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Issue: *The Year in Ecology and Conservation Biology***The empty forest revisited**David S. Wilkie,¹ Elizabeth L. Bennett,¹ Carlos A. Peres,² and Andrew A. Cunningham³¹Wildlife Conservation Society, Bronx, New York. ²Centre for Ecology, Evolution and Conservation, School of Environmental Sciences, University of East Anglia, Norwich, United Kingdom. ³Institute of Zoology, Zoological Society of London, Regent's Park, London, United KingdomAddress for correspondence: David S. Wilkie, Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY 10460. dwilkie@wcs.org

Tropical forests are among the most species-rich ecosystems on the planet. Some authors argue that predictions of a tropical forest extinction crisis based on analyses of deforestation rates are overly pessimistic since they do not take account of future agricultural abandonment as a result of rural–urban migration and subsequent secondary regrowth. Even if such regrowth occurs, it is crucial to consider threats to species that are not directly correlated with area of forest cover. Hunting is an insidious but significant driver of tropical forest defaunation, risking cascading changes in forest plant and animal composition. Ineffective legislation and enforcement along with a failure of decision makers to address the threats of hunting is fanning the fire of a tropical forest extinction crisis. If tropical forest ecosystems are to survive, the threat of unsustainable hunting must be adequately addressed now.

Keywords: bushmeat; tropical forest; defaunation**Introduction**

Tropical forests are among the most species-rich ecosystems on the planet, containing approximately 20%, 60%, and 70% of all known mammals, birds, and amphibians, respectively. Analysis of deforestation rates in the humid tropics has triggered fears of a tropical forest extinction crisis (e.g., Millenium Ecosystem Assessment).¹ Wright and Muller-Landau² assert that such predictions are overly pessimistic since they take no account of future rural–urban migration and subsequent options for secondary regrowth that would stem the tide of extinctions. Although thorough in their analysis of forest loss and regrowth based on Food and Agriculture Organization of the United Nations (FAO) data, Wright and Muller-Landau take no account of a key threat to species that is not directly correlated with area of forest cover (but see Ref. 3). Of known threats to tropical forest biodiversity, hunting is the most extensive, and also the most challenging to detect.⁴ Yet, hunting has long been recognized as a primary cause of species depletion in otherwise-undisturbed tropical forests, leading to the “empty forest syndrome”⁵ and to cascading declines of other plants and animals.^{6–9} In this paper, we explore how

hunting is driving tropical forest defaunation, thus contributing to a tropical forest extinction crisis in ways not readily detectable using forest change cover assessments alone.

Overexploitation potentially affects all tropical forest species, both plant and animal. In this paper we focus on terrestrial vertebrates as they often are the focus of international conservation concern, are more readily detectable than other animal taxa, are important to local livelihoods, and their loss potentially has major implications for forest structure, function, and resilience.

Hunting*Forest defaunation from hunting*

In tropical forests across the globe, wild animals are hunted for local consumption and for sale to local or distant consumers as food, trophies, medicines, and pets.^{10,11} Although many extant species have been hunted sustainably in the past, recent changes are rapidly increasing the extent and scale of hunting. First, hunting rates are often directly correlated with human population densities in and around the site,¹² which continue to increase in many tropical forest areas. In Central African countries, for

Table 1. Relative importance of threats to tropical forest vertebrates (reptiles have not yet been assessed)

Taxon	Total number of species found in tropical forests	Number of tropical forest species under threat ^a	Number (%) species in tropical forests threatened by				
			Habitat loss/ degradation	Invasive species	Hunting Pathogens/ parasites	accidental mortality or persecution	Pollution
Mammal	1035	435	364 (84)	24 (6)	11 (3)	167 (38)	10 (2)
Bird	5918	868	823 (95)	200 (23)	57 (7)	298 (34)	52 (6)
Amphibian	4461	1507	1393 (92)	75 (5)	344 (23)	78 (5)	446 (30)
Total	11414	2810	2580 (92)	299 (11)	412 (15)	543 (19)	508 (18)

^aClassified as vulnerable, endangered, critically endangered, or extinct in the wild. All data from the 2007 IUCN Red List (www.iucnredlist.org).

example, human populations increased by an average of >2% per year between 1990 and 2005. Also, access to forests, often associated with logging and other extractive industries,^{13–15} has increased alongside improved hunting technologies and the commercialization of hunting.¹⁶ Commercial hunting increasingly supplies highly organized, often illegal, globalized wildlife trade networks (e.g., see Ref. 17). Hunting across much of the tropics is already unsustainable, presenting the most serious threat to mammals and birds after habitat loss (Table 1).

Tropical forests are low-productivity habitats for mammals and, even though significant variation exists,¹⁸ mammalian biomass is often an order of magnitude lower than in more-open tropical habitats.¹¹ This greatly increases the likelihood that even relatively low levels of hunting will be unsustainable for many species. Tropical forests can only support about 1 person/km² if they depend exclusively on wildlife for their protein,¹¹ and human population densities are higher than this across all but a few parts of the tropics today.

Tropical forest animals vary in their vulnerability to extirpation through overhunting.^{19–21} Factors that make species especially vulnerable include (1) low intrinsic rate of population increase, that is, long-lived and/or large-bodied species (e.g., primates, carnivores, elephants, tapirs, and other large ungulates);²² and (2) behavioral traits that facilitate hunting, such as communal nesting or large-group living, enabling several animals to be killed at one

time (e.g., see Ref. 23); spectacular or audible displays, enabling easy detection; and slow movement, enabling easy capture.

Large-bodied species are particularly vulnerable to extirpation from hunting for several reasons. First, they tend to cover large areas and so are potentially exposed to many hunting locations, and hunting in one area can deplete animals from a wider area. Second, hunters actively select them, since large animals generate the highest value per unit effort invested in hunting. Even when large-bodied animals become scarce, hunters of multispecies prey assemblages continue to hunt any individuals encountered. Hunters' preference for large-bodied animals is likely to result in the local extinction of large species as long as the densities of small species remain sufficiently high to support continued hunting in that area.²⁴

Prolonged hunting at levels above those that can be defined as sustainable leads to local declines and extirpations, although interpretation of observations can be complex due to source-sink dynamics. As central place foragers, human hunters lower wildlife densities around villages and other centers of hunting activity, but those areas might be supplied from adjoining less-hunted source populations. Hence, hunts might be more sustainable than implied by surveys close to hunting villages alone.^{20,25,26} Despite such complexities, in general, populations of hunted species throughout the tropics are typically at lower densities than nonhunted populations (Table 2).

Table 2. Declines in population densities of tropical forest mammals due to hunting

Location	Country	Percentage by which densities of targeted species are reduced in moderately and heavily hunted forest	Reference
101 Amazonian sites	Brazil	90	Peres, ⁸³ Peres & Palacios ³²
Quehueiri-ono	Ecuador	35.3	Mena <i>et al.</i> ⁸⁴
Mbaracayu	Paraguay	53.0	Hill and Padwe ²⁵
Ituri I	D.R. of Congo	42.1	Hart ⁸⁵
Ituri II	D.R. of Congo	12.9	Hart ⁸⁵
Mossapoula	C. African Republic	43.9	Noss ⁸⁶
Seven sites in Sarawak and Sabah	Malaysia	62.4	E.L.Bennett, unpublished data
Nagarahole	India	75.0	Mahusudan and Karanth ⁸⁷
Makokou	Gabon	43.0 to 100	Lahm ⁸⁸
Mbaracayu	Paraguay	0 to 40	Hill <i>et al.</i> ⁸⁹
Mata de Planalto	Brazil	27 to 69	Cullen <i>et al.</i> ⁹⁰

As hunting becomes increasingly commercial, “boom and bust” patterns often occur at any one site: hunting rates initially increase when remote forests become connected to markets, then rapidly decline as wildlife populations are depleted.²⁷ Following depletion, consumers seek supplies from other species or other areas, causing ever-expanding depletion zones. Hunting in Bioko, Equatorial Guinea, has reduced primate populations by 90% in some areas and to local extinction in others.²⁸ In Kilum Ijim, Cameroon, most large mammal species, including elephants, buffalo, bushbuck, chimpanzees, leopards, and lions, have become locally extinct within the past 50 years through hunting.²⁹ Of 57 mammal, bird, and reptile species hunted throughout the Congo Basin, 60% are harvested unsustainably.³⁰ Half of the major protected areas in Southeast Asia have lost at least one large mammal species due to hunting; most have lost many more³¹ (Wildlife Conservation Society information). Hunting is depleting pangolin populations throughout their natural range across Asia; both Asian mainland species are now listed as Endangered (<http://www.iucnredlist.org/>). More than 50% of Asia’s freshwater turtle species are now endangered due to overharvesting for trade (<http://www.iucnredlist.org/>). In Vietnam, 12 large animal species have become extinct, or virtually extinct, in the past 50 years mainly due to hunting (J.

Walston, personal communication, 2010). Across 101 Amazonian forest sites, hunting drastically reduced the mean aggregate population density (and biomass) of the 12 most important game vertebrates from 115 individuals/km² (980 kg/km²) in non-hunted sites to only 19 individuals/km² (89 kg/km²) in heavily hunted sites.³² In the 16 years since the seminal paper by Redford,⁵ the “empty forest syndrome” is now a reality throughout much of Asia³¹ and Africa^{33,34} and is spreading rapidly to more sparsely settled tropical forest regions.³⁵ Moreover, hunting often operates synergistically with other threats, especially forest fragmentation^{36–38} and disease,^{39,40} sounding the death knell for many species.

Factors contributing to unsustainable hunting

Hunter-gatherers and forager-farmers are typically among the poorest and most economically and politically isolated families in society.⁴¹ For poor rural families living in close proximity to the forest, the use of wild animals for food, clothing, medicines, and ornamentation is an economic necessity in the absence of feasible substitutes.⁴² Wildlife is also a critical source of income for many rural people who have few alternatives.⁴³ In rural Gabon, hunting accounts for 15–72% of household incomes, with the proportion rising in poorer, more remote communities.⁴⁴ The relationship between poverty and hunting is complex and varies between

sites.^{34,45} In Gabon, households with more male labor and financial capital to pursue both hunting and trapping obtain most of the benefits from selling wild meat,^{44,46} but in eastern Democratic Republic of Congo, the poor are financially more dependent on hunting than are the rich.⁴⁷

The hunting of many species is driven by an urban, and increasingly international,⁴⁸ luxury market. Consumers might choose to eat wild meat either as a status symbol because it is more expensive than alternatives such as livestock, or to retain a connection to a cultural past.⁴⁹ Taste preference, though often touted as a driver of bushmeat consumption, may not, in fact, be an important factor according to a taste test conducted in Gabon.⁵⁰ Although wild meat is only a small part of the urban consumer's protein diet (e.g., approx. 2% for urban families in Gabon,⁵¹), large urban populations make them a significant driver of hunting. For wildlife products of high unit value (e.g., tiger bone, bear gall bladder), demand in urban centers is linked to increasing wealth, especially in East and Southeast Asia.⁵²

Roads play a role in facilitating many types of unsustainable hunting.^{15,53–55} For wildlife products of high unit value, hunters are willing to travel long distances even in the absence of roads or other transportation infrastructure. Wild meat has a relatively low value-to-weight ratio, however, so is seldom traded in the absence of roads. As roads reach remote forests, wildlife populations become targeted by commercial hunters and by recent colonists who might not have had time to produce agricultural commodities to generate food and income. Frontier logging concessions typify this pattern, especially since logging companies frequently regard wild meat as a free subsidy to feed their workers,¹³ with logging roads improving connectivity between wildlife and markets.⁵⁶ Even for high-value products such as ivory and rhino horn, which can be sought in remote forests, roads facilitate both the hunting and transport of the wildlife. Typically, the advent of roads leads to rapid increases in commercial hunting and subsequent population crashes of exploited species. In Congo, wildlife densities, as reflected by hunting return rates, decreased by more than 25% within a single three-week period after logging roads opened in an area.⁵⁶ In Sarawak, no primates or ungulates remained in areas of forest that had been accessible for at least a year.⁵⁷ In Bolivia, hunting in accessible logging concessions re-

duced wildlife populations to levels that, according to workers, “was not worth the effort to hunt.”⁵⁸ If roads through tropical forests spread unchecked, hunting and massive loss of wildlife to distant markets will result in whole forests becoming defaunated of animals larger than about 1 kg and sometimes even smaller.⁵⁹

A final factor contributing to unsustainable hunting is weak governance. The legal framework to manage hunting is weak or nonexistent in many tropical forest countries, often because management responsibility has been placed in the hands of state agencies lacking sufficient resources, trained personnel, or a supportive political environment. Local communities who live close to the resource usually lack the legal authority or experience to manage wildlife effectively.⁶⁰ Moreover, civil conflict or high levels of corruption, which occur in many tropical forest countries, reduce effective wildlife management, especially for high-value species.^{61,62} Although the legal situation differs with country and among continents, some patterns are similar.

- In Amazonian countries, hunting is ubiquitous and on a large scale.^{33,63} Wildlife legislation is poorly refined, poorly enforced, perceived as inappropriate by impoverished subsistence hunters in remote areas, and ignored by consumers in urban centers.
- In Central Africa, hunting rules and regulations are often part of the forestry laws, with hunting authorized through licenses (see Ref. 64 for a critical review). Hunting is therefore not an illegal activity per se and can include the right to sell the animal. Furthermore, laws recognize user rights for local populations, allowing traditional hunting. Most laws, however, forbid, among others, hunting at night and the use of nets and metal snares, thus outlawing most hunting practiced by local communities: villagers or pygmies do not hold licenses, steel wire is the preferred material for snares, and some species are only hunted at night.
- Laws vary greatly across Southeast Asia. Overall, countries tend to recognize the necessity for strict trade controls while recognizing the subsistence hunting rights of local peoples. Most have serious weaknesses and loopholes, but weak governance, enforcement, and implementation thwart their effectiveness rather

than intrinsic weaknesses in the laws themselves.

Globally, weak governance is compounded by lack of local consultation in decision making and management, insufficient resources, and inadequately trained managers. Exceptions are sites where long-term programs involve multiple partners with different and complementary skill-sets, scientific monitoring, and long-term relationship building.^{60,65}

Consequences of empty and half-empty forests

In large forest swathes across the globe, unsustainable hunting has caused severe defaunation, leading to local and, in some cases, global extinctions. Although short-term impacts of defaunation can be predicted to a reasonable degree, second-order effects are largely unknown but might have profound, long-term consequences for the persistence of other taxa, and the structure, productivity, and resilience of forests by disrupting the complex webs of interactions.⁶⁶ The implications of this for loss of ecosystem function are still not fully understood, although many studies show that tropical forests depleted of large vertebrates experience reduced seed dispersal, altered patterns of tree recruitment, shifts in the relative abundances of species,^{67–71} and various types of functional compensation.⁷²

Depleted species might be replaced by others that perform similar ecosystem functions, although some species or functional groups are less readily replaced than others. “Keystone species,” “ecosystem engineers,” and organisms with high “community importance values” refer to species whose loss have disproportionate ecosystem impacts compared to others.^{73,74} The loss of these animals can result in dramatic changes to ecosystems.^{5,75} Some predicted changes have been empirically demonstrated,⁷⁶ while others have yet to be shown or have so far proved to be inexact.¹⁶ Examples of overhunted species whose loss induces ecosystem changes are as follows:

- elephants, which have a major role in modifying vegetation structure and composition, including forest succession and regeneration patterns;^{77,78}
- top predators, whose extirpation triggers both prey hyperabundance (leading to in-

creased browsing or grazing intensity to the point where forest regeneration can be inhibited or prevented) and increases in mesopredators, causing overpredation on smaller species;⁶⁷

- wild pigs and some rodents, which are among the most active seed predators, and reduced population densities can have major effects on seedling survival and forest regeneration;^{32,79} and
- fruit bats, which are major seed dispersers, and their depletion can seriously affect forest structure and regeneration.⁸⁰

Species do not have to be entirely extirpated from a forest for significant ecosystem function to be lost. In “half-empty forests,”⁸¹ species might be sufficiently reduced to be ecologically extinct: although still present in the community, they no longer interact significantly with other species.⁸⁰

The way forward

Human intrusion into the world’s remaining tropical forests is almost ubiquitous, enhanced by the spread of logging and roads.¹³ Few areas remain free from the human footprint.⁸² This is especially acute in the highly impacted remaining forest patches in Asia and West Africa. However, even within intact regions of the Brazilian Amazon, few areas remain inaccessible to hunters,³⁵ and even low densities of households in hunting communities can deplete populations of large-bodied vertebrates.⁷²

Defaunation and the consequent broader impacts on tropical forest communities are particularly insidious threats to biodiversity because they cannot readily be detected and mapped by remote sensing approaches, require painstaking studies on the ground to quantify, and presenting the findings to policy makers in an arresting way is a challenge. Yet the situation is urgent as faunas required to perpetuate entire biological communities have already been widely disrupted across large swathes of the humid tropics.

Rarely does loss of wildlife resources enter national policy debates and never is it included in national systems of accounts.²⁰ The wider species and environmental losses of defaunation in tropical forests are seldom even considered by politicians. Recognition of the importance of wildlife for ecosystem and human well being is an important first step;

until this happens, wildlife will continue to be perceived as valueless by national policy makers who have no incentive to promote policy reforms or to enforce their implementation.

Critical steps to rectify the problems across the tropical forest world include the following:

- local, national, and international policies that recognize the critical importance of maintaining healthy faunal communities in tropical forests, both to conserve their full biodiversity, and also the vast environmental, livelihood, and economic systems that they support. Definitions of “forests” in legislation and treaties (e.g., Kyoto Protocol and its successors) should include the presence of intact faunal communities;
- developing systems of management that involve all relevant players, from governments to local communities and technical experts, to ensure realistic, transparent, long-term, and sustainable management systems; and
- learning lessons from successes and failures to develop good management practices for the mitigation of defaunation in tropical forests. These include the effective management of large protected areas where hunting and human incursion are negligible; control of hunters and wildlife carriage along transportation infrastructure, especially rivers and roads; effective management of commercial hunting and wildlife trade from source areas to potential consumers; import and export controls, trained customs officials; capacity and incentives to ensure enforcement of regulations; and monitoring systems to allow for rapid adaptive management as soon as significant changes are detected.

Wright and Muller-Landau⁸³ did not take into account faunal losses in tropical forest communities, so their view of the tropical forest world was overly optimistic. There is a tropical forest extinction crisis. The crisis is, however, largely unseen. The world’s tropical forests are losing their fauna as wildlife populations become depleted and species are lost through overexploitation. If tropical forest ecosystems are to continue to provide valued provisioning, regulatory, and cultural services, threats that risk the loss of most large-bodied wildlife species must be addressed now.

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Conflicts of interest

The authors declare no conflicts of interest.

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