Hunting and Plant Community Dynamics in Tropical Forests: A Synthesis and Future Directions

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ABSTRACT

This synthesis builds on the preceding articles of this Special Section and has three goals. We first review the nascent literature that addresses indirect effects of hunting for tropical forest plant communities. Next, we highlight the potential indirect effects of hunting for other groups of organisms. Our final goal is to consider what could be done to ameliorate the demographic threats to harvest-sensitive game species caused by unsustainable hunting. Three conclusions are possible at this time concerning the impact of hunting for tropical forest plant communities: (1) Hunting tends to reduce seed movement for animal-dispersed species with very large diaspores; (2) Hunting reduces seed predation by granivorous vertebrates for species with large seeds; and (3) Hunting alters the species composition of the seedling and sapling layers. The cascading effects of hunting are already known to affect bruchid beetles and dung beetles and are likely to affect other, nongame taxa. To ameliorate these problems, several lines of research should be further explored to facilitate the development of game management plans including: (1) alternative use of sources of animal protein; (2) income supplementation for local people from sources other than wild meat; (3) outreach and extension activities for communities; (4) recognition and facilitation of the shifting of attitudes towards hunting; (5) implementation of community-based wildlife management programs in regulated-use areas such as extractive reserves; and (6) landscape-scale conservation planning that maximizes the source-sink dynamics of harvested and unharvested game populations and enforces game regulations in strictly protected areas.

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Key words: bushmeat; management plans; plant community structure; seed dispersal; seed predation.

THE HUMAN HARVEST OF WILD FOREST VERTEBRATES for subsistence or commerce has profound implications for the structure and dynamics of tropical forests. The harvest of preferred game species is unsustainable virtually throughout the tropics (Milner-Gulland *et al.* 2003). Game harvest studies in tropical forests have shown that most unregulated, commercial hunting for wild meat is unsustainable (Robinson & Bennett 2000), and that even subsistence hunting driven by local demand can severely threaten many medium to large-bodied vertebrate populations (Corlett 2007, Peres & Palacios 2007). Preferred game species have been extirpated from many tropical forests, and widespread local extinction events seem to be inevitable outside the most effectively protected areas unless their harvest can be controlled (Bodmer *et al.* 1997, Fa *et al.* 2001, Corlett 2007, Peres & Palacios 2007). Nongame species are also indirectly affected wherever hunting disrupts ecological interactions with game species (Peres & Dolman 2000). The preceding articles in this special section have quantified the impact of hunting for preferred game species and other vertebrates of Southeast Asian and Amazonian forests (Corlett 2007, Peres & Palacios 2007) and documented indirect impacts of hunting for plant regeneration in Cameroon, Mexico, Panama, and Peru (Beckman & Muller-Landau 2007, Dirzo *et al.* 2007, Nunez-Iturri & Howe 2007, Wang *et al.*

2007, Wright *et al.* 2007). This synthesis builds on these articles and has three goals.

We first review the nascent literature that addresses indirect effects of hunting for tropical forest plant communities. Where sufficient data are available, we extract quantitative metrics from each study to evaluate whether hunting has consistent effects across sites and species. Our second goal is to highlight the potential indirect effects of hunting for other groups of organisms including invertebrates. Our final goal is to consider policies and actions to ameliorate the demographic threats to harvest-sensitive game species caused by unsustainable hunting.

INTERACTIONS AMONG HUNTING, GAME SPECIES, AND PLANTS

We ask whether hunting has consistent effects on plants that can be generalized and identify areas where additional studies are needed. We limit consideration to studies that compare 'protected' forests, with limited hunting and relatively intact vertebrate faunas, to 'hunted' forests, with more intense hunting and more disturbed vertebrate faunas. We exclude forest fragments smaller than 100 ha because fragmentation alters forest microclimates and leads to the extirpation of species that are not hunted such as forest interior

insectivorous birds (*e.g.*, Laurance *et al.* 2002, Lees & Peres 2006). The arbitrary 100-ha threshold should help to isolate the effects of hunting from these and additional effects of fragmentation. We are aware of only 12 studies that compare some aspect of tropical plant biology in protected and hunted forests within areas larger than 100 ha.

Four of these studies evaluate community-level properties of the seedling or sapling layers. Hunting invariably alters seedling and sapling species composition (Dirzo & Miranda 1991, Roldán & Simonetti 2001, Nuñez-Iturri & Howe 2007, Wright *et al.* 2007); however, hunting has inconsistent effects on other, emergent community-level metrics. Seedling density increases (Dirzo & Miranda 1991), decreases (Roldán & Simonetti 2001), or is unchanged (Wright *et al.* 2007) by hunting. Seedling and sapling diversity decreases (Dirzo & Miranda 1991) or is unchanged (Roldán & Simonetti 2001, Wright *et al.* 2007) by hunting. These inconsistent community-level responses suggest that similar inconsistencies are likely to characterize the interspecific interactions that relate hunting and plant responses despite pervasive changes in seedling and sapling species composition.

We distinguish between direct interactions of plants and the vertebrate species persecuted by hunters and indirect interactions between plants and animal species that hunters ignore. Published studies focus largely on direct interactions including predispersal seed predation, primary and secondary seed dispersal, postdispersal seed predation and leaf herbivory or browsing (but see Dirzo 2001, Wright 2003). Predispersal seed predators consume developing or mature seeds taken directly from the fruit-bearing plant. Browsers remove leaf tissue, which reduces plant carbon balance and often kills seedlings. The largest browsers can also break and uproot saplings and even trees. We are aware of only one study that addresses hunting and predispersal seed predation (Beckman & Muller-Landau 2007) and two studies conducted at Las Tuxtlas, Mexico, which address browsing (Dirzo 2001, Dirzo & Miranda 1991). In each case, the effect of hunting is large with browsing damage and predispersal seed predation by game species both decreasing where hunters are active; however, single-site comparisons preclude generalization. New studies are needed to evaluate hunting effects for browsing and predispersal seed predation.

The remainder of this brief review examines effects of hunting for seed dispersal and postdispersal seed predation. Two studies have evaluated the impact of hunting for plant species composition with respect to seed dispersal modes. Where hunters are active, species with seeds dispersed by game species are less abundant, whereas species with seeds dispersed by abiotic means and by small animals that are not hunted are more abundant in the seedling and sapling layers (Nuñez-Iturri & Howe 2007, Wright *et al.* 2007). Once again, two site comparisons preclude generalization, and new studies are needed to evaluate hunting effects with respect to seed dispersal modes.

Seven studies address additional effects of hunting for animal-mediated seed dispersal. We used data from these seven studies to evaluate the general hypothesis that reductions in seed dispersal associated with hunting fall disproportionately on species with larger diaspores. This is largely because large diaspores are primarily dispersed by a small subset of large-bodied frugivores (*e.g.*, Peres &

Roosmalen 2002, Poulsen *et al.* 2002). These large-bodied frugivores bear a disproportionately heavy fraction of the hunting pressure at any given site (Jerozolimski & Peres 2003, Fa *et al.* 2005) and succumb to the most severe population declines in overhunted areas (Peres & Palacios 2007). We extracted average proportions of seeds removed at protected and hunted sites to calculate a seed removal ratio (defined as the average proportion removed at hunted sites divided by the average proportion removed at protected sites). Hunting is associated with a reduction in seed removal when this ratio is less than one. We were able to calculate this seed removal ratio for 16 plant species across 14 comparisons between protected sites and paired sites with similar, nonzero hunting intensities (Fig. 1). The symbol types in Figure 1 capture an important methodological difference among studies. Seed removal was from fruiting trees, which incorporates primary and secondary dispersal (circles in Fig. 1), or from randomly located depots of 20–40 seeds, which captures secondary dispersal only (triangles). Seed removal incorporates seeds that are deposited when viable and are successfully dispersed as well as seeds that are consumed and killed. The fate of removed seeds was
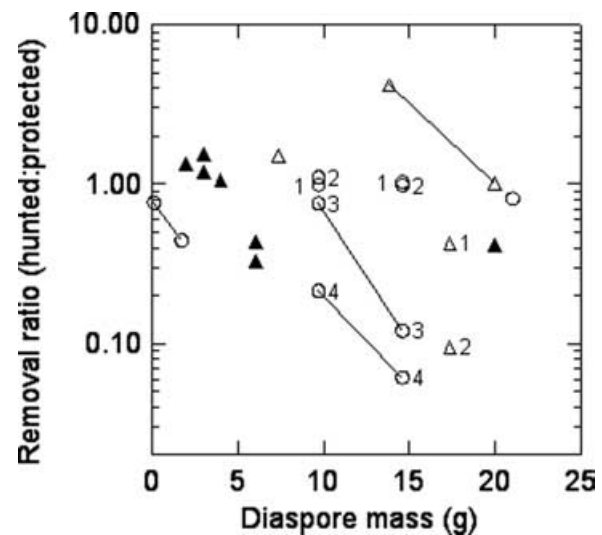

FIGURE 1.   The relationship between diaspore mass and the impact of hunting for seed removal. The vertical axis captures the relative impact of hunting as a ratio of the proportion of seeds removed for hunted sites relative to protected sites. Hunting reduced seed removal when this ratio is less than one. Seeds were removed from the seed-bearing tree (circles) or from randomly located, experimental depots (triangles). Two studies compared seed removal for multiple levels of hunting intensity for three species, and numbers located beside symbols represent differences in ranked hunting intensity for these three species (each species has a single diaspore mass). Four studies compared seed removal for multiple species for the same hunted and protected sites (data points connected by solid lines for two-species comparisons; solid triangles for a seven-species comparison). The integers beside symbols represent between-site differences in ranked hunting intensity for the three species evaluated in these two studies, where each species is characterized by a single diaspore mass. Data are taken from Beckman & Muller-Landau (2007), Forget & Jansen (2007), Galetti *et al.* (2006), Guariguata *et al.* (2000, 2002), Roldán & Simonetti (2001) and Wright *et al.* (2000).

unknown for most studies, and we therefore refer to seed removal rather than seed dispersal.

The seed removal ratio varied widely across species and sites (Fig. 1). This variation is caused in part by uncontrolled differences among studies in hunting intensity between protected and hunted sites. Two studies evaluated hunting intensity at multiple sites and illustrate the effect of differences in hunting intensity for the seed removal ratio (Wright *et al.* 2000, Galetti *et al.* 2006). The seed removal ratio declines as hunting intensity increases for all three species.

To control for variation associated with differences in hunting intensity, we used comparisons among species for the same protected and hunted sites to evaluate the hypothesis that reductions in seed removal associated with hunting are greater for species with larger diaspores. In four two-species comparisons, the seed removal ratio was invariably smaller for the species with the larger diaspore (symbols connected by solid lines in Fig. 1). In a seven-species comparison, the seed removal ratio and diaspore mass were negatively correlated (solid triangles in Figure 1; Spearman rank correlation coefficient $= -0.87$; $P < 0.05$, Guariguata *et al.* 2000). These results support the hypothesis that species with larger diaspores suffer disproportionate reductions in animal-mediated seed dispersal where hunting occurs. This effect of seed size presumably holds because hunters at these four forest sites target primarily large-bodied frugivore species that are more likely to disperse large diaspores from woody liana and tree species (*cf.* Peres & Roosmalen 2002, Poulsen *et al.* 2002).

This suggests an apparent paradox. Despite reduced seed dispersal, species with large diaspores tend to become more abundant not less abundant in the seedling layer where hunters are active in Mexico and Panama (Dirzo & Miranda 1991, Dirzo *et al.* 2007, Wright *et al.* 2007). The resolution of this apparent paradox lies with seed predators. Hunting is widely predicted to lead to reductions in postdispersal seed predation by granivorous vertebrates for large-seeded species. Seven studies now support this prediction (Wright *et al.* 2000, Roldán & Simonetti 2001, Wright & Duber 2001, Guariguata *et al.* 2002, Galetti *et al.* 2006, Beckman & Muller-Landau 2007, Dirzo *et al.* 2007; for *Dipteryx*). Hence, reduced seed predation increases seed survival, and this will tend to offset the negative consequences of reduced seed dispersal for seedling densities of species with large diaspores. There is a further complication, however, because total seed predation incorporating all seed predators might actually increase with hunting (Guariguata *et al.* 2002, Galetti *et al.* 2006 for *Carapa*). This effect is possible when other seed predator species that are spared from hunting increase in numbers where hunting occurs.

INTERACTIONS AMONG HUNTING, INVERTEBRATES, AND PLANTS

Two well-documented examples illustrate how hunting can indirectly affect populations of invertebrates and plant species. In the first example, the seeds of three coccosoid palm species are killed by granivorous mammals (agoutis, peccaries, and squirrels) that hunters pursue and by bruchid beetles that hunters ignore (Fig. 2). Bruchid larvae develop inside and kill seeds (Johnson & Romero 2004). Granivorous mammals respond differently to larval-infested seeds with some species consuming infested and uninfested seeds in proportion to their abundance and other species consuming infested seeds in preference to uninfested seeds (Silvius 2002, Gálvez & Jansen 2007). Each grub-infested seed consumed by a mammal kills a larval bruchid. Hence, the number of bruchids that survive to recruit to the adult population increases where hunters reduce mammal abundances. This increase (expressed as the ratio of the mean proportion of bruchid-infested seeds at hunted to protected sites) ranges from fourfold to 70-fold for the three coccosoid palms illustrated in Figure 2 (panels D–F). This increase in the population of insect seed predators raises the possibility that total seed predation might increase even where seed predation by mammals decreases. Many insects develop inside seeds, and increased abundances of such seed predators might be a widespread indirect consequence of hunting.

Hunting also indirectly impacts invertebrate seed dispersers, such as dung beetles. Dung beetles have interacted with vertebrate frugivores for as much as 80 Myr (Chin & Gill 1996). Dung beetles inadvertently benefit seeds when they bury dung that contains seeds, which protects the buried seeds from predators and fungi (Estrada & Coates-Estrada 1991, Vulinec 2000). Dung beetle abundance and diversity both decline wherever dung-producing vertebrates decline (Nichols *et al.,* in press). Several studies demonstrate that habitat degradation reduces dung beetle populations (Vulinec 2002, Feer & Hingrat 2005, Harvey *et al.* 2006, Nichols *et al.,* in press). Andresen and Laurance (2007) recently demonstrated that hunting-induced declines in mammal abundances have similar negative effects on dung beetles even when the forest itself is undisturbed. The cascading effects of hunting are already known to affect bruchid beetles and dung beetles and are likely to affect other nongame taxa. Peres & Dolman (2000), Dirzo (2001), and Wright (2003) outline many other possible indirect consequences of hunting for animals and plants in tropical forests.

Three conclusions are possible at this time concerning the impact of hunting for tropical forest plant communities. First, hunting tends to reduce seed movement for animal-dispersed species with very large diaspores (Fig. 1). Second, hunting reduces seed predation by granivorous vertebrates for species with large seeds ($N = 7$ studies); however, indirect changes in the abundances of other seed predators can offset the decrease in predation by granivorous vertebrates (Fig. 2). Many other possible interactions between plants, game species, and nongame species remain entirely unexplored. Finally, hunting alters the species composition of the seedling and sapling layers each time this possibility has been considered ($N = 4$ studies). Altered plant species composition seems inevitable given the wide range of strengths of interaction between particular game species, particular plant species, and other interacting species. Future studies that capitalize on the large-scale manipulation of vertebrate abundances being maintained by hunters throughout the tropics will provide additional insight into these interspecific interactions and their role in determining the structure and dynamics of
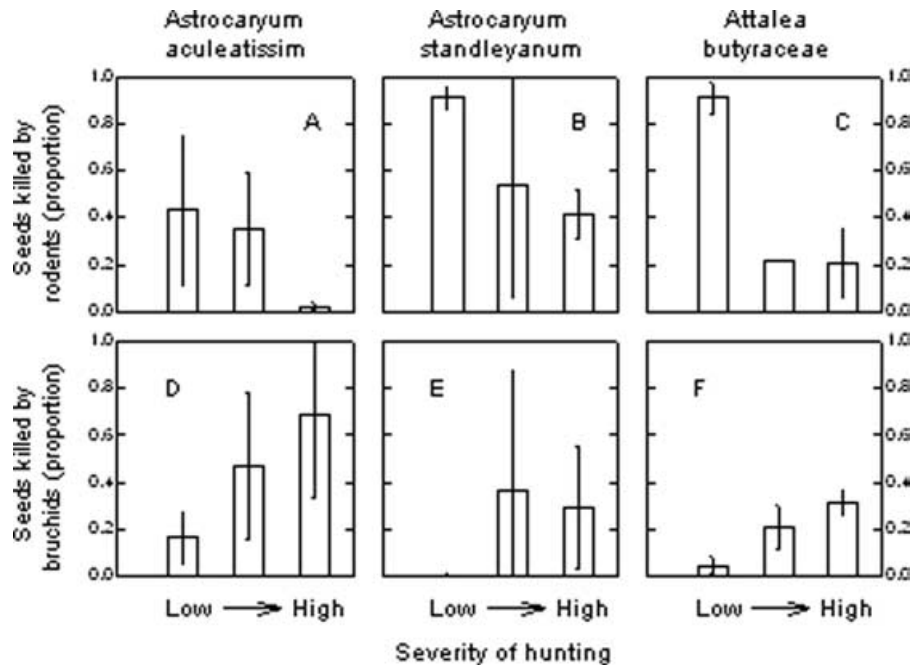
FIGURE 2.   The proportion of palm seeds killed by rodents declines with the severity of poaching (panels A–C) and the proportion killed by bruchid beetles increases (D–F) for three coccosoid palm species. Some of the principal rodent seed predators (agoutis, peccaries, and squirrels) are hunted. *Astrocaryum aculeatissim* is from the Atlantic coastal forest of Brazil. *Astrocaryum standleyanum* and *Attalea butyraceae* are from central Panama. The histograms and error bars represent means over sites ± one standard deviation. Data are taken from Galetti *et al.* (2006) and Wright *et al.* (2000).

tropical forest plant communities. Research also has an important role to play if hunting is to be changed from an unsustainable to a sustainable basis in the tropics.

A SUSTAINABLE FUTURE FOR GAME SPECIES IN TROPICAL FORESTS

OBSTACLES TO SUSTAINABLE HUNTING.—Several obstacles that are rather unique to the tropics must be overcome before hunting can become a sustainable activity. These problems include individual poverty, weak governance, workforce and infrastructure associated with enforcement of hunting laws, and poor knowledge of hunted species' density. In developed countries, hunting is largely a successfully regulated and sustainable recreational activity. In contrast to this scenario, in many developing countries hunting is largely a livelihood necessity involving many poorly known species, with little or no regulations, and is unsustainable.

Poverty limits the successful regulation of hunting in many ways. Furthermore, ethical issues of regulating hunting in regions where poverty holds are a serious concern. Hunting often provides a significant source of protein for otherwise impoverished people (Peres 2000, Hill 2002). The harvest, transport, and marketing of wildlife species also provide a significant source of household income at all stages of the supply chain (Cowlishaw *et al.* 2005). Efforts to control the wild meat trade must examine and address all levels of the supply chain (Cowlishaw *et al.* 2005). Poor rural people

are only likely to reduce hunting if they do not suffer short-term economic loss (Bodmer 1995). Poverty also influences the types of regulations that are likely to be successful. Quotas or bag limits related to the sex or age of game species may be impractical when the hunter's livelihood is at stake, and a more profitable alternative prey item might not be encountered that day (Noss & Cuéllar 2001). As an example, the harvest of wild species at one site in Peru is related to reproductive productivity and abundance and not to hunter preference (Bodmer 1995). Poverty creates an imperative to harvest every valuable animal encountered.

Weak governments and limited availability and institutional enforcement of game management regulations present a second, related problem that will limit the successful management of game harvest. Many tropical countries have no restrictions or poorly enforced restrictions on hunting (Verdade & Campos 2004). Hunting is often considered a birthright and is tolerated by local law enforcement. For example, Brazil has banned hunting since 1967, yet local people often discuss hunting openly (Vulinec *et al.* 2006, Peres & Palacios 2007). Elsewhere enforcement can be entirely absent (Anadu *et al.* 1988). Governments often lack the capacity or political will to enforce game laws in many developing tropical countries.

The lack of information about population densities of game species in tropical regions poses a further challenge to developing management programs. The successful regulation of hunting requires biological information provided by wildlife managers (Mugisha & Jacobsen 2004). Reproductive rates and carrying capacities of game species must be known to set sustainable yields

(Caughley 1985, Bodmer & Puertas 2000). Even where hunting is strictly regulated, the timing and length of hunting seasons and limits on the ages, sex, and overall harvest must be monitored and readjusted on a regular basis (Kokko & Lindstroem 1998, Biederbeck *et al.* 2001). In most developed countries, sport hunters pursue game species under strict regulations that have been tried and tested over many years and population densities are constantly monitored. The successful management of game in tropical forests will require sustained implementation of game monitoring programs.

POSSIBLE SOLUTIONS TO THESE PROBLEMS.—The most frequently proposed solutions to these problems fall into two broad categories. The first is to restrict who can hunt at the local level. In the Bolivian Chaco, for example, local communities favor prohibiting hunting by outsiders, banning commercial hunting, protecting plants important to wildlife, and establishing hunting zones, but oppose proposals to limit hunting to the more abundant species (Noss & Cuéllar. 2001). In western Amazonian forests, multiple-use zones allow local populations economic benefits from hunting and other extractive activities (Naughton-Treves *et al.* 2003). However, throughout Central and South America, rural people are often unaware of wildlife management regulations (including the boundaries of multiple-use zones), or the regulations are ignored due to lack of enforcement. More importantly, preferred game species including large herbivores, large carnivores, and many primates are often harvested at unsustainable rates in otherwise successful multiple-use zones (Bodmer *et al.* 1997, Altrichter & Almeida 2002, Naughton-Treves *et al.* 2003, Peres & Nascimento 2006). Attempts to restrict who hunts where have often met with limited success.

The second broad category of proposed solutions focuses on offsetting the economic loss incurred when hunting is restricted. For example, Bodmer and Lozano (2001) evaluated the relationship between rural development and sustainable wildlife use in the Peruvian Amazon. They proposed a management plan that would reduce the current harvest rate of some species causing short-term economic losses for hunters and long-term economic gains as hunting became sustainable. Bodmer and Lozano (2001) also suggest economic compensation to offset the short-term losses including payments to people who do not hunt, payment to patrol and prevent outsiders from hunting, and for transportation and health services. Other proposals that compensate local people to limit hunting or shift the costs to their wealthy neighbors include trophy-hunting programs (Lewis & Alpert 1997), hunting restrictions for large landholders (Hoogesteijn & Chapman 1997), and payments for wildlife damage to crops and domestic animals (Verdade & Campos 2004). Funding limits all proposals to regulate hunting through payments to offset the opportunity costs of reduced protein acquisition or economic losses through crop damage.

SUCCESS STORIES OF WILDLIFE MANAGEMENT IN THE TROPICS.—Despite the widespread lack of resources to redress the problems that lead to unsustainable hunting, several programs showcase the sustainable management of tropical forest game species. Malaysia has a relatively strong economy that provides economic alternatives to hunting for livelihoods of people in many rural communities. Furthermore, Malaysia has relatively strong government institutions that allow them to enforce environmental regulations. For example, the national parks of Malaysia are among the most effective in the wet tropics at reducing the incidence of forest fires (Wright *et al.,* in press). Kawanishi and Sunquist (2004) found no evidence of poaching and observed signs of all the medium-to-large terrestrial mammals expected to occur in the well-protected Taman Negara National Park of peninsular Malaysia. A master plan is in place to manage wildlife throughout Sarawak, Malaysia (Wildlife Conservation Society & Sarawak Forest Department 1996). The Master Plan for Wildlife in Sarawak included the enactment and strict enforcement of a new law that bans trade in wild animals and their parts, controls the availability of shotgun cartridges, and bans hunting in logging concessions. The management plan also includes education programs, involves local communities in management of protected areas, and shares financial benefits from protected areas with local communities.

Another success story comes from the People´s Republic of Congo (Elkan 2000, Elkan *et al.* 2006). The Congolese Government, a private timber company, and the World Conservation Society are working together to control hunting within a large logging concession adjoining the Nouabale Ndoki National Park. This program is largely successful due to the efforts of trained forest guards who prevent hunters from using wire snares and high-caliber firearms, enforce no-hunting zones, and prohibit any harvest of endangered species. Wildlife transportation is only allowed within the concession; wildlife cannot be transported out of the concession. Education programs are provided for logging company staff and local communities, and the economic feasibility of alternative protein sources is being evaluated. Similar suggestions have been made for managing the bushmeat crisis throughout the Congo Basin (Wilkie & Carpenter 1999). The success of this approach in the logging concession adjoining the Nouabale Ndoki National Park is evident from the now frequent observations of gorillas and chimpanzees in the area (Elkan 2000). As in Malaysia, the application of unusual levels of resources led to the successful management of hunting.

DIRECTIONS FOR FUTURE RESEARCH

EFFECTS OF HUNTING ON TROPICAL FORESTS.—Based on our review in the first section of this synthesis, we present three recommendations to increase the value of future studies evaluating the effect of hunting on tropical forest plant communities. First, the intensity and duration of hunting should be quantified for each site to facilitate future comparisons across studies. Hunting intensity might be quantified by recording the presence/absence of species most susceptible to hunting or the abundances of species less susceptible to hunting (see Bodmer *et al.* [1997] for hunting susceptibility). The duration of hunting is also crucial, because the long lifetimes of many forest organisms will introduce time lags after hunting alters interspecific interactions. Our second recommendation concerns

the plant species chosen for study. To date, there is an intense bias toward species with the largest diaspores (Fig. 1). For example, the two lightest diaspores in Figure 1 are heavier than the diaspores of 47 and 90 percent of 252 woody species with known diaspore masses from Barro Colorado Island, Panama (S. J. Wright, pers. obs.). A more representative sample of plant species will be required to evaluate many possible impacts of hunting; even the relationship between diaspore mass and the impact of hunting for seed movements might change when a more representative sample of plant species has been studied. Ideally, plant species would be chosen at random or in proportion to their abundances. Our final recommendation concerns plant species descriptions. There is a growing consensus concerning a modest number of functional plant traits that provide insight into the ecology of plant species (Cornelissen *et al.* 2003). These traits include seed mass, wood density, specific leaf area, and adult height among others. The inclusion of these traits in future studies would facilitate answers to several interesting problems. As an example, does hunting favor light-demanding pioneer species at the expense of shade-tolerant, climax species?

Recommendations for future research may be summarized from the papers presented in this Special Section as follows. (1) More studies need to document the effect of selective defaunation on tropical forests (Peres & Palacios 2007); (2) Ecological redundancy needs to be evaluated in nonhunted vertebrates within any particular community to recognize compensatory behavior that may help deter some of the negative effects of hunting of large and medium vertebrates (Stoner *et al.* 2007); (3) More research on the mechanisms structuring plant communities need to be compiled in order to help us predict how plant species respond when their seed dispersers are extirpated (Beckman & Muller-Landau 2007); (4) Long-term demographic and genetic impact of the loss of vertebrate dispersal agents need to be evaluated for more species and locations (Wang *et al.* 2007); (5) Long-term studies with comparable methodologies in sites representing different positions along the defaunation gradient are crucial for recognizing general emerging patterns of consequences of mammal defaunation; this information will be valuable in developing conservation, management, and restoration programs (Dirzo *et al.* 2007); and (6) Studies should be designed to take advantage of landscape-scale variation in the density of plant species and guilds, and in community composition, to investigate the density dependence and composition-dependence of ecological processes. These types of studies will provide information to quantify to what degree plant abundance affects seed predation and seed dispersal, mortality due to other natural enemies, life history transition rates, and ultimately reproductive rates (Muller-Landau 2007). Finally, a deficiency of studies from the Paleotropics restrict our ability to evaluate the effect of hunting on tropical forests; we therefore identify Paleotropical studies as a future research priority.

DEVELOPING HUNTING MANAGEMENT PLANS FOR TROPICAL AREAS.—In a global review Milner-Gulland *et al.* (2003) evaluate overhunting of wildlife for bushmeat and conclude that this issue must be addressed within a larger economic and institutional context that runs all the way from household economics to global trade. They emphasize that the successful conservation and sustainability of hunted wildlife would involve the collaboration of local people, resource extraction companies, governments, policy makers, and researchers. Corlett (2007) suggests that the control of hunting and trade in wildlife should be the first priority for governments, NGOs, and individual conservationists in tropical and subtropical Asia. Several lines of research that need to be further explored to facilitate the development of game management plans in tropical forests include: (1) alternative use of terrestrial and aquatic sources of animal protein, including small domestic livestock and aquaculture; (2) income supplementation for local people from sources other than wild meat; (3) outreach and extension activities for local communities; (4) recognition and facilitation of the shifting of attitudes towards hunting throughout tropical landscapes; (5) implementation of sound community-based wildlife management programs in regulated-use areas such as extractive reserves; (6) appropriate landscape-scale conservation planning that can maximize the source-sink dynamics of harvested and unharvested game populations; and (7) enforcement of game regulations in strictly protected areas, which are an essential component to any landscape management plan. Finally, hunting management plans will depend upon the target region; thus, specific data will need to be collected for each site. Resources are needed to develop similar plans appropriate to local culture and species and to implement those plans.

Ecological theory suggests that large areas of tropical forests will tend to return to their original structure and species composition wherever hunting can be controlled (Muller-Landau 2007); however, the funding to successfully control hunting remains at issue. We echo the recommendations of Bennett and Robinson (2000)— governments, aid agencies, policy makers, and conservation organizations need to incorporate hunting management into their development planning. For example, most timber certification programs do not directly consider wildlife or explicitly consider the harvest of game animals in their detailed guidelines. The Forest Stewardship Council (FSC), which perhaps has some of the highest standards for timber certification, is no exception (Bennett 2000). It is imperative that FSC and other similar programs in the certified tropical timber industry begin to explicitly include game management regulations as a requirement in logging concessions and other forestry operations before these can be defined as sustainable and gain access to more lucrative markets.

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LITERATURE CITED

ALTRICHTER, M., AND R. ALMEIDA. 2002. Exploitation of white-lipped peccaries *Tayassu pecari* (Artiodactyla: Tayassuidae) on the Osa Peninsula, Costa Rica. Oryx 36: 126–132.

ANADU, P. A., P. O. ELAMAH, AND J. F. OATES. 1988. The bushmeat trade in southwestern Nigeria: A case study. J. Hum. Ecol. 16: 199–208.

ANDRESEN, E., AND S. LAURANCE. 2007. Possible indirect effects of mammal hunting on dung beetle assemblages in Panama. Biotropica 39: 141–146.

BECKMAN, N., AND H. C. MULLER-LANDAU. 2007. Differential effects of hunting on pre-dispersal seed predation and primary and secondary seed removal of two Neotropical tree species. Biotropica 39: 328–339.

BENNETT, E. L. 2000. Timber certification: Where is the voice of the biologist? Conserv. Biol. 14: 921–923.

BENNETT, E. L., AND J. G. ROBINSON. 2000. Hunting for sustainability: The start of a synthesis. *In* J. G. Robinson, and E. L. Bennett (Eds.). Hunting for sustainability in tropical forests, pp: 499–519. Columbia University Press, New York, New York.

BIEDERBECK, H. H., M. C. BOULAY, AND D. H. JACKSON. 2001. Effects of hunting regulations on bull elk survival and age structure. Wildl. Soc. Bull. 29: 1271–1277.

BODMER, R. E. 1995. Managing Amazonian wildlife: Biological correlates of game choice by detribalized hunters. Ecol. App. 5: 872–877.

BODMER, R. E., AND E. P. LOZANO. 2001. Rural development and sustainable wildlife use in Peru. Conserv. Biol. 15: 1163–1170.

BODMER, R. E., J. F. EISENBERG, AND K. H. REDFORD. 1997. Hunting and the likelihood of extinction of Amazonian mammals. Conserv. Biol. 11: 460–466.

CAUGHLEY, G. 1985. Harvesting of wildlife: past, present, and future. *In* S. L. Beasom, and S. F. Roberstson (Eds.). Game harvest management, pp. 3–14. Cesear Kleberg Wildlife Research Institute, Kingsville, Texas.

CHIN, K., AND B. D. GILL. 1996. Dinosaurs, dung beetles, and conifers: Participants in a Cretaceous food web. Palaios 11: 280–285.

CORLETT, R. T. 2007. The impact of hunting on the mammalian fauna of tropical Asian forests. Biotropica: In press.

CORNELISSEN, J. H. C., S. LAVOREL, E. GARNIER, S. DÍAZ, N. BUCHMANN, D. E. GURVICH, P. B. REICH, H. TER STEEGE, H. D. MORGAN, M. G. A. VAN DER HEIJDEN, J. PAUSAS, AND H. POORTER. 2003. Handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust. J. Bot. 51: 335–380.

COWLISHAW, G., S. MENDELSON, AND J. M. ROWCLIFFE. 2005. Structure and operation of a bushmeat commodity chain in Southwestern Ghana. Conserv. Biol. 19: 139–149.

DIRZO, R. 2001. Plant-mammal interactions: Lessons for our understanding of nature, and implications for biodiversity conservation. *In* M. C. Press, N. J. Huntly, and S. Levin (Eds.). Ecology: Achievement and challenge, pp. 319–335. Blackwell Science, Oxford, UK.

DIRZO, R., AND A. MIRANDA. 1991. Altered patterns of herbivory and diversity in the forest understory: A case study of the possible consequences of contemporary defaunation. *In* P. W. Price, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson (Eds.). Plant-animal interactions: Evolutionary ecology in tropical and temperate regions, pp. 273–287. Wiley & Sons, New York, New York.

DIRZO, R., E. MENDOZA, AND P. ORTÍZ. 2007. Size-related differential seed predation patterns in a heavily defaunated Neotropical rain forest. Biotropica 39: 355–362.

ELKAN, P. 2000. Managing hunting in a forest concession in northern Congo. *In* E. L. Bennett, and J. G. Robinson (Eds.). Hunting of wildlife in tropical forests: Implications for biodiversity and forest peoples, pp. 28–29. The World Bank, Washington D.C.

ELKAN, P., S. W. ELKAN, A. MOUKASSA, R. MALONGA, M. NGANGOUE, and J. L.D. SMITH. 2006. Managing threats from bushmeat hunting in a timber concession in the Republic of Congo. *In* W. F. Laurance, and

C. A. Peres (Eds.). Emerging threats to tropical forests, pp. 393–416. University of Chicago Press, Chicago, Illinois.

ESTRADA, A., AND R. COATES-ESTRADA. 1991. Howler monkeys (*Alouatta palliata*), dung beetles (Scarabaeidae) and seed dispersal: Ecological interactions in the tropical rain forest of Los Tuxtlas, Mexico. J. Trop. Ecol. 7: 459–474.

FA, J. E., C. A. PERES, AND J. MEEUWIG. 2001. Bushmeat exploitation in tropical forests: An intercontinental comparison. Conserv. Biol. 16: 232–237.

FA, J. E., S. F. RYAN, AND D. J. BELL. 2005. Hunting vulnerability, ecological characteristics and harvest rates of bushmeat species in Afrotropical forests. Biol. Conserv. 121: 167–176

FEER, F., AND Y. HINGRAT. 2005. Effects of forest fragmentation on a dung beetle community in French Guiana. Conserv. Biol. 19: 1103–1112.

FORGET, P.-M., AND P. A. JANSEN. 2007. Hunting increases dispersal limitation in the tree *Carapa procera*, a nontimber forest product. Conserv. Biol. 21: 106–113.

GALETTI, M., C. I. DONATTI, A. S. PIRES, P. R. GUIMARÃESJr., AND P. JORDANO. 2006. Seed survival and dispersal of an endemic Atlantic forest palm: The combined effects of defaunation and forest fragmentation. Bot. J. Linn. Soc. 151: 141–149.

GÁLVEZ, D., AND P. A. JANSEN. 2007. Bruchid beetle infestation and the value of *Attalea butyracea* endocarps for Neotropical rodents. J. Trop. Ecol. In press.

GUARIGUATA, M. R., H. ARIAS-LE CLAIRE, AND G. JONES. 2002. Tree seed fate in a logged and fragmented forest landscape, northeastern Costa Rica. Biotropica. 34: 405–415.

GUARIGUATA, M. R., J. J. ROSALES ADAME, AND B. FINEGAN. 2000. Seed removal and fate in two selectively logged lowland forests with contrasting protection levels. Conserv. Biol. 14: 1046–1054.

HARVEY, C. A., J. GONZALEZ, AND E. SOMARRIBA. 2006. Dung beetle and terrestrial mammal diversity in forests, indigenous agroforestry systems and plantain monocultures in Talamanca, Costa Rica. Biodiver. Conserv. 15: 555–585.

HILL, C. M. 2002. Primate conservation and local communities—Ethical issues and debates. Am. Anthropol. 104: 1184–1194.

HOOGESTEIJN, R., AND C. A. CHAPMAN. 1997. Large ranches as conservation tools in the Venezuelan llanos. Oryx 31: 274–284.

JEROZOLIMSKI, A., AND C. A. PERES. 2003. Bringing home the biggest bacon: A cross-site analysis of the structure of hunter-kill profiles in Neotropical forests. Biol. Conserv. 111: 415–425.

JOHNSON, C. D., AND J. ROMERO. 2004. A review of evolution of oviposition guilds in the Bruchidae (*Coleoptera*). Rev. Brasil. de Entomol. 48: 401–408.

KAWANISHI, K., AND M. E. SUNQUIST. 2004. Conservation status of tigers in a primary rainforest of Peninsular Malaysia. Biol. Conserv. 120: 329–344.

KOKKO, H., AND J. LINDSTROEM. 1998. Seasonal density dependence, timing of mortality, and sustainable harvesting. Ecol. Model. 110: 293–304.

LAURANCE, W. F., T. E. LOVEJOY, H. L. VASCONCELOS, E. M. BRUNA, R. K. DIDHAM, P. C. STOUFFER, C. GASCON, R. O. BIERREGAARD, S. G. LAURANCE, AND E. SAMPAIO. 2002. Ecosystem decay of Amazonian forest fragments: A 22-year investigation. Conserv. Biol. 16: 605–618.

LEES, A. C., and C. A. PERES. 2006. Rapid avifaunal collapse along the Amazonian deforestation frontier. Biol. Conserv. 133: 198–211.

LEWIS, D. M., AND P. ALPERT. 1997. Trophy hunting and wildlife conservation in Zambia. Conserv. Biol. 11: 59–68.

MILNER-GULLAND, E. J., E. BENNETT, K. ABERNETHY, M. BAKARR, R. BODMER, J. S. BRASHARES, G. COWLISHAW, P. ELKAN, H. EVES, J. FA, C. A. PERES, C. ROBERTS, J. ROBINSON, M. ROWCLIFFE, AND D. WILKIE. 2003. Wild meat: The big picture. Trends Ecol. Evol. 18: 351–357.

MULLER-LANDAU, H. C. 2007. Predicting the long-term effects of hunting on plant species composition and diversity in tropical forests. Biotropica 39: 372–384.

NAUGHTON-TREVES, L., J. L. MENA, A. TREVES, N. ALVAREZ, AND V. C. RADELOFF. 2003. Wildlife survival beyond park boundaries: The impact of

slash-and-burn agriculture and hunting on mammals in Tambopata, Peru. Conserv. Biol. 17: 1106–1117.

NICHOLS, E., T. LARSEN, S. SPECTOR, A. L. DAVIS, F. ESCOBAR, M. FAVILA, K. VULINEC, AND THE SCARABAEINAE RESEARCH NETWORK. In press. Dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. Biol. Conserv.

NOSS, A. J., AND R. L. CUÉLLAR. 2001. Community attitudes towards wildlife management in the Bolivian Chaco. Oryx 35: 292–300.

NUÑEZ-ITURRI, G., AND H. F. HOWE. 2007. Bushmeat and the fate of trees with seeds dispersed by large primates in a lowland rainforest in western Amazonia. Biotropica 39: 348–354.

PERES, C. A. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. Conserv. Biol. 14: 240–253.

PERES, C. A., AND P. DOLMAN. 2000. Density compensation in Neotropical primate communities: Evidence from 56 hunted and non-hunted Amazonian forests of varying productivity. Oecologia 122: 175–189.

PERES, C. A., and H. S. NASCIMENTO. 2006. Impact of game hunting by the Kayapó of southeastern Amazonia: Implications for wildlife conservation in tropical forest indigenous reserves. Biodivers. Conserv. 15: 2627–2653.

PERES, C. A., AND E. PALACIOS. 2007. Basin-wide effects of game harvest on vertebrate population densities in Neotropical forests: Implications for animal-mediated seed dispersal. Biotropica 39: 304–315.

PERES, C. A., AND M. VAN ROOSMALEN. 2002. Patterns of primate frugivory in Amazonia and the Guianan shield: Implications to the demography of large-seeded plants in overhunted tropical forests. *In* D. Levey, W. Silva, and M. Galetti (Eds.). Seed dispersal and frugivory: Ecology, evolution and conservation, pp. 407–423. CAB International, Oxford, UK.

POULSEN, J. R., C. J. CLARK, E. F. CONNOR, AND T. B. SMITH. 2002. Differential resource use by primates and hornbills: Implications for seed dispersal. Ecology 83: 228–240.

ROBINSON, J. G., AND E. L. BENNETT. 2000. Hunting for sustainability in tropical forests. Columbia University Press, New York, New York.

ROLDÁN, A. I., AND J. A. SIMONETTI. 2001. Plant-mammal interactions in tropical Bolivian forests with different hunting pressures. Conserv. Biol. 15: 617–623.

SILVIUS, K. M. 2002. Spatio-temporal patterns of palm endocarp use by three Amazonian forest mammals: Granivory or 'grubivory'? J. Trop. Ecol. 18: 707–723.

VERDADE, L. M., AND C. B. CAMPOS. 2004. How much is a puma worth? Economic compensation as an alternative for the conflict between wildlife conservation and livestock production in Brazil. Biota Neotropica 4: 1–4.

VULINEC, K. 2000. Dung beetles (Coleoptera: Scarabaeidae), monkeys, and conservation in Amazonia. Florida Entomol. 83: 229–241.

VULINEC, K. 2002. Dung beetle communities and seed dispersal in primary forest and disturbed land in Amazonia. Biotropica 34: 297–309.

VULINEC, K., J. LAMBERT, AND D. J. MELLOW. 2006. Primate and dung beetle communities in secondary growth rainforests: Implications for conservation of seed dispersal systems. Int. J. Primatol. 27: 855–879.

WANG, B. C., M. T. LEONG, T. B. SMITH, AND V. L. SORK. 2007. Hunting of mammals reduces seed removal and dispersal from the Afrotropical tree, *Antrocaryon klaineanum* (Anacardiaceae). Biotropica. In press.

WILDLIFE CONSERVATION SOCIETY AND SARAWAK FOREST DEPARTMENT. 1996. A master plan for wildlife in Sarawak. Wildlife Conservation Society and Sarawak Forest Department.

WRIGHT, S. J. 2003. The myriad effects of hunting for vertebrates and plants in tropical forests. Perspect. Plant Ecol. Evol. Syst. 6: 73–86.

WRIGHT, S. J., AND H. C. DUBER. 2001. Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the palm *Attalea butyraceae*, with implications for tropical tree diversity. Biotropica 33: 583–595.

WRIGHT, S. J., A. HERNÁNDEZ, AND R. CONDIT. 2007. The bushmeat harvest alters seedling banks by favoring lianas, large seeds and seeds dispersed by bats, birds and wind. Biotropica 39: 363–371.

WRIGHT, S. J., G. A. SANCHEZ-AZOFEIFA, C. PORTILLO-QUINTERO, AND D. DAVIES. In press. Poverty and corruption compromise tropical forest reserves. Ecol. Appl.

WRIGHT, S. J., H. ZEBALLOS, I. DOMÍNGUEZ, M. M. GALLARDO, M. C. MORENO, AND R. IBÁÑEZ. 2000. Poachers alter mammal abundance, seed dispersal and seed predation in a Neotropical forest. Conserv. Biol. 14: 227–239.