
Synergistic Effects of Subsistence Hunting and Habitat Fragmentation on Amazonian Forest Vertebrates

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Abstract: *Subsistence game hunting has profound negative effects on the species diversity, standing biomass, and size structure of vertebrate assemblages in Amazonian forests that otherwise remain largely undisturbed. These effects are likely to be considerably aggravated by forest fragmentation because fragments are more accessible to hunters, allow no (or very low rates of) recolonization from nonharvested source populations, and may provide a lower-quality resource base for the frugivore-granivore vertebrate fauna. I examined the likelihood of midsized to large-bodied bird and mammal populations persisting in Amazonian forest fragments of variable sizes whenever they continue to be harvested by subsistence hunters in the aftermath of isolation. I used data from a comprehensive compilation of game-harvest studies throughout Neotropical forests to estimate the degree to which different species and populations have been overharvested and then calculated the range of minimum forest areas required to maintain a sustainable harvest. The size distribution of 5564 Amazonian forest fragments—estimated from Landsat images of six regions of southern and eastern Brazilian Amazonia—clearly shows that these are predominantly small and rarely exceed 10 ha, suggesting that persistent overhunting is likely to drive most midsized to large vertebrate populations to local extinction in fragmented forest landscapes. Although experimental studies on this negative synergism remain largely unavailable, the prospect that increasingly fragmented Neotropical forest regions can retain their full assemblages of avian and mammalian species is unlikely.*

Efectos Sinérgicos de la Cacería de Subsistencia y la Fragmentación del Hábitat sobre Vertebrados de Bosques en la Amazonía

Resumen: *La cacería de subsistencia tiene efectos negativos profundos sobre la diversidad de especies, la biomasa y estructura de las comunidades de vertebrados en bosques de la Amazonía que de otra forma están poco perturbadas. Estos efectos se agravan considerablemente por la fragmentación del bosque porque los fragmentos son más accesibles a los cazadores, no permiten la recolonización por poblaciones no cazadas o disminuyen las tasas de recolonización y pueden proporcionar una base de recursos de menor calidad para la fauna de vertebrados frugívoro-granívoros. Examiné la posibilidad de persistencia de poblaciones de aves y mamíferos medianos a grandes en fragmentos de bosque de tamaño variable si continúan sujetos a la cacería de subsistencia como una consecuencia del aislamiento. Utilicé datos de una compilación extensiva de estudios de cacería en bosques neotropicales para estimar el grado en que diferentes especies y poblaciones han sido sobre explotadas y calculé el área de bosque mínima requerida para mantener una cosecha sostenible. La distribución de tamaños de 5564 fragmentos de bosque amazónica, estimado a partir de imágenes de Landsat de seis regiones del sur y del este de la Amazonía brasileña indica claramente que estos fragmentos son principalmente pequeños y que rara vez exceden los 10 ha, lo que sugiere que la sobre cacería persistente probablemente lleve a la extinción local de poblaciones de vertebrados de tamaño mediano a grande en paisajes boscosos fragmentados. Aunque estudios experimentales de este sinérgico negativo no están disponibles, la perspectiva de que las regiones neotropicales cada vez más fragmentadas, puedan retener las comunidades completas de aves y mamíferos poco es probable.*

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Introduction

Subsistence hunting of wild vertebrates is one of the most widespread forms of nontimber resource extraction in tropical forests and results in profound consequences for the population biomass, species diversity, and size structure of the residual faunal assemblage (Wilkie & Carpenter 1999; Peres 2000a; Robinson & Bennett 2000). But this is a highly invisible, diffuse activity practiced by millions of increasingly market-integrated forest hunters worldwide, and the severity of this contemporary defaunation process is only beginning to be realized. Unlike other anthropogenic patterns of forest disturbance, overhunted areas cannot be efficiently mapped at large spatial scales using conventional remote-sensing techniques, and detecting the effects of game harvest in situ is at best a challenge. We can therefore only speculate on the extent to which large-bodied vertebrates are being reduced in numbers or extirpated in different tropical forest regions. Yet vast expanses of previously remote wilderness areas are becoming increasingly accessible to hunters, who in many areas are driving a number of sensitive game species to local extinction (Peres 1990, 1996; Redford 1992; Fang et al. 1999; Robinson et al. 1999; Fa & Peres 2001).

Different forms of human-induced disturbance in tropical forests often co-occur, so their effects may operate synergistically. For example, subsistence hunting targeted to large-bodied vertebrates often takes place in forest landscapes previously subjected to selective logging (Wilkie et al. 1992; Bennett & Dahaban 1995; Oates 1996; Robinson et al. 1999), slash-and-burn agriculture and fragmentation (Robinson 1996), and, more recently, surface wildfires that scorch the forest understory and kill a large proportion of the canopy trees (Cochrane et al. 1999; Peres 1999a). Yet most studies of faunal responses to structural and nonstructural habitat disturbance treat these as entirely independent. As a result, the interactions between hunting and different scales of forest disturbance—which may be favorable, detrimental, or neutral to different species of large vertebrates—remain poorly understood.

Studies of tropical game hunting have almost entirely overlooked fragmented forest regions, partly because the vast majority of forest dwellers who still rely heavily on terrestrial animal protein tend to be confined to large, remote tracts of undisturbed forest or naturally fragmented forest landscapes (Redford & Robinson 1987; Fa & Peres 2001). But there is no clear evidence to suggest that hunting pressure on forest wildlife declines for reasons other than game depletion as forest frontiers assaulted by logging and agriculture become increasingly fragmented. Indeed, the initial fragmentation process is often associated with an influx of human migrants (Alves et al. 1998; Instituto Brasileiro de Geografia e Estatística 2000), who rely heavily on meat from forest vertebrates,

so hunting is often ubiquitous in fragmented forests (Robinson 1996). Wildlife populations stranded in forest fragments therefore are expected to face the double threat of habitat fragmentation and overhunting.

Forest fragmentation could aggravate the effects of hunting by (1) initially reducing and isolating vertebrate populations averse to the surrounding habitat matrix (Malcolm 1997; Gascon et al. 1999); (2) reducing or precluding recolonization of overharvested areas from adjacent underharvested or nonharvested areas (Robinson 1996); (3) increasing the perimeter-to-area ratio and the amount of core forest habitat accessible to hunters on foot; and (4) further reducing the area of suitable habitat for species averse to forest edges (Laurance et al. 2000). It remains unclear whether any level of game harvest could be defined as sustainable in highly fragmented landscapes, because few studies have quantified large-vertebrate abundance within forest fragments differentially affected by a history of hunting (but see Chiarello 1999; Cullen et al. 2000).

I provide empirical estimates of the size of hunting catchment areas required to maintain a sustainable harvest for a group of 12 key game-vertebrate taxa of Amazonian forests, based on a comprehensive compilation of Neotropical hunting studies. To evaluate the conservation prospects of these species in hyperfragmented forest landscapes, I compared estimates of sustainable harvest area to the actual size of forest fragments remaining in postfrontier regions of Brazilian Amazonia. I attempted to predict the size of hunted and nonhunted forest fragments required to maintain viable populations of a set of 46 vertebrate species surveyed during a long-term series of line-transect surveys. Finally, I discuss how contemporary fragmentation processes could disrupt the source-sink dynamics that help maintain the long-term sustainability of game harvests over large spatial scales.

Methods

Estimates of Population Density

Population-density estimates are based on a standardized series of line-transect surveys of diurnal vertebrates undertaken over a 14-year period (1987–2000) at 30 Amazonian forest sites. Although well over 100 species weighing ≤ 150 g were recorded, I focused on a limited number of diurnal species. These consisted of 46 species (or species groupings) of midsized to large-bodied vertebrates, including primates, ungulates, squirrels, caviomorph rodents, coatis, edentates, cracids, tinamids, trumpeters, Wood-quails, and tortoises (for scientific names and body weights, see Appendix). Density estimates for nocturnal mammals, including pacas (*Agouti paca*), armadillos (e.g., *Dasytus* sp., *Priodontes maximus*), arboreal procyonids (*Potos flavus*, *Bassaricyon gabbii*),

and night monkeys (*Aotus* sp.) were obtained from the few sites where night surveys were carried out (e.g., Janson & Emmons 1990; Peres 1999b).

Survey sites that had not been subjected to hunting for at least three decades prior to wildlife surveys were defined as nonhunted. All other sites were assigned to one of three broad classes of hunting pressure—light, moderate, and heavy—on the basis of semistructured interviews with hunters. Hunters who had lived at each forest site for at least 2 years were interviewed about the frequency, intensity, and species selectivity of local game-harvest practices. Present and past human population density and distribution were quantified on the basis of interviews, and the number of households in each area was revealed by high-resolution (1:250,000) RADAM maps (1973–1981) of each survey area (Peres 2000a).

Population surveys at each site were conducted along two line transects of between 4.5 and 5.0 km in length cut and walked during 13 to 15 rainless days, usually within a period of <1 month. Three nonhunted sites—Urucú, Kayapó Reserve, and Igarapé Curimatá—were surveyed more than once over the years. A cumulative census effort of 1728 km walked was carried out at 13 nonhunted and lightly hunted sites. In 17 moderately to heavily hunted sites, 1415 km were walked. The majority of transects in hunted areas originated 200–300 m from navigable rivers (for dugout canoes and small motorboats) and were placed perpendicularly to the river channel, thus gradually sampling increasingly inaccessible areas. Only two transects started near unpaved roads, which were used occasionally by hunters on bicycles or on foot. In all cases, numbers of detection events within 500-m sections of each transect were initially transformed into a detection rate (per 10 km walked) to control for slight differences in cumulative sampling effort. Further details on the forest sites surveyed, sampling procedures, and derivation of population-density estimates can be found elsewhere (Peres 1997, 1999c, 2000b).

Estimates of Sustainable Harvest Areas

I compiled game-harvest profiles available from the literature by initially assembling the 19 anthropological studies reviewed by Redford and Robinson (1987), which encompassed 23 samples documenting kills brought into 6 colonist and 17 Indian settlements. To these samples I added 9 more recent studies of *caboclo*, rubber-tapper, and colonist settlements in different parts of Brazilian (Ayres et al. 1991; Martins 1992; Cauro 1995; Muchagata 1997), Peruvian (Alvard 1993; Bodmer 1994; Hiraoka 1995; Begazo & Bodmer 1998), and Colombian (Alonso 1997) Amazonia and 9 studies of Indian villages in Suriname (Mittermeier 1991), Amazonian parts of Brazil (Milton 1984, 1991), Ecuador (Vickers 1991; Mena et al. 2000), and Bolivia (Stearman 1990; Stearman & Redford 1995; Townsend 2000). In addition, I included two unpublished

game-harvest studies undertaken over a sampling period of at least 2 years (C. Peres and H. Nascimento, unpublished data). The first of these studies was conducted at Vila Moura, a small *caboclo* settlement located along the upper Tefé river of central Amazonas, Brazil (sampling effort = 35 consumers \times 750 days), and the second from the Kayapó Indian village of A'Ukre (231 consumers \times 550 days) located along the Riozinho River, an eastern Amazonian subtributary of the Xingú River.

My compilation is therefore based on game-hunting studies in the Amazon basin and adjacent forest regions and includes only two studies in Neotropical forests at higher latitudes (Yucatán Peninsula, Mexico [Jorgenson 1995]; eastern Paraguay [Hill & Padwe 2000]). This analysis thus excludes Neotropical hunting studies restricted largely to open-canopy environments (e.g., Leeuwenberg & Robinson 2000) and harvest data from nonforest portions of village harvest areas encompassing a forest-savanna mosaic (Townsend 2000).

Whenever available, information extracted from each harvest study included village size (number of consumers), village age (of a given settlement in years), duration of the study (days), area harvested by hunters of a given village (hereafter, harvest area), and numbers of animals harvested for each target species. For comparative purposes, harvest data from studies of various duration were annualized and expressed in terms of numbers of animals of each species harvested per consumer year (annual per capita harvest rate). For a group of 12 key target game taxa (consisting of single species or functionally equivalent congeners), observed harvest rates were then compared with those expected to maintain a maximum sustainable harvest, as derived from Robinson and Redford's (1991) model based on the maximum finite rate of increase (λ_{\max}) and the population density of a species. In the case of these species, I incorporated the best available density estimate for each study area, rather than the "predicted densities" used by Robinson and Redford (1991), which tend to overestimate the number of animals that can be sustainably harvested, particularly in Amazonian terra firme forests (Peres 2000b).

In several cases, species-specific density estimates were obtained and reported in the same or related studies from nonhunted areas in the vicinities of village harvest areas (e.g., Bodmer et al. 1997; Begazo & Bodmer 1998; Mena et al. 2000; C. P. & H. Nascimento, unpublished data). Otherwise, I matched each harvest sample to the most robust density estimate available for the same forest type from the nearest nonhunted or lightly hunted forests, based on line-transect surveys carried out in the same region (e.g., Janson & Emmons 1990) or from our own network of survey sites (Peres 1999b, 2000a, 2000b, unpublished data).

The minimum areas required to maintain a sustainable harvest (hereafter, sustainable harvest areas) were then calculated for each of the 12 taxa on the basis of village-

specific harvest rates observed during each study. The sustainable harvest area for a given game population was therefore proportionally smaller or larger than its observed village harvest area, according to the ratio between its observed harvest rate (OH) and sustainable harvest rate (SH). A species was thus defined as underharvested within a given harvest area if $OH/SH < 1$ and overharvested if $OH/SH > 1$.

Finally, the forest areas required to accommodate a population of 500 animals of each game taxon were also calculated on the basis of the range of density estimates available for nonhunted and lightly hunted areas surveyed to date (Peres 2000b, unpublished data). This arbitrary population size was chosen because it is often assumed to be the minimum necessary to maintain long-term demographic and genetic viability (Soulé & Wilcox 1980).

Estimates of Forest Fragment Size

Estimates of forest fragment sizes are based on six 1992 Landsat multispectral scanner satellite images acquired from the Basic Science and Remote Sensing Initiative (BSRSI) at Michigan State University (BSRSI 1998). With a ground-track spacing of 172 km at the equator and a swath width of 185 km, each of these scenes covered an area of nearly 32,000 km². The six scenes selected encompassed hyperfragmented parts of western (central and eastern Rondônia), southern (Alta Floresta, Mato Grosso), and eastern (southeastern Pará; and northern Tocantins) Brazilian Amazonia (Fig. 1) and included some of the highest recorded deforestation rates as of 1991–1994 at the level of quarter-degree cells (Alves et al. 1998).

These scenes were representative of the range of forest fragmentation patterns along the highly seasonal “deforestation arch” of Amazonia resulting from large-scale cattle ranching, agricultural settlement programs, and other deforestation activities. Classified images were thresholded into either forest or nonforest areas and were represented by black or white pixels, respectively, to maximize fragment contrast for further analysis. The reasonably high spatial-resolution data (30-m pixels) allowed a fairly clear distinction between major classes of land cover, and those interpreted as either primary or secondary forest were simply defined as forest. I deliberately used this conservative approach to avoid underestimating the size of forest fragments embedded within successional mosaics, and because several Amazonian ungulates, small- and mid-sized primates, caviomorph rodents, and cracids can use regrowth (*capoeiras*) lying immediately adjacent to primary forest (C.P., unpublished data). Other thematic features identified in the BSRSI images (e.g., water, clouds, cloud shadows, and natural scrub savannas or *cerrados*) were excluded from the fragment metrics analysis. Further details on digital image preprocessing and analysis, field validation, and accuracy assessment are available from BSRSI (1998).

Thresholded images were analyzed at the Geotechnical Microanalysis and Micromorphology Centre (GMMC), University of East Anglia, with SEMPER (Synoptics 1995), a versatile image-analysis and processing software package that can be readily extended to incorporate new algorithms. A batch SEMPER program was used initially to remove entirely isolated pixel clusters (hereafter, true isolates) that were not embedded in the nonforest matrix. True isolates were stored in a separate image, and each separate fragment was analyzed for shape and size.

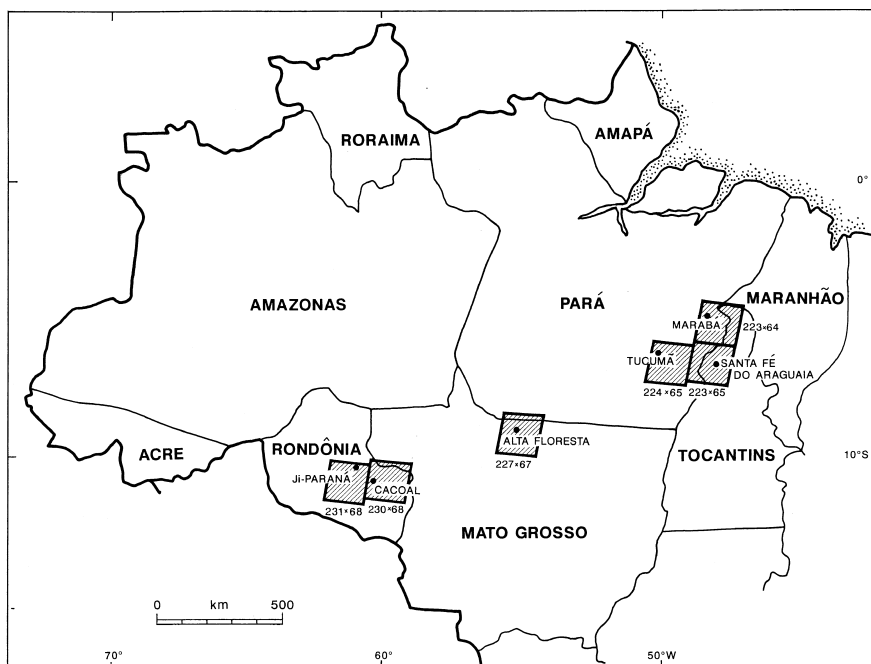


Figure 1. Location of the six Landsat scenes in Brazilian Amazonia analyzed in this study.

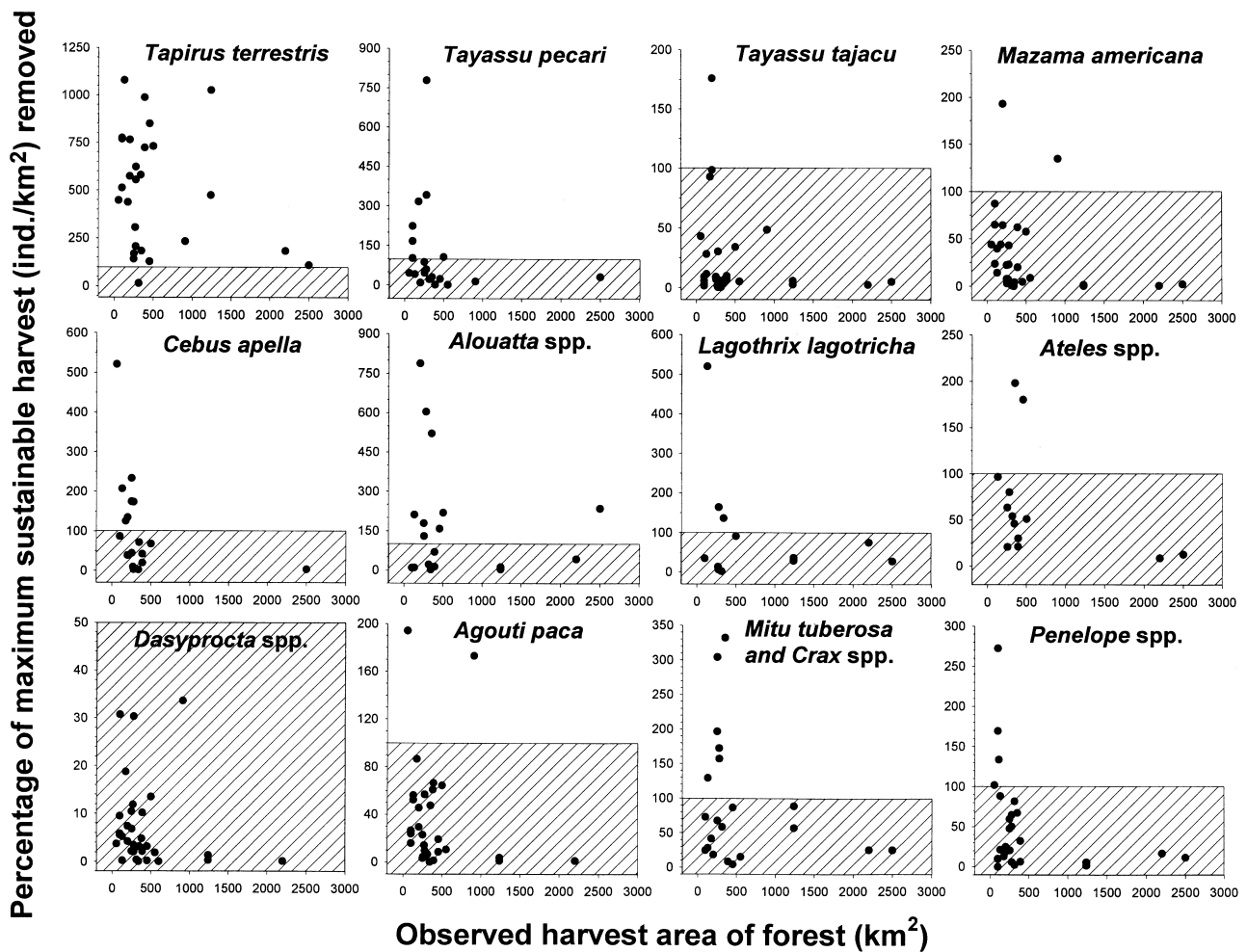


Figure 2. Relationship between forest harvest area and percentage of the maximum annual sustainable harvest of 10 mammal and 2 bird taxa known to be removed by subsistence hunters in different studies. Solid circles above the 100% line represent overharvested game populations; those below the 100% line (within hatched rectangles) may or may not have been underharvested. Common English names are listed in Appendix.

Remaining forest patches weakly connected to the skeletal forest matrix by narrow joins of a single pixel radius (hereafter, quasi-isolates) were mathematically identified and selectively eroded so that any connections of 30–60 m were broken off, creating a new set of fragments. This disconnection was achieved by a multistage process in which the remaining forest area was eroded by removing a one-pixel strip (equivalent to 30 m in width) around each edge. The erosion separated further fragments, but they were all reduced in size. Consequently, this eroded image was reprocessed to define the lines defining the skeletal zones of influence (SKIZ). The SKIZ image is thus a series of lines defining the break points in the thinly connected regions of forest. By using a boolean algebraic expression such that the original image was disconnected where there was a SKIZ line, a second set of fragments was obtained that could be processed in the same manner as the first set. This approach

ensured that the original areas of these new fragments remained unchanged.

Further erosion cycles removing successively more pixels are possible but were not done at this stage. I measured the area of true isolates and those generated by the first erosion cycle by noting the number of pixels included in each isolate. The fragment-size data I present exclude all one-pixel fragments (0.09 ha) that could reflect single features, such as large trees, isolated in the nonforest matrix.

Results

Observed and Sustainable Harvests

Observed harvest areas in continuous Neotropical forests across all studies were on average $410 \pm 64 \text{ km}^2$ ($n =$

Table 1. Estimated proportions of the maximum sustainable harvest removed and sustainable harvest area requirements for 12 large vertebrate taxa pursued by subsistence hunters in Amazonian forests.

Vertebrate taxa	Percent removed ^a	Sustainable harvest area (km ²) ^b	n ^c	Minimum viable forest area (km ²) ^d	
				this study	Redford & Robinson 1991
<i>Tapirus terrestris</i>	512 ± 372	2003 ± 475	28	4413 ± 9138 (28)	1621 ± 1792 (5)
<i>Tayassu pecari</i>	119 ± 175	298 ± 99	23	253 ± 101 (28)	195 ± 169 (5)
<i>Tayassu tajacu</i>	23 ± 38	69 ± 19	29	262 ± 512 (31)	117 ± 121 (10)
<i>Mazama americana</i>	34 ± 44	112 ± 44	28	242 ± 111 (31)	197 ± 188 (7)
<i>Cebus apella</i>	108 ± 126	209 ± 40	18	51 ± 45 (23)	75 ± 74 (21)
<i>Alouatta</i> spp.	209 ± 282	864 ± 303	20	295 ± 425 (23)	86 ± 126 (27)
<i>Lagothrix lagotricha</i>	95 ± 143	443 ± 132	12	44 ± 28 (14)	61 ± 28 (5)
<i>Ateles</i> spp.	66 ± 60	258 ± 64	13	113 ± 57 (13)	83 ± 79 (7)
<i>Dasyprocta</i> spp.	7 ± 9	26 ± 10	30	88 ± 34 (33)	94 ± 110 (8)
<i>Agouti paca</i>	37 ± 46	127 ± 52	30	107 ± 38 (32)	37 ± 37 (8)
<i>Mitu tuberosa/Crax</i> spp. ^e	109 ± 98	369 ± 67	25	221 ± 137 (28)	303 (1)
<i>Penelope</i> spp. ^e	47 ± 60	125 ± 31	29	72 ± 39 (33)	92 (1)

^aMean ± SD percentage of the maximum annual sustainable harvest that was known to be removed from a given harvest area.

^bMean ± SD minimum area required to maintain a sustainable harvest if observed harvest rates within a harvest area were to be maintained.

^cNumber of independent samples (village harvest areas and game populations) considered.

^dMean ± SD minimum area required to maintain a nonhunted population size of 500 individuals based on available density estimates in nonhunted areas according to this study and Redford and Robinson (1991). Numbers in parentheses refer to numbers of density estimates.

^eEstimates for these bird taxa were derived from densities provided by Begazo and Bodmer (1998).

53) in size but ranged widely from 56 to 2500 km², depending on means of transport and occasional seasonal incursions into distant parts of an indigenous territory. In many cases, however, these sizeable harvest areas were not sufficiently large to preclude overhunting: 68 populations of 11 of the 12 large-bodied vertebrate taxa I considered were overharvested according to the model of Robinson & Redford (1991) (Fig. 2). For example, tapirs were harvested at an average rate five-fold greater than their maximum sustainable harvest at each site, and only one of the 28 harvests examined for this species was potentially sustainable. A large proportion of the populations of white-lipped peccaries, brown capuchin monkeys, howler monkeys, woolly monkeys, and curassows were also overharvested, whereas the other taxa were mostly underharvested (Table 1). *Dasyprocta* sp. was the only one of the 12 taxa considered that had been consistently underharvested in all harvest areas (<40% of sustainable harvest in all cases).

There was a clear negative relationship between the size of a harvest area and the degree to which a given population had been overharvested (Spearman rank tests $p < 0.05$ in all 12 cases). When all species were considered, only five harvest areas of >1000 km² were associated with annual offtakes (individuals/km/year) falling beyond the 100% line, indicating parity between the observed and the predicted sustainable harvest (Fig. 2). Of all 68 cases of overharvest, 60 occurred within harvest areas <500 km² in size, which were most frequently used by hunters on foot radiating out from established villages.

Sustainable Harvest-Area Requirements

Estimates of the minimum forest area required to maintain a sustainable harvest were calculated for each species at each site on the basis of observed harvest rates, whether or not these were defined as sustainable (Table 1). The resulting distributions of sustainable harvest areas were highly variable across species and were often highly skewed toward large harvest areas, apparently reflecting the predominance of low population-density estimates derived from nonhunted areas. Some taxa (e.g., agoutis, pacas, and common guans) required modal harvest areas of <100 km², whereas other species usually required areas of >1000 km² (Fig. 3). Even for species that are reasonably resilient to hunting pressure, such as pacas and common guans, over half the estimates of sustainable harvest area exceeded 100 km². The average size of the sustainable harvest areas was <100 km² for only two taxa, agoutis and collared peccaries (Table 1), and for most species the average harvest area fell in the range of 100–500 km². The highest estimates were accounted for by exceptionally low-density populations of howler monkeys and tapirs. In hunted areas, the tapir was by far the most spatially demanding species, on average requiring a sustainable harvest area exceeding 2000 km² (range, 45–12,702 km²).

These estimates of the size of forest areas required to maintain a sustainable harvest, given levels of extraction documented to date, were by necessity restricted to otherwise largely undisturbed forest landscapes. We can now attempt to examine the prospects for the persistence of viable large-vertebrate populations in fragmented

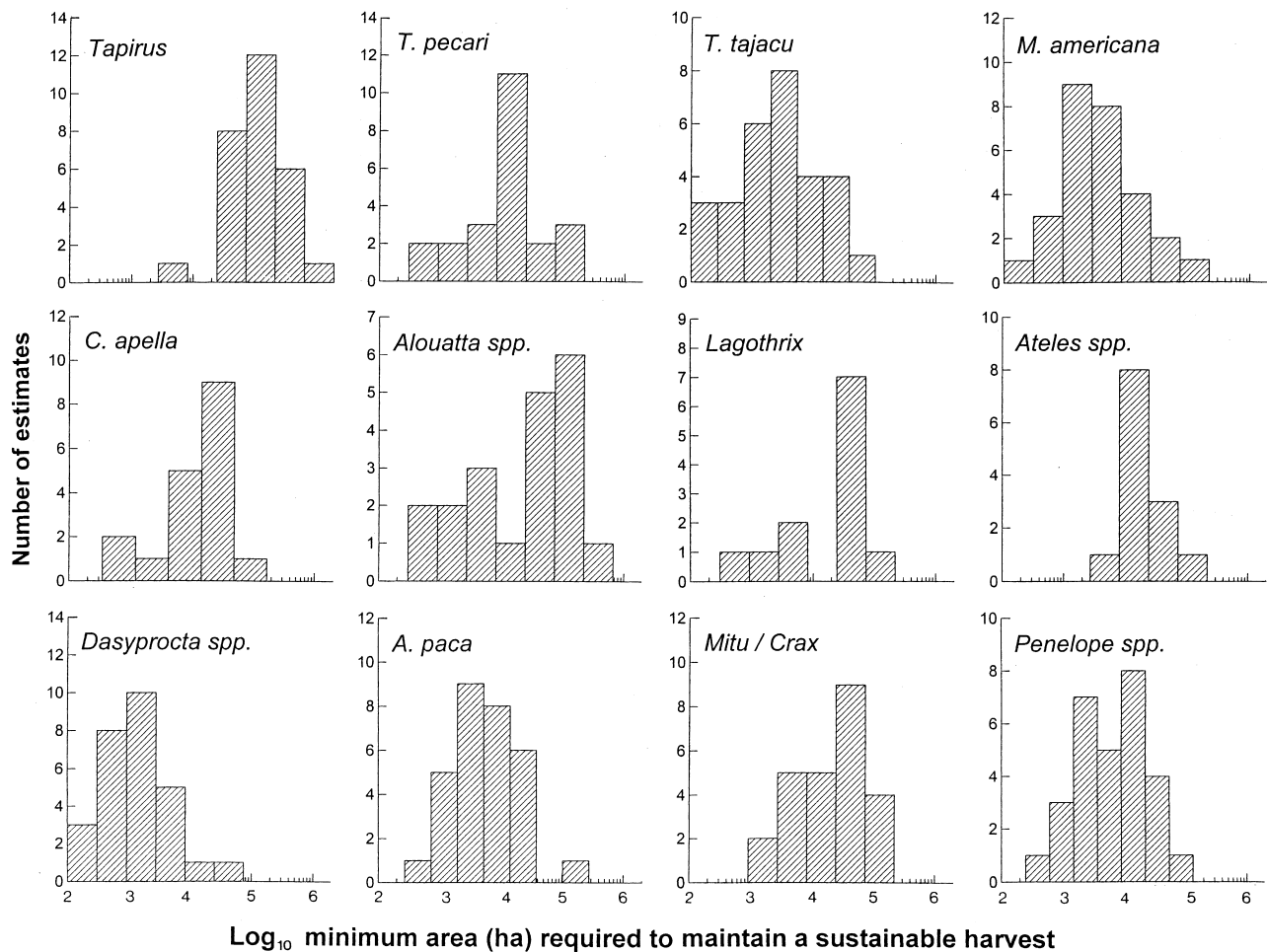


Figure 3. Distribution of estimates of forest harvest area required to maintain a sustainable harvest for 12 large-vertebrate game taxa in Amazonian forests.

forest regions of Amazonia if observed levels of extraction were to remain roughly constant.

Size of Amazonian Forest Fragments

In total, size estimates were derived for 5564 forest fragments, including both entirely and partially isolated fragments resolved by means of all six Landsat scenes. The proportion of each scene consisting of either continuous or fragmented forest cover ranged from 50% in Santa Fé do Araguaia of northern Tocantins to 81% in Cacoal of eastern Rondônia (Ji-Paraná, 72%; Alta Floresta, 79%; Tucumã, 77%; Marabá, 57%). When only true isolates were considered, mean isolate size was <2 ha in all but one region, northern Tocantins. The modal size of true isolates was smaller than 1 ha in all regions, even though all single-pixel features were excluded from the analysis (Fig. 4). When all regions were considered, only three entirely isolated fragments exceeded 100 ha and only one exceeded 1000 ha. In one region, eastern Rondônia, it was impossible to geo-

metrically discern a single truly isolated pixel cluster, despite high deforestation rates since the late 1970s. The typical “fish-bone” deforestation pattern in the west part of this region, caused by major roads and their perpendicular arteries, resulted in a considerable amount of connectivity. This essentially amounted to a “shredded” forest cover rather than a landscape characterized by archipelagos of small forest patches, which is more typical of regions dominated by large cattle ranches. Similar to other regions, however, successive erosions at different pixel radii generated quasi-isolates that were on average only 0.5 ha in size.

Nearly isolated forest patches were significantly larger than those that had been entirely isolated in all regions (analysis of variance on \log_{10} -transformed fragment area; range of F values, 60–179, $p < 0.0001$ in all five regions with isolates in both categories), but their average size in different regions still ranged between 3.1 and 7.2 ha. Again, increasingly larger quasi-isolates declined rapidly, with only seven exceeding 100 ha in all regions combined, and only 2 exceeding 1000 ha. Only 17 of all 5564

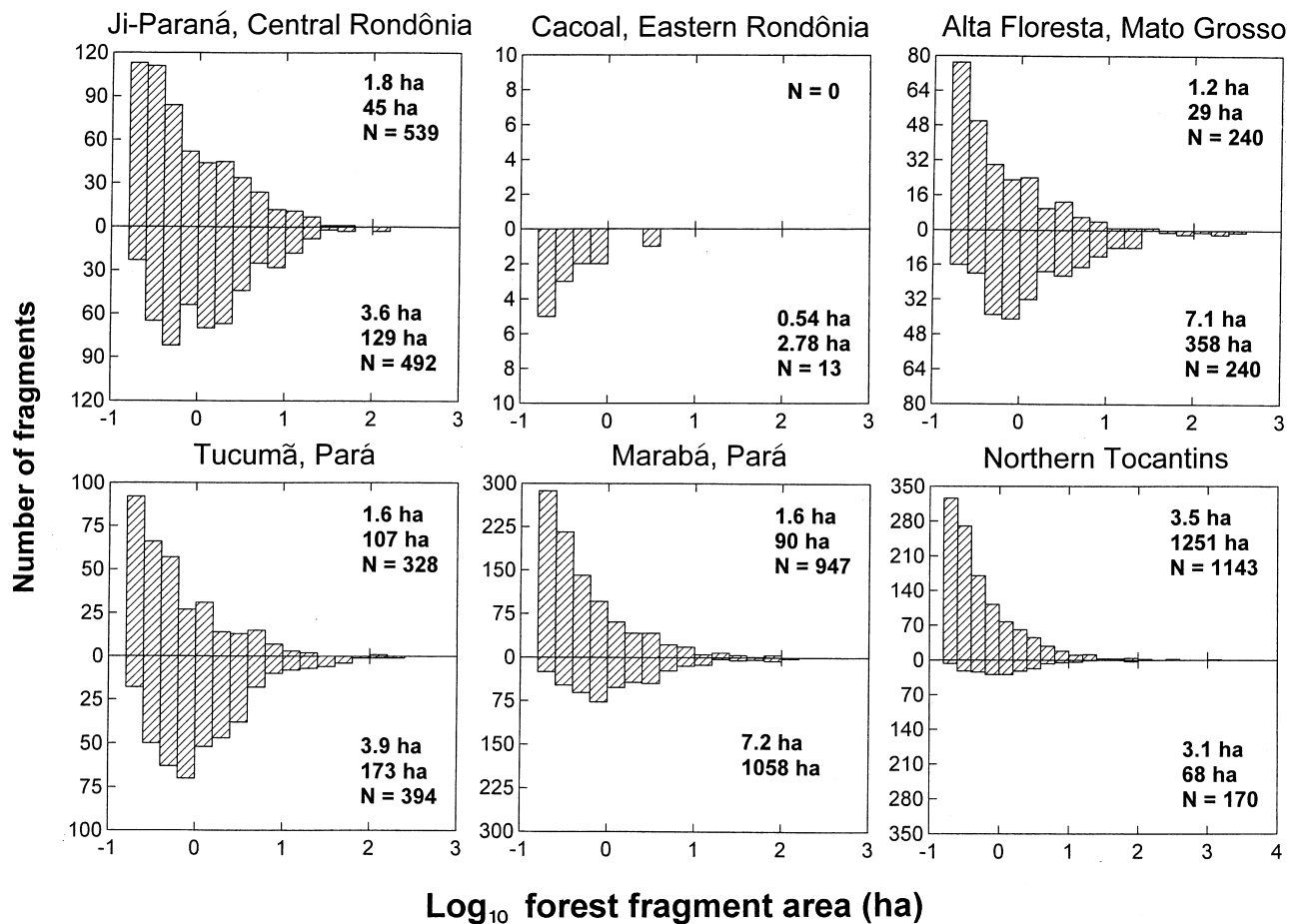


Figure 4. Distribution of forest fragment sizes within six cloud-free hyperfragmented scenes of southern and eastern Brazilian Amazonia. Fragments that had been entirely isolated in the nonforest matrix are shown above the upper half of each histogram. Those that had been weakly connected to the continuous forest matrix (quasi-isolates) are shown at the bottom. Data in the corners are the average and maximum size (ha), respectively, of fragments detected and the number (n) of fragments measured. Region names correspond to those listed in Fig. 1.

entirely or nearly isolated forest patches considered here were >100 ha in size, and only 2 were >1000 ha.

Predicted Extinctions within Hunted and Nonhunted Fragments

On the basis of population density estimates obtained for 46 large-vertebrate taxa surveyed at 13 nonhunted and lightly hunted forests and 17 moderately to heavily hunted Amazonian forests (species list in Appendix 1), I attempted to predict the number of local extinctions that would occur as forest fragment area is gradually contracted. For these purposes, a species was defined as locally extinct within a hypothetical fragment area if more than 50% of the available density estimates resulted in a population size equal to zero ($n = 0$). Two local extinction curves were then generated on the basis of density

and population-size estimates derived from forest sites pooled into two levels of hunting pressure.

According to these projections, fragments of >10,000 ha were reasonably robust to extinctions, particularly if they had been subjected to little or no hunting (Fig. 5). Gradually smaller fragments would, however, rapidly lose a large fraction of their original species assemblage. For example, 30 (65%) of the vertebrate species I considered would be retained within fragments 1000 ha or smaller if they could enjoy a reasonable level of protection and could be spared from persistent hunting. In contrast, moderately to heavily hunted fragments of 1000 ha would retain only 16 (35%) of the species, and those of 500 ha only 10–11 (22–24%) of the species. Retention of over half of all species would require areas of at least 600 ha if they were nonhunted to lightly hunted, but at least 2000 ha would be needed if they had been persistently hunted. Likewise, persistence of 90% of the

species would require fragments of about 11,000 ha if they had been exposed to moderate to heavy hunting, but only 3000 ha would be needed if they had not. The two local extinction curves eventually converged in fragments of ≤ 100 ha, which were able to retain only 4% of all species, presumably because the majority of species are unable to persist in very small fragments whether or not they had been hunted.

Discussion

Forest-Area Requirements

Although forest fragments of even a few hectares are unquestionably valuable to tropical biodiversity (Turner & Corlett 1996), data presented here clearly indicate that remaining forest patches in hyperfragmented regions of Brazilian Amazonia serve a limited conservation role for midsized to large forest vertebrates. This is particularly the case for true fragments or shredded forest areas that cannot be protected from continued incursions by subsistence hunters in the aftermath of fragmentation. Game hunting substantially amplifies the overall spatial requirements of viable large-vertebrate populations, which are already considerable even under the best-case sce-

nario of nonhunted, entirely undisturbed Neotropical forests in reasonably productive systems (e.g., Thiollay 1989; Janson & Emmons 1990; Terborgh et al. 1990; Peres 1997, 1999b; Fragoso 1998).

The forest area required to maintain a sustainable harvest was often considerably larger than the minimum area required to accommodate a nonharvested population of 500 animals. This was particularly the case for the four primate taxa, which are associated with low λ values and at best comprise "bad" game species if the realistic prospects of maintaining sustainable harvests even in continuous forest are considered (Peres 1990, 1999d). Townsend (2000) found that the estimated area required to produce a sustainable harvest in the Sirionó region of Bolivia also vary greatly across species, from 20 km² for red brocket deer to 720 km² for white-lipped peccaries; all ungulates in her study required areas of >500 km². Hill and Padwe (2000) estimate that the Aché of eastern Paraguay would need at least a 450-km² area—including both intensively and underharvested areas—in order to achieve a landscape-wide sustainable harvest at current rates of meat consumption. In these terms, an area of about 3.8 km² of forest per consumer would be necessary. Yet in most tropical regions continuous-forest areas in the order of 450–500 km² are rarely referred to as forest fragments, and the majority of remaining tropical forest fragments and protected areas are well below this size (e.g., Gascon et al. 2000).

The majority of the forest fragments in the six regions I examined were far too small to support any of the vertebrate species considered here, and a nonrandom, nested simplification of their vertebrate faunas is to be expected. Agoutis, red brocket deer, and collared peccaries comprised the only species that could be harvested in some of the fragments examined, largely because of their relatively high reproductive rates and population densities and tolerance to second-growth mosaics. Of the 5564 fragments analyzed, 99.8% were between 0.11 and 100 ha, whereas minimum viable areas necessary to maintain hunted or nonhunted game populations are several orders of magnitude larger. For example, minimum areas required to accommodate either a nonhunted population of 500 or a sustainably harvested population (given the range of observed harvest rates) were in the range of 1000–10,000 ha for all species except tapirs, which could have even larger spatial requirements.

The insufficient size of these fragments is supported by an independent fragment metrics analysis based on a 1992 Landsat Pathfinder scene of an 8500-km² region of central Rondônia, which identified only 40 forest fragments of >1000 ha in a sample of 2076 fragments (M. Cochrane & C. Barber, unpublished data). That their mean fragment size (191 ± 77 ha) was larger than those in my analysis was due mostly to the exclusion of all pixel clusters of <3 ha.

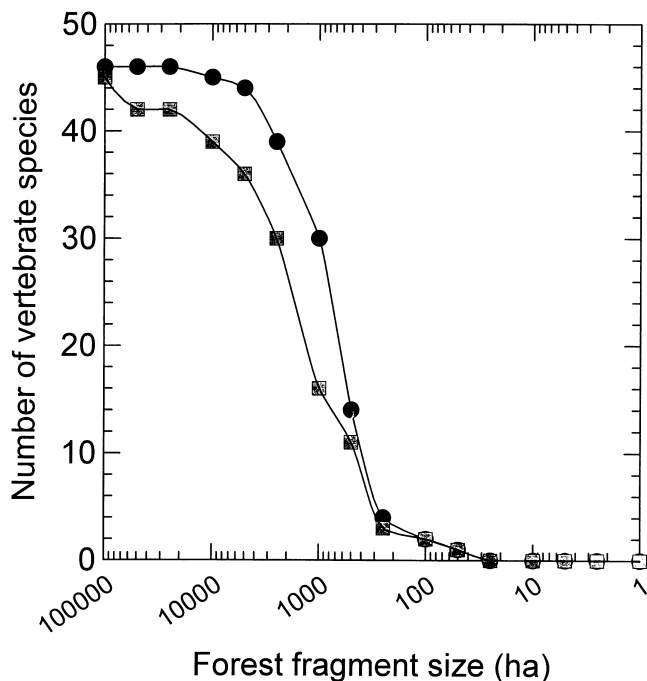


Figure 5. Predicted local extinctions for 46 vertebrate taxa surveyed in Amazonian forests (Appendix) as a function of forest fragments of varying size subjected to either little or no hunting (solid circles) or moderate to heavy hunting (shaded squares).

The clear inverse relationship between local extinction rate and habitat area is supported by empirical evidence from parks in the Atlantic Forest (Willis 1979), East Africa (Newmark 1996), and North America (Newmark 1995). But fragment-area requirements predicted for large Neotropical forest mammals in this and previous studies (Redford & Robinson 1991; Santos-Filho 1995) can be 250-fold greater than those of temperate-forest counterparts in the American Midwest, where fragments as small as 40 ha can retain all the post-settlement mammal fauna surviving beyond 1850 (Matthiae & Stearns 1981). This can be attributed partly to the paucity of true deciduous-forest specialists in the remnant mammal fauna of much of North America compared with Amazonian forest mammals larger than 500 g. Most Amazonian forest mammals are matrix-intolerant, reluctant to cross even small forest gaps, and are almost always restricted to closed-canopy evergreen environments.

With the exception of social species living in large, wide-ranging groups that occur at low densities (e.g., *Tayassu pecari*, *Lagothrix* spp., *Cacajao* spp.), most Neotropical mammal species can persist in forest fragments of >1000 ha in the complete absence of hunting (e.g., Bierregaard et al. 1992; Granjon et al. 1996; Cullen 1997; Malcolm 1997; Chiarello 1999; Gascon et al. 1999; Wright et al. 2000). For example, spider monkeys were found in approximately half (17/37) of a set of relatively small forest fragments surveyed in the Sierra de Santa Marta of southern Mexico (Silva-Lopez 1995) and are abundant in dry-forest fragments in Costa Rica (Chapman et al. 1989), provided that hunting activities are controlled. Likewise, in the State of São Paulo of southeastern Brazil, small populations of brown capuchin monkeys and colored peccaries persist in a number of small, privately owned forest fragments (150–450 ha) surrounded by pastures and intensive sugar-cane monoculture, as long as they are protected from hunting (Chiarello 2000; E. H. Ditt, personal communication).

Hunting can thus affect a greater range of species and in many cases override the effects of fragmentation alone by driving populations to local extinction before the faunal “relaxation” process is completed and new equilibrium conditions are reached. In some cases, the effects of hunting can be more perverse than those of fragment size per se, even for large-group-living species such as Amazonian bearded-saki monkeys, which can be far more abundant in smaller forest areas protected from hunting than in larger unprotected areas (Ferrari et al. 1999). Hunting-induced mortality striking the core of forest fragments could thus be seen as analogous to that affecting wide-ranging large carnivores straying outside park boundaries, which has been shown to be a greater contributor to local extinctions than population size per se (Woodroffe & Ginsberg 1998). In the absence of hunting, therefore, fragmentation appears to have little

direct short-term effects on the persistence of large vertebrates, except perhaps in forest patches of <250 ha (cf. Robinson 1996).

Breakdown of Source-Sink Dynamics

Populations of large-bodied Neotropical forest vertebrates are usually associated with significant negative density differentials between nonhunted and hunted forests (Peres 1990, 1996, 2000b; Glanz 1991; Bodmer et al. 1997; Cullen 1997; Mena et al. 2000; Wright et al. 2000). As reviewed here, a number of studies have shown that harvest levels are often well above those expected to be sustainable (Alvard et al. 1997; Robinson & Bodmer 1999). Yet these harvests appear to have been maintained over time, and surprisingly few local extinctions have been reported for persistently overhunted but finite harvest areas embedded within large, unbroken forest landscapes. To a large degree, this is presumably a function of repeated immigration into chronically overhunted areas from surrounding nonhunted or lightly hunted areas (Joshi & Gadgil 1991). Thus, colonization and extinction events will often not occur independently across forest patches exposed to varying degrees of hunting pressure.

In the context of island biogeography, Brown and Kodric-Brown (1977) referred to this as the “rescue effect,” because populations within increasingly depleted harvest areas would be repeatedly rescued from local extinction by continual immigration from adjacent source areas. In relation to game harvest, this concept was recently discussed by Novaro et al. (2000) and illustrated in terms of tapir metapopulation dynamics within large forest areas harvested at various intensities. They concluded that immigrants from neighboring areas may have a key role in replenishing locally depleted subpopulations, although virtually nothing is known about the population flows and dispersal patterns of Neotropical game species.

An indirect test of this hypothesis relates to the gradual depletion of preferred game stocks expected to occur around increasingly older village settlements. If populations in depleted harvest areas were relatively sealed to outside immigrants, one would expect to see a gradual decline in yields of overharvested closed populations as the age of the settlement (years) increases. In this study, however, annualized per capita harvest rates across all available Neotropical hunting studies were not significantly depressed by settlement age in 10 of the 12 game taxa considered, once the effects of village size (number of consumers) and observed harvest area were controlled for (backward stepwise multiple regression on log-transformed values). This was particularly surprising for tapir, the most frequently overharvested species, and supports the hypothesis that immigrants from surrounding areas can rebuild depleted subpopulations and replenish local game stocks (cf. Novaro et al. 2000).

Spider monkeys and white-lipped peccaries comprised the only two taxa for which settlement age had a significantly negative coefficient at an alpha-to-remove of 0.15 (*Ateles* sp., -1.02 , $F = 7.6$, $p = 0.02$; *T. pecari*, -0.54 , $F = 3.2$, $p = 0.09$). Spider monkeys have the lowest λ_{\max} value of any of the species considered (Robinson & Redford 1991), whereas white-lipped peccaries live in large, low-density herds that can rapidly succumb to local extinction resulting from recurrent slaughter of local herds following the establishment of new village settlements (Peres 1996).

There is little evidence, therefore, that repeated use and long-term depletion of a harvest area necessarily leads to lower yields in continuous tracts of undisturbed forest, provided that consumer numbers remain sufficiently low in relation to the size of game stocks. This is presumably because of the compensatory effects of immigration from adjacent underharvested (or nonhunted) areas. Indeed, at large spatial scales this pattern has so far been maintained for over 12,000 years of indigenous occupation and game harvest in Amazonia, which in low-productivity forests has been periodically relieved by the temporal dynamics of village resettlement (Roosevelt 1994).

Because density estimates incorporated into extinction projections (Fig. 5) were obtained from continuous tracts of forest, the extinction curve for persistently hunted forests did not take into account disruptions that the fragmentation process might cause to the flow of immigrants from nonhunted to overhunted areas. Yet dispersal from source populations is likely to be drastically reduced with changes in landscape structure and loss of connectivity between habitat patches (Dunning et al. 1992). Although local extinction and recolonization rates should be affected by the intensity and selectivity of the harvest, the size, shape, and productivity of hunting areas, and the ratio between the size of overharvested and underharvested areas, this form of source-sink dynamics is likely to be severely affected in highly fragmented forest landscapes. This effect may be further aggravated if remaining forest patches are small relative to the size of observed harvest areas and embedded in a hostile matrix of unsuitable habitat allowing little or no movement across patches.

In lowland Amazonia, primary-forest fragments are typically isolated by an inhospitable matrix consisting of grass- and shrub-dominated degraded pastures that are unlikely to be used or traversed by most terrestrial and all arboreal forest vertebrates. This is reflected in the surprisingly species-poor large-vertebrate faunas occurring in natural Amazonian savannahs even in the absence of hunting. Potential dispersal attempts from nearby areas of continuous forest are also unlikely to be successful, because exposed animals are more likely to be detected and killed even if they can move across degraded pastures. In reality, therefore, the predicted extinction curve

for hunted fragments (Fig. 5) should be considerably steeper and shifted farther to the left, thus requiring even larger forest fragments for any given level of species persistence.

What remains unclear is whether gradually dwindling populations stranded in fragments can be entirely extirpated before they become economically extinct or no longer worth pursuing. Subsistence hunters in Neotropical forests become less selective as local game stocks decline, resulting in the virtual disappearance of the most preferred species from village harvest profiles (A. Jerolimski & C.P., unpublished data). Opportunistic killing of increasingly rarer species is thus expected to continue as long as the incentive to harvest more abundant alternative species can be summoned.

These incentives can be maintained by mid-sized terrestrial species, such as agoutis and nine-banded armadillos, that can cope reasonably well with fragmentation and forest edges and that have relatively high reproductive rates. In addition, villagers harvesting chronically depleted areas are known to resort eventually to highly unprofitable species as small as spiny rats (*Proechimys* sp., Hiraoka 1995) and common possums (*Didelphis marsupialis*; Suárez et al. 1995), which are unlikely to be driven to local extinction by the combined effects of hunting and fragmentation (e.g., Fonseca & Robinson 1990). Species differences in hunter preference, population size, reproductive rates, and matrix tolerance should thus largely determine the nonrandom nested structure of residual species assemblages across the entire size range of overhunted fragments within a region.

Hunting-Mediated Local Extinctions in Fragments

Clear empirical support for the prediction that large vertebrates in Neotropical forest fragments cannot survive can be found in post-settlement regions that have already lost most of their forest cover. On the basis of a comprehensive survey of archived accounts from hunters and naturalists who witnessed the exponential contraction of the Brazilian Atlantic forest in the mid-1800s, Dean (1997) has repeatedly suggested that an interaction between hunting and fragmentation is driving forest vertebrates to regional extinction. Few Neotropical forest studies, however, have attempted to quantify patterns of large-vertebrate occurrence or abundance within fragments of variable size in old frontier regions that remain exposed to hunting (but see Glanz 1991; Oliver & Santos 1991; Cullen 1997; Pinto & Rylands 1997; Chiarello 1999).

Table 2 presents a brief compilation of some of the available evidence from Neotropical forests, which remains largely anecdotal. An apparently consistent trend suggests increasingly impoverished forest fragments in several regions as fragments continue to be assaulted by a range of disturbance patterns that almost always include

hunting (Gascon et al. 2000; Silva & Tabarelli 2000). Preferred target species have been extirpated from small forest patches of Mesoamerican forests in mainland Panama, even where hunting pressure is light (Glanz 1991; Wright et al. 2000). In the western part of the state of São Paulo, Brazil, Cullen (1997) found that tapirs, white-lipped peccaries, and brocket deer have been rapidly driven to local extinction in semideciduous Atlantic forest fragments averaging <2000 ha in size and exposed to heavy hunting pressure. In the highly fragmented Atlantic forest of southern Bahia, 99% of a set of 418 interviews conducted by L. P. Pinto (personal communication) indicated that large ungulates (tapirs and white-lipped peccaries) and midsized to large primates (yellow-breasted capuchins, howler monkeys, and woolly-spider monkeys) are virtually extinct within a 37,000-km² study region (Pinto & Rylands 1997). Although this was the first part of Brazil settled by Europeans, primate meat had been, or was still being, consumed by over half the population of low-wage rural workers in cacao plantations.

The Alagoas Curassow (*Mitu mitu*) is perhaps the most noteworthy example of a large Neotropical bird driven to global extinction in the wild by both habitat fragmentation and hunting. Historically, the species was endemic to a small forest region of northeastern Brazil (Alagoas and eastern Pernambuco) that was rapidly converted to sugar-cane monoculture in the seventeenth and eighteenth century. Although some relict populations survived in small, inadequately protected fragments well into the 1900s, one of the last records of the species was a bird killed by a hunter in 1984. The species is now thought to survive only in captivity under the guard of a few cracid collectors (Sick 1997).

In central Amazonia, spider monkeys, bearded sakis, and brown capuchins are excluded from 100-ha forest "reserves" following isolation (Rylands & Keuroghlian 1988), but local extinctions of large vertebrates at these sites were almost certainly accelerated by cattle-ranch

workers taking advantage of the initial overcrowding effect and easy pickings created by clear-cuts in adjacent properties (L. Emmons, personal communication). In western Brazilian Amazonia, interviews I conducted (1987–1993) with over 120 rubber tappers suggest that most midsized to large forest vertebrates had already been extirpated from the vast majority of small fragments (<300 ha) located along the extension of the Transamazon Highway into Acre (Rio Branco to Cruzeiro do Sul). Undoubtedly, most local extinctions of species larger than 1 kg were caused primarily by hunting. I suspect that the same would hold for most of the highly fragmented "deforestation arch" of Amazonia, from central and eastern Rondônia to northern Mato Grosso, and eastern and northeastern Pará, whether or not forest connectivity has been entirely eroded. On the conservative assumption that this effect extends 1 km from the nearest forest edge, then an area of at least 357,000 km² has already been defaunated of its large-game vertebrates by the combined effects of hunting and fragmentation throughout the entire Brazilian Amazon (Skole & Tucker 1993).

The same trends probably hold for other tropical forest regions, although data remain scarce. In western Madagascar, where vertebrates are also hunted for food within forest remnants, the presence of a large core area free of hunting disturbance is one of the most important conditions for primate conservation in fragments, and many fragments have lost their large-bodied lemur species to hunting (Smith 1997). Indeed, lemur species richness in this region is most severely affected by an index of "cultural impact," defined as the sum of all visible evidence of forest disturbance including hunting (Smith et al. 1997). Many of the bird and mammal extinctions in remaining forest fragments of Singapore—including three species of pheasant, three species of deer, and wild pig—were undoubtedly caused or accelerated by hunting (Corlett & Turner 1997; R. Corlett, personal communication). Hunting has also apparently increased extinc-

Table 2. Cases of local vertebrate extinctions within Neotropical forest fragments that were aggravated by subsistence hunting.

Neotropical region (forest type)	Local extinctions reported	Source
Veracruz, southern Mexico (evergreen forest)	<i>Tapirus</i> , <i>Tayassu pecari</i> , <i>T. tajacu</i>	Dirzo & Miranda 1991; Estrada et al. 1994
Mainland Panama (semideciduous forest)	<i>Tapirus</i> , <i>Tayassu pecari</i> , <i>T. tajacu</i>	Glanz 1991; Wright et al. 2000
Extension of BR-364 into Acre, western Brazilian Amazonia (Amazonian terra firme forest)	<i>Tapirus</i> , <i>Tayassu pecari</i> , <i>Cebus apella</i> , <i>Ateles chamek</i> , <i>Lagothrix lagotricha</i> , <i>Cacajao calvus</i> , <i>Dinomys branickii</i> , <i>Mitu tuberosa</i> , <i>Aburria pipile</i>	C. Peres, unpubl. data
Western State of São Paulo, Brazil (semideciduous Atlantic forest)	<i>Tapirus</i> , <i>Tayassu pecari</i>	Cullen 1997; Cullen et al. 2000
Espírito Santo, southeastern Brazil (evergreen Atlantic forest)	<i>Tapirus</i> , <i>Tayassu pecari</i> , <i>T. tajacu</i> , <i>Mazama</i> spp. <i>Priodontes</i> , <i>Dasyprocta</i>	Chiarello 1999
Southern Bahia, Brazil (evergreen Atlantic forest)	<i>Tapirus</i> , <i>Tayassu pecari</i> , <i>Cebus xanthosternos</i> , <i>Alouatta fusca</i> , <i>Brachyteles arachnoides</i>	L.P. Pinto, pers. comm.; Oliver & Santos 1991

tion rates of fragmented bird and mammal populations in parts of Sulawesi (T. O'Brien & M. Kinnard, personal communication), Uganda (C. Chapman, personal communication), and southern Mexico (A. Cuarón, personal communication).

My results suggest that the prospects for wildlife conservation in post-frontier tropical forest regions, such as southern and eastern Amazonia, look rather bleak unless hunting activities are regulated carefully. Given current trends, we can expect our legacy to be a landscape dominated by relatively empty forest patches.

If Amazonian vertebrate metapopulations within forest landscapes consisting of fragments with varying degrees of connectivity are ever to be harvested sustainably, their spatial structure will have to be explicitly considered when game management programs are designed. Some large, partially connected forest patches in private or public nature reserves should be entirely protected as refugia for source subpopulations that can supply occasional immigrants to smaller, less-productive or less-protected patches.

In a theoretical analogy, optimal harvesting of a metapopulation counter intuitively involves harvesting the more productive subpopulations less intensively than the less productive populations because of the importance of between-patch diffusion (Tuck & Possingham 1994). In some cases, patch colonization and extinction dynamics could be more significant for the regional persistence of a species than the internal dynamics of single patches (Gilpin & Hanski 1991). But most important, without solid regional networks of large, strictly protected forest reserves and wildlife sanctuaries, we are unlikely to contain the relentless hemorrhage of some of the most charismatic components of our tropical forest fauna.

Acknowledgments

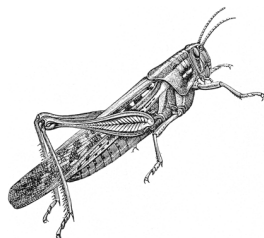
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Appendix

Nomenclature and body mass of 46 vertebrate taxa of the Brazilian Amazon considered in this study.

Vertebrate taxa and Common English name ^a	Genus	Species included	Mean adult body mass (g) ^b
Reptiles			
testudines			
tortoises	<i>Geochelone</i>	<i>G. carbonaria</i> , <i>G. denticulata</i>	4,580
Birds			
tinamids			
Small Tinamous	<i>Crypturellus</i>	<i>C. variegatus</i> , <i>C. cinereus</i> , <i>C. undulatus</i> , <i>C. soui</i>	205–540
Large Tinamous	<i>Tinamus</i>	<i>T. guttatus</i> , <i>T. tao</i> , <i>T. major</i>	800–2,000
phasianids			
Wood-quails	<i>Odontophorus</i>	<i>O. gujanensis</i> , <i>O. stellatus</i>	310
cracids			
Chachalacas	<i>Ortalis</i>	<i>O. guttata</i> , <i>O. motmot</i>	415
Common Guans	<i>Penelope</i>	<i>P. jacquacu</i> , <i>P. pileata</i>	1,250–1,280
Piping Guans	<i>Aburria</i>	<i>A. pipile</i>	1,200
Curassows	<i>Mitu</i>	<i>M. tuberosa</i>	3,000–3,060
	<i>Crax</i>	<i>C. globulosa</i> , <i>C. fasciolata</i>	
psophiids			
Trumpeters	<i>Psophia</i>	<i>P. leucoptera</i> , <i>P. viridis</i> , <i>P. crepitans</i>	990
Mammals			
edentates			
common armadillos	<i>Dasybus</i>	<i>D. novencinctus</i>	3,140
seven-banded armadillos	<i>Dasybus</i>	<i>D. kappleri</i>	10,900
giant armadillos	<i>Priodontes</i>	<i>P. maximus</i>	32,000
collared anteaters	<i>Tamandua</i>	<i>T. tetradactyla</i>	4,600
common sloths	<i>Bradypus</i>	<i>B. variegatus</i> , <i>tridactylus</i>	4,300
sciurids			
dwarf squirrels	<i>Microsciurus</i>	<i>M. flaviventer</i>	96
bolivian squirrels	<i>Sciurus</i>	<i>S. ignitus</i>	220
amazon red squirrels	<i>Sciurus</i>	<i>S. spadiceus</i>	600
rodents			
acouchies	<i>Myoprocta</i>	<i>M. pratti</i> , <i>M. acouchy</i>	950
agoutis	<i>Dasyprocta</i>	<i>D. fuliginosa</i> , <i>D. agouti</i>	3,200–4,500
paca	<i>Agouti</i>	<i>A. paca</i>	8,500
pacarana	<i>Dinomys</i>	<i>D. branickii</i>	8,000
ungulates			
collared peccary	<i>Tayassu</i>	<i>T. tajacu</i>	25,000
white-lipped peccary	<i>Tayassu</i>	<i>T. pecari</i>	32,000
gray brocket deer	<i>Mazama</i>	<i>M. gouazoubira</i>	18,000
red brocket deer	<i>Mazama</i>	<i>M. americana</i>	30,000
lowland tapir	<i>Tapirus</i>	<i>T. terrestris</i>	160,000
primates			
pygmy marmosets	<i>Cebuella</i>	<i>C. pygmaea</i>	150
saddle-back tamarins	<i>Saguinus</i>	<i>S. fuscicollis</i>	390
moustached tamarins	<i>Saguinus</i>	<i>S. mystax</i> , <i>S. imperator</i>	510
goeldi's monkeys	<i>Callimico</i>	<i>C. goeldii</i>	560
squirrel monkeys	<i>Saimiri</i>	<i>S. boliviensis</i> , <i>S. sciureus</i>	940
night monkeys	<i>Aotus</i>	<i>A. nigriceps</i> , <i>A. trivirgatus</i>	1,050
dusky titi monkeys	<i>Callicebus</i>	<i>C. cupreus</i> , <i>C. moloch</i>	950
collared titi monkey	<i>Callicebus</i>	<i>C. torquatus</i>	1,200
saki monkeys	<i>Pithecia</i>	<i>P. albicans</i> , <i>P. irrorata</i> , <i>P. monachus</i>	2,200
bearded saki monkeys	<i>Chiropotes</i>	<i>C. satanas</i> , <i>C. albinasus</i>	2,650
white uakaries	<i>Cacajao</i>	<i>C. calvus</i>	3,175
brown capuchins	<i>Cebus</i>	<i>C. apella</i>	2,910
white-face capuchin	<i>Cebus</i>	<i>C. albifrons</i>	2,700
howler monkeys	<i>Alouatta</i>	<i>A. seniculus</i> , <i>A. belzebul</i>	6,500
woolly monkeys	<i>Lagothrix</i>	<i>L. lagotricha</i>	8,710
spider monkeys	<i>Ateles</i>	<i>A. paniscus</i> , <i>A. chamek</i> , <i>A. marginatus</i>	9,020
procyonids			
kinkajou	<i>Potos</i>	<i>P. flavus</i>	2,600
olingo	<i>Bassaricyon</i>	<i>B. gabbii</i>	1,300
tayra	<i>Eira</i>	<i>E. barbara</i>	4,800
coati	<i>Nasua</i>	<i>N. nasua</i>	3,100

^aSpecies sharing the same ecological functional groups were assigned to a common taxon (or ecospecies).

^bBody mass data from Terborgh et al. (1990), Janson & Emmons (1990), Bodmer 1994, Peres (2000b), and C. Peres & H. Nascimento (unpublished data).