
Extent of Nontimber Resource Extraction in Tropical Forests: Accessibility to Game Vertebrates by Hunters in the Amazon Basin

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Abstract: Extractive activities targeting a wide range of nontimber forest products (NTFPs) are ubiquitous in tropical forests, yet the extent of structurally intact forests in a given region affected by this form of cryptic disturbance is poorly documented. We conducted a basin-wide geographic information system analysis of the nonmotorized accessibility of Amazonian NTFP extraction and estimated the proportion of the Amazon drainage basin within Brazil (3.74 million km²) that can be accessed on foot from the nearest navigable river or functional road. We use a long-term series of standardized line-transect vertebrate censuses conducted throughout the region to illustrate the effects of physical accessibility on wildlife densities in terms of hunting pressure as a function of distance from the nearest point of access. Population abundance in large-bodied, prime-target species preferred by game hunters tended to increase at greater distances from the access matrix, whereas small-bodied species ignored by hunters usually showed the reverse trend. In addition, we estimated the proportion of presumably inviolate core areas within nature, extractive, and indigenous reserves of Brazilian Amazonia that are prohibitively remote and unlikely to be overhunted; for instance, only 1.16% of the basin-wide area is strictly protected on paper and is reasonably safe from extractive activities targeted to game vertebrates and other valuable NTFPs. Finally, we discuss the concept of truly undisturbed wildlands in the last major tropical forest regions by distinguishing potentially overharvested areas from those that remain largely or entirely pristine and that maintain viable populations of a full complement of harvest-sensitive species.

Alcance de la Extracción de Recursos no Maderables en Bosques Tropicales: Acceso a Vertebrados de Caza por Cazadores en la Cuenca del Amazonas

Resumen: Las actividades de extracción enfocadas en un amplio rango de productos forestales no maderables (NTFPs) son omnipresentes en los bosques tropicales. Sin embargo, la extensión de bosques estructuralmente intactos en una determinada región afectada por esta forma de perturbación criptica ha sido escasamente documentada. Realizamos un análisis GIS del acceso no motorizado para la extracción NTFP en el Amazonas y estimamos la proporción de la desembocadura de la cuenca amazónica (~3.74 millones de km²) a la cual se puede acceder a pie a partir del río navegable o la carretera funcional más cercana. Utilizamos series de censos de vertebrados a largo plazo empleando transectos en línea estandarizados a lo largo de la región para ejemplificar los efectos del acceso físico sobre las densidades de vida silvestre en términos de presión de caza como función de la distancia al punto de acceso más cercano. La abundancia poblacional de especies de cuerpo grande que son blancos preferidos por los cazadores tendió a crecer a mayores distancias de la matriz de acceso, mientras que las especies de cuerpo pequeño ignoradas por los cazadores generalmente muestran la tendencia inversa. Además, estimamos la proporción de áreas medulares presuntamente inviolables dentro de las reservas naturales, extractivas e indígenas del Amazonas brasileño que son prohibitivamente remotas y poco probables de ser sobreexplotadas: por ejemplo, solo el 1.16% del área de la cuenca estrictamente proyectada en papel está razonablemente a salvo de las actividades extractivas de los vertebrados de caza y otras NTFPs valiosas. Finalmente, discutimos el concepto de tierras silvestres verdaderamente

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no perturbadas en las grandes regiones de bosque tropical restantes diferenciando las áreas potencialmente sobreexplotadas de aquellas que son en su mayor parte o totalmente prístinas y que mantienen poblaciones viables de un complemento total de especies sensibles a la cosecha.

Introduction

Many tropical nature reserves are lamentably understaffed, lack the necessary financial resources and infrastructure for conservation, and exist only on paper. Although protected areas that have been delineated on the map, rather than effectively implemented, can be protected from habitat loss (Bruner et al. 2001), many population-level threats to biodiversity may continue to affect them. These include a wide range of illegal extractive activities such as selective logging, fishing, and harvest of forest vertebrates, medicinal plants, and other nontimber plant products for either subsistence or commercial purposes (Kramer et al. 1997). Other detrimental effects arising from virtually undetectable human use include displacement of wildlife from desirable habitat, accidental surface fires, chemical pollution, and introduction of exotic species and pathogens.

The weak institutional capacity of national environmental agencies can be further aggravated by reserve-design considerations that facilitate rather than discourage unlawful human incursions into protected areas (Peres & Terborgh 1995). From a landscape perspective, poorly designed reserves may include those with an insufficient core area of undisturbed primary habitat, high perimeter-to-area ratios, poor overall connectivity between primary habitats, and a biased mosaic of the original landscape, where crucial habitat types have been left unprotected. From a defensibility perspective, long-term biological integrity may be compromised in poorly implemented reserves containing multiple entry points left unguarded along public means of access, such as rivers and roads. These can be compounded by human enclaves that continue to deplete or degrade natural resources and extractive settlements that have free access to reserve boundaries, whether or not they are shielded by a buffer zone (Terborgh & Peres 2001).

Gradients of human disturbance often have nonlinear or threshold effects on species and ecosystems depending on convenient means of physical access (Gill et al. 1996). Physical access depends on factors such as remoteness, topographic barriers, availability of transport systems, and overland and waterway conveyances. In lowland forest regions, reserve core areas beyond a given distance from the fluvial and road network are more likely to have passive protection from human use even in the absence of strictly enforced regulation. Accessible areas could thus function as demographic sinks for har-

vest-sensitive target species, just as core areas immune to human disturbance could serve as sources. However, this would depend largely on the life history, metapopulation dynamics, and subsistence value of the resource population, and the intensity and spatial structure of the harvest activity (e.g., Joshi & Gadgil 1991; Novaro et al. 2000).

Because of the high subsistence or commercial value of bushmeat, forest vertebrates are one of the most important and ubiquitously harvested nontimber forest products (NTFPs) in the tropics (Redford 1992; Robinson & Bennett 2000). For example, the market value of wildlife meat harvested by the zero-income rural population of Brazilian Amazonia, estimated at some U.S. \$191 million/year, is second only to that of timber (Peres 2000a). Forest extractivists wielding guns often operate within the boundaries of poorly defended conservation areas if they have free access to NTFPs, which, on average, are more abundant in protected areas than in unprotected areas. In the case of large vertebrates, this occurs if poachers are either unaware of hunting restrictions or run little or no risk of being penalized (Leader-Williams & Albon 1988). In Amazonian forests, hunting is one of the most important causes of large-vertebrate population decline in areas that otherwise remain undisturbed, whether or not they are formally protected (Peres 2000a, 2000b). Hunting is often the most important threat to wildlife even in forests affected by selective logging (Thiollay 1989), fragmentation (Peres 2001:225), and understory fires (Barlow et al. 2002). Indeed, local park authorities often report that hunting is one of the greatest threats to their conservation areas (Peres & Terborgh 1995; Sá et al. 2000).

Levels of hunting pressure within reserves are largely a function of active protection resulting from effective law enforcement, or passive protection due to prohibitive physical access. This argument holds for both game vertebrates and other classes of NTFPs harvested during incursions on foot by millions of tropical-forest dwellers worldwide, including fruits, seeds, lianas, fibers, resins, gums, spices, dyes, elastic and nonelastic latex, palm-hearts, and medicinal plants (Richards 1993; Peters 1994; Emperaire & Lescure 2000). Although the negative demographic effects of such harvest practices remain unclear, they are likely to be aggravated by the burgeoning human populations currently inhabiting the world's biodiversity hotspots (Cincotta et al. 2000). This is particularly the case for tropical regions such as Amazonia that re-

main largely exposed to unregulated exploitation of forest resources.

Nontimber extractive activities under the forest canopy cannot be readily detected over large spatial scales with conventional remote-sensing techniques. The unknown extent and intensity of such cryptic disturbance has therefore bedevilled attempts to monitor the integrity of apparently intact forest ecosystems (Bryant et al. 1997; Groombridge & Jenkins 2000). Yet NTFP extraction may spell the distinction between truly undisturbed areas characterized by a full complement of biological diversity and those that have already been degraded by local extinctions of harvest-sensitive species resulting from a long history of overexploitation.

We approached the issue of nontimber extractive disturbance by examining the extent of the Amazon basin and its protected areas that are accessible to forest dwellers on foot. We then used field data from hunted survey sites to show the effects of accessibility on the abundance of large-bodied vertebrates, a prime example of frequently harvested NTFPs. We also estimated the potential levels of game depletion within protected areas. Finally, we assessed the discrepancy between potential and realized

accessibility by considering the rural human population density within and outside protected areas in order to identify which reserves are most vulnerable to unregulated resource depletion.

Methods

Study Area

Our study area was the entire drainage basin of the Amazon River within Brazil (Fig. 1a). This encompasses some 3.7 of the 6 million km² of the entire Amazon Basin, which excludes the drainage areas of the Rio Tocantins, Rio Araguaia, and smaller catchments that may be part of "Legal Brazilian Amazonia" (5×10^6 km²) but do not contribute to the Amazon discharge. The Amazonian part of the states of Maranhão and Tocantins and large parts of eastern Pará, eastern Amapá, and northern Mato Grosso were thus excluded. In any case, many parts of these regions have been deforested and can no longer support NTFP extraction.

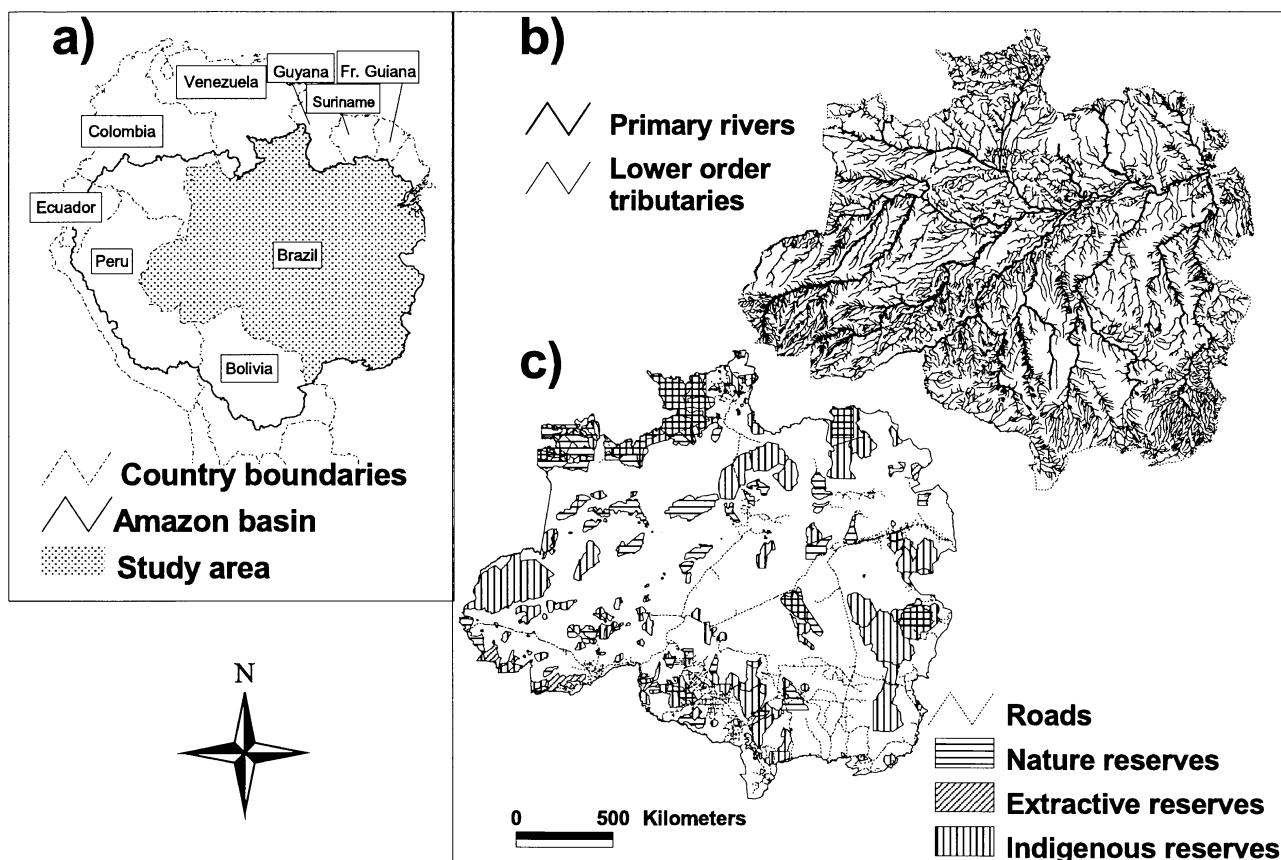


Figure 1. Study region showing (a) the Amazon drainage basin within Brazil (shaded area) and (b) its navigable river network. Hatched polygons and dotted lines (c) indicate the basin-wide geographic distribution of reserves and roads, respectively. Boundaries between contiguous conservation units may not be shown in every case.

Basin-Wide Accessibility

We used a geographical information system (GIS) to evaluate the extent to which Amazonian forests are potentially harvested by forest dwellers on foot, given feasible means of access from the nearest navigable river or road. The locations of all perennial rivers were extracted from the Digital Chart of the World (DCW), which is derived from mapping at a scale of 1:1,000,000 (Fig. 1b). This fluvial network was cross-referenced with high-resolution Landsat images and reprocessed at the remote-sensing lab of the University of São Paulo at Piracicaba, Brazil, to enhance its consistency and positional accuracy. The network included rivers up to fourth-order tributaries of the Amazon, thus excluding thousands of lower-order, subcanopy perennial and seasonal streams. Moreover, the linear fluvial network we used only took into account the visible river channels, thus excluding the small-scale sinuosity of rivers and extra-channel areas, such as riparian zones, extensive floodplains of large rivers, and other backwater forms of access such as lakes, *levees*, and *paranás*. All these factors ensured that the river network we considered provided a conservative estimate of overall accessibility.

Human access to and disturbance in remote areas tends to increase with higher road density. The locations of existing all-weather primary roads and secondary dirt roads (including highways and all unpaved roads that permit motorized traffic) were taken from a 1995 map of legal Amazonia (1:3,000,000 scale; Instituto Brasileiro de Geografia e Estatística [IBGE] 1995; Fig. 1c). We excluded an unknown number of narrow, precarious, unpaved roads that are lightly travelled by local peoples on bicycles, carts, and other nonmotorized vehicles but that effectively dissect many remote interfluvial areas, which again underestimates the potential accessibility to NTFPs.

We combined the river and road data sets to produce an overall digital map of access points. We then assessed the potential accessibility of the entire Brazilian Amazon Basin within ArcInfo GIS by calculating the distance from the nearest access point in 1-km bands. In particular, we calculated the total areas within a walking radius of 9 km from the nearest point of access. This provides an appropriate estimate of total accessible areas, because extractive activities targeted to valuable NTFPs in Amazonian forests become increasingly prohibitive beyond this 9-km distance threshold from the nearest village or active household (A. Jerozolimski & C.P., unpublished review).

We used a land-cover map, based on 1993 Advanced Very High Resolution Radiometer (AVHRR) imagery and classified according to the South America seasonal land-cover regions (U.S. Geological Survey 2001), to exclude all areas that were originally unforested or had been recently deforested. This map was reclassified into a secondary map of forested and unforested areas based on main vegetation types and personal knowledge.

Our analysis then focused on the accessibility of con-

servation areas within officially recognized boundaries of all strictly protected areas (SPAs) and extractive and indigenous reserves obtained from the IBGE (1995) map of Brazilian Amazonia, which was updated to include more recent reserves (Fig. 1c). The SPAs included nature reserves under different tiers of government administration, including national parks, biological reserves, and ecological stations. Extractive reserves were defined as those in which nontimber exploitation is legally permitted and included extractive reserves and sustainable-development reserves under state management. To this functional group we added the national forests, which are officially designated for sustainable forestry initiatives but in many ways converge with extractive reserves. We also included indigenous reserves comprised of Indian lands, Indian areas, and other officially recognized categories of indigenous territories (Ricardo 1999). We then evaluated the degree of access to all conservation areas by juxtaposing the reserve boundaries with the potential accessibility map of the Amazon Basin.

Effects on Vertebrate Abundance

Wildlife population-density estimates were based on a standardized series of diurnal line-transect censuses of mid-sized to large-bodied vertebrates undertaken over 14 years (1987–2000) at 30 Amazonian forest sites. Although over 100 species weighing at least 150 g have been recorded, we focused on only 25 vertebrate taxa that are amenable to line-transect surveys (Table 1). Abundance estimates for nocturnal mammals were excluded from this analysis because night surveys were carried out at only a few sites.

Survey sites that had been subjected to hunting for at least three decades prior to surveys were assigned to one of three broad classes of hunting pressure—light, moderate, and heavy—on the basis of semistructured interviews with hunters who had resided at each site for at least 2 years. Interviews were designed to assess the frequency, intensity, and species selectivity of game-harvest practices in each study area, the human population density at the time of the surveys and in past decades, and the number and spatial distribution of active households, which were cross-referenced with 1:250,000 RADAM charts (Peres 2000a).

Wildlife surveys at each site were conducted along two to four transects of between 4500 and 5000 m, which were cut and marked every 50 m and left undisturbed for 1 day before census walks were initiated. Each transect was walked for 13 to 15 consecutive days without rain, usually within a period of 1 month, and all target species were recorded following visual and/or acoustic detection (Peres 1999).

We evaluated how distance from the nearest points of physical access available to hunters on foot affected wildlife abundance within 500-m sections of 45 transects surveyed at 21 forest sites subjected to either moderate

Table 1. Characteristics of species of Amazonian forest vertebrates and the effects on their abundance of distance from the hunter-access network.

<i>English common name</i>	<i>Scientific name</i>	<i>Body mass (kg)</i>	<i>Hunter preference^a</i>	λ^b	r_s^c	p^c
Wood Quail	<i>Odontophorus</i> spp.	0.3	0	1.80	-0.891	0.001
Small Tinamou	<i>Crypturellus</i> spp.	0.4	1	1.90	-0.248	0.489
Great Tinamou	<i>Tinamus</i> spp.	1.2	3	1.50	-0.648	0.043
Trumpeter	<i>Psophia</i> spp.	1.2	2	1.30	0.612	0.060
Common Guan	<i>Penelope</i> spp.	1.3	3	1.49	-0.139	0.701
Razor-billed and other curassows	<i>Mitu tuberosa/Crax</i> spp.	3.0	4	1.47	0.624	0.054
Bolivian squirrel	<i>Sciurus ignitus</i>	0.2	0	3.60	-0.673	0.033
Red Amazon squirrel	<i>Sciurus spadiceus</i>	0.6	1	3.50	-0.952	0.000
Acouchy	<i>Myoprocta</i> spp.	0.8	0	3.00	-0.648	0.043
Agouti	<i>Dasyprocta</i> spp.	4.0	3	3.00	-0.879	0.001
Coati	<i>Nasua nasua</i>	3.1	1	1.26	0.212	0.556
Saddle-back tamarin	<i>Saguinus fuscicollis</i>	0.4	0	1.35	-0.842	0.002
Moustached tamarin	<i>Saguinus mystax</i>	0.5	0	1.35	-0.673	0.033
Squirrel monkey	<i>Saimiri</i> spp.	0.9	0	1.28	-0.770	0.009
Dusky/red titi monkey	<i>Callicebus cupreus/moloch</i>	1.1	0	1.26	-0.650	0.058
Collared titi monkey	<i>Callicebus torquatus</i>	1.2	0	1.26	-0.850	0.004
Saki monkey	<i>Pithecia</i> spp.	2.2	2	1.18	-0.685	0.029
White-face capuchin	<i>Cebus albifrons</i>	2.7	2	1.18	0.600	0.088
Brown capuchin	<i>Cebus apella</i>	2.9	3	1.15	-0.336	0.312
Howler monkey	<i>Alouatta</i> spp.	6.5	3	1.17	-0.806	0.005
Woolly monkey	<i>Lagothrix lagotricha</i>	8.7	4	1.15	0.915	0.000
Spider monkey	<i>Ateles</i> spp.	9.0	4	1.08	-0.467	0.174
Collared peccary	<i>Tayassu tajacu</i>	25.0	4	3.49	0.939	0.000
Red/gray rocket deer	<i>Mazama</i> spp.	30.0	4	1.49	-0.079	0.829
Lowland tapir	<i>Tapirus terrestris</i>	160.0	4	1.22	0.903	0.000

^aDegree of hunter preference on a scale of 0 (always ignored) to 4 (never ignored).

^bMaximum finite rate of population increase.

^cSpearman correlation coefficients between overall detection rate per unit of census effort within 500-m sections of transects and distance from the access matrix.

or heavy hunting pressure. This amounted to a cumulative census effort of 2753 km conducted over 576 census walks. To control for possible habitat effects of river edges, the origin of all transects accessed via rivers was placed 250–300 m away from the river bank, and transects were cut perpendicularly to the main axis of the river channel. These rivers were navigable for at least dugout canoes and small motorized boats used by local extractivists. Line transects thus penetrated increasingly inaccessible areas farther inland from the nearest point of access used by subsistence game hunters on foot. Only three transects began near unpaved roads that were occasionally traveled by nonmotorized hunters (on bicycles), but these also penetrated increasingly inaccessible terra firme forest areas.

To control for slight differences in census effort along transects, we transformed numbers of species-specific detection events within each 500-m transect segment into a mean detection rate per cumulative distance walked within each section of all transects. This was necessary because transect length (4.5–5.0 km) was variable and census walks were occasionally aborted prior to the end of the transect because of unfavorable weather; 10 segments across all transects thus defined increasingly distant accessibility zones, which were used to evaluate distance effects on local species abundance. Detection

rates for all social species are presented as the number of groups (rather than individuals) detected per 10 km walked because there is no evidence that differences in hunting pressure along transects at any given site affect the group size of the social species surveyed. Further details on the forest sites sampled and data analysis are provided by Peres (1999, 2000a).

The 25 vertebrate taxa we examined were classified according to (1) dietary class, (2) degree of preference for forest habitat along major rivers, and (3) degree to which they are preferred by local subsistence hunters in lowland Amazonia. In addition, the adult body mass and finite rate of population increase (λ) of each game species was obtained from the literature as a measure of body size and maximum reproductive rate, respectively. These variables were then related to the effects of accessibility on the abundance of each species along transects in hunted areas.

Effects of Accessibility within Protected Areas

To assess the significance of potential hunter access to protected game stocks, we estimated the relative decline in wildlife population sizes across reserves that would be predicted if our distance-abundance relationships became ubiquitous throughout the Brazilian Amazon. We

achieved this by applying these relationships to each of the six animal taxa showing a positive distance response to estimate the proportion of a population size within a reserve that would be lost at 1-km intervals, up to and including 6 km, from the combined river and road networks. Other species were either unaffected or detrimentally affected by increasing isolation from fluvial and road access. We then calculated the relative change in animal numbers resulting from incursions by game hunters by taking the midpoint of each distance zone and estimating the overall percentage decline on the basis of the observed abundance-distance functions.

In the interest of simplicity, we assumed that population sizes within reserves were not affected by hunting beyond 6 km from the access network. This core reserve area would presumably maintain populations that would remain unaffected by demographic sinks. With the exception of lowland tapir (*Tapirus terrestris*), for which the impact of game harvest extended well beyond the 6- to 7-km buffer zone, this appears to be a reasonable assumption. The rates of decline for this species were thus likely to be underestimated.

Because data on the usage intensity of the access network are unavailable, our analysis is based solely on the locations of rivers and roads. We assumed, however, that the discrepancy between the potential and realized threats of accessibility to protected areas is a function of the rural population density in a region. We therefore overlaid the boundaries of all municipal areas in Brazilian Amazonia (IBGE 2000) with those of existing reserves. We used an area-weighted average to estimate the mean rural population density for each protected area because data on human population density within and around the boundaries of each reserve were unavailable. The estimates were based on the most recent Brazilian national census (IBGE 2001). Given that data on the spatial distribution of active extractive households are also unavailable at this scale, mean rural population density is likely to provide the best, albeit crude, measure of local extractive pressure on NTFPs. However, some of the mean population densities are based on large municipal areas partly or entirely enclosed within the Brazilian Amazon basin (mean = $20,034 \pm 25,584 \text{ km}^2$; range = $609\text{--}166,343 \text{ km}^2$, $n = 197$), and local residents may not always represent permanent users of a given reserve.

Results

Basin-Wide Accessibility

Most of lowland Amazonia is potentially accessible on foot mainly via its extensive dendritic and sinuous river network consisting of thousands of lower-order streams. The total of 235,495 km of rivers dominated the access network, whereas the 31,917 km of roads represented

only 11.9% of the network. This resulted in an average density of navigable rivers and roads of 0.0714 km/km^2 , or 71 m of access routes for each square kilometer of the Brazilian Amazon Basin. Most of the protected and unprotected area across the region can be reached on foot, and the total inaccessible area declined exponentially as a function of walking radius (Fig. 2). If the entire basin was considered, 64.7% of the total area of nearly $3.74 \times 10^6 \text{ km}^2$ fell beyond a 3-km buffer from the nearest point of access, but this proportion declined to 50.7% if only the basin area under forest cover was considered. The total area beyond a walking radius of 9 km was 24.3% of the entire basin and 19.7% of the basin-wide forest cover.

The total conservation area of any denomination covered approximately $1.4 \times 10^6 \text{ km}^2$, or approximately 38.0% of the Brazilian Amazon Basin (Fig. 2). Over two-thirds (69.7%) of this total area fell beyond a 3-km distance that can be easily reached on foot from nearby rivers or roads, and this proportion declined to 57.2% when only the forest area within any reserve category was considered. However, only 11.1% of the aggregate area of all indigenous, extractive, and nature reserves fell beyond 9 km from any access point, and this area was further reduced to 9.4% when only the reserve forest cover was considered. Moreover, when we considered only the 3.8% of the basin represented by SPAs, only $43,485 \text{ km}^2$ of the entire region fell beyond this 9-km threshold. Therefore, only 1.16% of the total basin-wide area is both strictly protected on paper and reasonably safe from potential extractive activities targeted to game vertebrates and other valuable NTFPs.

The exponential decline in inaccessible area at increasing distances from rivers and roads was steeper for the

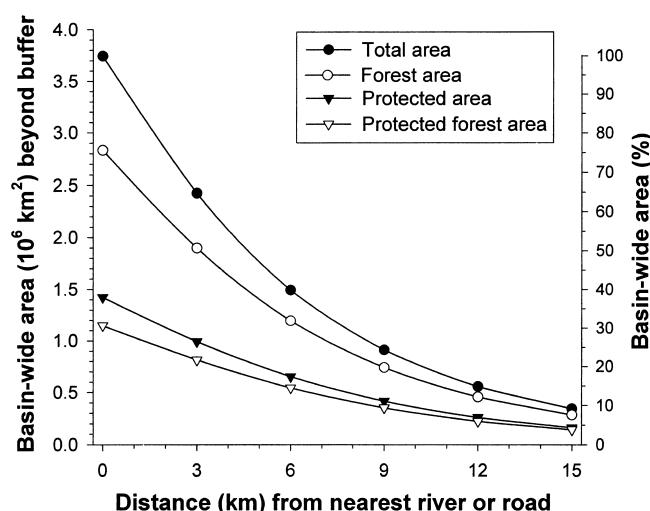


Figure 2. Total core forest area in the Brazilian Amazon basin that remains inaccessible as a function of straight-line distances from the nearest point of access.

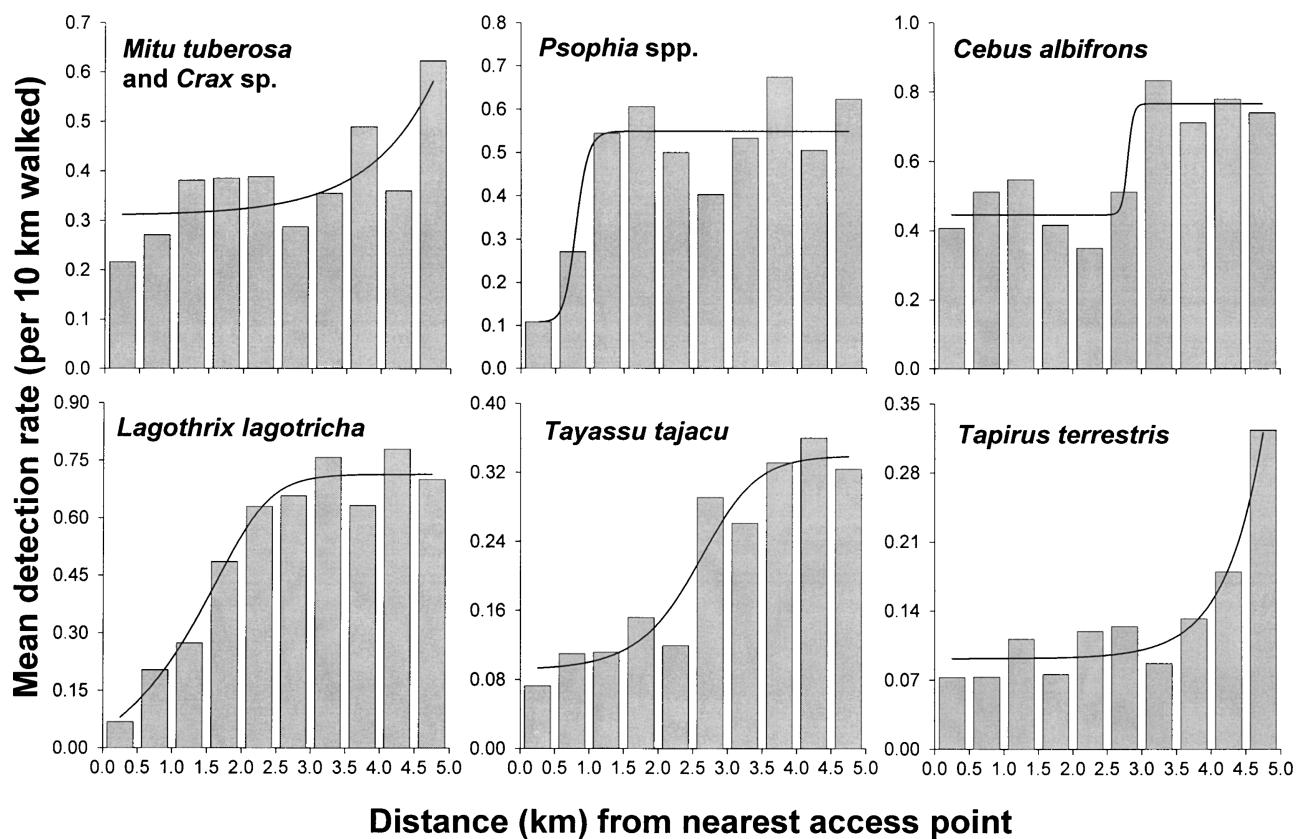


Figure 3. Examples of vertebrate game species (or functional groups) showing strong positive relationships between local population abundance and distance from the access matrix.

Amazon Basin as a whole than for all conservation areas combined (Fig. 2). This suggests that the aggregate forest area under any degree of protection is less physically accessible to forest extractivists than the larger matrix of unprotected areas under public jurisdiction and communal or private ownership.

Accessibility and Vertebrate Abundance

The relationship between local wildlife abundance and distance from the nearest points of access varied across species. Several species (or functional groups) showed markedly higher densities at increasingly greater distances from the nearest river or road (Fig. 3). In four out of six cases, these positive relationships were best represented by a sigmoid function that eventually tapered off beyond a given threshold distance (<5 km) from the access network. These critical distances, which presumably describe a partial or complete release from human hunting pressure, ranged between approximately 1500 m for trumpeters to over 5000 m for tapirs (Table 2; English names given in Table 1). Given the levels of hunting pressure in our survey sites, transects of 5 km thus appeared to be sufficiently long to capture the asymptotic relationships between accessibility distance and the local abundance of most vertebrate species marked by a positive response.

The abundance of most species surveyed, however, showed either a strong negative relationship (Fig. 4) or no discernible relationship with hunting range (Table 1). The sign and strength of distance-dependent responses on the local abundance of different species were largely

Table 2. Potential effects of hunter access in protected areas of Brazilian Amazonia for game species showing higher local abundance at greater distances from rivers and roads.

Game species	Threshold distance (km) ^a	Core population (%) ^b		
		SPA	IR	entire basin
<i>Psophia</i> spp.	1.5	92.0	90.9	89.7
<i>Mitu tuberosa</i> and <i>Crax</i> spp.	>5.0	75.8	73.4	70.9
<i>Cebus albifrons</i>	3.0	88.1	86.8	85.3
<i>Lagothrix lagotricha</i>	3.2	86.8	85.1	83.3
<i>Tayassu tajacu</i>	4.0	80.6	78.6	76.1
<i>Tapirus terrestris</i>	>5.0	63.2	59.6	56.0

^aMinimum distance from the access matrix at which local populations were apparently released from hunting pressure in the forest sites surveyed.

^bPercentage of population sizes in all strictly protected areas (SPA), indigenous reserves (IR), and the entire Amazon Basin that would remain unaffected by game harvest given the species-specific release function in relation to the access matrix, as documented in this study.

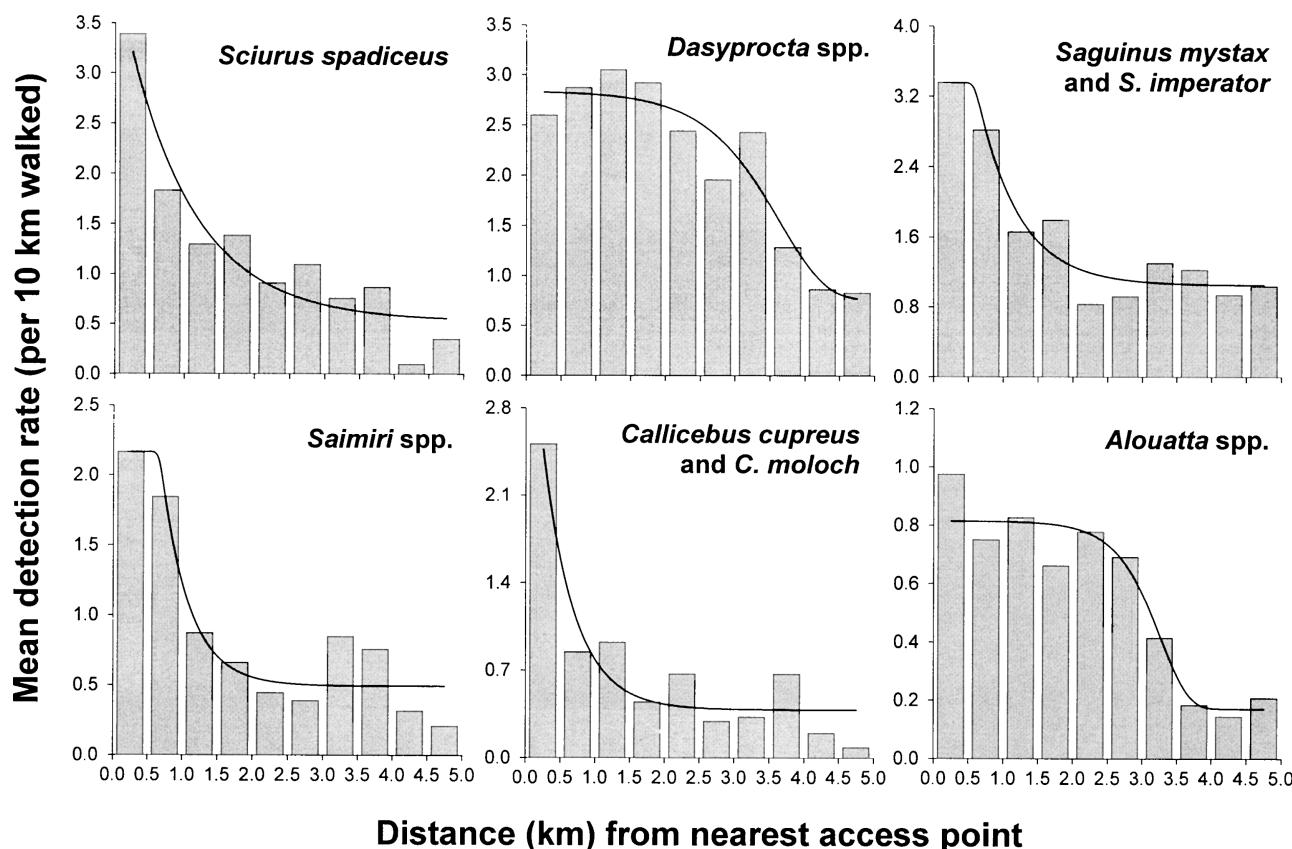


Figure 4. Examples of vertebrate game and nongame species (or functional groups) showing strong negative relationships between local population abundance and distance from the access matrix.

determined by the degree of preference of game hunters, species body mass, and dietary class. Susceptible game species showing a positive relationship included large-bodied birds and mammals preferred by subsistence hunters, such as Razor-billed Curassows, trumpeters, white-faced capuchin monkeys, woolly monkeys, collared peccaries, and lowland tapirs. A multiple-regression model including all species variables explained 53% of the variance in the Spearman correlation coefficient (r_s) between overall detection rate and distance from the nearest river

or road (Table 3). The finite rate of increase (λ) and preference of different species for alluvial and floodplain forests had little effect on the overall abundance-distance relationship and were thus excluded from the model through a backward-elimination procedure.

Small-bodied species ignored by game hunters, such as large squirrels, saddle-back tamarins, and squirrel monkeys, typically showed abundance declines in areas increasingly farther from the access matrix. However, some mid-sized to large-bodied game species showed a fairly clear

Table 3. Multiple-regression model^a of the effects of vertebrate species traits on the relationship between local population abundance and distance from the access network in hunted areas.^b

Variables	Regression coefficient	SE	Standardized coefficient	Tolerance	df	F	p
Retained							
adult body mass	0.238	0.111	0.572	0.314	1	4.615	0.044
hunter preference	0.162	0.103	0.404	0.338	1	2.478	0.130
dietary class	0.441	0.186	0.458	0.596	1	5.617	0.027
Removed							
riparian habitat selection	-0.286	—	—	0.893	1	1.776	0.198
lambda (λ)	0.155	—	—	0.827	1	0.492	0.491

^a $r = 0.730$; $r^2 = 0.533$, $n = 25$.

^bDefined as the nonparametric correlation (r_s) between number of detection events per unit of census effort and distance from the nearest point of access (see text).

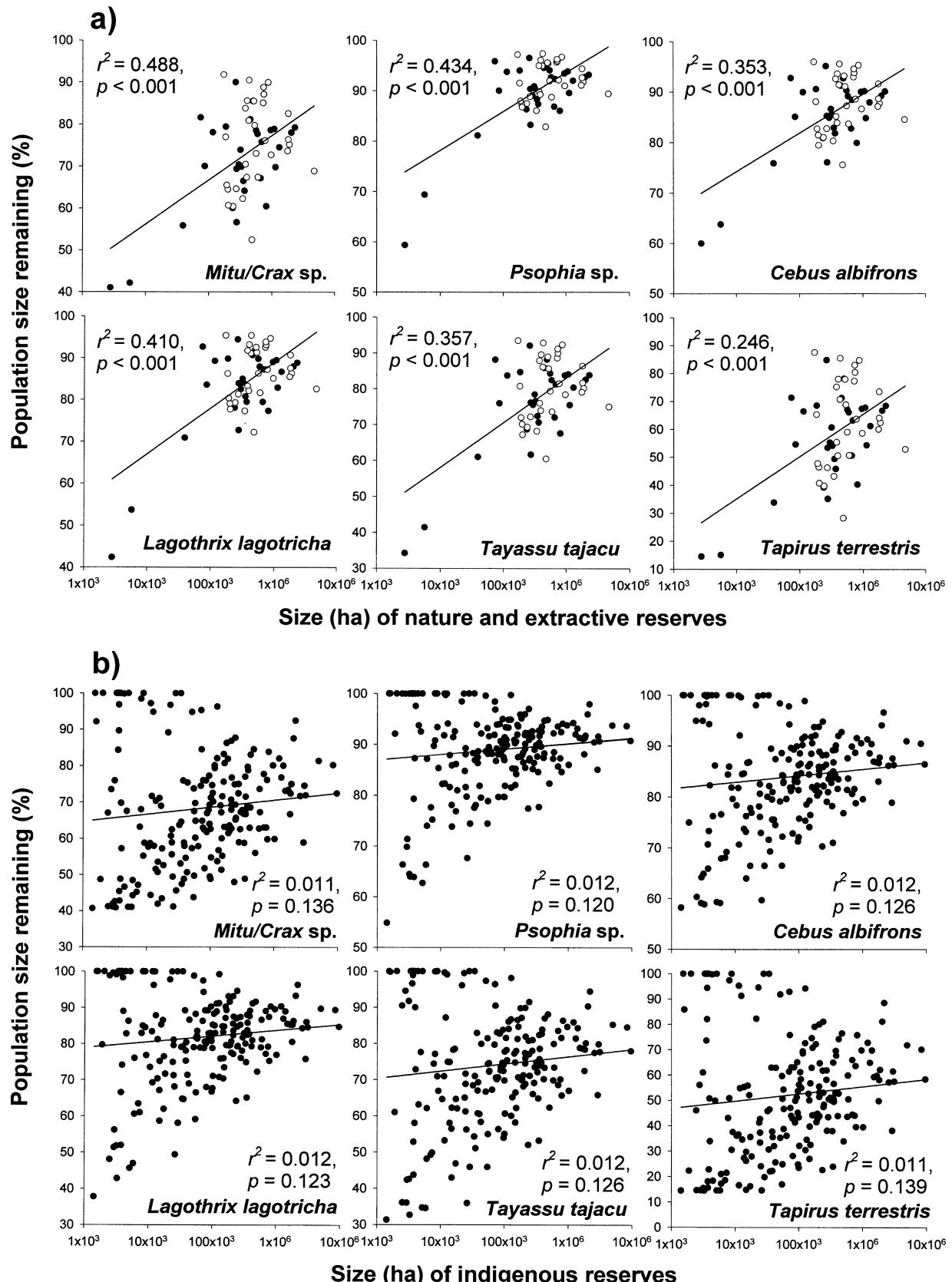


Figure 5. Relationships between the size of (a) 59 nature and extractive reserves and (b) 198 indigenous reserves in Brazilian Amazonia and the relative reduction in reserve population sizes for different harvest-sensitive species within areas accessible on foot, assuming a 6-km radius from the nearest point along navigable rivers and/or functional roads.

negative distance response, partly because of their strong preference for riparian and floodplain forests. These species may also be common in adjacent terra firme forest under some influence of fluvial dynamics. This was the case for howler monkeys and agoutis, which became rarer in more remote areas where hunting pressure was presumably lower. The regression model clearly indicated, however, that the overall effects of habitat selection were far outweighed by those of species body mass and hunter preference, even though rivers may boost forest productivity for some species.

Effects on Wildlife within Protected Areas

The potential impact of hunting was dependent on the species considered should observed abundance/distance relationships eventually become ubiquitous across the entire region (Table 2). For example, trumpeters, which are either ignored by hunters or rapidly recover at increasing distances from access points, are least affected along the accessibility gradient and may lose only 10% of their basin-wide population size. However, a similar scenario would deplete at least 44% of all tapirs across the Amazon basin because this species is strongly affected within 6 km of an access point. Core populations in SPAs and indigenous reserves that were unaffected by hunting were larger than core populations across the entire basin (Table 2), again suggesting that reserves (and particularly SPAs) are on average less accessible than the wider unprotected forest matrix.

The size of core populations showing a positive distance response was expected to increase in large reserves because these areas are more likely to have fewer access points and thus offer greater passive protection from extractive activities. We examined this possibility by estimating the relative size of core populations for each SPA and extractive and indigenous reserve and then plotting the predicted values against reserve size.

Although few SPAs and extractive reserves were surveyed, there were positive relationships between reserve size and the percentage of the population of each game species that was safe from hunting (range of $r^2 = 0.25$ –0.49; Fig. 5a). However, the line intercepts were lower for tapir, woolly monkey, collared peccary, and curassow, indicating that small nature reserves, given their present geographic position, were more likely to expose a larger proportion of these populations than populations of trumpeter and white-face capuchin monkey. Large reserves were thus particularly important for large-bodied species such as tapirs, which were greatly affected by hunting several kilometers inland from the nearest access points. In contrast, reserve size was least important for trumpeters and those species least sensitive to hunting, which thus showed a negative distance response.

A similar pattern emerged for the more numerous indigenous reserves, although the overall effect of reserve

size decreased (Fig. 5b). Several small indigenous reserves were relatively inaccessible, protecting virtually 100% of their core populations because they were far from rivers or roads. Large reserves tended to protect large core populations, whereas small reserves ranged widely in the degree to which their wildlife populations were vulnerable to hunters. Therefore, the density of access points within existing indigenous reserves did not necessarily increase with decreasing reserve size. Target species were not necessarily safe from hunting by legal indigenous occupants, however, who are often less constrained by the access matrix.

For the threat of hunter access to large tracts of nominally protected areas to be realized, extractive communities need to live within or near reserves and enjoy free access to their forest resources. Based on data on game abundance, the greatest impact of hunting occurs within 6 km of an access point, although hunters are often prepared to walk much longer distances if necessary. We therefore plotted reserve size against the reserve area within 6 km of a river or road and the potential hunting threat as measured by the mean rural population density of each reserve. The results for SPAs, extractive reserves (Fig. 6a), and indigenous reserves (Fig. 6b) indicate that although there is considerable variance in overall accessibility, most reserves still occur in sparsely populated regions subjected to relatively low consumer pressure.

Discussion

Our study covers the largest and least-disturbed river basin under the jurisdiction of a single country, but most of this area is deceptively accessible. Over three-quarters of the basin area can be reached on foot if people are prepared to walk up to 9 km from an access point. Moreover, the actual accessibility may be considerably larger because of inevitable underestimates in the river and road network as already discussed.

The fate of undisturbed wilderness areas throughout lowland Amazonia is thus more likely to be a function of the scale of extractive activities determined by consumer demand and technology than of constraints on physical access per se. This should help dispel the argument in priority-setting conservation workshops that there is little urgency in setting aside SPAs in roadless wilderness areas because they are not imminently threatened by the existing transportation infrastructure (e.g., Biodiversity Support Program 1995; Instituto Socio Ambiental 1999). Indeed the availability of many inexpensive but legitimately titled landholdings and the relatively small political costs of creating new reserves in remote, sparsely populated, pristine forest areas present huge, socially acceptable conservation opportunities that may no longer exist within two decades (Peres 2002). Regional

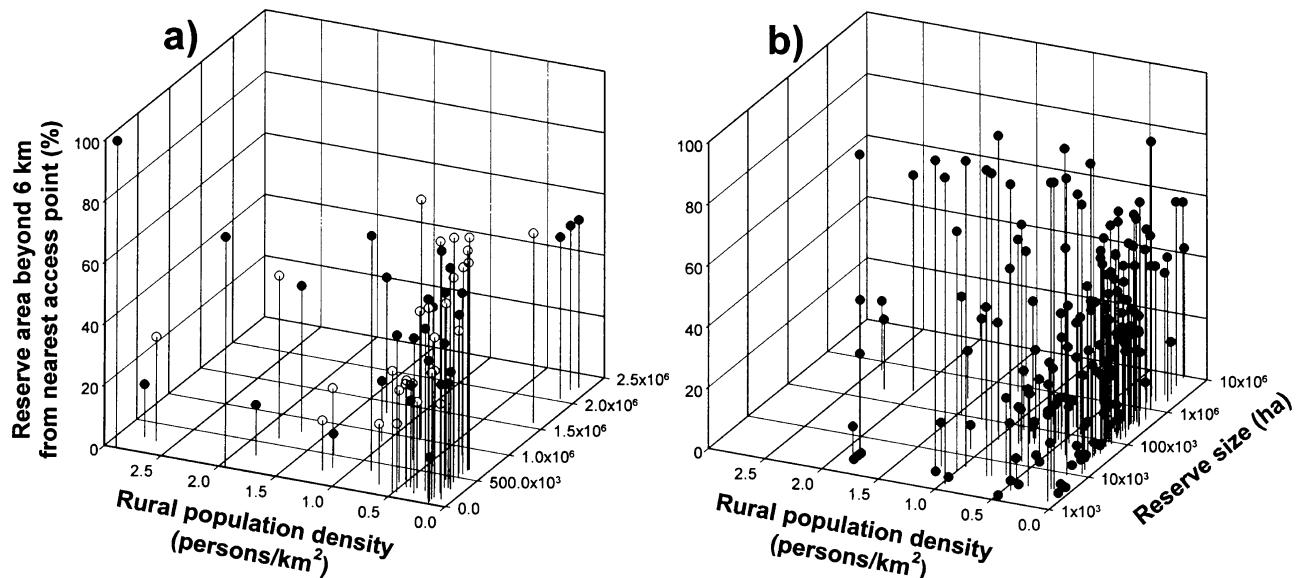


Figure 6. Relationships between the size of (a) nature reserves (solid circles), extractive reserves, and national forests (open circles) and (b) indigenous reserves of Brazilian Amazonia, their rural population density, and total core area beyond 6 km from the existing access matrix.

conservation strategies thus need to be tailored to different scales of threats and forest disturbance. These may range from overhunting and other forms of NTFP over-exploitation in otherwise undisturbed forests to degraded forests that are imminently threatened by deforestation but still retain a largely intact canopy cover.

Game Abundance Responses

The effects of hunter access were clearly detected along forest transects for a significant fraction of the game species surveyed. These typically included large-bodied forest vertebrates that cope poorly with hunting because they exhibit low reproductive rates and are consistently singled out by hunters (Bodmer et al. 1997; Peres 2001a), who are often willing to wander far from the nearest river or road to kill preferred game species.

Depending on fuel availability, use of the fluvial network can be greatly facilitated by increasingly affordable outboard motors for dugout canoes. Greater transportation efficiency substantially expands the hunting range of local communities and fatally disrupts the lateral movements and metapopulation dynamics of several game species that make daily or seasonal incursions into riparian habitats. Unhunted riparian forests are found in only a few SPAs or those well beyond a minimum distance from the nearest settlement. Amazonian floodplain forests, fabled for their sheer megafaunal abundance, would hardly exist without either effective law enforcement or extremely prohibitive access. Forest areas abutting whitewater rivers, which account for most of the hunted sites sampled (Peres 2000a), tend to be more productive,

capture a seasonal influx of alluvial nutrients, and present a higher habitat diversity. This partially explains why several hunting-tolerant vertebrate species were actually more abundant in the most accessible areas near rivers, which runs against the harvest gradient (Fig. 4). This is consistent with the lower densities of many vertebrate populations in remote terra firme forests of lowland Amazonia compared with those in floodplain forests (Peres 2000a, 2000b). The positive distance-abundance relationships for several large vertebrate species in hunted sites (Fig. 3) are thus likely to be reversed in unhunted sites. Howler monkeys, for instance, are widely harvested in floodplain forests, but their numbers typically decline abruptly in remote, poor-habitat areas farther inland, even though these are unhunted (Peres 1997). Herein lies an additional justification for maintaining large reserves encompassing natural mosaics of floodplain and terra firme forests (Peres & Terborgh 1995). The population sizes of many game species will be larger in reserves incorporating a heterogeneous mosaic of upland and floodplain forests, provided that the latter do not function as sinks. The effects of distance from rivers thus have important implications for the landscape design of protected areas and the effective size of their wildlife populations.

Population Declines within Reserves

The estimated population declines within protected areas did not take into account the effects of density dependence or metapopulation dynamics across the harvest gradient. Rather, they are based on observed levels of abundance along all census transects in hunted for-

ests, which presumably already accommodate the intrinsic demographic processes of density regulation and dispersal within continuous forest landscapes.

The source-sink dynamics of game populations within reserves could break down, however, should they become increasingly isolated from the adjacent unprotected forest landscape (Peres 2001a), although this is unlikely to happen in very large reserves.

There were apparently few cases of reserves containing rural population densities above which hunting is problematic if we assume that densities of bushmeat consumers of >1 person/km 2 are largely unsustainable (Robinson & Bennett 2000). The majority of reserves in Brazilian Amazonia are still embedded within a context of low human population density that rarely exceeds 2 persons/km 2 . Reserves in areas containing rural population densities >1 person/km 2 included 7 of 30 SPAs (23.3%), 5 of 31 extractive reserves and national forests (16.1%), and 32 of 196 indigenous reserves (16.3%). Densely populated small reserves with proportionally large forest areas within < 6 km from a river or road are likely to be most at risk from NTFP exploitation. A prime example is the entirely accessible Sauim-Castanheira Ecological Reserve (109 ha), which was created within the urban perimeter of Manaus to protect a population of the endemic bare-faced tamarin (*Saguinus bicolor*). This reserve has not retained any of the prime game species.

Cryptic Disturbance in Protected Areas

Potential access to existing reserves can only be a threat if reserves are poorly defended. Throughout Amazonia, reserves are almost invariably decreed on paper but neglected by government agencies. Indeed, Amazonian reserves tend to be chronically understaffed, underfunded, and entirely vulnerable to a wide range of external and internal threats (Peres & Terborgh 1995). Local officials from Instituto Brasileiro do Meio Ambiente (IBAMA)—the Brazilian environmental agency charged with park protection—are often starved of resources and logistical support, demoralized, and thus forced to overlook extractive violations against protected areas under their jurisdiction. For instance, the IBAMA Tefé office, allegedly one of the best funded in the State of Amazonas, consists of a team of only four officials, who attempt the unattainable task of enforcing conservation policy over 251,000 km 2 of forest, including four protected areas (C.P., personal observation). In Brazil the problem of inadequate park implementation extends in even the most developed parts of the country: 40 of the 60 federal SPAs created outside the Amazon prior to 1994 remain understaffed, with $<50\%$ of a sufficient number of park guards and officials (Sá et al. 2000). Such chronic understaffing applies to 25 of the 26 federal reserves in Amazonia even after 7 years of their decree. Consequently, systematic resource exploitation is reported by virtually all park managers interviewed. Examples of

Brazilian biological reserves that are strictly protected on paper but degraded by hunting and other extractive practices include Sooretama (Chiarello 1999) and Una (R. Pardini, personal communication) in the Atlantic forest, and Gurupí (Lopes & Ferrari 2000) and Abufarí in Amazonia (C.P., unpublished data).

NTFP Extraction and Roads

Poorly defended reserves may not be an immediate problem in sparsely populated areas. Since the Amazonian road-building program was initiated in the 1960s, however, roads have been spanning an increasingly greater expanse of interfluvial regions. One of the major effects of paved roads is their crucial role in the migration of hundreds of thousands of new settlers into terra firme forests, providing a new pool of resource extractors to threaten the integrity of poorly protected areas (Fearnside & Ferreira 1984). Such extractive activities often escalate beyond local subsistence needs because, by reducing transport costs, roads can generate the commercial demand for NTFPs from other areas. This threat is likely to increase as the paved highway network is expected to more than double within the next two decades under the Avança Brasil Program (Laurance et al. 2001). In addition, roads represent a direct threat to conservation areas and subsidize a greater range of economic activities resulting in large-scale forest disturbance, wildfires, and deforestation (Nepstad et al. 2001; Peres 2001b).

Our analysis included 31,917 km of roads of any type in an area nearly 15 times greater than Britain. Although this currently amounts to an average road density of only 0.0085 km/km 2 , it results in a substantial road-effect zone in terms of the extent of NTFP extraction, and this will certainly increase in the future. To put this in perspective, 100% of the Amazon Basin could eventually become accessible if the density of road and fluvial access points increases to 0.119 km/km 2 , which would require 177,089 km of new roads. Under these conditions, the viability of all populations of large-bodied vertebrates in effectively unprotected areas would be threatened by both forest fragmentation and overhunting. By comparison, an estimated 15–20% of U.S. territory is directly affected by 630,000 km of unpaved public roads (mean = 1.2 km/km 2). Yet a road density of approximately 0.6 km/km 2 appears to be the maximum tolerable for a naturally functioning landscape containing viable populations of large carnivores, such as wolves and mountain lions (Forman & Alexander 1998). In many respects, these top predators encapsulate the North American concept of roadless wilderness much like woolly monkeys, white-lipped peccaries, and tapirs are hallmarks of large tracts of effectively protected or extremely remote Amazonian forests.

Given the presently pathetic institutional capacity to enforce environmental policy, roads in lowland Amazonia are just as detrimental to wildlife populations as in

the Congo Basin (Wilkie et al. 2000), Malaysia (Laidlaw 2000), and elsewhere (Forman & Alexander 1998; Trombulak & Frissell 2000). Indeed, the trend of declining wildlife densities with increased road access is ubiquitous throughout Asian (Chin & Bennett 2000), African (Eves & Ruggiero 2000), and Neotropical forests (Ayres et al. 1991). In northern Congo, roads increase the local demand for bushmeat, provide hunters with easier access to isolated forests, and increase bushmeat exports to new markets (Wilkie et al. 2000). Distance from the end market and road conditions are key determinants of the hunting pressure on populations of two endemic wild pig species in Sulawesi, Indonesia (Clayton et al. 1997). Indeed, in the absence of effective protection, the presence of large areas of prohibitive access may be the best predictor of large-vertebrate population viability and other indicators of ecosystem integrity in many tropical forest regions.

Implications for Reserve Design

The results of our analysis have important implications for the design of new nature reserves. Large reserves safeguard larger core areas, which increases their passive defensibility value, in addition to several other conservation benefits (Terborgh & Soulé 1999; Etienne & Heesterbeek 2000). Poorly guarded reserves containing a high density of access points will be more difficult to defend, but passive defensibility may not be an issue if a reserve is well protected then. Given the glaring deficiencies in implementing law enforcement in existing reserves in most of the tropics, and uncertainties as to how this will improve in the future, it makes sense to design reserves containing as much core habitat as possible.

To increase their passive defensibility, reserves need to be placed in areas of low river and road density, and it follows that they should capture entire subcatchment boundaries rather than match river or road contours. In addition, any potential threat should be minimized whenever possible by selection of areas with a low human population density and few entry points to monitor. Manu in Peru and Jaú in Brazil are prime examples of Amazonian national parks encompassing entire major watersheds with only one riverine entrance requiring permanent vigilance.

Distinguishing Core Tropical Wilderness Areas

Despite considerable advances in remote sensing, there have been few attempts to quantify the extent to which cryptic disturbance by NTFP extractivists has affected the world's forests. The World Resources Institute defined as "frontier forests" those areas that are relatively undisturbed by human activity and are large enough to maintain their full biota, including viable populations of wide-ranging species (Bryant et al. 1997). In a coarse-scale GIS analysis conducted by the Global Forest Watch

(2002), frontier forests were estimated to comprise some 40% of the world's remaining forests, nearly 40% of which were under moderate to high threat of degradation from selective logging, mining, and agricultural clearance, which can be detected from space, and several forms of NTFP exploitation, which cannot (Global Forest Watch 2002). There was no mention in this study of the extent and intensity of hunting disturbance, which requires both a remote-sensing and a field-based approach.

Much of lowland Pan-Amazonia is deceptively accessible, with truly pristine primary forests—defined as those completely without human intervention and including a full complement of harvest-sensitive species—comprising only a small fraction of the apparently intact land cover. Hunting alone could substantially reduce the population size of key game species from protected areas, even under the context of low rural population density. There are many other examples of commercially important Amazonian NTFPs that were once widely distributed but have since been depleted or driven to local extinction in all but the most remote areas, including the oil of *pau rosa* trees (*Aniba roseadora*), which is widely employed in the perfume industry; the medicinal oil of copaiba trees (*Copaifera* sp.); latex from several tree species (e.g., *Couma utilis*, *C. macrocarpa*, *Manilkara bidentata*); the highly resistant fiber of *Heteropsis* spp. (Araceae) vines, and a wide range of medicinal and hallucinogenic plants. These NTFPs are often extracted unsustainably if the one-off harvest event is destructive and leads to high levels of adult or juvenile mortality. To these we can add all the game vertebrates referred to here showing positive distance responses to the accessibility matrix. More sustainably harvested NTFPs involving little or no adult mortality include the collection of fruits or seeds from Brazilnut (*Bertholletia excelsa*), andiroba (*Carapa procera* and *C. guianensis*), and cumarú trees (*Dypterix odorata*) and several arborescent palms (but see Vasquez & Gentry 1989). Few studies have attempted to quantify the long-term effects of systematic seed depletion, however, which could result in a severe demographic bottleneck.

This clearly raises serious doubts about the role of NTFP extraction in sustainable natural forest management in Amazonia at a time when conservation programs and rural development directives from the central government have encouraged and subsidized NTFP harvest and trade. Promoting short-term income-generating alternatives to the detriment of the long-term protection of harvest-sensitive species may do more harm than good to the social welfare and biological integrity of the Amazon.

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