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The myriad consequences of hunting for vertebrates and plants in tropical forests

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Abstract

Humans hunt forest vertebrates throughout the tropics. Many preferred game species consume flowers, fruit, seeds and/or leaves, and these interactions will cause their harvest to ramify through forests. Three related issues will determine how severely the harvest of forest vertebrates influences the plant community. First, the types of species selected by hunters and the intensity of the harvest will determine which vertebrates are removed and which remain. Second, the possible presence of ecologically similar, non-game species able to expand their activities to fulfill the ecological role of heavily exploited species will determine how severely the harvest disrupts ecological relationships between the community of forest vertebrates and the community of forest plants. Finally, hunters will alter plant species composition if the harvest of vertebrates differentially affects mutualists or pests of particular plant species. Hunters will also alter plant diversity if the harvest of vertebrates disrupts ecological mechanisms that permit plant species to coexist. I examine hunter selectivity, the intensity of the hunt, possible compensation by non-game species, and the types and strengths of interactions among game species and plants for tropical forests to determine when and where these outcomes occur.

Key words: folivores, Janzen-Connell hypothesis, plant diversity, pollinators, seed dispersers, seed predators

Introduction

Humans hunt forest vertebrates throughout the tropics. Many preferred game species consume fruit, seeds and/or leaves, and these interactions will cause their harvest to ramify through forests (Emmons 1989). Frugivores inadvertently disperse seeds, which sets the spatial template for plant recruitment. Granivores kill seeds, which reduces potential plant recruitment, whereas browsers often kill seedlings and always reduce leaf area and plant carbon balance. Preferred game species also interact with other, non-preferred forest vertebrates. Carnivores, many of which are hunted themselves, prey upon both game species and non-game species. Non-game species may also compete with game species. Humans disrupt this web of

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This paper is dedicated to the memory of Agent Marcelino Castillo of the National Police of the Republic of Panama. Agent Castillo was murdered by a poacher while patrolling the Barro Colorado Nature Monument in June 1992.

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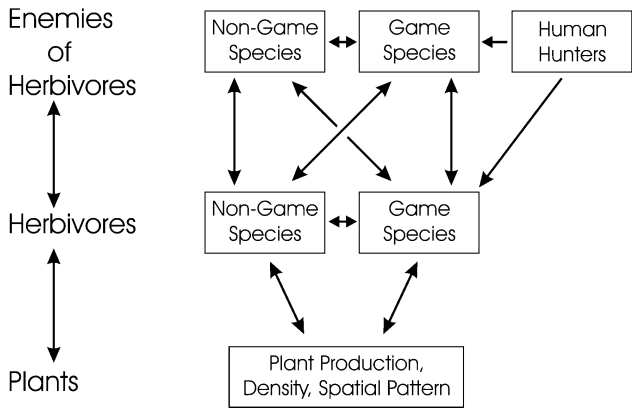

Fig. 1. A schematic model representing interactions among hunters, preferred game species, non-game animals, and plants. The single-headed arrows emerging from hunters represent their direct effect on game species. The double-headed arrows among game species, non-game species, and plants represent the web of natural interactions that may cause the direct effects of hunters on game species to cascade to include a much wider range of indirect effects on plants and non-game animals.

interactions wherever forest vertebrates are harvested (Fig. 1). This review addresses the consequences for the biota left behind in tropical forests.

The review is organized in four sections around four issues which will determine how severely the harvest of forest vertebrates influences the plant community. The first section integrates the types of species selected by hunters and the intensity of the harvest. Selectivity varies continuously among vertebrate species from universally preferred (many ungulates) to rarely or never hunted (small bats and rats). Selectivity and intensity are difficult to separate because hunters routinely expand the range of species harvested wherever the abundance of preferred species is low (Peres & Dolman 2000). Selectivity and intensity determine which vertebrates are removed and which remain.

The second section concerns the possible presence of ecologically similar, non-game species able to expand their activities to fulfill the ecological role of heavily exploited species. The extraordinary number of vertebrate species that inhabit many tropical forests suggests that the potential for such ecological redundancy is high. The selectivity of hunters, the intensity of hunting pressure, and the compensatory potential of both game and non-game species will jointly determine how severely hunters disrupt ecological relationships between the community of forest vertebrates and the community of forest plants.

The third section addresses indirect effects for plants mediated by interaction with the animals that hunters harvest. Particular vertebrate species may be mutualists (pollinators or seed dispersal agents), pests (seed predators or browsers), or neutral toward particular plant species. Hunters will alter plant species composition if the harvest of vertebrates differentially affects mutualists or pests of particular plant species (Emmons 1989; Wright et al. 2000). The final section addresses the further possibility that hunters will alter plant diversity if the harvest of vertebrates disrupts ecological mechanisms that permit plant species to coexist (Dirzo & Miranda 1991; Dirzo 2001; Wright & Duber 2001). Hunter selectivity, the intensity of the hunt, and compensation by non-game species will determine when and where these outcomes occur.

The intensity and selectivity of the hunt

Redford (1992) created the image of an 'empty forest', where mammals and birds were entirely extirpated and their ecological roles went unfilled, to emphasize the threat to biodiversity posed by hunters in tropical forests. Are there 'empty' tropical forests? And, if so, where and under what circumstances have hunters extirpated game species?

Spatial variation in hunting pressure has two primary causes. First, laws potentially protect selected forests. Where these laws are enforced, the abundance of game species can change markedly at an artificial border (Wright et al. 2000). Unfortunately, truly protected forests are rare in developing tropical countries. The 59-km^2 Barro Colorado Nature Monument, Panamá, which is among the best protected, illustrates the problem. Twenty-one game wardens and forest police are dedicated to the protection of the Monument. The national police arrested 150 poachers inside the Monument during the 1990s and confiscated their weapons and equipment. A poacher murdered a policeman during hot pursuit in 1992 (Wright et al. 1994) and remains in prison in 2003. Nonetheless poachers continue to reduce the abundance of game species in all but the central core of the Monument, which is protected by an additional water barrier (Wright et al. 2000).

Very few forest reserves enjoy this level of protection in developing tropical countries. Rather, the norm is for high levels of hunting that greatly reduce the abundance of game species within 'protected' forests (Alvard 2000; Fitzgibbon et al. 2000; Hart 2000; Hill & Padwe 2000; Madhusudan & Karanth 2000; Noss 2000; O'Brien & Kinnaird 2000). Wilson (2002) proposed that a relatively modest global investment of 30 billion US dollars would secure all existing protected lands in the tropics. This seems unlikely. The political and social will to deny the subsistence economy is lacking. Laws protect wildlife successfully in developed nations because their citizens have economic alternatives. Laws are unlikely to protect wildlife in developing tropical nations as long as large numbers of

their citizens survive at a subsistence level. For many species, sustainable management (Bodmer & Puertas 2000; Hill & Padwe 2000) may be the only viable alternative to local extirpation and eventual global extinction.

The second cause of spatial variation in hunting pressure, simple spatial isolation, is much more likely to protect wildlife in developing tropical countries. Hunting pressure is predictably intense near villages and roads and decreases markedly with isolation from humans over distances of just 10 to 20 km (Fimbel et al. 2000; Hart 2000; Hill & Padwe 2000; Mena et al. 2000; Peres 2000). Today, the full range of levels of hunting pressure can be found in the tropics. Hunting is completely absent from remote, depopulated forests. Examples include large parts of French Guiana and the headwaters of selected rivers and interfluvial areas in the Amazon Basin (Peres 2000; P.M. Forget, pers. comm., June 2002). Hunting by indigenous people armed with traditional weapons also still occurs (Robinson & Bennett 2000). At the other extreme, present levels of hunting are unsustainable near villages and roads throughout the tropics (Robinson & Bennett 2000) and are unsustainable over the entire Congo Basin for 60% of African forest mammals (Fa et al. 2002). Hunting is particularly severe in logging concessions and in forests fragmented by anthropogenic activity (Whitmore 1997; Robinson et al. 1999; Peres 2001). Tropical nations plan to develop the last great tropical forests (Laurance et al. 2001). Hunting pressure will increase unless the planned development spurs economic growth that reduces the number of subsistence hunters.

What are the likely consequences for forest vertebrates? – Humans have hunted forest vertebrates for perhaps 10 millennia in the Neotropics, 40 millennia in Southeast Asia, and much longer in Africa. Extant vertebrates are survivors. However, the nature of the hunt is changing. Indigenous people armed with traditional weapons and living at relatively low population density are being replaced by modern people armed with guns and able to export skins, live animals and smoked meat to essentially infinite markets. Modern hunters and trappers have caused the extinction of at least 80 animal species since 1600 (WCMC 1992). It is now possible to identify the types of mammal species that are most severely threatened in tropical forests.

Choices made by hunters and the ability of the chosen species to withstand exploitation will jointly determine which species are at greatest risk. Recent colonists and local indigenous people often prefer the same species, although indigenous hunters tend to take a wider range of species (Redford & Robinson 1987). The universally preferred game species are at greatest risk. They tend to be large, because large size makes their capture rewarding, and to possess behavioral traits that make them easy to locate. These traits include frequent vocalization, travel in noisy social groups, and predictable return to salt licks, dens or fruiting trees. Preferred game species include ungulates and large primates throughout the tropics and large rodents (>1 kg) wherever they occur (Robinson & Bennett 2000). Many carnivores may also be preferred, but this possibility is rarely evaluated perhaps because carnivores are often rare. Less preferred species larger than 1 kg in mass include nocturnal opossums and carnivores, secretive primates, and several edentates (anteaters, sloths and armadillos). The mammal species least likely to be hunted are all small and include bats, most rodents, and the smallest primates.

The ability of wild species to withstand exploitation by humans varies with generation time, longevity of individuals, and maximum potential growth rates of populations (Pimm 1991). Bodmer et al. (1997) confirmed these relationships for forest mammals in Amazonian Peru. Hunters markedly reduced the abundance of preferred game species with long generation times (high age to first reproduction), long-lived individuals (high age at last reproduction), and low potential rates of population increase. In contrast, the same hunters had relatively little effect on the abundance of equally preferred species with short generation times, short-lived individuals, and rapid potential rates of population increase. Large primates and many ungulates (tapirs, rhinoceros, bovids, most deer) share long generation times, extended longevity, and low potential population growth rates and are highly sensitive to hunting (Redford & Robinson 1991; Bodmer et al. 1997; Robinson & Bennett 2000). Large rodents and selected ungulates (pigs, smaller duikers) are equally preferred by hunters, tend to have shorter generation times and higher potential population growth rates, and are less sensitive to hunting (Bodmer et al. 1997; Alvard 2000; Hart 2000). The choice of species made by hunters and the differential susceptibility of the chosen species determine the relative abundances of game species left in the forest and set the stage for compensatory shifts among non-game species.

Compensatory changes among animals

Compensatory changes may occur among the remaining, non-game species after hunters harvest game species. The abundance of non-game species may increase if their competitors or predators are harvested, or decrease if their prey is harvested. Attention has focused on possible compensatory changes mediated by competition.

Overlap in resource requirements, competition, and the potential for compensatory change are expected to be greatest among closely related species. For example, overlap in diet among large arboreal frugivores was greatest among congeneric hornbills and among congeneric primates, intermediate among primates from different genera, and least among primates and hornbills in an African forest (Poulsen et al. 2002). Closely related species are also expected to share traits that influence sensitivity to hunting (body size, behavior, generation time, longevity). Thus, the potential for compensatory change may be limited because hunters tend to have similar impact on closely related species.

The limited evidence available suggests that compensatory change is surprisingly common. The clearest example of compensatory change occurs among New World monkeys of the family Cebidae (Peres & Dolman 2000). The different cebids have broadly overlapping diets, and agonistic interspecific interactions are commonplace. The largest cebids include woolly, spider and howler monkeys (*Lagothrix*, *Ateles* and *Alouatta*, respectively). These large, conspicuous, diurnal monkeys comprise a single subfamily and share low population growth rates, extended longevity, and high sensitivity to hunting (Bodmer et al. 1997; Peres & Dolman 2000). In contrast, several smaller cebids, including saki monkeys and uakaries (*Pithecia* and *Cacajao*, respectively), are rarely hunted. Moderate hunting pressure reduces the abundance of the larger, preferred cebids, which, in turn, allows the abundance of the smaller, less preferred species to increase (Peres & Dolman 2000). The species composition of Cebidae in forests subjected to moderate hunting reflects missing competitive interactions with preferred game species.

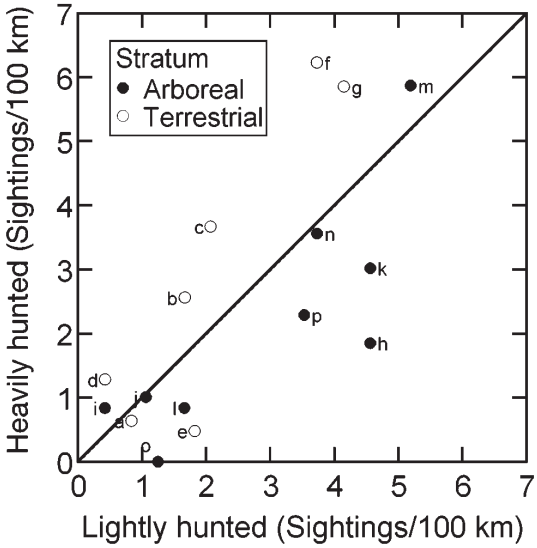

Fig. 2. The relationship between the abundance of game species at lightly and more heavily hunted sites provides evidence for possible compensatory changes among frugivores from different forest strata in northeastern Peru. The 45° line represents equal abundance. Hunters reduced the abundances of seven of nine arboreal frugivores (letters h through p). In contrast, the abundances of five of seven terrestrial frugivores (a through g) were actually greater at more heavily hunted sites, suggesting a compensatory increase. In an analysis of covariance, abundance under heavier hunting was the response variable, abundance under lighter hunting was the covariate, the strata-covariate interaction was not significant ($F_{1,12} = 3.29$, $P = 0.10$), and the stratum main effect was significant in the reduced model ($F_{1,13} = 6.84$, $P < 0.05$). Letters represent species as follows: (a) *Tayassu pecari*, (b) *T. tajacu*, (c) *Mazama americana*, (d) *M. gouazoubira*, (e) *Tapirus terrestris*, (f) *Dasyprocta fuliginosa*, (g) *Myoprocta pratti*, (h) *Lagothrix lagothrica*, (i) *Alouatta seniculus*, (j) *Cacajao calvus*, (k) *Cebus apella*, (l) *C. albifrons*, (m) *Pithecia monachus*, (n) *Callicebus cupreus*, (o) *Ateles paniscus*, and (p) *Samimiri* spp. Data are from Bodmer et al. (1997).

Compensation may also occur among phylogenetically unrelated species that share a common resource. For example, arboreal frugivores have first access to fruit while terrestrial frugivores depend on fallen fruit and often congregate beneath arboreal frugivores. During a year of very low fruit production by most plant species in central Panama, arboreal frugivores including squirrels and primates switched to immature fruit which subsequently exacerbated famine among terrestrial frugivores including artiodactyls and caviomorph rodents (Wright et al. 1999). Hunting reveals a similar relationship between arboreal and terrestrial frugivores in Amazonian Peru. Bodmer et al. (1997) contrasted the abundance of 16 frugivorous mammals in two forests subjected to different intensities of hunting and noted that large rodents and artiodactyls were more abundant at the more heavily hunted site. I re-plotted their data to contrast the relationships between hunting and abundance for arboreal and terrestrial species (Fig. 2). The abundance of most arboreal frugivores was lower at the more heavily hunted site. In contrast, the abundance of most terrestrial frugivores including several of the most highly preferred game species (peccaries and deer) was unexpectedly greater at the more heavily hunted site (Fig. 2). This result again suggests an asymmetric competitive relationship. Arboreal frugivores preempt fruit but are unaffected by terrestrial frugivores. Again, the abundance of the vertebrates remaining in forests subjected to hunting reflects the absence of interactions with game species.

The potential for compensatory change will also vary with hunting pressure and the range of species selected by hunters (Fig. 3). In Amazonia, hunters take mostly the largest cebids in lightly hunted forests, smaller cebids in moderately hunted forests, and finally still smaller callitrichids (tamarins and marmosets) in severely overhunted forests (Peres & Dolman 2000). The potential for compensatory change among

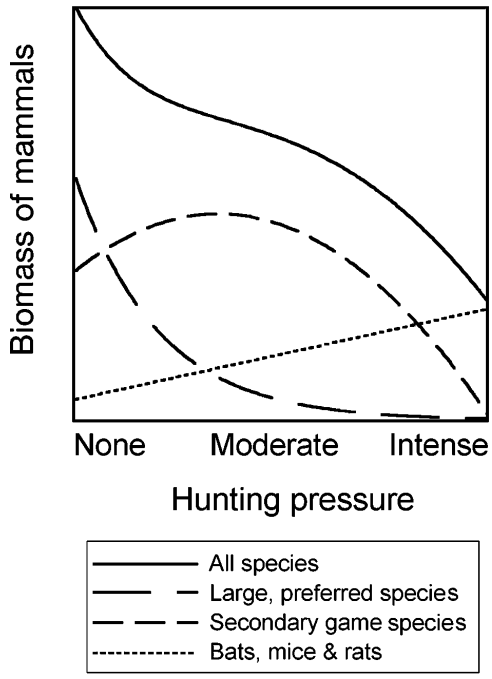

Fig. 3. Predicted shifts in the composition of mammal community structure with hunting in tropical forests. Large-bodied, preferred game species dominate community biomass in the absence of hunting but decline rapidly as hunting pressure increases (see Peres 2000 for an example). Smaller, secondary game species initially increase due to competitive release but then decline as preferred species are extirpated and hunters shift to secondary targets (see Peres & Dolman 2000 for an example). More speculatively, bats, mice and rats are not hunted and increase steadily with hunting pressure. Compensation is also likely to be incomplete so that the total biomass summed over all mammal species declines steadily as large-bodied species become rare and smaller species become more abundant.

New World primates falls to zero as the proportion of species actively hunted increases.

Bats, mice, and rats remain in the most heavily hunted forests (although even they are taken by some indigenous peoples). Diet overlap can be substantial among bats and arboreal frugivores and among mice, rats, and other terrestrial frugivores (Handley et al. 1991; Adler 1995). The potential for compensatory increases in abundance in heavily hunted forests has never been evaluated for bats and has been evaluated just once for small terrestrial mammals (Wright et al. 2000). Extraordinarily high abundances of common opossums (*Didelphis marsupialis*) and spiny rats (*Proechimys* spp.) in small forest fragments in the Atlantic coastal forests of Brazil and in central Panama suggest that these small mammals have the potential to increase dramatically where their competitors and/or predators are absent (Fonseca & Robinson 1990; Adler 1996). Possible compensatory responses of bats, mice, and rats to hunting merit further attention because these smallest mammals disperse many seeds and can also be voracious seed predators.

Figure 3 summarizes the probable relationship between the intensity of hunting pressure and the biomass of preferred and secondary game species and non-game species. The total biomass of all vertebrates and the biomass of the larger, preferred game species decline steadily with increasing hunting pressure. The biomass of secondary game species may undergo compensatory increases as preferred species are reduced, but then decline as preferred species become rare and hunters switch to secondary species (Peres & Dolman 2000). The biomass of non-game species that are never hunted may increase steadily with hunting pressure. This last possibility has not been evaluated. Insects may also increase in numbers where vertebrate defaunation occurs (Dirzo 2001). The indirect effects of hunting for forest plants will depend partly on the ability of non-game species to fill the ecological roles of game species.

Indirect effects on plants

Vertebrates consume nectar, pollen, flowers, fruit, seeds, and leaves, and thereby disperse pollen and seeds, kill seeds and seedlings, and reduce leaf area. My review of the potential indirect effects of hunters for plants is organized around these plant-vertebrate interactions. Just two studies have directly examined the consequences of hunting for plant-vertebrate interactions in tropical forests (Wright et al. 2000; Wright & Duber 2001). Additional studies, which provide insight into the consequences of vertebrate defaunation, include experiments that exclude vertebrates from otherwise intact forest and comparisons of forest fragments inhabited by different vertebrate species. The relevance of these additional studies is questionable, however. Exclusion experiments and hunters affect different vertebrate species, and forest fragmentation also alters the physical environment, which, in turn, affects plants and animals. Therefore, I draw on exclusion and fragmentation studies sparingly and only to illustrate potential effects of hunting for plants in tropical forests.

Pollinators

Pollen is dispersed by animals or by wind. Animals are particularly important in tropical forests, where a vast array of insect species and a smaller number of vertebrate species disperse pollen (Roubik 1992). Small birds and bats are important pollinators; however, their small size and specialized nectar-rich diets ensure that they are unlikely to be affected either directly or indirectly by hunters. Primates and several other potential game species also visit large flowers (E. Mendoza & R. Dirzo, pers. comm., Jan 2003). It is not

generally known whether these larger vertebrates are effective pollinators. Smaller vertebrates (bats and hummingbirds) and large insects (bees and Lepidoptera) also visit most of the same large flowers and may be effective pollinators (Roubik 1992). Hunters may alter pollen vectors and pollen dispersal for selected plant species with large flowers.

Seed dispersal agents

The seeds of most plants are dispersed by vertebrates or by wind. Vertebrates are particularly important in tropical forests (Levey et al. 1994), where preferred game species, secondary game species, and non-game species all disperse seeds. Vertebrate defaunation is expected to alter seed dispersal.

Three types of study have evaluated this possibility. The first catalogues primary seed dispersal agents, identifies plant species whose only primary dispersal agents are the large birds and primates most sensitive to hunting and habitat fragmentation, and warns that these plant species are at risk (Bond 1994; Chapman & Onderdonk 1998; Silva Cardoso & Tabarelli 2000; Peres & van Roosmalen 2002). The second type of study contrasts primary seed dispersal for conspecific populations from continuous, continental forests versus forest fragments or islands. The extent of dispersal of animal-dispersed seeds is relatively greater in larger forests than in smaller forests and parallels the number of species of frugivorous vertebrates present (Pizo 1997; Bleher & Böhning-Gaese 2001; Cordeiro & Howe 2001). These studies highlight the potential consequences of hunting for primary seed dispersal.

Primary dispersal agents remove seeds from seed-bearing plants, while secondary dispersal agents move fallen seeds to a new position. Secondary dispersal agents can be crucial (Forget et al. 2002). For example, the black agouti *(Dasyprocta fuliginosa)* disperses and buries fallen pods of the tree *Hymenaea courbaril*. Seedlings recruit successfully where agoutis are present, but fail where agoutis are absent on small islands in Lago Guri, Venezuela (Asquith et al. 1999). Smaller rodents also cache fallen seeds (Adler 1996; Brewer & Rejmanek 1999). In tropical forests, most seeds disappear quickly when left in the open where they are exposed to all terrestrial vertebrates (mean = 73% for ten tree populations). Complementary experiments with seeds placed in fenced enclosures with small holes (25–64 cm^2), where they are exposed only to small rodents, demonstrate that small rodents alone remove 15–100% of the seeds removed by all vertebrates (mean = 69% for the same ten tree populations; data compiled from Terborgh et al. 1993; Terborgh & Wright 1994; Brewer & Rejmanek 1999; Feer & Forget 2002; Guariguata et al. 2002). The net effect of hunting on seed dispersal is not obvious given the strong possibility of compensatory, secondary dispersal by small rodents.

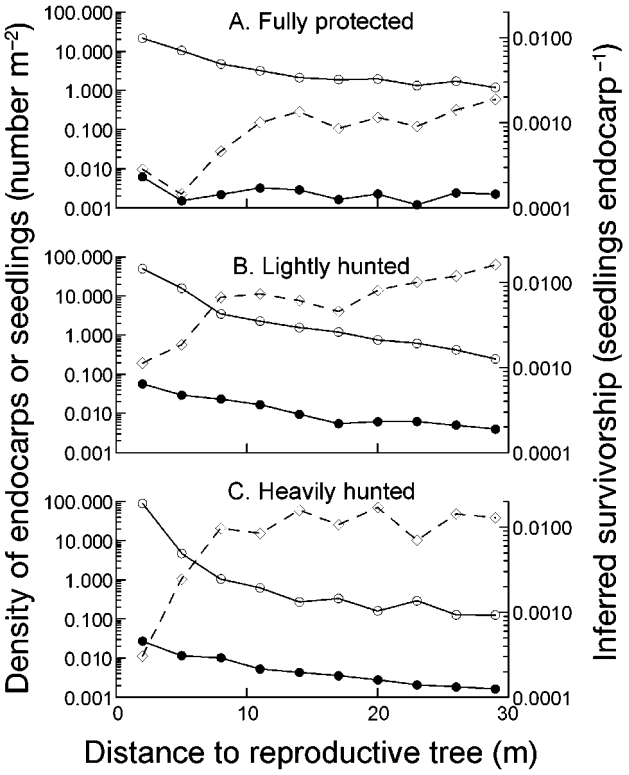

Fig. 4. Post-dispersal density of seeds (open circles, solid line), density of seedlings (solid circles and line), and inferred seed/seedling survivorship (open triangles, dashed line) related to distance to the nearest reproductive tree for the palm *Attalea butyraceae* at protected (panel A), lightly hunted (panel B), and heavily hunted (panel C) sites in central Panama. Reduced seed dispersal and increased seed survival where hunters were active caused seedling density to increase dramatically near conspecific trees and to drop off more rapidly with distance (redrawn from data in Wright & Duber 2001).

I am aware of just two studies that examined the effect of hunting on seed dispersal (Wright et al. 2000; Wright & Duber 2001). Three primate species, two carnivores, and four rodents disperse the seeds of the palms *Astrocaryum standleyanum* and *Attalea butyraceae* in central Panama. Hunters prefer seven of the nine dispersal agents and avoid one primary dispersal agent, the red-tailed squirrel (*Sciurus granatensis*), and one secondary dispersal agent, the spiny rat *(Proechimys semispinosus)* (Wright et al. 2000). The seeds of both palms are encased in large, stony endocarps, which decay slowly and are easily located on the forest floor. This facilitates estimates of final dispersal distances, which incorporate both primary and secondary dispersal, relative to nearest conspecific adults. For both species, the percentage of seeds dispersed away from seed-bearing trees declined from

more than 85% of all seeds at sites with zero to moderate hunting to less than 10% of all seeds at sites with intense hunting (Wright et al. 2000). For *Attalea butyraceae*, hunting also reduced dispersal distances for those seeds that were successfully dispersed away from seed-bearing trees (Fig. 4). Hunters altered seed dispersal distances and the spatial template for subsequent seedling regeneration. The dramatic impact of hunting for seed dispersal of these two palms is likely to be repeated for the many tropical forest plants whose seeds are dispersed by large birds and mammals.

Seed predators

Seed predators are largely restricted to insects, mammals and birds (Janzen 1971). Important seed predators include preferred game species, secondary game species and non-game species among tropical forest vertebrates. Microbes also kill seeds, and the potential for compensatory seed mortality is great if insects and microbes multiply where game species are harvested. Nevertheless, hunters are likely to alter patterns of seed predation.

Two types of study illustrate the potential effects of vertebrate defaunation for seed predation. Experiments that protect seeds placed on the forest floor demonstrate that terrestrial vertebrates locate and kill most seeds after primary dispersal (Fig. 5). Reduced post-dispersal seed predation has the potential to increase the density of viable seeds by an order of magnitude where hunters harvest game species. Birds and arboreal mammals also include voracious pre-dispersal seed predators (Janzen 1971), and viable seed rain density may increase after hunters remove game species. This possibility has not been evaluated. The second type of study contrasts seed predation for large, continuous forests versus forest fragments or islands. Levels of post-dispersal seed predation were similar in a large continuous forest and a 250-ha forest fragment; however, the major seed predators were rodents and insects in the continuous forest and birds in the forest fragment (Pizo 1997). These studies highlight the enormous potential for vertebrate defaunation to alter patterns of seed predation. Protection from terrestrial vertebrates may increase numbers of viable seeds by an order of magnitude or more. However, compensatory seed predation by other species may destroy virtually all of those seeds. What actually happens in forests subjected to hunting?

Again, I am aware of just two studies that examined the relationship between hunting and seed predation (Wright et al. 2000; Wright & Duber 2001). Three rodents and two bruchid beetles are predators of mature seeds of the palms *Astrocaryum standleyanum* and *Attalea butyraceae* in central Panama. White-faced mon-

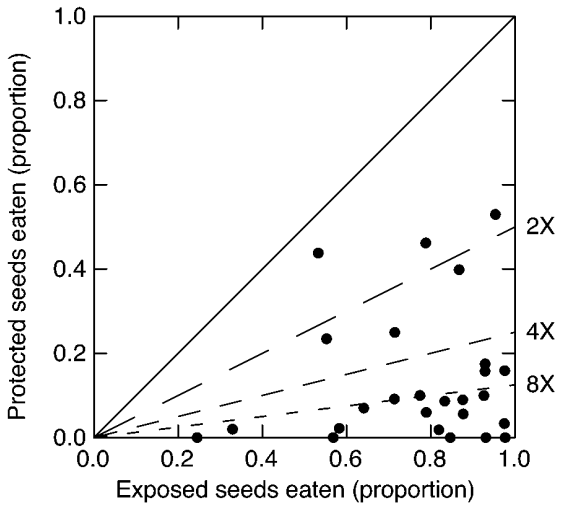

Fig. 5. The relationship between the proportion of dispersed seeds killed when exposed to insects and vertebrates (exposed seeds) or when protected from vertebrates but exposed to insects (protected seeds). Each symbol represents a plant species. The proportion of seeds eaten was two, four, eight (labeled dashed lines) or more times greater when seeds were exposed to vertebrates as well as insects. All seeds were placed on the forest floor, exposed seeds were available to both insects and vertebrates, and protected seeds were enclosed in 1.27-cm mesh cages that provided free access to insects but excluded vertebrates. Seeds were censused biweekly and the cause of mortality was noted. Drawn from data in Notman & Gorchov (2001).

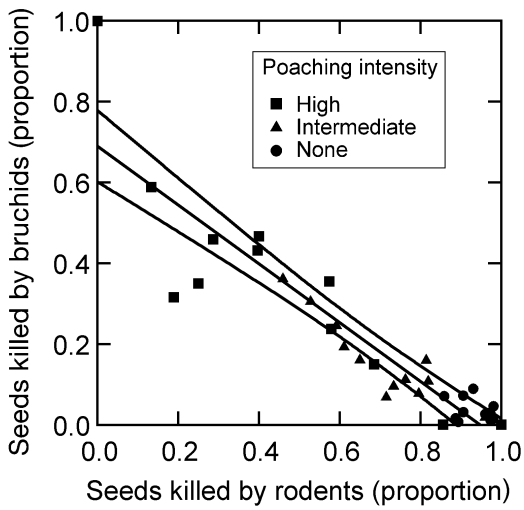

Fig. 6. The relationship between bruchid beetles and rodents as seed predators of the palm *Attalea butyraceae* in central Panama. Rodents killed most seeds where poaching was absent, and beetles killed most seeds where poaching was most intense. The solid lines represent the least squares linear regression and its 95 percent confidence limits. Its slope (–0.73 ± 0.048 [±95% confidence limits]) indicates that beetles only partially compensated where seed predation by rodents fell to low levels. Redrawn from data presented by Wright & Duber (2001).

keys (*Cebus capucinus*) also eat immature *Astrocaryum standleyanum* seeds during periods of food shortage (Wright et al. 1999). There are no other predispersal seed predators of either palm. The red-tailed squirrel (*Sciurus granatensis*) is a primary dispersal agent as well as a seed predator. The agouti (*Dasyprocta punctata*) and the spiny rat (*Proechimys semispinosus*) are secondary dispersal agents as well as seed predators. The agouti is a preferred game species, spiny rats may be taken in snares, and squirrels are not hunted (Wright et al. 2000). For both palm species, the percentage of dispersed seeds killed collectively by the three rodents declined from more than 85% at sites with zero to moderate hunting to less than 50% at sites with intense hunting (Wright et al. 2000). Bruchids compensated partially but were able to locate and kill an average of only 73% of the seeds that escaped rodents (Fig. 6). Largely as a consequence, the survival of dispersed seeds and seedling density increased by an order of magnitude where hunters were active relative to sites where hunters were absent (Fig. 4). Hunters are likely to have similar effects for the many tropical plant species with large seeds that are eaten by game species.

Folivores

Insects and mammals as well as a few lizards and birds consume leaves. With the notable exception of sloths in the Neotropics, the mammalian folivores of tropical forests are virtually all preferred game species. As with seed predation, insects could potentially compensate after hunters remove vertebrates (Dirzo 2001). Hunters are likely to alter patterns of herbivory on leaves.

Experiments that exclude terrestrial vertebrates demonstrate the potential consequences of hunting. Forest seedlings are particularly susceptible because a single encounter with a browser can easily be fatal. Factorial experiments with seedlings transplanted into two forest microhabitats (tree-fall gap versus shaded understory) and two treatments (control versus protected from browsers) have been performed in Panama and northeastern Australia (Howe 1990; Molofsky & Fisher 1993; Osunkoya et al. 1993). I treated species as replicates and site as a third factor (Panama versus Australia) and used a three-way analysis of variance to analyze mean annual seedling survival (using the angular transformation to fulfill normality assumptions). Survival was marginally significantly greater in gaps (Fig. 7; $F_{1,28} = 3.44$, $P = 0.074$), and highly significantly greater with protection from browsers (Fig. 7; $F_{1,28} = 10.8$, $P < 0.01$). None of the interactions was significant ($P > 0.25$). In a second experiment performed in the shaded understory in Panama and Peru, first-year seedling survival and the density of seedlings increased when terrestrial vertebrates were excluded (Terborgh & Wright 1994). Hunters are likely to cause a consistent increase in seedling density when they remove terrestrial browsers from tropical forests.

Dirzo & Miranda (1991) compared the seedling layer of tropical forests at Montes Azules and Los Tuxtlas, Mexico. The mammal fauna of Montes Azules is intact, while poachers and habitat fragmentation have combined to reduce populations of caviomorph rodents and to extirpate ungulates from the 750-ha Las Tuxtlas reserve. The percentages of seedlings with evidence of damage by browsing mammals were 0% and 29% at Las Tuxtlas and Montes

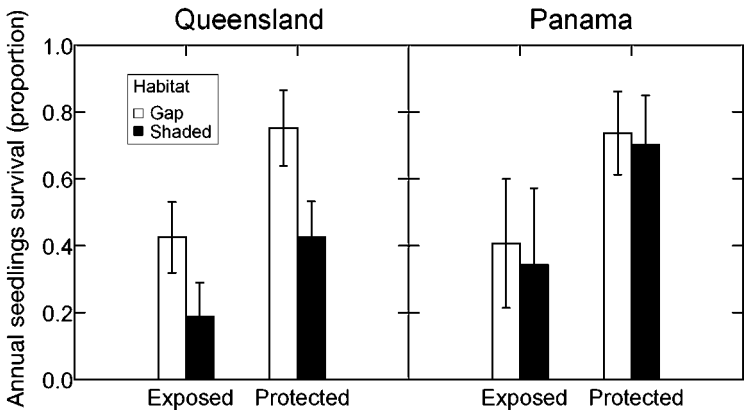

Fig. 7. Vertebrate herbivores (protected versus exposed) and understory microhabitat (gap versus shade) influence seedling survival in northern Australia and in Panama. Seedlings were germinated in screened houses, were transplanted to tree-fall gaps or the shaded understory, and were either left exposed to all animals or were immediately protected by a wire fence that excluded vertebrates but allowed ready access by insects. Survival was measured about one year later. Survival was greater in tree fall gaps (open bars) than in the shaded understory (solid bars), and the survival of seedlings protected from vertebrates was greater in both microhabitats. Data are means (±1SE) for six and three species for Australia and Panama, respectively. Drawn from data presented by Howe (1990), Molofsky & Fisher (1993) and Osunkoya et al. (1993).

Azules, respectively. Dense carpets of seedlings covered the forest floor at Las Tuxtlas, but not at Montes Azules. Dense carpets of seedlings also develop inside fences that exclude all terrestrial mammals in central Panama (W. Carson, unpubl. data), but not at nearby sites subjected to intensive hunting where white-tailed deer (*Odocoileus virginianus*) and collared peccary (*Tayassu tajacu*) persist in small numbers (Wright et al. 2000). These case studies suggest that the complete extirpation of browsing ungulates will profoundly alter the understory of tropical forests.

The biomass of arboreal vertebrate folivores ranges from 1.5 to 5 times greater than the biomass of terrestrial vertebrate folivores in tropical forests, and arboreal vertebrate folivores may consume up to 200 kg of leaves per hectare per year (Leigh 1999). Natural levels of herbivory limit growth and reproduction by shrubs in the understory of tropical forests (Marquis 1984; Sagers & Coley 1995). The possibility that arboreal folivores have similar effects on trees has not been evaluated. And, the potential impact when hunters remove large arboreal folivores is another open question.

Plant diversity

Partial vertebrate defaunation may alter the ecological mechanisms that permit hundreds to thousands of plant species to coexist in most tropical forests. There is a growing consensus that the following mechanisms contribute to plant diversity in tropical forests: negative density dependence, regeneration niche differences, intermediate disturbance, recruitment limitation, and the spatial pattern of recruitment relative to conspecific adults (the Janzen-Connell hypothesis) (reviewed by Wright 2002). I will now evaluate the contribution of vertebrates to these mechanisms and the possible consequences of hunting for plant diversity.

Negative density dependence

Negative density dependence occurs when nearby conspecifics impair performance. Allelopathy, intraspecific competition, and the facilitation of pests may all contribute. Negative density dependence constrains locally abundant species, which favors coexistence by opening space for otherwise less successful species.

Vertebrates acting as pests could contribute to negative density dependence among plants, but this seems unlikely. Most vertebrates forage over relatively large areas and are polyphagous, taking seeds or leaves from a wide variety of plant species. For 27 populations of tropical forest plants, the rates of consumption of seeds or seedlings by vertebrates were measured near conspecific adults, where initial seed density was higher, and further from conspecific adults, where initial seed density was lower (Hammond & Brown 1998). Vertebrate depredations were independent of distance to conspecific adult and/or local seed/seedling density for 25 of the 27 populations. Vertebrates rarely kill dispersed seeds or established seedlings in a density-dependent manner in tropical forests. Arboreal vertebrates are also unlikely to behave in a density-dependent manner because the crowns of individual trees are large relative to individual vertebrates and even entire social groups. Vertebrate defaunation is unlikely to disrupt negatively density-dependent interactions among tropical forest plants.

Regeneration niches, intermediate disturbance, and recruitment limitation

In contrast, vertebrates clearly contribute to the processes that facilitate plant species coexistence in the regeneration niche, intermediate disturbance, and recruitment limitation hypotheses. All three hypotheses posit spatial variation in the environment and environment-dependent competitive hierarchies among plant species. The regeneration niche hypothesis emphasizes environmental conditions that influence recruitment and early regeneration (Grubb 1977). Plant species coexist because a particular set of conditions favors the early regeneration of each species. We have seen that terrestrial vertebrates routinely locate, consume, and kill dispersed seeds and established seedlings (Figs. 5, 7). Hence, terrestrial vertebrates are an important component of the environmental variation that influences recruitment and early regeneration. We have also seen that the level of vertebrate-induced mortality varies widely among plant species (Fig. 5). This variation is key. When hunters alter the community of terrestrial vertebrates, they also indirectly alter the relative advantages enjoyed by different plant species. For example, when hunters remove the larger terrestrial vertebrates, plant species with large seeds and ineffective seed and seedling defenses benefit more than other plant species with minute seeds and/or effective seed and seedling defenses. Hunters indirectly alter the competitive balance among plant species. As a consequence, plant species composition and plant diversity will change.

The intermediate disturbance hypothesis embellishes the regeneration niche hypothesis with disturbances that occasionally kill established plants and reset competitive interactions (Connell 1978). Patchy disturbances permit species with different regeneration requirements to coexist over a landscape. Long distance dispersal is an added key process. Plants associated with recent disturbance must eventually disperse seeds

to newly disturbed patches to escape competition, and plants associated with mature forests must disperse seeds to colonize more recently disturbed patches. Seed dispersal between patches will vary with the distance between patches, the number of viable seeds produced in the source patch, and the distances individual seeds are dispersed (Clark et al. 1998). Birds and mammals are the principal dispersal agents for many tropical forest plants and are also likely to reduce viable seed production through pre-dispersal seed predation and possibly folivory (see *Indirect effects on plants* above). Vertebrates facilitate between-patch dispersal as dispersal agents and reduce between-patch dispersal as seed predators and possibly as folivores. This raises new opportunities for hunters to alter the equipoise among plant species. For example, hunters may reduce the dispersal of large, animal-dispersed seeds by harvesting their dispersal agents; have no effect on the dispersal of wind-dispersed seeds; and increase the dispersal of small, animal-dispersed seeds if the harvest of large frugivores stimulates compensatory increases among smaller frugivores. Again, plant species composition and plant diversity will change.

The recruitment limitation hypothesis embellishes the regeneration niche hypothesis with the occasional failure of the superior competitor, which allows an inferior competitor to win a regeneration site by default (Hurtt & Pacala 1995). The superior competitor may fail because too few viable seeds are produced, seed dispersal is too limited, dispersed seeds are killed, and/or established seedlings are killed. We have seen that vertebrates contribute to each of these processes and that the strength of vertebrate-plant interactions varies widely among species for each process. Again, the stage is set for hunters to alter plant species composition and plant diversity.

The Janzen-Connell hypothesis

The spatial pattern of plant regeneration is widely believed to contribute to plant species coexistence (Janzen 1970; Connell 1971). Many plant pests are host specific and congregate near large adult trees or at dense aggregations of seeds or seedlings. If these pests prevented regeneration near parent trees, then only seeds dispersed away from conspecific adults would survive. This could prevent single species dominance and maintain space for the regeneration and coexistence of additional tree species (Armstrong 1989). If hunters were to alter the spatial pattern of plant regeneration, this could in turn alter plant diversity.

Janzen (1970) modeled the spatial pattern of plant recruitment as the product of the density of dispersed seeds and their survival probability. Wright & Duber (2001) used his model as modified by Hubbell (1980) to explore possible consequences when hunters harvest seed dispersal agents and seed predators (Fig. 8). Seed density (I) and survival probability (P) are exponential functions of distance to the nearest conspecific tree. The population recruitment curve (PRC) is the

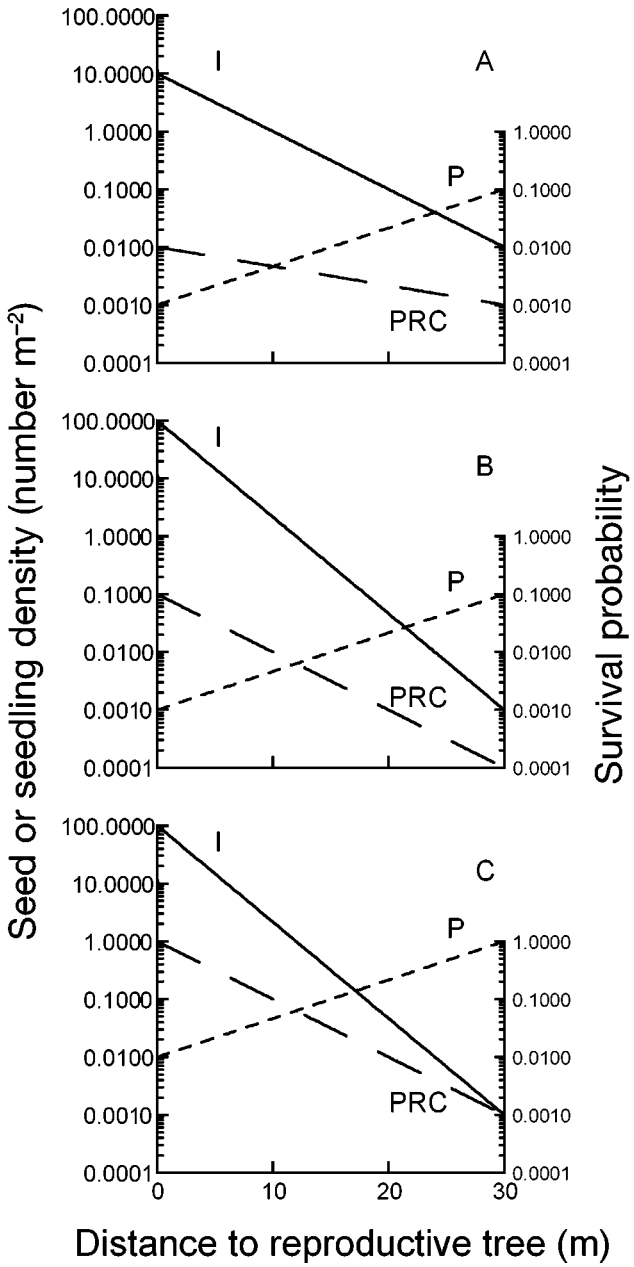

Fig. 8. Predicted spatial pattern of plant regeneration for a fully protected forest (panel A), a forest with reduced seed dispersal (panel B), and a forest with reduced seed dispersal and increased seed and seedling survival (panel C). Following Janzen (1970) as modified by Hubbell (1980), seed density (I, solid line) declines, survival probability (P, short dashed line) increases, and seedling density (PRC, long dashed line) declines with distance to the nearest reproductive conspecific. A recent analysis of seed survival for 53 tropical species suggested the functions for I, P, and PRC in panel A (Harms et al. 2000). Changed values in panels B and C represent qualitative predictions.

product of P and I and is also an exponential function of distance. Seed density invariably declines with distance from seed-bearing trees (Howe & Smallwood 1982) and survival probability usually increases with distance, although there are exceptions (McCanny 1985; McCanny & Cavers 1987; Hammond & Brown 1998). The harvest of large birds and mammals is predicted to reduce seed dispersal distances and to make the seed density-distance relationship (I) steeper. All else equal, the steeper seed density-distance relationship will cause a steeper population recruitment curve (Figs. 8b vs. 8a). The harvest of terrestrial vertebrates is predicted to increase seed and seedling survival and to shift the survival-distance relationship (P) upwards. A change in slope is not expected because terrestrial vertebrates tend to forage over large areas so that seed and seedling survival is reduced by similar amounts everywhere (Hammond & Brown 1998). All else equal, an upward shift in the survival-distance relationship will cause an upward shift in the population recruitment curve (Figs. 8c vs. 8b). Both changes predicted for the spatial pattern of plant regeneration when hunters disrupt mammal communities will increase seedling recruitment near conspecific trees.

These changes were all observed for the palm *Attalea butyraceae* in central Panama (Fig. 4). The slope of the relationship between seed density and distance to the nearest reproductive conspecific was progressively steeper at more intensively hunted sites (Fig. 4). The proportion of seeds inferred to survive increased by similar amounts at all distances at more intensively hunted sites (Fig. 4). And, the density of seedlings increased disproportionately near conspecific adults at more heavily hunted sites (Fig. 4). To the extent that low recruitment near conspecifics facilitates plant species coexistence, a decline in plant diversity may be anticipated.

A tentative synthesis and future directions

A tentative synthesis must recognize the web of interspecific interactions disrupted by hunters (Fig. 1). To begin, consider the indirect effects of game species on plants (the double-headed arrow between herbivorous game species and plants) for an intensively hunted forest. Assume preferred large birds and mammals have been extirpated. Then, relative to a pristine forest, the missing plant-animal interactions are predicted to cause the following:

1. More viable seeds produced because pre-dispersal seed predators are absent.
2. More viable seeds produced because arboreal folivores are absent.
3. Fewer seeds dispersed because seed dispersal agents are absent.
4. Fewer dispersed seeds killed because terrestrial seed predators are absent.
5. Fewer seedlings killed because terrestrial folivores are absent.

Predictions 1 and 2 have yet to be evaluated, while single case studies have confirmed Predictions 3, 4 and 5 (Dirzo 2001; Dirzo & Miranda 1991; Wright et al. 2000; Wright & Duber 2001).

Additional indirect effects occur among animals. Again, assume preferred large birds and mammals have been extirpated. Then, relative to a pristine forest, the missing animal-animal interactions are predicted to cause the following:

6. Compensatory increases among non-game species that consume fruit, seeds, and leaves because hunters harvest larger competitors.
7. Compensatory increases among non-game species because hunters harvest predators.

Two case studies have confirmed Prediction 6 (Bodmer et al. 1997; Peres & Dolman 2000), but Prediction 7 has yet to be evaluated. Compensatory increases among animals may mitigate the indirect effects predicted from missing plant-animal interactions. In fact, Predictions 1 through 5 are not directly testable. Rather, only net differences between pristine and hunted forests can be evaluated. These net differences integrate missing interactions between plants and game species, missing interactions between game species and non-game species, and ongoing interactions between plants and non-game species.

Indirect effects, which are further removed from hunters, may also occur. These additional indirect effects would ramify through more than one of the double-headed arrows in Fig. 1. A few possible predictions chosen only because they have been evaluated follow:

8. If plant (seedling) density increases, then insect herbivores multiply.
9. If insect herbivores multiply, then their predators and parasites multiply.

Prediction 8 has been confirmed for two beetles and one caterpillar, and Prediction 9 has been confirmed for a parasite of the caterpillar (Wright et al. 2000; Dirzo 2001; Wright & Duber 2001).

Predictions 8 and 9 are reminiscent of the familiar debate concerning the roles of top-down versus bottom-up forces in the control of community structure. Spatially structured plant populations provide still further complications. Again, a few possibilities chosen only because they have been evaluated follow:

10. If spatial patterns of plants (seeds, seedlings, saplings) change, then patterns of attack by herbivores change.
11. If plant and herbivore spatial patterns change, then patterns of attack by predators and parasites of the herbivores change.

Prediction 10 has been confirmed for a caterpillar and rejected for a beetle, and Prediction 11 has been confirmed for a parasite of the caterpillar (Dirzo 2001; Wright & Duber 2001). A tremendous variety of predictions is possible contingent upon an equal variety of possible changes in vertebrate and plant populations following hunting.

Future research will take three directions. First and foremost, additional comparative studies are needed to evaluate the first-order indirect effects of partial vertebrate defaunation (Predictions 1 through 7 above). There are compelling reasons to expect these indirect effects to vary with climate and especially with the local fauna (Wright et al. 2000). For example, partial vertebrate defaunation is associated with dense seedling carpets in Mexico but not in Panama (Dirzo & Miranda 1991; Wright et al. 2000). The absence of medium sized rodents (particularly *Proechimys* spp.) from Mexican rain forests may contribute to this difference (Wright et al. 2000). The second direction to be taken by future research will involve experimental manipulations designed to probe causal relationships between partial vertebrate defaunation and associated indirect effects (Asquith et al. 1997, 1999; Dirzo 2001). Third, future research will target the myriad higher order indirect effects that may follow after partial vertebrate defaunation (a few examples include Predictions 8 through 11 above; Dirzo 2001; Wright & Duber 2001). As this research agenda is completed, the long-term consequences of partial vertebrate defaunation for plant diversity will become evident.

Conclusions

Human extraction of vertebrates from tropical forests has reached alarming levels (Redford 1992). Hunters who take just a few animals per square kilometer per year depress the abundance of preferred game species and are virtually invisible to outside observers (Mena et al. 2000; Bodmer et al. 1997; S.J. Wright, pers. observ.). Hunting is nearly ubiquitous within perhaps 20 km of villages, roads, and navigable rivers throughout the tropics (Robinson & Bennett 2000). The number of truly protected sites near humans is vanishingly small (Bennett et al. 2000; Wright et al. 2000). I personally have encountered hunters or their constructions in the Barro Colorado Nature Monument, Panama; the La Selva Biological Station, Costa Rica; the Biological Diversity of Forest Fragments Project, Brazil; and the Pasoh Forest Reserve, Malaysia. Hunters color our understanding of these forest reserves, which are dedicated to research, and of virtually all unprotected tropical forests.

Gradients of hunting intensity and vertebrate defaunation can still be found throughout the tropics today and offer an opportunity to explore the consequences of many interspecific interactions. A handful of studies have documented how partial vertebrate defaunation affects plants and non-game vertebrates (Predictions 1 to 7 above). Higher-order effects are only beginning to be considered (Dirzo 2001; Wright & Duber 2001). It is too early to predict the long-term consequences of vertebrate defaunation for the composition and diversity of tropical forest plant communities with confidence. There is, however, ample reason for concern.

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