
Effects of Subsistence Hunting on Vertebrate Community Structure in Amazonian Forests

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Abstract: *Subsistence hunting affects vast tracts of tropical wilderness that otherwise remain structurally unaltered, yet distinguishing hunted from nonhunted tropical forests presents a difficult problem because this diffuse form of resource extraction leaves few visible signs of its occurrence. I used a standardized series of line-transect censuses conducted over a 10-year period to examine the effects of subsistence game harvest on the structure of vertebrate communities in 25 Amazonian forest sites subjected to varying levels of hunting pressure. Crude vertebrate biomass, which was highly correlated with hunting pressure, gradually declined from nearly 1200 kg km⁻² at nonhunted sites to less than 200 kg km⁻² at heavily hunted sites. Hunting had a negative effect on the total biomass and relative abundance of vertebrate species in different size classes at these forest sites, but it did not affect their overall density. In particular, persistent hunting markedly reduced the density of large-bodied game species (>5 kg), which contributed a large proportion of the overall community biomass at nonhunted sites (65–78%) and lightly hunted sites (55–71%). Nutrient-rich floodplain forests contained a consistently greater game biomass than nutrient-poor unflooded forests, once I controlled for the effects of hunting pressure. Conservative estimates of game yields indicate that as many as 23.5 million game vertebrates, equivalent to 89,224 tons of bushmeat with a market value of US\$190.7 million, are consumed each year by the rural population of Brazilian Amazonia, which illustrates the enormous socioeconomic value of game resources in the region. My cross-site comparison documents the staggering effect of subsistence hunters on tropical forest vertebrate communities and highlights the importance of considering forest types and forest productivity in game management programs.*

Efectos de la Cacería de Subsistencia sobre la Estructura de la Comunidad de Vertebrados en Bosques Amazónicos

Resumen: *La cacería de subsistencia afecta amplias extensiones de los trópicos que permanecen estructuralmente inalterados. Sin embargo, distinguir bosques tropicales sujetos a cacería de aquellos bosques no sujetos a cacería representa un problema difícil porque esta forma difusa de extracción de recursos deja pocas señas visibles de su ocurrencia. Utilicé una serie estandarizada de censos en transectos por un período de diez años para examinar los efectos de la cacería de subsistencia sobre la estructura de comunidades de vertebrados en 25 sitios sujetos a distintos niveles de presión de cacería en la Amazonia. La biomasa de vertebrados, altamente correlacionada con la presión de cacería, declinó gradualmente desde 1200 kg km⁻² en sitios sin cacería hasta 200 kg km⁻² en sitios con cacería. La cacería tuvo un efecto negativo sobre la biomasa total y la abundancia relativa de especies de vertebrados en diferentes clases de tamaño en estos sitios, pero no afectó su densidad total. Particularmente, la cacería persistente marcadamente redujo la densidad de especies de tamaño grande (>5 kg), que contribuyeron una proporción significativa de la biomasa total de la comunidad en sitios sin cacería (65–78%) y sitios con poca cacería (55–71%). Los bosques inundables, ricos en nutrientes, consistentemente presentaban una mayor biomasa de especies cinegéticas que los bosques no inundables, pobres en nutrientes, una vez que controlé los efectos de la presión de cacería. Estimaciones conservadoras del rendimiento cinegético indican que alrededor de 23.5 millones de vertebrados, equivalentes a 89,224 toneladas de carne con un valor de US\$190.7 millones, son consumidos cada año por la población rural de la Amazonia brasileña, lo cual ilustra el enorme valor socioeconómico de los recursos cinegéticos de la región. Mi comparación de sitios documenta el asombroso efecto de la cacería de subsistencia sobre las comunidades de vertebrados y resalta la importancia de considerar a los bosques y su productividad en programas de manejo cinegético.*

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Introduction

Subsistence hunting of terrestrial vertebrates is a widespread phenomenon in tropical forests that has recently attracted much attention from applied ecologists and anthropologists (Robinson & Redford 1991; Robinson & Bennett 1999 and references therein). Yet little is known about the community-wide consequences of persistent game hunting on tropical vertebrate faunas. Anecdotal reports indicate that areas affected by game extraction in tropical forests range from remote headwater regions of western Brazilian Amazonia, where small groups of Amerindians may still hunt sustainably, to parts of west Africa accessible through logging roads, where market hunters are now trapping, snaring and shooting almost every terrestrial vertebrate larger than 1 kg (e.g., Johansson 1995; McRae 1997). Even small-scale subsis-

tence hunting, however, can result in marked population declines in large-bodied birds and mammals (Terborgh et al. 1986; Thiollay 1986; Peres 1990; FitzGibbon et al. 1995), which in turn may reverberate at other trophic levels and eventually affect tropical forest dynamics. For example, the demographics of plant populations that have long depended on strong interactions with large vertebrates may be disrupted in the absence of (1) adequate treatment and dispersal of large seeds by large frugivores (e.g., Alexandre 1978; Chapman & Chapman 1995; Peres & van Roosmalen 1996); (2) large granivores and herbivores that mediate competitive interactions through selective seed predation and seedling browsing (Dirzo & Miranda 1991; Terborgh & Wright 1994); and in some cases (3) direct physical disturbance caused by habitat "landscapers" such as large forest mammals.

Table 1. Key habitat features and game abundance of 24 forest sites surveyed in the Brazilian Amazon and Cocha Cashu, Peru.

Site localities ^a	Latitude (S), longitude (W)	River type ^b	Hunting pressure	Survey distance (km)	Date of survey	Game density (ind. km ²)	Game biomass (kg km ²)	Mean body mass (kg)
Oligotrophic Forests								
1. Urucu	4°50', 65°16'	B (hw)	none	359	3/88-9/89	232	693	2.98
2. Igarapé Açú	4°35', 64°29'	B (c)	none	51	5/87	207	712	3.44
3. SUC-1	4°50', 65°26'	B (hw)	none	47	2/88	177	665	3.76
4. Oleoduto	4°42', 65°23'	B (c)	none	124	5/94	174	582	3.35
5. Igarapé Curimatá	4°26', 65°39'	B (c)	none	305	10-11/96	167	662	3.98
6. Igarapé Jaraquí	4°21', 66°31'	B (l)	moderate	50	2-3/88	175	281	1.61
7. Riozinho	4°28', 67°06'	B (c)	light	44	12/88	208	504	2.42
8. Vira Volta	3°17', 66°14'	W (l)	light	110	5-6/92	235	553	2.35
9. Vai Quem Quer	3°19', 66°01'	W (l)	light	107	5/92	189	429	2.27
10. Barro Vermelho I	6°28', 68°46'	W (c)	moderate	117	10-11/91	214	412	1.92
12. Condor	6°45', 70°51'	W (c)	light	119	9-10/91	263	673	2.56
13. Penedo	6°50', 70°45'	W (c)	heavy	102	8-9/91	208	204	0.98
14. Sobral	8°22', 72°49'	W (hw)	heavy	109	2-3/92	233	178	0.76
15. Porongaba	8°40', 72°47'	W (hw)	heavy	115	2/92	255	222	0.87
16. São Domingos	8°55', 68°20'	W (c)	heavy	52	6/87	213	175	0.82
Eutrophic Forests								
11. Altamira ^c	6°35', 68°54'	W (c)	light	113	11-12/91	328	835	2.54
17. Fortuna ^c	5°05', 67°10'	W (c)	heavy	56	5-6/87	255	380	1.49
18. Kaxinawá Reserve	9°23', 71°54'	W (hw)	heavy	92	8-9/93	261	325	1.24
19. Cocha Cashu ^d	11°54', 71°22'	W (hw)	none	—	—	409	1030	2.52
20. Kayapó Reserve ^c	7°46', 51°57'	C (hw)	light	224	9-11/94,95	227	904	3.98
21. Lago da Fortuna	5°05', 67°10'	W (c)	moderate	48.0	5-6/87	387	615	1.58
22. Barro Vermelho II	6°28', 68°46'	W (c)	moderate	91.4	10-11/91	242	471	1.95
23. Boa Esperança	6°32', 68°55'	W (c)	light	102	11-12/91	404	1164	2.88
24. Nova Empresa	6°48', 70°44'	W (c)	moderate	96.0	8-9/91	209	455	2.18
25. Sacado	6°45', 70°51'	W (c)	moderate	92.4	9-10/91	177	352	1.99

^aSite numbers correspond to those in Fig. 1.

^bGeochemical characteristics of the watershed: W, white-water; B, black-water; C, clear-water rivers. Hydrological position of survey sites in parentheses: hw, headwaters; c, central; l, lower sections of the rivers.

^cBecause of their atypically nutrient-rich soil geochemistry, these mesotrophic terra firme forest sites were grouped with alluvial and várzea sites.

^dData from Terborgh et al. (1990); Janson & Emmons (1990).

In addition to such ecological services, game vertebrates often contribute a critical direct-use resource to tribal and nontribal peoples throughout the humid tropics (Hart 1978; Anstey 1991; Bodmer 1994; Bodmer et al. 1994; Calouro 1995; Melnyk & Bell 1996; Clayton et al. 1997) and have been considered a limiting factor to the population growth and cultural development of Neotropical forest indigenous societies (Gross 1975). Selective defaunation of otherwise undisturbed tropical forests through overhunting of large vertebrates may thus have important socioeconomic consequences, reducing the extractive value of primary forests to local peoples and their potential ecotourism value. This, in turn, may weaken the support from local constituencies to retain primary forest cover as a land-use option, particularly within Indian reserves, which account for nearly one-fifth of Amazonia (Peres & Terborgh 1995).

In this paper, I evaluate the effect of game harvest by subsistence hunters on the structure of Amazonian forest vertebrate communities. I provide a large-scale, cross-site comparison of vertebrate abundance using data from a long-term series of standardized surveys conducted at forest sites under varying degrees of hunting pressure. I focus on community-wide rather than species-specific responses to hunting pressure in terms of the standing density and biomass of forest vertebrates. In addition, I

examined the influence of forest type as defined by hydrological regimes on abundance responses to hunting by comparing nutrient-rich (eutrophic) floodplain forests with nutrient-poor (oligotrophic), unflooded forests. Finally, I attempt to assess the socioeconomic importance of subsistence hunting to rural people of Amazonia by estimating the total number and market value of game vertebrates killed each year in Amazonian Brazil.

Methods

Species Surveyed

This study is based on a standardized series of line-transect surveys of diurnal vertebrates undertaken over a 10-year period (1987–1996) at 25 Amazonian forest sites (Table 1; Fig. 1). Although over 100 vertebrate species with an adult body mass greater than 100 g were recorded, I focused on a limited number of diurnal primary consumers comprising the most important game vertebrates, including primates, ungulates, squirrels, caviomorph rodents, cracids, tinamous, trumpeters, wood-quails, and tortoises. These species were grouped into four size classes taking into account their body size distribution (species names and body weights given by Peres 1999a):

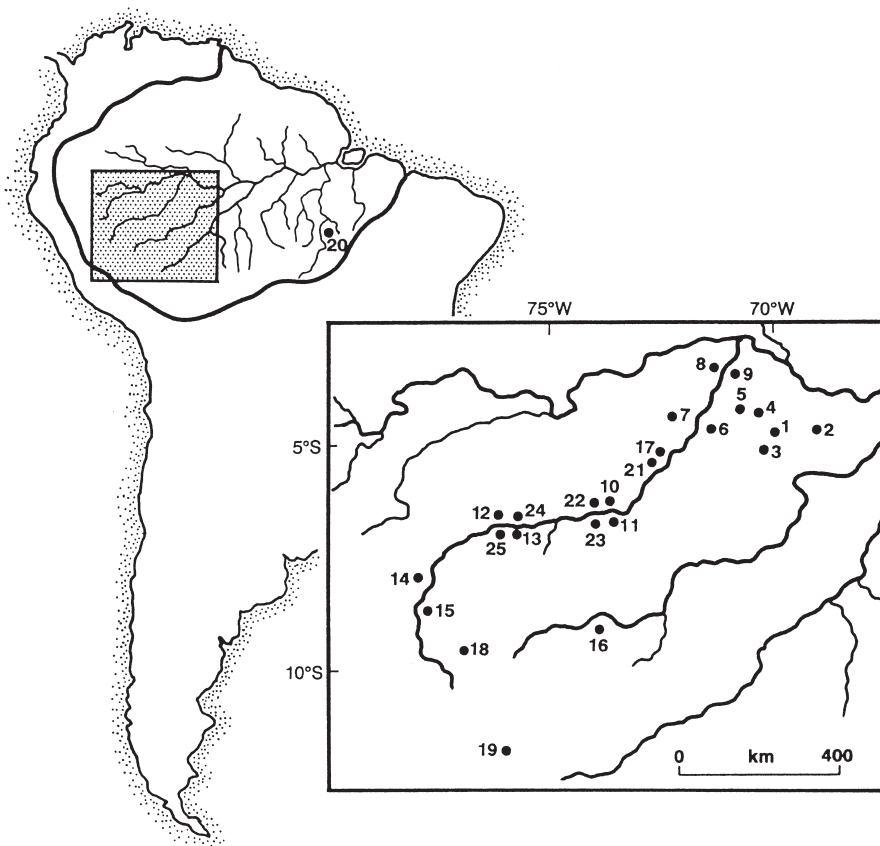


Figure 1. Location of Amazonian forest sites censused. Site numbers correspond to those listed in Table 1.

- (1) Small species (<1 kg): all squirrels (*Microsciurus* and *Sciurus* spp.); acouchis (*Myoprocta* spp.); callitrichid primates (pygmy marmosets [*Cebuella pygmaea*], tamarins [*Saguinus* spp.], and Goeldi monkeys [*Callicimico goeldii*]); squirrel monkeys (*Saimiri* spp.); wood-quails (*Odontophorus* spp.); and small tinamous (*Crypturellus* spp.).
- (2) Medium species (1–5 kg): tortoises (*Geochelone* spp.); large tinamous (*Tinamus* spp.); trumpeters (*Psophia* spp.); Common and Piping Guan (*Penelope* spp. and *Aburria pipile*); curassows (*Crax* spp. and *Mitu mitu*); agoutis (*Dasyprocta* spp.); and all cebid primates other than the Atelinae (titi monkeys [*Callicebus* spp.], saki monkeys [*Pithecia* spp.], bearded sakis [*Chiropotes satanas*], uakaries [*Cacajao calvus*], and capuchin monkeys [*Cebus* spp.]).
- (3) Large species (5–15 kg): howler monkeys (*Alouatta* spp.), woolly monkeys (*Lagothrix lagothricha*), and spider monkeys (*Ateles* spp.).
- (4) Very large species (>15 kg): collared peccary (*Tayassu tajacu*), white-lipped peccary (*T. pecari*), red brocket deer (*Mazama americana*), gray brocket deer (*M. gouazoubira*), and lowland tapir (*Tapirus terrestris*).

I refer to these taxa collectively as game vertebrates because they are or could be harvested by subsistence hunters in Amazonia. Although these taxa include a relatively small number of species, they represent the bulk of the vertebrate biomass in Neotropical forests (Eisenberg & Thorington 1973; Terborgh 1983; Terborgh et al. 1990; Peres 1999b). The diurnal line-transect surveys I conducted captured most game species pursued by hunters in Amazonian forests. The main exceptions are the two sloth genera (*Bradypus* and *Choloepus*), a few other species of nocturnal mammals, and a few infrequently harvested taxa of large-bodied avian frugivores that tend to be highly mobile in the forest canopy and notoriously difficult to census.

Sampling Sites

Sampling sites consisted of 17 unflooded (hereafter *terra firme*) forests, five forests predictably flooded on a seasonal basis (hereafter *várzea*), one alluvial forest inundated at irregular supra-annual intervals, and one transitional *terra firme*-palm forest with small enclaves of edaphic savannas (*cerrados*). All sites were located in several major river basins of eastern (upper Rio Xingú: 1 site) and western Brazilian Amazonia (Rio Juruá, Tarauacá, Jutai, Purús, Tefé, and Urucu: 23 sites; Fig. 1). Data from the southern Peruvian alluvial forest of Cocha Cashu, Manu National Park, were also incorporated into the analysis. This is the only additional Amazonian forest for which reliable density estimates are available for all

large-bodied bird (Terborgh et al. 1990) and mammal species (Terborgh 1983; Janson & Emmons 1990).

Survey sites were assigned to one of two broad categories of forest types according to soil types and differences in seasonal influx of alluvial sediments, which in lowland Amazonia are the primary sources of exogenous soil macronutrients that may affect large-scale forest productivity (Irion 1978; Duivenvoorden & Lips 1995). I thus classified all sites into either *terra firme* (oligotrophic) or alluvial-floodplain (eutrophic) sites according to nutrient concentrations in 20 soil samples collected at each site along census transects (C. Peres, unpublished data). The only exceptions were the mesotrophic *terra firme* forests of Fortuna, Altamira, and Kayapó Reserve, which were similar in nutrient profile to alluvial forest sites such as Kaxinawá Reserve.

Twenty-five sites (6 nonhunted and 19 hunted) were thus considered. Nonhunted sites were defined as those entirely uninhabited by Amerindians, detribalized Amazonians (*caboclos*), and rubber tappers, and those that offered no enduring evidence of hunting activity this century (e.g., ax marks on core hardwoods, old scars on the bark of large latex trees). These sites could not be easily reached on foot by hunters, and access to them by investigators was gained largely with helicopters and small aircraft. The term *nonhunted* is thus reserved for pristine forests of remote interfluvial basins and headwater regions of Amazonia, rather than for areas rarely visited by hunters in the last few decades. Hunting at all hunted sites was carried out with shotguns, because the rapid transition from traditional weapons to firearms has now reached even some of the most remote parts of Amazonia (Peres 1993), including the three Indian reserves sampled (Kaxinawá Reserve, Kayapó Reserve, Penedo).

Because reliable data on game harvest were not available, it was difficult to accurately reconstruct the history of hunting at hunted sites over the last several decades. I thus simply assigned them to one of three broad categories of hunting pressure—light, moderate, and heavy—on the basis of (1) semi-structured interviews (with hunters who had lived at each hunted site for at least 2 years prior to surveys) about the frequency, intensity, and species selectivity of local game harvest practices, and (2) present and past human population density and distribution quantified on the basis of interviews and the number of households in each area, as revealed by high-resolution (1:250,000) maps of each census area (RADAM 1973–1981).

Human population density at all but two hunted sites had either remained stable or declined since the RADAM surveys, because many sites along the Juruá River have been subject to rural exodus to urban centers. I also took into account the direct evidence of hunting activity that was detectable at the time of surveys (e.g., frequency of shotgun sounds heard, occurrence of hunting trails, hammock “waiting” stations, old campsites). This

kind of evidence, however, can be a poor predictor of the history of hunting pressure in an area because (1) hunting activity often varies considerably on a seasonal basis, (2) the behavior of hunters in an area was often affected by our presence, and (3) the effective life span of most residual signs of prior hunting activity is ephemeral. Interviews with hunters, on the other hand, were unbiased with respect to fear of disclosing illegal hunting activities because interviewees in such remote areas were unaware and did not appear to be suspicious of legal issues concerning game hunting.

The density of species thought to be most susceptible to hunting was not used to infer the hunting pressure at a given site because rates of game recovery may also be affected by other environmental gradients, such as hydrological regime and forest type (Peres 1999a, 1999b). I therefore assumed that this crude four-point scale of hunting pressure was the most refined this classification could afford in the absence of more accurate records of game harvest by present or past human populations.

Population Density Estimates

Surveys were conducted over an average of 113.5 ± 78.0 km (range, 44–359 km; Table 1), for a total of 2724 km walked at 24 sites. Population densities at Cocha Cashu were calculated from a range of methods, including home-range mapping and strip-census surveys using the King estimator (Janson & Emmons 1990). Line-transect censuses were conducted from early morning to midday (0600–1130 hours) by trained observers walking between two and four transects of 4–5 km in length, which were cut and marked every 50 m. Transects within terra firme sites abutting floodplain forests were cut inland, perpendicularly to the river. Newly prepared transects were left to “rest” for at least 1 day before each survey was initiated. At previously hunted sites, we avoided using hunter trails and rubber-tapper trails (*estradas*) regardless of their linearity because that could potentially introduce detection biases resulting in density underestimates. Censuses were conducted on clear or overcast but not on rainy days, at walking velocities of approximately 1.25 km/hour, by one observer per transect and were usually completed within a 30-day period. The potential effects of seasonality on vertebrate community dynamics, which can be pronounced in seasonally flooded forests (Peres 1997a), were accommodated by surveys in this forest type being undertaken on roughly the same months of the year, coinciding with the low-water season. Surveys taking place throughout the annual cycle were thus restricted to the relatively aseasonal terra firme forests, which tend to contain stable large-vertebrate assemblages throughout the year (e.g., Peres 1997a).

I derived density estimates for each species from either the hazard rate or uniform models with a cosine ad-

justment (Buckland et al. 1993) using perpendicular distances from the transect to the first animal sighted. For a few highly vocal species (e.g., *Alouatta* spp., *Callicebus* spp.), observations resulting from acoustic cues (at extreme distances from the transect) were excluded because they were detrimental to the performance of model estimators. Because detection probabilities could be biased toward species in large, uncohesive groups, a correction factor based on the mean group spread of each social species was also incorporated into the model (Peres 1997a). These models provided the best fits for species-specific data sets as determined by the minimum Akaike information criterion (Buckland et al. 1993). In the case of relatively rare species, I avoided unrealistic distortions caused by small sample sizes by pooling all surveys yielding fewer than 40 independent sightings (Burnham et al. 1980) and then deriving density estimates based on site-specific sampling efforts. This procedure was justified because between-site variances in perpendicular distances, which could have resulted from potential differences in detection probabilities, were no greater than those within sites (analysis of variance [ANOVA], $p > 0.05$ in all cases).

I calculated population densities for social species using mean group sizes at each site from the fraction of total group counts considered accurate. Because data on the size structure of populations of each species were unavailable, I estimated crude population biomass using the mean body weight of a given species, simply defined as 80% of the average body mass of adult males and females in Amazonian populations (data from Janson & Emmons 1990; Terborgh et al. 1990; Bodmer 1994; C. Peres & H. Nascimento, unpublished data). Densities (D) were assumed to be >0 if a species had been recorded at a site either during or outside our census routine. On the other hand a species was assumed locally extinct ($D = 0$) at a hunted site if local interviewees unanimously agreed that it had once been common but had not been sighted for at least 5 years. Further details on the physiognomy of the sampling sites and survey methodology can be found elsewhere (Peres 1997a, 1999a, 1999b, 1999c).

Estimates of Game Harvest

Patterns of wildlife use in Neotropical forests have been reviewed by Redford and Robinson (1987) in terms of the average number of animals consumed per capita per annum. That review was based on 19 anthropological studies encompassing 23 samples documenting kills brought into 17 indigenous and 6 colonist settlements. Those studies did not take into account the game mortality from animals that were fatally wounded but not retrieved by hunters. Consumption rates, therefore, can severely underestimate the total mortality actually resulting from game hunting, which for some taxonomic

groups may correspond to nearly twice the number actually reaching village households (e.g., Peres 1991). Using kill rates based on these hunting studies and human population data from the 1980 Brazilian national census, Redford (1993) estimated that as many as 19 million game animals are killed each year in rural Brazilian Amazonia. Here I provide new estimates of the total number of game vertebrates consumed in Brazilian Amazonia on the basis of the 23 samples reviewed by Redford and Robinson (1987), plus eight additional game harvest profiles spanning a sampling period of between 1 and 4 years. Four of these studies targeted caboclo, rubber-tapper, and colonist settlements of different parts of Brazilian (Martins 1992; Calouro 1995; Muchagata 1997) and Peruvian Amazonia (Bodmer 1994), whereas two studies targeted Indian villages in Ecuadorian (Mena et al. 1999) and Bolivian Amazonia (Townsend 1999). In addition, I include two unpublished game harvest studies we have undertaken over a sampling period of at least 2 years (C. Peres & H. Nascimento, unpublished data). The first of these was obtained from a small caboclo settlement located at Vila Moura, upper Tefé River, Amazonas, Brazil (35 consumers \times 750 days) and the second from the Kayapó Indian village of A'Ukre (133 consumers \times 542 days) located along the Riozinho River, an eastern Amazonian tributary of the Xingú River.

On the basis of these 31 samples, estimates of the average number of animals of each species consumed per person per year were then multiplied by the size of the rural population of Brazilian Amazonia in low-income households who are most likely to depend on game resources (Table 2). The upper and lower limits of my estimates corresponded to the size of the total rural population within households with an aggregate income of <1 Brazilian minimum salary (BMS in September 1993 = US\$98/month) and <0.5 BMS (US\$49/month), respec-

tively. These critical values excluded the minimum-wage public and private sector of the rural labor force, leaving primarily zero-income households that must resort to hunting and fishing to meet dietary protein demands. Although many of the samples I compiled were intrinsically biased toward areas of high game consumption, these crude, basin-wide estimates could still be highly conservative because they exclude (1) 55% of the entire human population of Amazonia corresponding to urban centers (cities, towns, and large villages), even though these are often subsidized with game meat; (2) all areas dominated by agricultural landscapes in the southern Amazonian states; (3) all areas outside the phytogeographic limits of Amazonia (Fig. 1); (4) all households with an aggregate income >1 BMS, which are assumed to be far more reliant on wage labor and food purchases, including domesticated animal protein rather than bushmeat; (5) several game species of more restricted geographic distribution for which average harvest rates remain unavailable; and (6) all species comprising <1.5% of the total weight of game taken in a given sample, which were also excluded by Redford and Robinson (1987).

Results

Hunting Pressure and Game Abundance

Vertebrate species censused at the 25 forest sites fall along a size-graded continuum, ranging from pygmy marmoset (0.15 kg) to lowland tapir (160 kg). As in other Neotropical forests, the vertebrate assemblages I censused were largely represented by small (16 species) and medium-sized taxa (18 species), rather than those in the two largest size classes (4 and 5 species, respectively). Because game harvest at hunted sites was highly

Table 2. Human population of Brazilian Amazonia^a that may be heavily subsidized by subsistence game hunting of forest vertebrates.

State of Amazonia	Total population	Rural population	Area (km ²)	Rural population density (km ⁻²)	Population in rural households with a joint income of less than ^b	
					1 BMS	0.5 BMS
Acre	446,480	170,160	153,698	1.11	98,522	38,456
Amapá	317,597	60,651	142,359	0.43	21,167	9,037
Amazonas	2,269,555	647,972	1,567,954	0.41	316,210	149,682
Pará	5,332,187	2,535,367	1,227,530	2.07	1,151,057	398,053
Rondonia ^c	1,291,214	539,613	238,379	2.26	315,134	153,250
Roraima	251,783	88,831	225,017	0.39	36,687	24,784
Tocantins ^c	990,760	419,226	277,322	1.51	27,250	10,523
Maranhão ^c	5,160,974	3,096,250	329,556	9.40	219,524	109,298
Mato Grosso ^c	2,246,757	600,827	903,569	0.66	39,204	14,330
Total	18,307,307	8,158,897	5,065,384	1.61	2,224,756	907,411

^aFundação Instituto Brasileiro de Geografia e Estatística 1996.

^bBrazilian minimum salary (BMS) based on wage values of September 1993 (1 BMS = US\$98 per month).

^cThe low-income rural population of these southern states of "Legal Amazonia" is adjusted by excluding all areas outside the phytogeographical limits of the region.

selective toward large-bodied taxa (Peres 1990; Bodmer 1995a), however, one would expect these species to take the brunt of the effects of game hunting.

Estimates of total game density and biomass at the 25 forest sites are presented in Table 1. Considering all species censused, overall biomass of the vertebrate community declined significantly with increasing levels of hunting pressure (one-way ANOVA on \log_e -transformed data, $F_{3,21} = 18.9$, $p < 0.001$; Fig. 2). The average body mass of the vertebrate fauna was therefore significantly reduced from the least to the most hunted sites ($F_{3,21} = 30.9$, $p < 0.001$), but the total number of animals occurring at different forest sites—which accounted for a small variation from 228 ± 92 individuals km^{-2} at nonhunted sites ($n = 6$) to 237 ± 23 individuals km^{-2} ($n = 6$) at heavily hunted sites—was not affected by hunting regime ($F_{3,21} = 0.34$, $p = 0.79$).

Because large-bodied taxa are by far the greatest contributors to the overall community biomass of nonhunted vertebrate communities (Fig. 3), even slight shifts in their densities resulted in major changes in their biomass. Overall community biomass at nonhunted sites (724 ± 156 kg km^{-2} , $n = 6$) was virtually the same as that of lightly hunted sites (723 ± 260 kg km^{-2} , $n = 7$) but substantially greater than that at moderately (431 ± 114 kg km^{-2} , $n = 6$) and heavily hunted sites (247 ± 85 kg km^{-2} , $n = 6$).

The combined density and biomass of species in different size classes clearly diverged across varying levels of hunting pressure (Fig. 3). Although small and medium-sized species were not obviously affected by hunting, the overall abundance of the two largest size classes was significantly depressed at moderately and heavily hunted sites both in terms of density (ANOVA on \log_e -transformed data; species 5–15 kg: $F_{3,21} = 7.7$, $p < 0.001$; species >15 kg:

$F_{3,21} = 29.7$, $p < 0.001$) and biomass (species 5–15 kg: $F_{3,21} = 9.0$, $p < 0.001$; species >15 kg: $F_{3,21} = 34.0$, $p < 0.001$; Fig. 3). In aggregate, species in the largest size classes accounted for an average density of 42 individuals km^{-2} at either nonhunted or lightly hunted sites but sharply declined to only 21 and 5 individuals km^{-2} at moderately and heavily hunted sites, respectively. In contrast, densities of small and medium-sized species, albeit relatively high at all sites, either remained unchanged or gradually increased from nonhunted to heavily hunted sites (Fig. 3), suggesting that they were either unaffected or covaried positively with some correlate of hunting pressure.

There was a ten-fold difference between the mean ungulate biomass at nonhunted (337 ± 19 kg km^{-2}) and heavily hunted sites (32 ± 8 kg km^{-2}). The large-bodied ateline primates also gradually declined from a mean biomass of 186 ± 32 kg km^{-2} and 191 ± 80 kg km^{-2} at nonhunted and lightly hunted sites, respectively, to 96 ± 25 kg km^{-2} and 20 ± 6 kg km^{-2} at moderately and heavily hunted sites. The pooled biomass of these two largest size classes thus declined 10-fold from an average of 523 ± 51 kg km^{-2} (72%) at nonhunted sites to 53 ± 14 kg km^{-2} (21%) at heavily hunted sites. Selective removal of large-bodied species was thus translated into pronounced shifts in the mean body mass of individual vertebrates present at different sites (Table 1), from as much as 3980 g at a nonhunted site (Igarapé Curimatá) to as low as 760 g at a heavily hunted site (Sobral).

These trends resulted in clear shifts in the overall vertebrate community structure: biomass densities were dominated by large-bodied frugivore-herbivores at nonhunted sites but by small and medium-sized frugivore-insectivores at persistently hunted sites. This can be seen in the relationships between hunting pressure and density and biomass that were strongly negative for large-bodied species but positive for small-bodied species (Fig. 4). Most noticeable was the staggering negative relationship between hunting pressure and the relative contribution of species weighing >5 kg to the overall vertebrate biomass ($r_s = -0.93$, $p < 0.001$, $n = 25$), which decreased from 65–78% and 55–71% at nonhunted and lightly hunted sites, respectively, to only 8–29% at heavily hunted sites. Considering medium-sized species (1–5 kg), this correlation was only marginally significant in terms of their overall density but strongly positive in terms of their biomass (Fig. 4).

Effects of Forest Type

The total vertebrate density at different sites was significantly affected by forest type but not by hunting pressure (analysis of covariance; Table 3). In contrast, both forest types and hunting pressure explained a comparable proportion of the variation in overall game biomass. In eutrophic forests subject to little or no hunting, the aggregate game biomass ranged from 850 to nearly 1200 kg km^{-2} , whereas that of oligotrophic forests did not exceed 712 kg km^{-2}

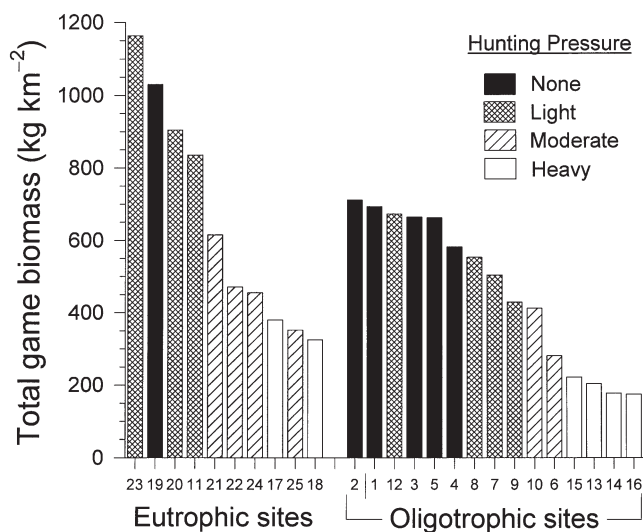


Figure 2. Total game biomass (ranked in decreasing order) of 10 eutrophic and 15 oligotrophic Amazonian forest sites subjected to varying levels of hunting pressure. Site numbers correspond to those shown in Table 1.

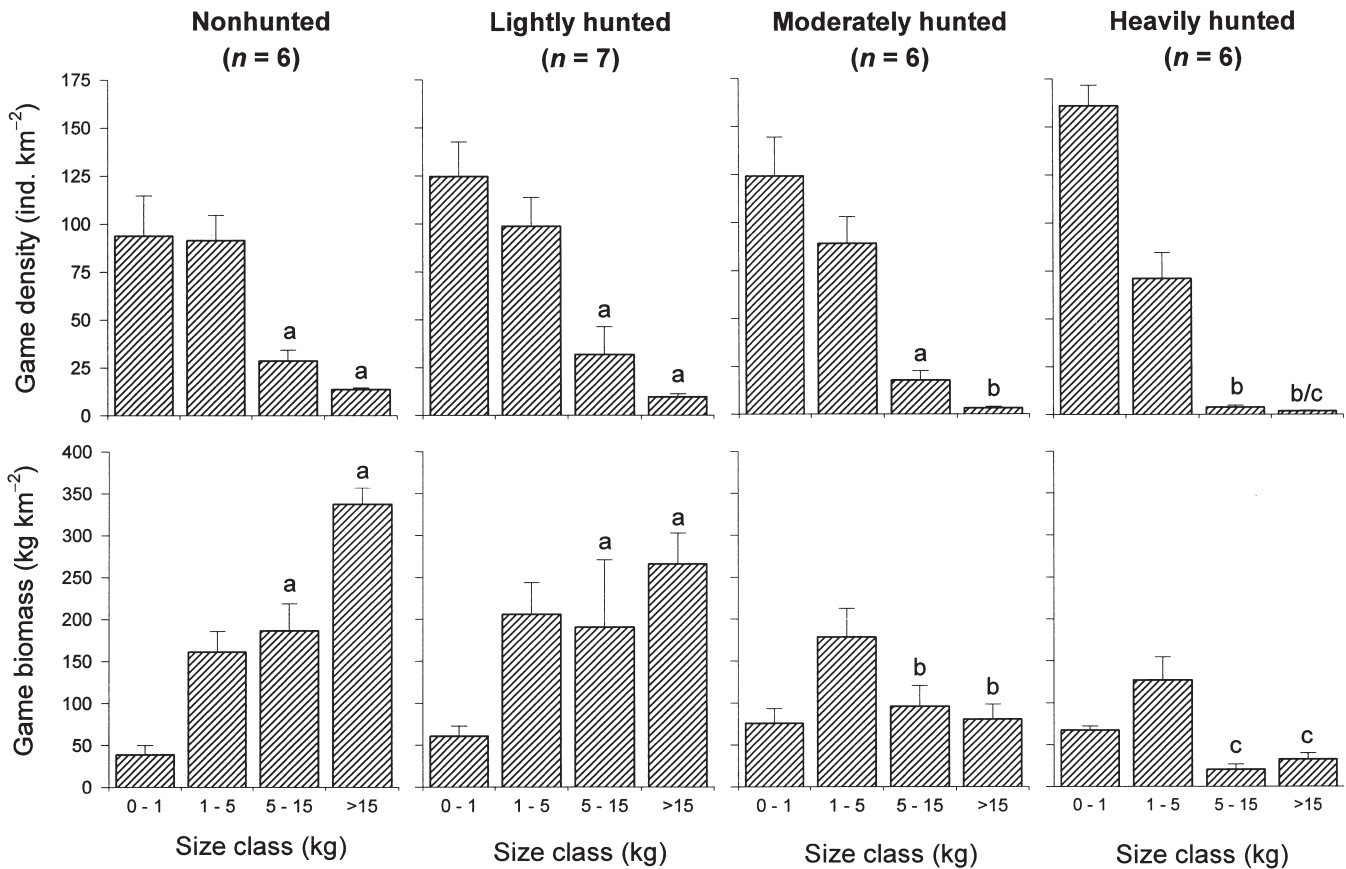


Figure 3. Total density and biomass (mean \pm SD) of game populations in four different size classes subjected to varying levels of hunting pressure. Vertebrate taxa included in each size class are listed in the text. For significant analyses of variance of \log_e -transformed density and biomass data, means are compared within each size class and across different levels of hunting; means that share the same letter do not differ significantly ($p < 0.05$) according to a Tukey multiple comparison test.

even where hunting had not taken place (Fig. 1). At the lower end of the scale, several heavily hunted oligotrophic forests had a game biomass lower than 200 kg km^{-2} , whereas the biomass of eutrophic forests never fell below 325 kg km^{-2} , even under the heaviest level of hunting pressure. Eutrophic forests thus appeared to be more productive and to sustain a greater vertebrate biomass than oligotrophic forests once the effects of hunting were controlled for. Combined with greater access to more productive fishery resources, this helps to explain the disproportionate concentration of extractive settlements along Amazonian alluvial, tidal, and várzea forests from pre-Columbian (Roosevelt 1989) to contemporary days because seasonal shifts between aquatic and terrestrial sources of animal protein are typical in these settlements (Pierret & Dourojeanni 1966; C. Peres & H. Nascimento, unpublished data).

Game Harvest in Brazilian Amazonia

Game consumption rates extrapolated for the whole of Brazilian Amazonia indicate that between 9.6 and 23.5 million reptiles, birds, and mammals are consumed each

year by the rural population in this region, corresponding to between 67,173 and 164,692 tons of terrestrial vertebrates harvested (Table 4). For mammals alone, this represents a total harvest of between 6.4 and 15.8 million individuals, corresponding to 60,426–148,150 tons of mammal biomass harvested. Considering the actual yields of edible meat (i.e., muscle mass and edible viscera; for different species, mean 55%, range 39–71% of body mass; data from Martins 1992; C. Peres & H. Nascimento, unpublished data) by excluding the proportion of each species mean body mass accounted for by all nonedible animal parts, the total game harvest corresponds to a mean of 62,808 tons (range 36,392–89,224 tons) of edible bushmeat. In economic terms, assuming that the mean substitution value of purchased bovine beef in small Amazonian settlements is US\$2.14/kg (C. Peres, unpublished data, 1998), this tonnage of wild meat would represent a mean annual market value of US\$134.2 million (range US\$77.8–190.7 million) for the whole of Brazilian Amazonia.

These basin-wide estimates of game harvest are conservative because they do not take into account a large fraction of the rural households above the critical in-

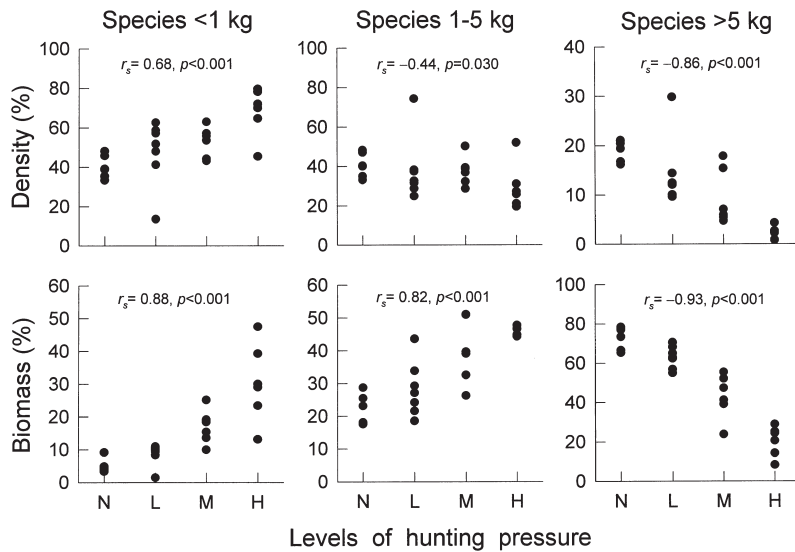


Figure 4. Relationship between level of hunting pressure (N, none; L, light; M, moderate; H, heavy) and the percent contribution of species within three size classes to the overall density and biomass of game vertebrates at 25 Amazonian forest sites. Spearman correlation coefficients (r_s) are shown for each scatterplot.

come level that are also heavily subsidized by game meat. This also applies to a large number of Amazonian hunters who are relatively wealthy and well equipped and come from urban households. Nevertheless, these estimates suggest the enormous socioeconomic importance of game vertebrates to Amazonian rural people. They also roughly support Redford's (1993) estimate of 19 million vertebrates consumed (including 14 million mammals) based on the 1980 population of Amazonian Brazil. The total mortality associated with hunting is far greater, however, because these estimates ignore all casualties from lethally wounded animals left unretrieved.

Discussion

Shifts in Vertebrate Community Structure

My study shows that game harvest can have a marked effect on the structure of Amazonian vertebrate communi-

ties largely because of selective overhunting, if not local extirpation, of large-bodied taxa (see also Peres 1990; 1996, 1999a). Vertebrate assemblages at forest sites exposed to increasingly heavier hunting pressure were dominated by small-bodied species, which accounted for a substantially lower crude biomass than did species in the two largest size classes. The enormous contribution to the game biomass of nonhunted sites made by large-bodied species, which are associated with long generation time and low fecundity, was clearly depressed at persistently hunted sites. Large vertebrates particularly sensitive to hunting, as inferred from large differences in population density between hunted and nonhunted areas, included large tinamous, Piping guan, curassows, trumpeters, white-lipped peccaries, tapirs, and all three genera of prehensile-tailed primates, but particularly woolly monkeys and spider monkeys (Peres 1999a). These trends are consistent with those found elsewhere in the Neotropics (Freese et al. 1982; Thiollay 1986; Glanz 1991; Silva & Strahl 1991; Bodmer 1995a).

Table 3. Mean (\pm SD) density and biomass of game vertebrates for each category of hunting pressure at 25 Amazonian forest sites.

Hunting pressure (n)	Overall game density (individual km^{-2})		Overall game biomass (kg km^{-2})	
	mean	SD	mean	SD
None (6)	227.6 ^a	92.4	723.7 ^b	156.4
Light (7)	264.9 ^a	76.0	723.1 ^b	260.0
Moderate (6)	234.0 ^a	79.0	431.1 ^c	113.9
Heavy (6)	237.4 ^a	23.2	247.2 ^d	85.1
All sites (25)	241.9	69.7	538.9	262.3
r^2		0.417		0.919
Hunting pressure, $F_{3,20}$		1.034		66.325 ^f
Forest type, $F_{1,20}$		11.917 ^e		46.808 ^f

^{a-d} Analysis of covariance, considering the effects of hunting pressure and forest types on game abundance, following transformation of density and biomass data (x) as $\log_e(x)$. Means that share letters in common do not differ significantly ($p < 0.05$) according to a Tukey multiple comparison test.

^e $p < 0.01$.

^f $p < 0.001$.

Table 4. Estimates of game vertebrate numbers and biomass harvested per year by the low-income rural population of Brazilian Amazonia.

Vertebrate species	Consumption rate ^a	No. of animals consumed ^b		Biomass harvested (tons)	
		minimum	maximum	minimum	maximum
Ungulates					
<i>Tayassu pecari</i>	0.6739	611,527	1,499,318	15,655.1	38,382.5
<i>Tayassu tajacu</i>	0.6083	551,949	1,353,248	11,039.0	27,065.0
<i>Mazama</i> spp.	0.3071	278,704	683,317	5,351.1	13,119.7
<i>Tapirus terrestris</i>	0.0523	47,422	116,269	6,070.0	14,882.4
Rodents					
<i>Cuniculus paca</i>	0.8055	730,886	1,791,959	5,700.9	13,977.3
<i>Dasyprocta</i> spp.	0.6649	603,312	1,479,177	2,171.9	5,325.0
<i>Myoprocta</i> spp.	0.0437	39,674	97,270	23.8	58.4
<i>H. hydrochaeris</i>	0.0927	84,094	206,179	1,345.5	3,298.9
<i>Sciurus</i> spp.	0.1422	128,991	316,256	61.9	151.8
<i>Coendou</i> spp.	0.0300	27,233	66,768	46.3	113.5
Lagomorphs					
<i>Sylvilagus brasiliensis</i>	0.0004	319	781	0.3	0.6
Primates					
<i>Alouatta</i> spp.	0.3429	311,143	762,850	1,617.9	3,966.8
<i>Ateles</i> spp.	0.2507	227,471	557,704	1,642.3	4,026.6
<i>Lagothrix lagotricha</i>	0.5621	510,057	1,250,539	3,555.1	8,716.3
<i>Cebus</i> spp.	1.0720	972,707	2,384,846	2,266.4	5,556.7
<i>Pithecia</i> spp.	0.0465	42,236	103,554	74.3	182.3
<i>Cacajao</i> spp.	0.0093	8,416	20,663	21.3	52.2
<i>Chiropotes</i> spp.	0.0347	31,532	77,308	68.1	167.0
<i>Callicebus</i> spp.	0.0404	36,640	89,833	30.8	75.5
<i>Aotus</i> spp.	0.0446	40,485	99,260	38.9	95.3
<i>Saimiri</i> spp.	0.0074	6,711	16,454	5.0	12.3
<i>Saguinus</i> spp.	0.0093	8,442	20,697	4.0	9.7
Edentates					
<i>Bradypus</i> spp.	0.0627	56,858	139,401	119.4	292.7
<i>Myrmecophaga tridactyla</i>	0.0131	11,851	29,056	71.1	174.3
<i>Tamandua tetradactyla</i>	0.0871	79,023	193,746	237.1	581.2
<i>Dasybus</i> spp.	0.6734	611,007	1,498,045	2,138.5	5,243.2
<i>Priodontes maximus</i>	0.0037	3,375	8,273	84.4	206.8
Carnivores					
<i>Nasua nasua</i>	0.3728	338,316	829,470	839.0	2,057.1
<i>Potos flavus</i>	0.0140	12,670	31,064	19.0	46.6
<i>Eira barbara</i>	0.0084	7,620	18,682	29.3	71.7
<i>Felis</i> spp.	0.0216	19,595	48,042	98.0	240.2
Total mammals	7.0977	6,440,266	15,789,999	60,425.7	148,149.7
Cracids					
<i>Crax/Mitu</i> spp.	0.2964	268,973	659,457	726.2	1,780.5
<i>Pipile cujubi</i>	0.1609	146,006	357,971	157.7	386.6
<i>Penelope</i> spp.	0.5425	492,241	1,206,857	566.1	1,387.9
<i>Nothocrax urumutum</i>	0.0082	7,409	18,166	17.8	43.6
<i>Ortalis</i> spp.	0.0148	13,420	32,903	5.0	12.2
Tinamids					
<i>Tinamus</i> spp.	0.2503	227,151	556,921	245.3	601.5
<i>Crypturellus</i> spp.	0.2522	228,811	560,989	86.9	213.2
Wood-quails					
<i>Odontophorus</i> spp.	0.0233	21,150	51,854	5.9	14.5
Trumpeters					
<i>Psophia</i> spp.	0.2256	204,739	501,972	221.1	542.1
Other game birds					
<i>Ara</i> spp.	0.0716	65,008	159,385	97.5	239.1
<i>Amazona</i> spp.	0.1335	121,164	297,065	72.7	178.2
<i>Cairina moschata</i>	0.0199	18,082	44,333	45.2	110.8
<i>Leptotila</i> spp.	0.3150	285,872	700,890	85.8	210.3
<i>Ramphastos</i> spp.	0.5358	486,173	1,191,982	243.1	596.0
<i>Pteroglossus</i> spp.	0.0237	21,487	52,682	6.4	15.8
<i>Ophistocomus boazin</i>	0.0038	3,470	8,507	6.9	17.0
Total birds	25.1653	22,834,269	55,984,193	145,249.8	356,117.9

continued

Table 4 (continued)

Vertebrate species	Consumption rate ^a	No. of animals consumed ^b		Biomass harvested (tons)	
		minimum	maximum	minimum	maximum
Testudines					
<i>Podocnemis expansa</i>	0.0652	59,149	145,019	1,774.5	4,350.6
<i>Podocnemis unifinis</i>	0.0428	38,793	95,111	310.3	760.9
<i>Chelus fimbriatus</i>	0.0025	2,300	5,639	11.5	28.2
<i>Geochelone</i> spp.	0.4459	404,634	992,065	1,820.9	4,464.3
Crocodylids					
<i>Melanosuchus niger</i>	0.0180	16,301	39,966	195.6	479.6
<i>Caiman</i> spp.	0.0098	8,891	21,799	44.5	109.0
Total reptiles	0.5842	530,068	1,299,599	4,157.2	10,192.5
Total all vertebrates	10.56	9,581,487	23,491,529	67,173.0	164,692.0

^aAverage annual per capita rate of game consumption based on data from 31 game harvest profiles from Amazonian Indian, caboclo, and colonist settlements (Redford & Robinson 1987; Martins 1992; Bodmer 1994; Calouro 1995; Muchagata 1997; Mena et al. 1999; Townsend 1999; C. Peres & H. Nascimento, unpublished data).

^bEstimates based on the total low-income rural population of Brazilian Amazonia (see text and Table 2). Minimum and maximum estimates are based on the total rural population from households with an aggregate monthly income value below 0.5 (<US\$49) and 1 BMS (<US\$98), respectively. Population sizes in marginal states of "Legal Amazonia" have been adjusted to account for areas falling outside the phytogeographic limits of the region.

Forest type is an important determinant of the patterns of abundance, diversity, and guild structure of Amazonian vertebrate communities (e.g., Peres 1997a, 1999b) and can be used as a good predictor of game abundance when considered in conjunction with hunting pressure. Game biomass in eutrophic forests was consistently greater than that of oligotrophic forests once the effects of hunting had been controlled for. This is remarkable given the substantial between-site heterogeneity in hydrological regimes, soil fertility, floristic composition, and forest structure caused by different regimes of natural disturbance (e.g., flooding regime, bamboo regeneration cycles, canopy gaps), all of which can account for some of the variation in vertebrate community structure in Amazonia (Janson & Emmons 1990; Terborgh et al. 1990; Peres 1999b).

These results stress the importance of incorporating the effects of forest types and productivity into the design of game management programs, which may emphasize only the demographic parameters of the target species that define game production and recovery potential in an average-quality habitat (e.g., Robinson & Redford 1991; Bodmer 1995b). For certain game species, physical distance to productive Amazonian habitats under the influence of major white-water rivers is actually a better predictor of population density than is hunting pressure per se (Peres 1997b). This suggests that although persistent hunting can drive populations of sensitive game species to local extinction even in the most productive habitats, extremely high levels of productivity can override the detrimental effects of game depletion at sites subjected to light or moderate hunting.

Socioeconomic Importance of Game Resources

Despite the widespread neglect of game populations in valuation studies of tropical ecosystems, it is clear that such "nontimber forest products" comprise a critical

subsidy from nature to tropical forest dwellers (Redford 1993). Indeed, the nutritional, social, psychological, and ritual importance of game resources is deeply entrenched in the culture of most tropical forest aborigines, who despite wide linguistic divergences often share common semantic references to a term meaning "craving for meat" (e.g., Garine & Pagezy 1990). A meal of any kind in many parts of rural Amazonia cannot be defined as such unless it is supplemented by game meat or fish. The availability of animal protein is also thought to be a critical environmental constraint to the size, distribution, density, cultural development, and permanence of indigenous settlements in lowland Amazonia (Gross 1975; Hames 1980; Vickers 1988), although this remains a controversial issue among anthropologists (Beckerman 1994).

Bushmeat often accounts for most of the animal protein consumed in small Amazonian villages, particularly where fish are scarce (e.g., terra firme forests drained by small clear-water streams) or difficult to catch (e.g., floodplain areas during the high-water season). The perceived value of the forest to indigenous peoples can therefore become considerably reduced as game populations become depleted or are driven to local extinction. Game depletion often generates an increasing demand for alternative sources of domesticated animal protein, which is grown mostly in newly created open habitats rather than under a closed-canopy forest. Indeed there is a widespread and growing pressure in overhunted forest landscapes of Amazonia to either raise domestic livestock locally or generate cash from other agricultural enterprises so that frozen (or chilled) beef from merchant "ice boats" (that are increasingly expanding their trade network) can be purchased. Such alternative sources of protein do not necessarily relieve wild vertebrate populations from persistent hunting pressure and contribute to the erosion of an important sociopolitical justification for maintaining the integrity of forest ecosystems.

Game Hunting versus Forest Disturbance

The Brazilian Amazon contains over one-third of the tropical forest remaining worldwide, much of which is still fairly remote. Until only a few decades ago, large-scale anthropogenic forest disturbance was relatively minor because access to most of the region was physically prohibitive and confined to a belt of forests not far from navigable rivers and settled by small, rural populations. Since the initiation of the federally funded highways program in the 1960s, access to new forest frontiers has increased enormously, but implementation of environmental legislation and enforcement of existing laws restricting resource extraction have failed to keep pace with the improved access.

On a large scale, signs of forest disturbance are most visible in areas converted to agriculture and pasture, fragmented forest mosaics, uncontrolled logging, mining operations, and hydroelectric dams (Skole & Tucker 1993). Compared to these patterns of structural habitat alteration, subsistence hunting is often viewed by policy makers and conservation organizations as a benign form of human disturbance, particularly because its detrimental effects are extremely difficult to detect at different spatial scales (Redford 1992). Indeed, identifying hunted but otherwise undisturbed tropical forest presents a difficult problem because hunting is a highly inconspicuous form of resource extraction that leaves few visible indicators of its occurrence. Game harvest should thus be seen as but one extreme of a graded continuum of anthropogenic forest disturbances that vary in the extent to which they are (1) detectable from space, (2) reversible, and (3) mediators of change to the entire ecosystem. This is reflected in current difficulties faced by international conservation organizations in distinguishing pristine tropical forests (i.e., nonhunted and structurally undisturbed) from those that have been defaunated to varying degrees but otherwise remain unaltered (e.g., Dinerstein et al. 1995; Bryant et al. 1997).

Game hunting is the single most geographically widespread form of resource extraction in Amazonia and can affect the core of even some of the largest and least accessible nature reserves (Peres & Terborgh 1995). No area accessible on foot within 10 km of the nearest navigable river or perennial stream is safe from hunting, particularly as firearms, ammunition, and outboard motors become increasingly affordable. Moreover, even if the political will were in place, enforcing restrictions on game harvest is largely impractical because hunting is a highly diffuse and undetectable form of resource extraction practiced on a small scale by millions of Amazonians.

Finally, the pervasive changes in vertebrate community structure associated with game hunting are clearly becoming more severe and widespread in Amazonia as (1) rapid rural population growth places heavier demands on game resources; (2) changes in land-use patterns degrade prime forest habitat, particularly for spe-

cies averse to second growth, small forest isolates, and forest edges (Robinson 1996); (3) changes in transport and weapon technology increase hunter mobility and game mortality over larger catchment areas (e.g., Yost & Kelley 1983); (4) increased integration into the market economy encourages sales of salted and smoked meat surpluses, thus blurring the distinction between subsistence and commercial hunting (Hart 1978); and (5) traditional practices break down, eliminating folklore, myths, and taboos that once served to protect forest wildlife.

Deleterious effects at the population or community level that may result from persistent game hunting will therefore be widespread and extremely difficult to control. Protecting wildlife within strictly protected nature reserves thus emerges as one of the few available mechanisms for preventing large vertebrate extirpation, at least in Amazonia. Other measures designed to safeguard the viability of sensitive game populations should rest on (1) the creation of game sanctuaries within indigenous and extractive reserves, which could serve as adjacent "source" areas for recolonization of overhunted "sinks," and (2) compliance with sustainable hunting practices through appropriate quota systems and hunting seasons, which could be enforced by either community-based managers or outside inspectors. The short-term opportunity costs of deliberate restraint should be far outweighed by the long-term benefits of a sustainable harvest (e.g., Bodmer 1994). Although much of the technical practicalities of sound game management are yet to be refined for tropical forests, these strategies are our best hope for reversing the widespread depletion or deletion of a set of species that may have a disproportionate influence on the overall forest dynamics and collectively may represent truly undisturbed forests.

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