Shield. Their data confirm that hunting decimates the larger species first, falls most heavily on frugivorous species across all body sizes, and actually favors several smaller species whose larger competitors and predators are hunted. The pervasive impact of hunting on large forest vertebrates sets the stage for the second component of this special section, which evaluates the indirect impact of hunting for tropical forest plants.

THE CONSEQUENCES FOR FOREST STRUCTURE AND DYNAMICS

Hunters persecute many species whose ecological interactions influence plant regeneration (Dirzo 2001, Wright 2003). These interactions include predispersal seed predation, primary and secondary seed dispersal, postdispersal seed predation, and leaf herbivory or browsing. Predispersal seed predators consume developing or mature seeds taken directly from the fruit-bearing plant. Primary seed dispersal agents also take fleshy fruit directly from the plant, but consume the fruit and inadvertently disperse living seeds. Secondary seed dispersal agents take fallen fruit or seeds from the ground and move them to new locations where the seeds are often stored or cached for future consumption. Postdispersal seed predators consume dispersed seeds. All browsers remove leaf tissue, which reduces plant carbon balance and often kills seedlings, while the largest browsers can break and uproot saplings and even trees. Collectively these interactions determine the number, locations, and survival of dispersed seeds and seedlings and, hence, the spatial template for all onward plant regeneration. The third paper in this special section (Stoner *et al.* 2007) reviews plant–mammal interactions for the major tropical regions and presents potential effects of mammal extirpation for plant regeneration.

The next five papers in this special section present case studies that evaluate the impact of hunting on plant–animal interactions and on the species composition and diversity of seedlings and saplings for forests in Cameroon, Mexico, Panama, and Peru. Beckman and Muller-Landau (2007) provide the first evaluation of the impact of hunting on predispersal seed predation. A large-seeded species experienced a significant reduction in predispersal seed predation by mammals where hunters were active while a second smaller-seeded species lacked predispersal seed predation by mammals everywhere. This result suggests that larger-seeded species will tend to produce a larger number of viable seeds where hunters are active.

Two papers evaluate the impact of hunting for seed dispersal. Given the grave impact of hunting on frugivores in Amazonian forests documented by Peres and Palacios (2007), the indirect effect on seed dispersal is expected to be particularly severe for species whose seeds are dispersed by game species. Beckman and Muller-Landau (2007) document significant decreases in primary seed dispersal for one species and in secondary seed dispersal for their second study species. Wang *et al.* (2007) find a similar significant increase in the number of seeds that failed to disperse and fell directly beneath a seed-bearing conspecific at hunted sites and use genetic evidence to refine their estimate of the true decline in seed movement. Frugivores disperse an unknown number of seeds between fruiting conspecifics as they move between fruiting trees. The proportion of such seeds—found beneath a seed-bearing conspecific that was not their genetic mother—was significantly lower at a site subject to hunting than at a second site that lacked hunters. These two studies provide direct evidence that hunting reduces seed dispersal for species whose seed dispersal agents include game species.

Two papers evaluate complementary hypotheses concerning postdispersal seed predation. Dirzo *et al.* (2007) and Wright *et al.* (2007) both hypothesize that predation on large seeds will be reduced where hunters remove large seed predators, and Dirzo *et al.* (2007) also hypothesize that predation on small seeds will be increased where small seed predators increase in numbers after hunters remove their larger competitors. Dirzo *et al.* (2007) use a series of experiments to evaluate all components of their hypothesis. Both studies document increased densities of large-seeded species in the seedling layer. Collectively, these studies suggest that hunting has opposing effects on large-seeded species—increasing viable seed production, decreasing seed dispersal, and increasing postdispersal seed survival—and that the net effect might be to favor large-seeded species. A different outcome is likely in Southeast Asian forests where seed predators tend to be smaller and are not hunted (Corlett 2007).

Two papers evaluate the impact of hunting on the density, species composition, and diversity of seedlings or saplings. Nuñez-Iturri and Howe (2007) and Wright *et al*. (2007) find substantial shifts in plant species composition with species whose seeds are dispersed by small, nongame animals and by abiotic means (primarily by wind) becoming increasingly more important where hunters are active. Wright *et al*. (2007) also document a dramatic increase in lianas where hunters are active and attribute this increase to the large proportion of lianas whose seeds are dispersed by wind. To summarize, these five papers demonstrate that hunting has pervasive effects on tropical forest plant communities altering levels of predispersal seed predation, primary and secondary seed dispersal, and postdispersal seed predation, which, in turn, alters seedling and sapling species composition.

Our empirical studies focus on seeds, seedlings and saplings. The lasting impact for adult trees and lianas whose longevities extend from decades to centuries remains unexplored. In the final original contribution in this special section, Muller-Landau (2007) provides a theoretical perspective on the lasting impact of hunting.

An encouraging conclusion is that the ecological forces that stabilize plant communities—negative density dependence due to interactions with natural enemies and niche partitioning—could reverse the effects of hunting on plant species composition rather quickly once a forest is protected and animals recover. A discouraging possibility is that plant species composition might shift to a new steady state with crucial plant species absent or at such low numbers that animals fail to recover. A solution to the pantropical wild meat crisis is urgently required before this possibility materializes and before game species are driven to extinction.

CONCLUSIONS

A final synthesis paper provides a meta-analysis of published studies that bear on the consequences of hunting for tropical forest plants. This meta-analysis identifies ubiquitous consequences for seed dispersal as well as consequences for seed predation and seedling recruitment that occur in some forests but not in others for reasons that are not yet understood. These reasons are likely to involve indirect effects that are yet further removed from the direct impact of hunters on forest vertebrates. Possibilities include altered spatial patterns of seedlings and saplings and dramatic increases in recruitment to the adult stage among insect seed predators. The unfortunate vertebrate removal experiment being maintained by hunters will provide many more insights into the ecological interactions that shape tropical forests.

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