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Hunting for Sustainability in Tropical Secondary Forests

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Abstract: *The interaction between land-use change and the sustainability of hunting is poorly understood but is critical for sustaining hunted vertebrate populations and a protein supply for the rural poor. We investigated sustainability of hunting in an Amazonian landscape mosaic, where a small human population had access to large areas of both primary and secondary forest. Harvestable production of mammals and birds was calculated from density estimates. We compared production with offtake from three villages and used catch-per-unit-effort as an independent measure of prey abundance. Most species were hunted unsustainably in primary forest, leading to local depletion of the largest primates and birds. The estimated sustainable supply of wild meat was higher for primary (39 kg* $\cdot$ *km*$^{-2}$ $\cdot$ *yr*$^{-1}$*) than secondary forest (22 kg* $\cdot$ *km*$^{-2}$ $\cdot$ *yr*$^{-1}$*) because four species were absent and three species at low abundance in secondary forests. Production of three disturbance-tolerant mammal species was 3 times higher in secondary than in primary forest, but hunting led to overexploitation of one species. Our data suggest that an average Amazonian smallholder would require* $\geq$*3.1 km*^{2} *of secondary regrowth to ensure a sustainable harvest of forest vertebrates. We conclude that secondary forests can sustainably provide only 2% of the required protein intake of Amazonian smallholders and are unlikely to be sufficient for sustainable hunting in other tropical forest regions.*

Keywords: bushmeat, deforestation, food security, game birds, hunting, large mammals, secondary forest, sustainability

Cacería para la Sustentabilidad en Bosques Tropicales Secundarios

Resumen: *La interacción entre cambio de uso de suelo y la sustentabilidad de la cacería es poco comprendida, pero es crítica para sustentar poblaciones de vertebrados cinegéticos y para la provisión de proteína para poblaciones rurales. Investigamos la sustentabilidad de la cacería en un paisaje heterogéneo en la Amazonía, donde una pequeña población humana tuvo acceso a extensas áreas de bosque primario y secundario. La producción aprovechable de mamíferos y aves se calculó a partir de estimaciones de la densidad. Comparamos la producción con la captura de tres aldeas y utilizamos la captura por unidad de esfuerzo como una medida independiente de la abundancia de presas. La mayoría de las especies fueron cazadas no sustentablemente en el bosque primario, lo que condujo a una reducción drástica de los primates y aves mayores. El suministro sustentable estimado de carne silvestre fue mayor para el bosque primario (39 kg*$\cdot$*km*$^{-2}$ *año*$^{-1}$*) que en el secundario (22 kg*$\cdot$*km*$^{-2}$$\cdot$*año*$^{-1}$*) porque cuatro especies estuvieron ausentes y tres especies tuvieron baja abundancia en los bosques secundarios. La producción de tres especies de mamíferos tolerantes a la perturbación fue tres veces mayor en el bosque primario que en el primario, pero la cacería llevó a la sobreexplotación de una especie. Nuestros datos sugieren que un pequeño propietario promedio requeriría* $\geq$ *3.1 km*^{2} *de bosque secundario para asegurar una cosecha sustentable de vertebrados. Concluimos que los bosques secundarios pueden aportar sustentablemente solo 2% de la ingesta de proteína para los pequeños*

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propietarios en la Amazonía y probablemente no son suficientes para la cacería sustentable en otras regiones con bosques tropicales.

Palabras Clave: aves cinegéticas, bosque secundario, cacería, carne de animales silvestres, deforestación, mamíferos mayores, seguridad alimentaria, sustentabilidad

Introduction

Overexploitation of hunted mammals and birds is common in tropical regions (Robinson & Bennett 2000; Milner-Gulland et al. 2003), where it is often accompanied by major changes in land cover (Achard et al. 2002). The interaction between land-use change and sustainability of hunting is poorly understood, but is critical for maintenance of hunted vertebrate populations and protein supply for the rural poor (Robinson & Bennett 2004).

Growth in the global extent of secondary forest (Wright 2005) has led some authors to herald their potential as hunting grounds (Lovejoy 1985; Wilkie & Lee 2004). It has been suggested that the wild-meat supply is higher in disturbed habitats than in primary forest due to canopy openness and greater abundance of understory vegetation (Robinson & Bennett 2004). Consequently, hunting in secondary forest could be rewarding for both forest dwellers who often live near successional mosaics and vulnerable primary forest specialists (that may be subjected to less persecution if hunters can obtain wild meat from secondary habitats).

Despite their potential, the value of secondary forests for wildlife conservation and rural people remains unclear. Demographic trends of declining rural populations (Wright & Muller-Landau 2006) are not consistent among regions (United Nations 2005), and expansion of industrial land uses in the tropics threatens to decouple deforestation from the number of rural farmers practicing slash-and-burn agriculture (Fearnside 2008). We address a third area of uncertainty and examine whether the wild-meat supply (harvestable biomass) of secondary forest can support local demand (hunting offtake).

Although the results of empirical hunting studies suggest that secondary forest can support substantial wild-meat offtakes (Wilkie 1989; Gavin 2007), harvest sustainability is unclear because offtakes have not been compared with reliable biomass and productivity estimates for hunted species. Similarly, a recent prediction of sustainable hunting from farm-fallow systems rests on the untested assumption that these landscapes are four times more productive for wildlife than native forest (Wilkie & Lee 2004). Furthermore, attempts to estimate wild-meat production and offtake from structurally heterogeneous landscapes have been hampered by the difficulty of measuring abundance of species with home ranges far larger than the secondary forest patches under study (Gardner et al. 2007).

We overcame these assumptions and methodological shortcomings by assessing sustainability of subsistence hunting in large areas (>10 km^2) of second-growth and primary forest within a landscape mosaic in the Brazilian Amazon. First, we assessed vertebrate depletion in hunted primary forests in our study region. Second, we tested specific predictions that secondary forests provide a greater supply of wild meat than primary forests and meat supply from second-growth may be greater than the demand from hunting (Robinson & Bennett 2004; Wilkie & Lee 2004).We used our results to consider the potential for sustainable hunting in secondary forests across the humid tropics.

Methods

Study Area

Our study area was a landscape matrix of upland primary terra firme forests, secondary forests, and industrial plantation forests located in the Jarí region of the northeastern Brazilian Amazon (00°27′00″–01°30′00″S, 51°40′00″–53°20′00″W; Fig. 1). The landholding incorporates approximately 500 km^2 of active *Eucalyptus* plantations on 5- to 6-year rotations and approximately 550 km^2 of postplantation secondary forest. This forest type is analogous to mature regrowth of farm-fallow agriculture. We tested sustainability of hunting in secondary forest, not younger secondary regrowth, which is an earlier transient phase of postagricultural succession. These secondary forest patches were all 10–20 years old, >10 km^2 in extent, and dominated by typical Amazonian pioneer species such as *Cecropia* spp., *Inga* spp., *Bellucia* spp., and *Vismia* spp. (J.B., unpublished data). They resulted from clearcutting of primary forests in the 1970s and 1980s and one or two rotations of commercial tree monocultures (*Eucalyptus* spp. and *Gmelina* spp.) lasting 5–10 years. These areas were deemed uneconomic because of the cost of transporting timber to the factory and were allowed to regenerate naturally following clearance and removal of exotic trees.

There are 30 nontribal communities embedded within the 2500-km^2 forest-plantation landscape, with a total rural population of approximately 5600 people (density of 2.2 people/km^2). Our study could be seen as a favorable testing ground for sustainable hunting in a secondary forest given the relatively low human population density,

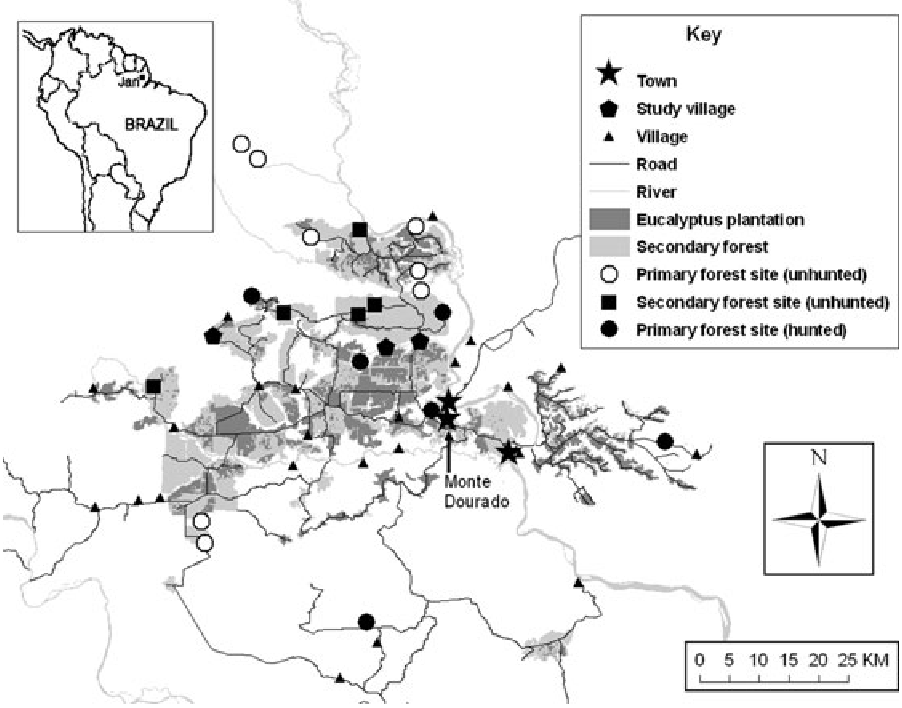

Figure 1. Map of the study area in the Jarí region of the northeastern Brazilian Amazon. Unshaded areas are primary forest.

large secondary forest patches, and extensive primary forest coverage. Most of the villages in Jarí are more than 50 years old because the region was a large Brazil nut (*Bertholletia excelsa*) concession prior to initiation of industrial plantation forestry in the early 1970s. Villagers in Jarí practice small-scale slash-and-burn agriculture, hunting, fishing, and forest extraction (especially Brazil nuts). The principal agricultural outputs are manioc, fruit, and vegetables (for local consumption and market sale). Hunting is almost exclusively for subsistence because of restrictions enforced by the Brazilian Institute for the Environment and Renewable Natural Resources (IBAMA) in the main urban center, Monte Dourado.

Faunal Surveys

Mammal and bird densities were estimated with standardized line transect surveys at eight unhunted and six hunted primary forest sites, and five large unhunted secondary forest areas (all >10 km^2). Our initial assessment of whether a site was hunted or unhunted was based on interviews with local hunters. Unhunted sites were in remote parts of the landscape with limited proximity or access to communities or urban areas. In addition, we recorded all hunting trails, shotgun shells, and hunters encountered during transect cutting and subsequent censuses. All unhunted sites were confirmed as unhunted because they either lacked direct or indirect signs of hunters, or signs were observed on only one occasion. We undertook 98 surveys in unhunted primary forest (cumulative census effort of 344 km), 74 surveys in hunted primary forest (225-km cumulative effort), and 78 surveys in unhunted secondary forest (268-km cumulative effort). All faunal surveys were conducted following Peres (1999) and undertaken on a monthly basis between May 2004 and November 2005 (see Supporting Information for details on sampling design).

Transects were walked slowly (1.25 km/h) by L.P. or a highly trained independent observer. Surveys began at 06:00–06:30 and finished at approximately 10:30. Censuses were not conducted in the rain. All medium-to-large mammals and easily detectable larger birds encountered were identified, noting species, detection cue (acoustic or visual), distance along transect, and perpendicular distance from the transect to the center of the cluster in the case of social species. Reliable group size counts were obtained whenever possible.

Harvest of Wild Meat

To assess wild-meat demand from primary and secondary forests, we measured the hunting offtake of three communities in the Jarí matrix—Bananal, São Militão, and Vila Nova. We recorded 957 vertebrate kills in 14,965 household days from January through December 2005. These three villages had immediate access to five habitat types: primary forest, *Eucalyptus* plantations, postplantation secondary forest, and the active and fallow agricultural plots of each village. We restricted our analyses to offtake from primary and large postplantation secondary forests (hereafter, secondary forests). We trained an assistant in each study village to collect information on all hunting forays made by community members. The villages were relatively small (≤ 19 households; 41 households in total), so we were able to visit all households nearly every day. Household members were interviewed by the local assistant following each hunting foray, irrespective of whether hunters successfully returned with a carcass. The assistant asked about hunt duration and timing, principal forest type(s) visited, local name of area visited, and the species killed (either captured or fatally wounded but not captured). Whenever possible, carcasses were weighed ($n = 770$) with Pesola scales (0–10 and 0–50 kg). L.P. made unscheduled data quality-control visits to each village at least twice monthly.

We carried out collaborative mapping with hunters to assess the hunting catchments around each village (Siren et al. 2004). We accompanied at least five hunters per village (≥ 10 accompanied trips per village) and used a GPS (12XL, Garmin, Olathe, Kansas) with an external antenna to map areas of primary forest and other habitats and to record area boundaries. L.P. accompanied hunters during wet and dry seasons to account for seasonal variation in hunting areas. We used a minimum convex polygon of the positional data collected to define the total catchment area of each village.

Data Analyses

FAUNAL DENSITY

We calculated densities of hunted species with the DISTANCE program (Buckland et al. 1993). We tested all detection functions for each species and fitted half-normal, negative exponential, or hazard-rate models, depending on which provided the best fit. Primary and secondary-forest detection curves were calculated separately for each species because structural differences between habitats affect detectability (Johns 1985). We used a minimum of 26 observations to calculate detection curves (primary forest mean = 64.1; secondary forest mean = 51.8). Perpendicular distance data were truncated only for brown capuchins (*Cebus apella*; 80 m) in primary and secondary forests. The number of encounters was insufficient to generate density estimates for the white-lipped peccary (*Tayassu pecari*) and tapir (*Tapirus terrestris*) in both forest types and the gray brocket deer (*Mazama gouazoupira*) in secondary forest. Only diurnal species were surveyed, so we do not present density estimates for some nocturnal mammals, namely paca (*Agouti paca*) and armadillos (*Dasypus* spp.).

HARVEST MODEL

We compared offtake of vertebrate species in primary and secondary forest with estimated levels of potential biological removal (PBR) (Wade 1998), which is the number of individuals of a species that can be sustainably removed per unit area per year. Sustainability measures based on Robinson and Redford's (1991) harvest model have been criticized, partly due to the effects of uncertainty in population growth rates (Slade et al. 1998) and overestimates in carrying capacity (Peres 2000; Milner-Gulland & Akçakaya 2001).

Potential biological-removal models use conservative minimum estimates of carrying capacity (D) and are frequently used in fisheries (Wade 1998; Johnston et al. 2000). Potential biological removal was developed to assess the impact of bycatch mortality on cetacean populations and uses the lower 95% confidence limit. Nevertheless, small sample sizes are common for censuses of low-density forest vertebrates (de Thoisy et al. 2008); therefore, variance around the mean is high. Moreover, for subsistence hunting, it is necessary to trade-off restraint in hunting yield with protein provision to the rural poor (cf. Kaimowitz & Sheil 2007). Consequently, we used mean D – 1 SE as our estimate of carrying capacity ($D_{\min}$). Thus,

$$\mathrm{PBR} = 0.6 D_{\min}(\lambda_{\max} - 1)F,$$

where $\lambda_{\max}$ is the maximum finite rate of increase and F is a mortality factor. Our modified PBR model assumes that maximum production occurs at 60% of carrying capacity, following Robinson and Redford (1991). Natural mortality based on longevity was accounted for with $F = 0.2$ for long-lived species and $F = 0.4$ for short-lived species, where F assumes the proportion of production that can be harvested.

We used catch-per-unit-effort (CPUE) as an independent check on population depletion because production models cannot detect whether a low offtake of a given species is an indication of a sustainable harvest or of stock depletion (Milner-Gulland & Akçakaya 2001). By recording hours spent hunting, rather than assuming an average, we reduced the potential for bias in CPUE estimates (Rist et al. 2008) between habitats. See Parry et al. (2009) for a more detailed description of our hunting-catchment delineation, determination of hunter effort, and an exploration of the biases inherent when comparing CPUE estimates.

Results

Large-Vertebrate Densities

We were able to estimate the density of seven mammal and six bird species (congeners for tinamous) (Fig. 2). Howler monkeys (*Alouatta macconnelli*) and black spider monkeys (*Ateles paniscus*) occurred at significantly lower densities at hunted sites than at unhunted sites (Fig. 2; Mann–Whitney: $U_{6,8} = -2.58, p < 0.01$; $U_{6,8} = -2.55$, $p < 0.01$, respectively). Population densities of red brocket deer (*M. americana*), gray brocket deer, collared peccaries (*T. tajacu*), and brown capuchin monkeys were not significantly different between hunted and unhunted sites. Agoutis (*Dasyprocta agouti*) were significantly more abundant in hunted than in unhunted sites

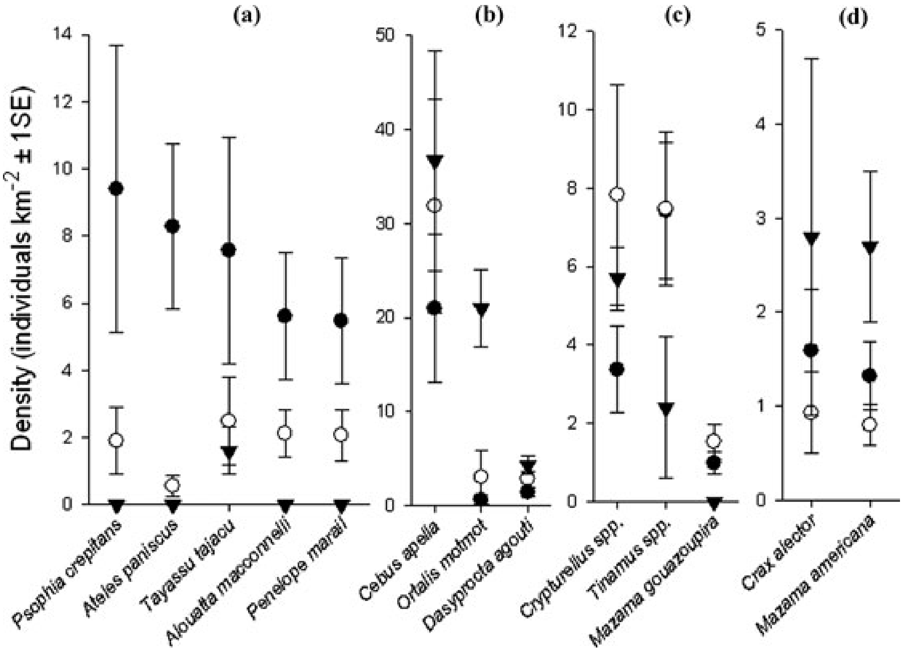

*Figure 2. Large-vertebrate densities (±1SE) in unhunted primary forest (PF) sites (*n = 8*), hunted sites (*n = 6*), and unhunted secondary forest (SF) sites (*n = 5*). (a) Species most common in unhunted primary forest, (b) least common in unhunted primary forest, (c) most common in hunted primary forest, (d) most common in unhunted secondary forest.*

($U_{6,8} = -2.20$, $p < 0.05$). Hunting had no significant effect on density of bird species, although Black Currasows (*Crax alector*), Marail Guans (*Penelope marail*), and Gray-winged Trumpeters (*Psophia crepitans*) were less abundant in hunted sites, whereas small tinamous (*Crypturellus* spp.) and Little Chachalacas (*Ortalis motmot*) were more abundant in hunted sites.

Overall, total vertebrate densities in the two forest types were similar (primary forest: 74.0 individuals/km^2; secondary forest: 77.3 individuals/km^2). Total biomass was higher in primary (444 kg · km^{-2}) than in secondary forest (277 kg · km^{-2}). Brown capuchin monkeys were the most abundant species in both forest types and more numerous in secondary forest than in primary forest, although this difference was not significant ($U_{5,8} = -1.03$, $p = 0.35$). Secondary forest supported 3 times the density of agoutis ($U_{5,8} = -2.65$, $p < 0.01$) and twice as many red brocket deer compared with primary forest, although this was not significant ($U_{5,8} = -0.82, p = 0.44$). Small tinamous and the smallest cracid, Little Chachalaca, were significantly more abundant in secondary forest ($U_{5,8} = -2.05$, $p < 0.05$; $U_{5,8} = -3.08$, $p < 0.05$, respectively). There was no significant difference in the density of Black Currasows in the two forest types ($U_{5,8} = -0.59, p = 0.62$). Two primates (spider monkeys and howler monkeys) and two bird species (Marail Guans and Gray-winged Trumpeters) were never recorded in secondary forest. Collared peccaries occurred at higher density in primary forest, as did large tinamous ($U_{5,8} = -1.78, p = 0.09$; $U_{5,8} = -2.49, p < 0.05$, respectively). Although gray brocket deer were observed in secondary forest, there were an insufficient number of encounters to calculate densities, and they were evidently more abundant in primary forest.

Wild-Meat Production

Estimated maximum sustainable harvest (MSH) of vertebrate biomass was higher in primary forest (38.7 kg · km^{-2} · yr^{-1}) than in secondary forest (22.3 kg · km^{-2} · yr^{-1}; Table 1). In primary forest, collared peccaries provided the highest potential sustainable production (22 kg · km^{-2} · yr^{-1} or 57% of the total) and no other species could provide more than 3 kg · km^{-2} · yr^{-1}. Nevertheless, in secondary forest three terrestrial mammal species (red brocket deer, collared peccary, and agouti) could each sustain a harvest of over 5 kg · km^{-2} · yr^{-1}. Birds contributed 3.2 kg · km^{-2} · yr $^{-1}$ to the MSH in primary forest and only 1.3 kg · km^{-2} · yr $^{-1}$ in secondary forest.

Hunting Sustainability

Hunting catchments of our focal communities did not overlap. Interviews with hunters also revealed that their hunting catchments did not overlap with those of other communities not monitored in this study (Fig. 1). Hunting was exclusively with shotguns, and hunters were occasionally accompanied by dogs. Five of the seven mammal species for which we were able to estimate densities were overhunted in primary forest. Of the other two, collared peccaries were harvested sustainably and brown capuchins were possibly harvested sustainably (Fig. 3). We were able to estimate densities for four mammal species in secondary forest. Only red brocket deer were harvested unsustainably, but it is unclear whether or not the other three mammal species were harvested sustainably (Table 2). The CPUE in secondary forests was at least 50% lower than in primary forest for capuchins, agoutis, gray brocket deer, and collared peccaries (Table 2).

Table 1. Calculations of maximum sustainable harvest (individuals km^{-2} · yr^{-1}; based on mean density−1 SE) and observed offtake from primary (PF) and secondary forest (SF) at three villages in the northeastern Brazilian Amazon.

	Mass[a]	λ	r	*Density*			*Primary forest estimated limits*[c]			*Observed offtake*[d]			*Secondary forest estimated limits*[c]			*Observed offtake*[d]		
Scientific name	*(kg)*	*max*[b]	*max*	*PF*	*SF*	*Life*	*P*	*H*	*H kg*	*BAN*	*SAO*	*VIL*	*P*	*H*	*H kg*	*BAN*	*SAO*	*VIL*
Primates																		
Cebus apella	3.24	1.15	0.14	13.1	25.0	long	1.18	0.24	0.5	0.06 (2)	0.32 (9)	0.10 (6)	2.25	0.45	1.46	0.07 (2)	0 (0)	0 (0)
Alouatta macconnelli	6.5	1.17	0.16	4.2	0	long	0.44	0.09	0.6	0.23 (8)	0.53 (15)	0 (0)	0	0	0	0 (0)	0 (0)	0 (0)
Ateles paniscus	9.02	1.08	0.07	5.8	0	long	0.25	0.05	0.3	0 (0)	0 (0)	0.13 (8)	0	0	0	0 (0)	0 (0)	0 (0)
Rodent																		
Dasyprocta agouti	4.2	3.0	1.1	1.0	3.4	short	1.16	0.46	2.0	0.99 (35)	1.10 (31)	0.36 (22)	4.03	1.61	6.8	0.34 (10)	0 (0)	0 (0)
Ungulates																		
Tayassu tajacu	21.7	3.49	1.25	4.2	0.9	long	6.28	1.26	21.9	0.23 (8)	0.32 (9)	0.70 (43)	1.37	0.27	5.94	0.03 (1)	0 (0)	0 (0)
Mazama americana	30	1.49	0.4	0.8	1.9	short	0.23	0.09	2.7	0.11 (4)	0.07 (2)	0.32 (20)	0.56	0.23	6.77	0.38 (11)	0.22 (2)	0.59 (2)
M. gouazoupira	18	1.63	0.49	0.6	0	short	0.24	0.10	1.8	0.11 (4)	0.11 (3)	0.21 (13)	0	0	0	0.03 (1)	0 (0)	0 (0)
Hunted birds																		
Tinamus spp.	1.1	4.38	1.48	5.7	0.7	long	11.48	2.30	2.53	0.03 (1)	0.43 (12)	0.02 (1)	1.39	0.28	0.31	0 (0)	0 (0)	0 (0)
Crypturellus spp.	0.4	2.0	0.69	2.3	4.9	long	1.36	0.27	0.11	0 (0)	0 (0)	0 (0)	2.92	0.59	0.23	0 (0)	0 (0)	0 (0)
Ortalis motmot	0.5	1.76	0.53	0.05	16.9	long	0.02	0.004	0.002	0.03 (1)	0 (0)	0 (0)	7.05	1.41	0.63	0 (0)	0 (0)	0 (0)
Penelope marail	2	1.49	0.40	3.6	0	long	1.06	0.21	0.43	0 (0)	0.04 (1)	0.02 (1)	0	0	0	0 (0)	0 (0)	0 (0)
Crax alector	3.1	1.46	0.38	0.9	1.0	long	0.26	0.05	0.16	0 (0)	0.18 (5)	0.11 (7)	0.27	0.05	0.17	0 (0)	0 (0)	0 (0)
Psophia crepitans	1.3	1.03	0.03	5.1	0	long	0.08	0.02	0.02	0 (0)	0.07 (2)	0.10 (6)	0	0	0	0 (0)	0 (0)	0 (0)
Total									38.69						22.29			

[a] *From our own data and Hilty (2003).*

[b] *From Robinson and Redford (1991), Begazo and Bodmer (1998), Cabot (1992), and Sherman (1996; personal communication).*

[c] *Abbreviations: P, production; H, harvestable portion of production; H kg, harvestable kilograms of production.*

[d] *Individuals km^{-2} · yr^{-1} (number of individuals killed in parentheses); village abbreviations: BAN, Bananal; SAO, São Militão; VIL, Vila Nova.*

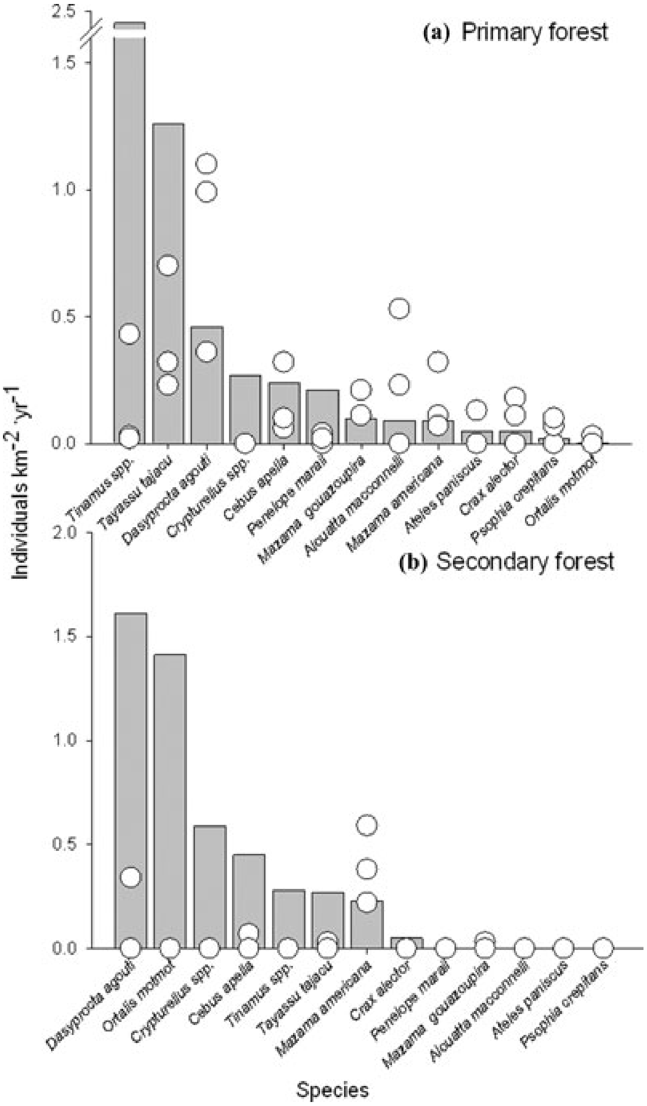

Figure 3. Maximum sustainable harvest estimates (based on mean density−1SE) of large vertebrates versus observed offtake from (a) primary and (b) secondary forest by three villages in the Brazilian Amazon.

The two large primate species were harvested unsustainably by all three communities. Howler monkeys were hunted above the MSH at two of the three communities, but none were killed by villagers of Vila Nova, which could be interpreted as evidence of previous depletion. Spider monkeys had been locally extirpated around Bananal and São Militão and were unsustainably harvested at Vila Nova.

Red brocket deer were unsustainably harvested in both primary and secondary forests. Two communities harvested this species above the MSH in primary forest, and the CPUE in primary forest was low, indicating depletion (Table 2). The CPUE for this species was 9 times higher in secondary forest, although levels of offtake were above the MSH for all three villages. Gray brocket deer were hunted above the MSH estimate for primary forest by all communities. Agoutis were harvested in primary forest above the MSH at all villages, but below the MSH in secondary forest. Capuchin monkeys were hunted above the MSH in primary forest by one community, but below the MSH in secondary forest in all cases. Collared peccaries were hunted below the MSH in both primary and secondary forests by all three communities. No birds were killed in secondary forest, despite their use of secondary forests in the Jarí region (Fig. 2). Curassows and Gray-winged Trumpeters were harvested above the MSH in primary forest by two communities.

Discussion

Overharvesting of forest wildlife for food is a major problem in Africa, Asia, and Latin America (Fa et al. 2002; Corlett 2007). In our study hunting severely depleted abundances of two large primates and caused a weaker reduction in density of the three largest birds, a pattern consistent with greater vulnerability of large-bodied Neotropical vertebrates to overexploitation (Peres & Palacios 2007). Overhunting of these species in primary forest highlights the potential importance of secondary forests as hunting grounds that could alleviate hunting pressure on vulnerable primary forest specialists.

Nevertheless, contrary to more optimistic conjecture (Lovejoy 1985; Robinson & Bennett 2004; Wilkie & Lee 2004), our findings suggest that existing Neotropical secondary forests will not provide a sufficient supply of wild meat to enable sustainable subsistence hunting, even at low human population densities. We found clear evidence of overhunting for some vertebrate species in both secondary and primary forests, even though the study region was sparsely populated and contained extensive areas of relatively undisturbed primary forests. On the basis of a modified form of the PBR model (Wade 1998) and the use of CPUE as an independent check for prey depletion, five of seven mammal and three of six bird species were overharvested in primary forest. In contrast, collared peccaries and agoutis were apparently harvested sustainably, the latter being resilient to hunting pressure due to high reproductive rates (Peres 2000). In secondary forests only red brocket deer were clearly being hunted unsustainably. Harvest sustainability of a rodent (agouti), a primate (brown capuchin), and an ungulate (collared peccary) remains unclear because these species were harvested below the predicted MSH, although at a low CPUE.

Community Composition

Tropical secondary forests could be four times more productive than primary forests (Wilkie & Lee 2004), where tree trunks and heavily defended leaves comprise a large

Table 2. Summary of sustainability indices for large mammals in primary forest (PF) and secondary forest (PF) for three villages within the Jarí landscape matrix in the Brazilian Amazon.

	No. of villages ≥ MSH[a]		*Effect of hunting—this study*[c]	*Effect of hunting Peres (2000)*	*CPUE in hunted sites* [d]		*Sustainable*	
Species	*PF*	*SF*	*PF*	*PF*	*PF*	*SF*	*PF*	*SF*
Primates								
Alouatta macconnelli	2	–	$-$ve**	$-$ve	0.6	0	no	–
Ateles paniscus	1	–	$-$ve**	$-$ve	0.2	0	no	–
Cebus apella	1	0	ns	ns	0.4	0.2	?	?
Rodent								
Dasyprocta agouti	2	0	+ve*	ns	2.0	0.9	no	?
Ungulates								
Mazama americana	2	3[b]	ns	$-$ve	0.5	4.7	no	no
M. gouazoupira	3	–	ns	$-$ve	0.4	0.09	no	–
Tayassu tajacu	0	0	ns	$-$ve	1.2	0.09	yes	?
Birds								
Crax alector	2	0	ns	$-$ve	0.3	0	no	?
Crypterellus spp.	0	0	ns	ns	0	0	yes	yes
Ortalis motmot	1	0	ns		0.02	0	?	yes
Penelope marail	0	–	ns	ns	0.05	0	no	?
Psophia crepitans	2	–	ns	$-$ve	0.2	0	no	–
Tinamus spp.	0	0	ns	$-$ve	0.4	0	yes	yes

[a] *Abbreviation: MSH, maximum sustainable harvest.*

[b] *Only two-thirds are exploited above MSH, although the third is close (0.22 vs. 0.23).*

[c] *Significant negative ($-$ve), positive (+ve), or no significant effect (ns) of hunting ($^{**}p < 0.01$; $^{*}p < 0.05$).*

[d] *Catch-per-unit-effort (CPUE) shown as kills per 100 h (including fatally injured but unretrieved animals).*

part of plant biomass (Waterman & McKey 1989). In addition, most primary production in primary forests is in the canopy, so there is little food available to terrestrial vertebrates (Hart 2000). Population densities (and associated production estimates) in secondary forests were two- to three-fold greater for capuchins, agoutis, red brocket deer, small tinamous, and Little Chachalacas. These disturbance-tolerant species have broad diets and, in addition to fruits, are able to exploit other secondary forest food resources such as insects, browse, and seeds (Simmen & Sabatier 1996; Gayot et al. 2004). Nevertheless, larger primates and several large bird species were absent from secondary forests in Jarí, which were dominated by species of low hunter preference and limited conservation value (Barlow et al. 2007; Parry et al. 2007). In addition, the sustainable harvest estimate of the collared peccary, a key hunted species, was four times lower in secondary forest than in primary forest.

Hunting Patterns

The potential of anthropogenic habitats as hunting grounds is further confounded by hunter preferences. Wildlife depletion in primary forest does not necessarily lead to more hunting in other habitats (Parry et al. 2009). Hunters may continue to hunt smaller and fast-breeding species, which may still expose vulnerable, increasingly scarce species to "piggyback extinction" (sensu Clayton et al. 1997). This is exacerbated when hunting is combined with the collection of other nontimber forest resources, such as Brazil nuts (Rumiz & Maglianesi 2001), which reduces the opportunity costs of time allocated to primary forest. Hunting techniques, whether diurnal or nocturnal, change between habitats, and it can be harder to detect smaller animals such as agoutis in more closed, secondary forest habitat (Johns 1985; Naughton-Treves et al. 2003). In addition, if large prey are abundant, smaller less-preferred species such as agoutis or capuchin monkeys might be ignored (Peres 2000), perhaps explaining the lower CPUE for agoutis in secondary forest. The CPUE may also be influenced by the different distribution of plant food resources among habitats (e.g., clustered fruiting vs. diffuse browse; Parry et al. 2007), which may influence prey movements and rates of prey encounter. The varying distribution of food resources among habitats could affect hunting methods and therefore bias CPUE estimates (Rist et al. 2008).

Sustainable Hunting?

Wilkie and Lee (2004) calculated that the average person (approximately 40 kg) would need 106 kg of undressed vertebrate biomass per year to meet their required protein intake (assuming zero consumption of domestic animals and purchased meats). Rural Amazonians living away from productive rivers would therefore require at least 4.8 km^2 of secondary forest per person to extract a sustainable animal protein supply on the basis of our production estimate of 22.3 $\text{kg} \cdot \text{km}^{-2} \cdot \text{yr}^{-1}$. Admittedly, this estimate excludes production for several important hunted species (tapir, white-lipped peccaries, armadillos, gray brocket deer, paca). Nevertheless, we can account for this by using their 40% contribution to the total harvestable production, as calculated by Wilkie and Lee (2004). These additional species would increase the estimated annual sustainable harvest to 37.2 kg $\cdot$ km^{-2} $\cdot$ yr^{-1}, although this is likely overestimated because white-lipped peccaries are wide ranging (Fragoso 1998) and almost invariably ephemeral visitors to second-growth patches. Yet even if this revised figure were accurate, an area of 2.8 km^2 of secondary forest per person would still be required to ensure a sustainable harvest. Our estimate of annual production is based on total biomass removed by hunting-induced mortality, which also includes unretrieved, but fatally wounded animals, which occurred in 9% of cases in Jarí. Thus, assuming that 9% of all animals killed were not retrieved, the actual "take-home" offtake from secondary forest is likely to be as low as 20.3 kg $\cdot$ km^{-2} $\cdot$ yr^{-1} (our estimate) or 33.9 kg $\cdot$ km^{-2} $\cdot$ yr^{-1} (accounting for all hunted species). This would increase the per capita secondary forest required to 5.2 km^2 (on the basis of a production estimate for the species we studied) or 3.1 km^2 (on the basis of a production estimate modified following Wilkie and Lee [2004]).

Although our estimates are based on many assumptions, their magnitude is implausible for most if not all regions of the humid tropics. In our study region the large areas of postplantation regrowth provided 1.8 km^2 of secondary forest per person (within 10 km of the study villages), combined with 0.3 km^2 of postagriculture secondary regrowth per person. This extent of secondary forest is much greater than the typical Amazonian context of smallholder agriculture. An average smallholding in the eastern Brazilian Amazon covers approximately 0.45 km^2, with 0.28 km^2 (61%) covered by secondary vegetation at any one time (Smith et al. 2003). Assuming an average family size of 4.7 people and correcting to account for all hunted species and collateral mortality, secondary vegetation could only sustainably supply 1.9% of the annual protein needs. Nevertheless, production of wild meat could be higher in secondary forests in the western Amazon, where overall forest productivity is higher (Malhi et al. 2004; Peres 2008).

There are other reasons to question the potential importance of secondary forests as havens for biodiversity conservation and a protein source for the rural poor. Deforestation can continue regardless of declining rural populations, and the notion that abandoned land will be left to regenerate is unlikely to hold true in many areas given the recent rapid expansion of industrial soy production in South America (Fearnside 2008) and oil palm in Southeast Asia (Fitzherbert et al. 2008). Sustainable hunting in secondary forests is also unlikely in Africa because rural populations are increasing (United Nations 2005), which reduces the chance of forest recovery (Wright & Muller-Landau 2006). The fecundity of prey communities will also affect hunting sustainability, and varies across regions. In Africa, for example, disturbance-tolerant rodents and duikers are highly fecund (Fa et al. 1995) and can provide a substantial offtake from secondary forest (Wilkie 1989). Nevertheless, a major difference in maximum sustainable-harvest potential compared with our estimates is unlikely because the population growth potential (rmax) of these African species is comparable to those of hunted vertebrates in the Neotropics (Wilkie & Lee 2004).

Model Limitations

The persistence of regional prey populations depends on the proportion of sink relative to source habitat (Pulliam 1988), yet our harvest model assumes no immigration and emigration. Although we used a static model of harvest sustainability that ignores changes in demand (Ling & Milner-Gulland 2006), hunting in our study region is predominantly for subsistence; hence, demand for wild meat is probably relatively stable. Nevertheless, our understanding of sustainability would be improved through temporal monitoring of either hunting catchment size (Clayton et al. 1997) or hunted populations (wildlife surveys or CPUE; Noss et al. 2005), in primary and secondary forests.

Conclusion

Our data suggest that secondary forests fall significantly short of providing the necessary reprieve to the widespread negative consequences of overhunting on tropical forest wildlife. Although secondary forests can provide a supplementary source of meat to local people (Robinson & Bennett 2004), our results cast serious doubt on the long-term sustainability of hunting in this forest type. Alternative solutions must be found to prevent local- or regional-scale extinction of vulnerable hunted species.

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Supporting Information

The line-transect protocol (Appendix S1) is available as part of the on-line article. The authors are responsible for content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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