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Emptying the Forest: Hunting and the Extirpation of Wildlife from Tropical Nature Reserves

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More than 18% of tropical rainforests are now covered by totally protected areas. If these were well protected, we could feel reasonably confident that current conservation strategies might succeed in preserving a substantial proportion of tropical biodiversity. However, in most parts of the tropics, poachers enter and leave reserves with impunity. On the basis of reports from the hunting literature, it seems likely that a majority of tropical nature reserves may already be considered empty forests*—meaning that all bird and mammal species larger than approximately two kilograms—barring a few hunting-tolerant species—have either been extirpated or exist at densities well below natural levels of abundance. The disruption of ecological functions caused by the loss of symbionts further compromises the capacity of these reserves to conserve biodiversity over the long term. A substantial shift toward improving the management and enforcement of tropical protected-area networks is required.*

Keywords: conservation, defaunation, extirpation, hunting, tropical forests

It has long been recognized that hunting poses a threat to the conservation of tropical wildlife, but the scale of the problem has increased immensely in recent years (Peres 2009). For example, in the early 1990s, an estimated six million animals were hunted annually in Malaysian Borneo, or approximately 36 animals per square kilometer (km^2) of forest (Bennett et al. 2000), and in Africa, four million metric tons of bushmeat are extracted from the Congo basin each year (Fa and Brown 2009). Across the tropics, the demand for wild meat is driving consumption rates that are several times sustainable levels (Peres 2009). Moreover, because of improved communications, markets can be located hundreds of kilometers from the source, so as wildlife supplies in one area are exhausted, the hunters simply move on to another. Behind them they leave an empty forest—a forest deprived of many of its more characteristic inhabitants and, perhaps more importantly, the ecological services they provide.

However, national parks and other totally protected areas now cover over 18% of tropical rainforests (Brooks et al. 2004). Therefore, if wildlife within reserves were well protected, we could feel reasonably confident that current conservation strategies might succeed in preserving a substantial proportion of tropical biodiversity. However, although protected-area systems in the tropics have been somewhat successful in reducing habitat clearance (Bruner et al. 2001, Brooks et al. 2009), they have been much less effective at preventing more insidious types of habitat degradation (Wright et al. 2007a). In most parts of the tropics, poachers enter and leave so-called protected areas with impunity.

Defaunation of tropical nature reserves

In tropical forests today, the abundance of wildlife is more closely correlated with patterns of hunting than with factors such as forest type, the area of the habitat, or its protected status (Woodroffe and Ginsberg 1998, Peres 2009). In Borneo, for example, small forest patches bordered by fishing communities may have abundant wildlife, whereas large remote protected areas have suffered declines due to the overexploitation of wildlife by local communities (Bennett et al. 2000, McConkey and Chivers 2004). Across the Amazon basin, animal abundances reflect the accessibility of an area to hunters rather than its protected status (Peres and Palacios 2007), whereas in West Africa, Brashares and colleagues (2004) found that the scale of bushmeat hunting was primarily determined by the availability of alternative protein sources. In contrast, both logging (Clark et al. 2009, Berry et al. 2010) and oil concessions (Laurance et al. 2008) have proven valuable wildlife sanctuaries when their managers have taken an active interest in controlling hunting.

Reserve authorities are, of course, reluctant to admit that they have enforcement issues, and extirpations from nature reserves are rarely reported. It is therefore difficult to obtain an accurate picture of how wildlife is faring in most reserves. However, on the basis of the hunting literature, it seems likely that a majority of tropical nature reserves can already be considered empty forests (box 1). Across Southeast Asia (Corlett 2007), from South China (Fellowes et al. 2004) to Laos (Nooren and Claridge 2001), Myanmar (Rao et al. 2010), Cambodia (Loucks et al. 2009), Thailand (Brodie

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Box 1. Homage to Lambir, or Where Have All the Animals Gone?

Lambir Hills National Park (N 4°20′, E 113°50′; 100–465 meters above sea level; 7000 hectares), in Borneo, is the world's most diverse forest yet studied. A plot of just 0.52 km^2 supports more tree species (1178 species) than the entirety of the temperate forests of the Northern Hemisphere (1166 species) (Wright 2005), and in 1984, when the park was first surveyed, Lambir also had an almost-intact vertebrate fauna (Shanahan and Debski 2002). However, in the early 1990s, local bushmeat markets expanded dramatically (Bennett et al. 2000). By 1994, two species had been extirpated from the park (Shanahan and Debski 2002), and in more recent surveys (2003–2007), a further 20% of the park's resident bird species and 22% of the mammal species were not recorded (see the supplementary material, available online at *http://dx.doi.org/10.1525/bio.2011.61.11.11*). Some naturally rare or secretive species may have been overlooked, but it is safe to conclude that many have been extirpated. These losses include 50% of the park's primate species and six out of seven hornbill species. In total, 90% of the totally protected species (under Sarawak law) formerly recorded in the park have been extirpated.

Other species persist only at very low densities. For example, just one bearded pig (*Sus barbatus*), normally among the most common of the larger mammals in Bornean forests, was recorded in 1127 camera-trap days (multiple traps were used) over an eight-month period (Azlan and Lading 2006). Similarly, hornbills were observed on just two occasions and giant squirrels (*Ratufa bicolor*) on only 5 in 25 days of observation at fruiting figs. In 1997, I observed five giant squirrels feeding simultaneously in the same tree.

Such losses clearly have ecological consequences for the forests at Lambir. Observations of animals feeding at fruiting figs indicate that assemblages of fruit-eaters have less than half as many species as they did 10 years ago (figure 1a, supplementary materials) and the abundances of several species that are still present have clearly declined. A large proportion of the observed fig crops fell to the ground uneaten, and other fruits, such as durian (*Durio* spp., figure 1b), can often be seen rotting on the ground.

The speed and extent of Lambir's defaunation is difficult to overstate. In less than 20 years, hunting has deprived Lambir of almost all of its more charismatic animals and has, in the process, substantially altered the ecology of the forest. How did such a fate befall the world's most diverse forest? Unfortunately, Lambir is typical of many—particularly smaller—reserves that through biogeographic and historical happenstance do not harbor glamorous A-list species, such as orangutans or rhinos, and, as a result, are bypassed by all the attention and funding. The focus of conservation efforts on such a tiny proportion of species, usually at larger and more remote sites, is condemning many reserves and a large proportion of tropical biodiversity to a fate similar to Lambir's.

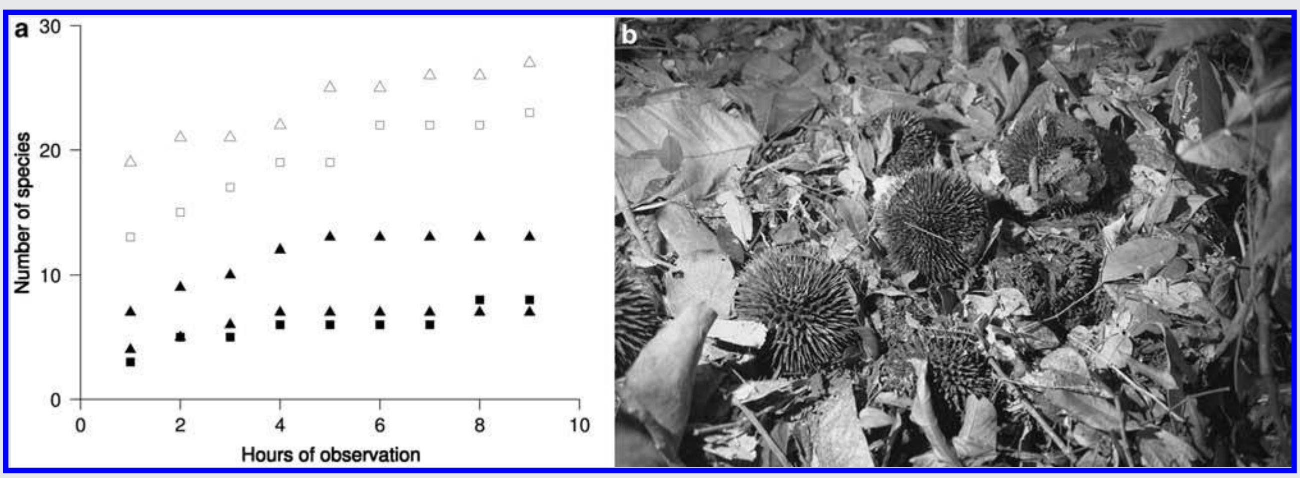

Figure 1. (a) Species accumulation curves for vertebrate fruit-eaters observed at two species of fruiting fig tree at Lambir in 1997–1998 (open symbols) and 2005–2007 (solid symbols) (see the supplementary materials available online at http://dx.doi.org/10.1525/bio.2011.61.11.11 *for methods).* Ficus subgelderi *(squares) has small fruit (about 12 millimeters in diameter), and* Ficus subcordata *(triangles) has very large fruit (about two centimeters in diameter and four centimeters long). Other fig species observed showed similar declines in frugivore assemblage diversity, and out of a total of 51 frugivore species observed at figs in 1997–1998, only 23 species were observed in 2005–2007. (b) Durians (*Durio *sp.) lying rotting on the forest floor. Durians are normally among the most sought-after fruit in Borean forests; however, there are few, if any, animals left in Lambir that can handle large fruits like these and, therefore, their seeds are no longer dispersed.*

et al. 2009), Malaysia (Bennett et al. 2000), and Indonesia (Lee 2000), nature reserves have suffered recent widespread declines in vertebrate populations, and the situation appears similar in other tropical areas with relatively high-density human populations, such as Madagascar (Dunham et al. 2008, Golden 2009), West and Central Africa (Fa and Brown

2009), the Brazilian Atlantic forest (Galetti et al. 2009), and Oceania (McConkey and Drake 2006).

The inaccessibility of forests in parts of Amazonia, Congo, and New Guinea undoubtedly affords wildlife some protection (e.g., Peres 2009) but, given the current rates of extraction, we can anticipate declines in wildlife populations in these regions as access improves (Levi et al. 2009). Only about 35%, 9%, and 1% of the Neotropic, Afrotropic, and Indo–Malayan regions, respectively, harbor intact megafaunal (more than 20 kilograms) communities (Morrison et al. 2007). Less well appreciated is that outside of these areas, almost all species larger than approximately two kilograms—barring a few hunting-tolerant animals—have often either been eliminated or exist at densities well below historical levels of abundance (Corlett 2007, Peres 2009). Indeed, the focus on megafauna has undoubtedly delayed an appreciation of the extent of the hunting problem. For example, previous studies on defaunation in tropical Asia have all been for reserves with still-complete or near-complete megafaunal communities, albeit at reduced densities (e.g., Datta et al. 2008). Most reserves are far more severely affected than these. In many, one may consider oneself lucky to see a squirrel!

Consequences of defaunation

Quite apart from a concern for the species directly affected by the hunting, studies on the consequences of defaunation have consistently indicated that the ecology of heavily hunted forests is severely disrupted. For example, hunters often target animals feeding at fruiting trees. As a result, the larger frugivorous mammals and birds are usually among the first species to be extirpated (see box 1). Such species constitute an important subgroup of seed dispersers that are capable of swallowing larger seeds and dispersing seeds greater distances. Therefore, in forests affected by hunting, the regeneration of large-seeded plants, which include many of the slower-growing canopy trees, is often inhibited relative to that of plants with smaller or abiotically dispersed seeds (McConkey and Drake 2006, Nuñez-Iturri and Howe 2007, Wang et al. 2007, Terborgh et al. 2008, Brodie et al. 2009, Holbrook and Loiselle 2009, Sethi and Howe 2009). Presumably, the spatial and genetic structures of plant populations are also affected, although studies in which these issues have been specifically addressed are lacking. Studies have shown that hunting can drastically alter several other important ecological processes, including seed predation (Roldán and Simonetti 2001, Beckman and Muller-Landau 2007, Dirzo et al. 2007, Wright et al. 2007b), seedling mortality (Roldán and Simonetti 2001, Nuñez-Iturri et al. 2008), nest predation (Posa et al. 2007), and prey availability for large carnivores (O'Brien et al. 2003). Unless animal populations in tropical reserves are properly protected, and in many cases this means that they must be restored, it cannot be assumed that so-called "protected" forests will survive in anything approximating a natural state.

Why are tropical conservation efforts failing to protect wildlife?

Much of the conservation effort in the tropics is still focused on extending the area under official protection rather than on improving the enforcement and management of existing reserves. Indeed, the metrics used to measure the effectiveness of conservation efforts are often based solely on the geographic extent of protected areas (e.g., Brooks et al. 2004, Joppa et al. 2008). However, in tropical developing countries, reserve-management authorities are often grossly underfunded and, in addition, have to contend with a gamut of secondary problems, such as limited political support, poor infrastructure, overstretched education systems, inefficient legal systems, and corruption (Bruner et al. 2001, Wright et al. 2007a, Yu et al. 2010). Under such circumstances, the capacity to administer reserves, to provide programs for developing alternative livelihoods for local people, or even just to pay the salaries of forest guards can be very limited (Yu et al. 2010). Many parks employ barely enough people to man the main entrance, let alone effectively patrol the boundaries. Statistics on the extent of tropical protected-area networks are meaningless unless they are coupled with information on the efficacy of the protection.

Furthermore, where efforts are being made to improve enforcement, the focus is disproportionately on a few select, often remote sites, which by dint of their remoteness are not usually the most immediately threatened (e.g., Cannon et al. 2007). This focus is derived largely from a preoccupation with charismatic species. However, arguments for using such species as flagships for conservation are based on the idea that they serve as a proxy for the protection of biodiversity as a whole. When the plight of a large proportion of reserves and the biodiversity they harbor is simply left off the agenda (see box 1), something is seriously amiss.

A related issue is that smaller reserves (1000–10,000 hectares) tend to be regarded as being of low conservation priority. However, such reserves are a critical component of protected-area networks in tropical regions with relatively little original forest cover remaining; they make up a substantial proportion of the habitat and biogeographic diversity, and often the only examples of species-rich lowland forest (*www.wdpa.org*). Smaller reserves can also support abundant wildlife when they are afforded adequate protection (box 2). Indeed, many of the problems commonly associated with small reserves reflect their proximity to human settlements (and a lack of enforcement) and have little or nothing to do with area effects (e.g., Woodroffe and Ginsberg 1998). Moreover, where there are valid concerns about area effects, such as in the long-term population viability of wide-ranging megafauna, the management of matrix habitats around and between reserves is often of greater importance than the size of reserves per se (Chazdon 2008, Prugh et al. 2008).

In many parts of the tropics today, hunting is the biggest threat to the conservation of biodiversity. The focus

Box 2. Small reserves can be effective wildlife sanctuaries: Sungai Wain, east Kalimantan.

Sungai Wain's (S 1°16′ E 116°54′; 9783 hectares) recent trajectory could not be more different from that of Lambir (box 1), but just 10 years ago, it appeared to be a lost cause. During the strong El Niño droughts in 1983 and 1998, approximately 60% of the reserve was burned (figure 2; Slik 2004). Simultaneously, it was suffering from poaching and illegal logging (Fredriksson and Nijman 2004). However, recognizing the importance of the forest for water security, in 2000, the city of Balikpapan set about improving Sungai Wain's protection. Regular enforcement patrols were established, and a few people were actually prosecuted. Simultaneously, monitoring and education programs and collaborative projects looking at alternative livelihoods for people living near the park were initiated. Today, despite its small size and relative isolation, Sungai Wain supports populations of many species that are rare elsewhere in Borneo (Fredriksson and Nijman 2004, Slik and Van Balen 2006), including all the species extirpated from Lambir that were formerly shared between the sites (39 species). There are 21 species of carnivore, 9 species of primate, and all 8 of Borneo's hornbill species. Moreover, it is an important site for sun bear (*Helarctos malayanus*, a relatively large carnivore) conservation (Fredriksson et al. 2007).

*Figure 2. The burned forest at Sungai Wain following the fires in 1998. Over 60% of the park was burnt, leaving only about 4000 hectares of primary forest. However, it remains an important site for sun bear (***Helarctos malayanus***) conservation. Photograph: Martijan Lammertink, Cornell Lab of Ornithology.*

Sungai Wain's success is clearly due to the carrot-and-stick approach: tough enforcement coupled with education and development programs. The strong support of the local government was perhaps the battle 80% won. Most importantly, however, the success in Sungai Wain demonstrates the potential of relatively small reserves for conserving biodiversity in a region with relatively little original rainforest remaining.

of conservation efforts on select, often remote sites fails to address the fundamental causes of this problem. A substantial shift toward improving countrywide or regionwide protection of wildlife in reserves is required. Such a shift would benefit charismatic megafauna, many other lesser-known but threatened species and, through the maintenance of ecological processes across small and large reserves alike, the greater part of tropical biodiversity.

Searching for solutions

No one can pretend that dealing with hunting is easy. Indeed, it is almost inevitably a significant social issue. Poor people in developing countries pay disproportionately for conserving tropical biodiversity, and local communities often regard the forest as their birthright and hunting—even of endangered species—as an important cultural tradition (Bennett et al. 1997). Nevertheless, it is also true that the extirpation of wildlife from nature reserves does not benefit anyone. For sustainable subsistence hunting in rainforests, human densities cannot exceed about one person per km^2 (Robinson and Bennett 2004). With 46 people per km^2 in the Neotropics, 99 in Africa, and 522 in Asia, average population densities are already one to two orders of magnitude too high for a sustainable protein supply that depends to any substantial degree on bushmeat (Bennett 2002). Indeed, for many consumers, bushmeat is already a luxury item. Domestic protein sources are often much cheaper, but people still enjoy hunting as a pastime and like to eat wild meat when they can get it. Moreover, in many places, a large proportion of bushmeat is shot by immigrant hunters and consumed in urban restaurants (e.g., Poulsen et al. 2009). Under such circumstances, authorities should not feel reluctant to enforce prohibitions on hunting.

An essential step forward would be achieved by shifting reporting away from simplistic area-based figures toward statistics that incorporate measures of effective enforcement, such as the intactness of assemblages (Scholes and Biggs 2005) and time-dependent changes in the abundance or distribution of hunting-sensitive species (e.g., large frugivores; see box 1). By exposing the inadequacies of current enforcement, this would apply more pressure on tropical nations to improve reserve management and wildlife protection in general. The international conservation community and donor agencies should also pay much more attention to interventions that will help improve the administration and enforcement of entire protected-area networks, such as guard-training programs and facilities (including modern patrolling technology and remote-detection equipment), legal capacity development, and training for extension officers. Of course, many such activities are already being run, but there is an urgent need to expand these programs and shift the emphasis from selected site-based activities to those targeting capacity development at national and regional levels. Targeted species conservation programs aimed at restoring wildlife populations in reserves are now vital and may also be an effective way of engaging local people, because such programs can provide employment for field assistants, can be tied to ecotourist ventures and education initiatives, and can generate local pride in a reserve. Again, there is a need to expand such efforts to a larger proportion of reserves and especially to those that, because of their proximity to human settlements, are most threatened. Finally, greater efforts must be applied to improving the management of wildlife in secondary forests and other matrix habitats in the landscape outside protected areas (Chazdon 2008, Koh and Wilcove 2008, Prugh et al. 2008).

Although guards and patrolling remain essential frontline activities, the conservation community also needs to consider supporting a wider range of governance options (Damania and Hatch 2005, Yu et al. 2010). For example, in Ghana, it was found that a significant fine applied to the sale of bushmeat in urban markets was sufficient to reduce hunting to sustainable levels (Damania et al. 2005). Moreover, enforcement at the point of sale can make use of existing capacity in the form of market inspectors and food-hygiene officers, and if fines are inadequate, alternative legal instruments, such as restaurant- or business-licensing laws, can be used to increase the penalties. This approach also has the benefit that people rarely have the same qualms about imposing fines on urban businesses as they might on rural hunters and, because guns are not (normally) involved, the danger is greatly reduced. Given the ubiquity of mobile phones, the probability of detecting wildlife crimes can be greatly increased by employing hotlines, particularly when reports are linked to generous rewards. By increasing the chance that hunters or wildlife traders get caught, such systems can greatly augment the deterrent effect of existing laws and penalties (Damania and Hatch 2005). Unfortunately, one rarely sees such systems employed at anything approaching their full potential. Many tropical nations earn large sums of money from nature-based tourism, but governments often remain ignorant of the essential role that wildlife and nature reserves play in underpinning the industry, and prefer instead to invest in golf courses. Partnerships with tour operators and government tourist agencies may therefore be an effective way of lobbying for improved wildlife management. Also, where tourist lodges own land next to reserves, they can serve as a buffer zone and help restrict poacher access (Yu et al. 2010). Similarly, developing partnerships with logging (Berry et al. 2010) or oil concessionaires (Laurance et al. 2008) may sometimes prove a more effective way of protecting wildlife than trying to work with cash-strapped nature reserve agencies.

Conclusions

In many parts of the tropics, hunting is now the biggest threat to tropical biodiversity. There is a need to acknowledge the unpalatable but undeniable fact that current tropical conservation efforts are failing. A large proportion of the conservation estate is already empty forest, and with the loss of important symbionts, we can anticipate that the ecosystems in such reserves will continue to degrade unless their wildlife populations are restored. A substantial shift toward improving the management and enforcement of tropical protected-area networks is required.

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