Impact of game hunting by the Kayapó of south-eastern Amazonia: implications for wildlife conservation in tropical forest indigenous reserves

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Abstract. Indigenous forest reserves represent approximately one fifth of Brazilian Amazonia and pose enormous challenges for sustainable natural resource management by native Amazonians. In collaboration with the Kayapó Indians of A'Ukre of southeastern Amazonia, we obtained a game harvest profile of over 1360 forest vertebrates consumed at this village over a 20-month period, including 743 mammals, 361 forest tortoises and 256 birds from a minimum of 42 game species. This amounted to a total of 13,775 kg of game animals harvested over the entire study (mean = 26.2 kg d^{-1}). We also obtained some 450 km of line transect census data of midsized to large-bodied vertebrates within the core hunting catchment of this village and in an unhunted but otherwise comparable site upriver of A'Ukre. Population density estimates of 16 of the 18 species censused were significantly depressed by hunting by central place foragers within the village catchment, and a number of harvest-sensitive prey species showed clear evidence of local depletion. For the time being, however, we can conclude that hunting was sustainable at the landscape scale largely because source-sink dynamics in the context of low village catchment density is made possible by large surrounding tracts of primary forest that remain unharvested or underharvested.

Introduction

Most Amazonian indigenous peoples have been officially conferred land tenure status over large territories under varying degrees of legal implementation. A total of 401 indigenous reserves have been legally designated in Brazilian Amazonia, accounting for a combined acreage of 104.3 million ha (= 20.8% of the region) or five times the area currently designated as strictly protected on paper (ISA 2004). Although over 99% of the native Indian population of Brazilian Amazonia (~180,000) inhabit these Indian Lands, they account for relatively low human densities (mean = 0.17 person km⁻²), providing encouraging prospects for sustainable management of natural resources, including game vertebrates.

The impact of rapidly changing patterns of resource extraction by indigenous peoples has become central to discussions on the long-term integrity of remaining tracts of tropical forests. While native Amazonians can be seen as legitimate allies of conservationists as legally empowered guardians of many biologically important wildlands (Schwartzman et al. 2000; Zimmerman et al. 2001), they can profoundly change forest structure and composition in the long run (Peres 1994; Terborgh 1999). This debate is particularly relevant to low-density animal populations that are selectively harvested over large areas, raising growing concerns over the role of indigenous reserves in biodiversity conservation.

Protein acquisition by indigenous peoples in lowland Amazonia relies heavily on wild meat from forest vertebrates (Redford and Robinson 1987; Jerozolimski and Peres 2003). Subsistence hunting becomes even more important in unflooded (*terra firme*) forest areas where aquatic sources of animal protein are often scarce. Subsistence hunters have access to most areas of Amazonia, affecting even the core of many nature and indigenous reserves (Peres and Lake 2003). Indeed, populations of many large-bodied tropical forest vertebrates have declined precipitously even in structurally undisturbed forests (Peres 2000a), a phenomenon that has become increasingly recognized at a pantropical scale (Fa and Peres 2001; Milner-Gulland et al. 2003).

The demographic viability of many game vertebrate populations depends on the rate at which different target species are harvested per unit time, the total hunting area exploited (hereafter, catchment area), and the site-specific annual productivity of different target species. In this paper, we examine the patterns of game harvest by the Kayapó Indians of southeastern Amazonia, and the extent to which these can be defined as sustainable. We focus on the Kayapó Indians because their impact as game hunters has been framed as a central issue in a prominent debate over the long-term role of indigenous reserves in tropical biodiversity conservation (Schwartzman et al. 2000; Terborgh 2000; Peres and Zimmerman 2001). We rely on a detailed game harvest profile obtained from Kayapó villagers at A'Ukre, with whom we have been working continuously over the past 11 years (Zimmerman et al. 2001). Game population densities were derived from wildlife surveys conducted in both an unhunted and a persistently hunted site, and then compared with sustainable harvest estimates for different game species. We then provide a general discussion on how the impact of subsistence hunting in Amazonian indigenous reserves can be mitigated.

The Kayapó of A'Ukre

The Kayapó are traditionally semi-nomadic hunter-gatherers who historically occupied the vegetation transitions between the central Brazilian scrublands (*cerrado*) and the seasonal forests of southeastern Amazonia (Vidal 1977). However, the Kayapó were gradually pushed by frontier expansion into their present closed-canopy forest domain, and they currently number some 3900 Indians scattered among 15 villages (Zimmerman et al. 2001). These are



Figure 1. Location of the study area (upper left inset map) along the Riozinho river, within the Kayapó Indian Land. Larger map shows the extent and distribution of indigenous territories in southeastern Brazilian Amazonia, including all officially recognized Indian Lands of southern Pará and northern Mato Grosso inhabited by the Kayapó.

distributed over six officially recognized Indian Lands of southern Pará and northern Mato Grosso, and comprise a combined acreage of 11,346,326 ha (Figure 1). This study was conducted at A'Ukre (7°41′15″ S; 51°52′25″ W), an average-sized Kayapó village located 220 km west of the nearest town (Redenção), and along the Rio Riozinho, a second-order tributary of the upper Rio Xingú. A'Ukre is one of six Indian villages located within the Kayapó Indian Land, a territory of 3.3 million ha inhabited by some 1946 Kayapó. During the study period, A'Ukre consisted of 133 villagers (mean density = 0.04 person km⁻²) belonging to 17 family units (mean = 7.9 people per family) distributed around a circular arrangement of family households. Children and dependent young represented 62.4% of the village population, which included 21 male hunters.

The Kayapó of A'Ukre territory is closed to outside hunters and forest extractors; river access is lengthy and treacherous because of rapids, waterfalls and lack of paved roads, and the village is accessible only by small aircrafts stationed at Redenção. Hunting at A'Ukre dates from the late 1970s and early 1980s when the village was formed by migrant families from the neighboring village of Kuben-Krã-Kein, located 5 days upriver by canoe. A'Ukre villagers control some 300,000 ha of the Kayapó Indian Reserve, which is unofficially bounded by three neighboring village territories (Moikarako, Kuben-Krã-Kein and Gorotire). The extent to which these areas are controlled by different communities became an issue only during the past two decades when communities began to vie for ownership of broadleaf mahogany trees (*Swietenia macrophylla*, Meliaceae), the most valuable forest resource in this region (Zimmerman et al. 2001).

Methods

Field sites

The study sites consisted primarily of highly seasonal transitional evergreen forests sustained primarily by clay soils. Canopy cover in this region is highly heterogeneous including more open forests dominated by *Attalea maripa* palms and large numbers of woody lianas; high *terra firme* forests, where large emergents such as Brazil-nut trees (*Bertholletia excelsa*, Lecythidaceae) were common; and small *cerrado* enclaves in areas of shallow soils that often expose the surface bedrock (Brasil 1974). Approximately, 70% of the A'Ukre territory is covered in forest, the remaining consisting of *cerrados* that are largely restricted to upland plateaus and rocky ridges (100–200 m a.s.l.). The *cerrados* are largely undisturbed and remain ungrazed by domestic livestock, whereas forest areas are largely undisturbed except for highly selective logging of mahogany trees along valley bottoms. Mean rainfall averages 1640 mm (N = 10 years) with a clearly demarcated dry season (June–September) that typically include 100 consecutive days without rain.

Game harvest profile

Game harvest at A'Ukre was examined during 542 days spread over a period of 20 consecutive months (November 1994–July 1996; Figure 2). This includes

a more intensive sampling period of 324 days over 14 months (June 1995–July 1996). All village households were visited on a daily basis and cooperation from villagers was facilitated by our long term working relationship with the Kayapó of A'Ukre (Zimmerman et al. 2001). In total, data on 1360 prey items were obtained. All terrestrial vertebrate kills brought into A'Ukre were identified, sexed, and weighed with a size-graded set of *Pesola*[©] scales (accurate to 10, 50 and 100 g). Additional information was obtained directly from hunters using a standard questionnaire, including hunter identity, the approximate location of the site where a given prey item was encountered, and weapon used. Kayapó hunters have an excellent cognitive map of the areas they hunt, and positional data on reported kill sites were verified in August 2000 when the entire A'Ukre catchment was mapped using GPS fixes of all main hunting sites. All 21 hunters living at A'Ukre during the study took part in data collection. A body weight survey of all inhabitants of A'Ukre was carried out in August 1996.

The number of animals of each species consumed at A'Ukre over the entire study was corrected to a full year (365 days) to provide an annualized observed harvest (OH) rate. The annual harvest rate per unit area within the core catchment (117 km²; see below) was also estimated. Estimates of the biomass harvested (kg km⁻²) were also calculated by multiplying the number of animals harvested by the species-specific mean body mass obtained from fresh, whole



Figure 2. Monthly variation in daily game biomass harvested at A'Ukre between November 1994 and June 1996. Two ungulate species – tapir and white-lipped peccary – accounted for a disproportionately large contribution to the overall harvest. Shaded squares and open circles indicate the sampling effort allocated to the harvest profile (in days) and mean monthly river water-level at the Pinkaití field station, respectively.

carcasses weighed during the entire study. Sample sizes for body mass data exceeded 10 weighed kills for 26 of the 42 vertebrate species in the harvest profile.

We also examined patterns of hunter selectivity considering the body mass of all target species for which both observed harvest and population density estimates were available. This was calculated using the Ivlev's selectivity index (S_i) , which ranges from -1.0 to +1.0 and compares availability (A) with utilization (U) as in $S_i = (U - A)/(U + A)$ (Bodmer 1995).

Hunting catchment area

The A'Ukre core catchment area was mapped with the aid of a GPS receiver and included (i) the forest area covered during single-day hunting forays within a radius of 8 km from A'Ukre and the Riozinho river for the most frequently hunted areas; and (ii) an additional 1-km wide forest strip of 8 km up and down from the village along the west bank of the river, where hunting was consistently restricted to shorter inland incursions. This resulted in an estimated core catchment area of 117 km². Data on kill locations obtained from A'Ukre hunters during daily interviews indicated that 68% of all animals captured (or 79% of the aggregate game biomass consumed at A'Ukre) were harvested within this core catchment. Hunting treks into more distant forest areas accounted for 210 kills (15.9%) taken during only 15 of the last 324 days of study, and were treated separately in the analysis. These data were thus excluded from calculations of sustainable harvest rates within the core catchment, but included in the total number of kills and game biomass consumed at A'Ukre.

Population density estimates

Line-transect surveys were conducted along several transects of 4–5 km in length, placed at two study sites with different histories of hunting pressure: (1) Pinkaití, a virtually unhunted area located 12–18 km upriver of A'Ukre, and (2) A'Ukre, a persistently hunted area in the vicinities of, and up to 5.5 km from, the center of this village (Figure 1). Although Pinkaití had been occasionally visited by A'Ukre hunters for as long as 20 years, hunting at this site had been discontinued 5 years prior to censuses when Pinkaití became a research station with continuous investigator presence (Zimmerman et al. 2001). Our total census effort amounted to a cumulative walking distance of 248.5 km at Pinkaití, conducted over four consecutive years (1994–1997), and 199.4 km at A'Ukre conducted over two years (1997–1999). Density estimates at these sites were then compared to examine the abundance responses of vertebrate species to persistent game harvest within the A'Ukre catchment area. This assumes that game density estimates were primarily a function of

hunting pressure rather than differences in forest structure and composition. This assumption appears to be valid because the Pinkaití and A'Ukre census areas were similar in terms bird, mammal and tree species composition, canopy gap structure, and distances from the river (Baider 2000, H. Nascimento and C. Peres, unpubl. data).

To avoid detection biases along hunting trails, all censuses were carried out on purpose-cut transacts which had been measured and marked every 50 m with the help of a $Hip - Chain^{\text{(B)}}$ to aid mapping of animal locations. Census walks were carried out on rainless days at a mean velocity of ca. 1250 m h⁻¹, with brief stops every 50–100 m to maximize detection of all acoustic or visual cues. During each encounter with a prey species (groups or individuals), we noted the time of day, species identity, group size, perpendicular distance (PD) to the trackline (with the aid of a Range Finder^(B)), and distance along the transect. Observations were terminated within 12 min of each detection event and, in the case of social species, only accurate group counts were used to estimate mean group size. Census walks were conducted in the morning (0700– 1100 h) and in the afternoon (1400–1800 h), corresponding to intervals of maximum activity for diurnal game species. Further details on survey methodology can be found in Peres (1999).

Population density estimates (ind. km^{-2}) at each area were derived using the Distance software, v. 3.5 (Laake et al. 1994) for all species that met the recommended minimum number of independent sightings (25–30) for reasonably robust model fits (Buckland et al. 1993; S. Buckland, pers. comm.). Because modeling independent detection events becomes increasingly difficult for smaller samples, we used the most effective strip-width method (Whitesides et al. 1988) for a few uncommon species by determining the fall-off point in the PD histograms. This consisted of the PD interval where the sighting frequency was equal to or less than 50% of the preceding level, and was used to calculate the effective strip-width (Whitesides et al. 1988). The species-specific census area was then used to estimate the overall density of each species on the basis of their detection frequencies.

Detection data for red brocket deer (*Mazama americana*) and grey brocket deer (*M. gouazoupira*) were pooled because identifications to species level during censuses were not always possible. The same was applied to both species of curassows (*Mitu tuberosa* and *Crax fasciolata*) and the two sympatric congeners of common guans (*Penelope pileata* and *P. superciliaris*) occurring in both census areas.

Sustainable harvest estimates

For a set of 24 game species (consisting of a single species or functionally equivalent congeners), observed harvest rates per km² (OH) were compared with maximum sustainable harvest (MSH) estimates derived from estimates of maximum production rates (P_{max}) using the Robinson and Redford (1991)

model. P_{max} was calculated on the basis of the maximum finite rate of increase (λ_{max}) and the local population density of each species. For the two most important ungulate species harvested by the Kayapó, these P_{max} estimates were marginally higher than those estimated using the Bodmer (1994) method (i.e. tapir: 0.082 vs. 0.074 ind. km⁻² year⁻¹; white-lipped peccary: 4.67 vs. 3.59, ind. km⁻² year⁻¹). Here we assume that density estimates obtained from field censuses at the unhunted site serve as a baseline for the A'Ukre village catchment. These best-available density estimates sidestep the use of 'predicted densities', as recommended by Robinson and Redford (1991) when no other density estimates are available, which in Amazonian *terra firme* forests tend to overestimate the MSH of game species (Peres 2000b).

Maximum intrinsic rates of increase (r_{max}) for mammal and some gamebird species were obtained from Robinson and Redford (1986) and Begazo and Bodmer (1998), respectively. Because r_{max} values were not available for a few game species, we considered approximate values from a closely related species.

Results

Kayapó game hunting

Hunting is arguably the most important subsistence activity for the Kayapó providing the bulk of their protein requirements. Hunting was carried out primarily by married men and throughout the year, although alternative aquatic sources of animal protein became very important during the dry season when the low water-level facilitates fishing (Figure 2). Although both traditional and modern hunting technology was used, most game vertebrates were killed with fire weapons (16- to 44-gauge shotguns), with the most frequently used weapon (20-gauge shotguns) accounting for 53% of all kills. However, tortoises were hand-captured and stored for later consumption, and three armadillo species were killed primarily with the aid of iron diggers. The use of bow-and-arrows was not recorded during the study, although white-lipped peccaries swimming across rivers were killed with traditional hardwood clubs. Hunting and feeding taboos against any given game species or body parts were rarely reported, but were related to special contexts such as newborn babies, illnesses in the family, and elderly persons.

Most Kayapó hunts consist of single-day incursions on foot into forest trails fanning out from the village, but some forays were aided by motorized dugout canoes that were largely restricted to areas near the village, usually due to fuel shortages. In single-day hunts, hunters (alone or in small groups) leave the village at 0600-0800 h and return just before dusk, thus limiting their effective range to distances that can be covered on foot within at most 12 h of daylight. On average, hunters went out on single-day hunts twice weekly and covered a maximum radius of 8–10 km from the village. In addition, Kayapó hunters also go on occasional hunting treks into more remote areas well outside the

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core village catchment, usually prior to traditional village feasts that required large amounts of meat. During these treks, most A'Ukre adult and adolescent males collectively move to a temporary base camp set up far from the village (12–26 km), from which they repeatedly disperse alone or in pairs, typically over a period of 3–28 days (mean = 7 days).

Patterns of game harvest

A total of 1360 forest vertebrates were consumed by the Kayapó of A'Ukre during the study, including 743 mammals (54.6% of all kills), 361 testudine reptiles (26.5%) and 256 birds (18.8%). These included 21 mammal, at least 19 bird, and two tortoise species (Table 1). Prey items obtained by Kayapó hunters weighed an average of 11.41 kg (\pm 24.29 kg, N = 1096), but ranged widely from Crested Oropendula (*Psarocolius decumanus*) weighing less than 0.3 kg to lowland tapir weighing over 175 kg. As shown in the overall distribution of prey body mass (Figure 3), however, potential prey items smaller than 1 kg were rarely taken by hunters who were able to concentrate primarily on a few species of large mammals, and two species of forest tortoises (*Geochelone* spp.) that were consumed primarily during ceremonial feasts involving all village members (Figure 4).

Kayapó hunters clearly exhibited a bias towards large-bodied target species as shown by an abrupt step transition from negative to positive Ivlev's indices of selectivity as the size of prey species increased. Prey body mass alone explained more than half of the overall variation in prey selectivity (r = 51.7%, $F_{1,22} = 23.5$, N = 24, p < 0.001), and mammal species larger than 30 kg



Figure 3. Size distribution of forest vertebrate kills consumed by the Kayapó of A'Ukre, in terms of the $(\log_{10}$ -transformed) body mass of all whole carcasses (adults and juveniles) individually weighed at the village.



Figure 4. Total number of kills (open circles) and prey biomass (shaded bars) harvested at A'Ukre during this study. Species are ranked according to their overall biomass contribution to the village offtake.

(giant armadillo, tapir and white-lipped peccary) were associated with highly positive selectivity values on the basis of their local population density. Red brocket deer comprised the only large-bodied forest prey species that was selected against. In contrast, small-bodied species (<3 kg) were always associated with negative selectivity values, and were often deliberately bypassed during hunting forays.

Brown capuchin monkeys, both tortoise species, and great long-nosed armadillos were the numerically dominant prey items, although large ungulates accounted for most of the biomass consumed (Figure 4). Primates, tapirs, peccaries, xenarthrans and large caviomorph rodents comprised the most important mammalian prey. In contrast, agoutis and all three species of cervids, including the white-tailed deer that was restricted to the cerrado plateaus of the A'Ukre territory, contributed with only a small number of kills. Capture of small rodents, marsupials, bats, canids, felids and mustelids were never reported or observed, although large cats such as puma and jaguar were perceived as a threat and occasionally killed. A'Ukre hunters also killed a number of bird species for food, including cracids, trumpeters, macaws and oropendulas, although gamebirds accounted for a modest contribution to the total biomass harvested. A small number of toucans, parrots, and oropendulas were also killed primarily for their feathers which were traditionally used in ornamental handcraft. In terms of biomass, 86.3%, 11.5% and 2.3% of the total game offtake was derived from mammal, reptile, and bird species, respectively (Table 1). Primates comprised the most important mammalian order in numeric terms accounting for 22.4% of all kills. Three ungulate species – lowland tapir, white-lipped peccary and collared peccary – comprised 11.7% of all kills and 56.2% of the total biomass harvested, and tapirs alone contributed with a staggering one third of the total game biomass consumed at A'Ukre (Figure 2). The monthly white-lipped peccary harvest, which provided the second highest contribution in terms of biomass (16.4%), was relatively erratic (Figure 2), and coincided with episodic hunting treks preceding ceremonial feasts or the occasional appearance of large herds moving through the village catchment.

A total of 13,775 kg of game animals were harvested over the entire study (mean = 26.2 kg day⁻¹), including 6323 kg harvested during the last 324 days of sampling (mean = 19.5 kg day⁻¹). Given that approximately 30% of this crude biomass is non-edible (Townsend 2000), we estimate that some 9642 kg of fresh game meat was actually consumed by the 133 Kayapó living in A'Ukre, resulting in a mean daily per capita rate of 138 g of game meat consumed. The number of animals killed within the A'Ukre catchment area accessed during single-day hunts represented 67.8% of the total harvest or 3.8 animals km⁻². This corresponded to 42.4 kg km⁻² or 78.5% of the total game biomass consumed at the village.

Effects of hunting on local game stocks

The aggregate game stock in the A'Ukre catchment within 6 km of the village (94 ind. km⁻²) was less than half of that at the unhunted Pinkaití site (223 ind. km⁻²). Population density estimates for 16 of 18 game species censused at both forest sites were significantly higher at Pinkaití (paired *t*-test, t = 3.38, P_{adj} , = 0.003, N = 18; Table 2). Surveys at A'Ukre failed to detect four game species (or signs of their presence) – tapir, white-lipped peccary, giant armadillo, and giant ant-eater – and this is consistent with information provided by Kayapó hunters. For most group-living target species, the smaller mean group sizes and lower group densities (Table 2). Consequently, the standing aggregate game biomass density at A'Ukre (232 kg km⁻²) was only 21% of that at Pinkaití (1098 kg km⁻²), reflecting a substantial overall difference in game biomass density of -59% from the unhunted to the hunted site.

Harvest-sensitive species including all midsized to large-bodied primates, tapir, white-lipped peccary, giant armadillo, razor-billed curassow, redthroated piping guan and tortoises showed the largest relative differences between Pinkaití and A'Ukre (Table 2 and Figure 5). On the other hand, coatis (*Nasua nasua*) and small tinamous (*Crypturellus* spp.) were actually more abundant in the heavily hunted area. However, small gamebirds such as small tinamous and marbled wood-quail (*Odontophorus gujanensis*) were not

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November 1994–June 1996).		4 5			3) I
Species	English name	Body mass (g) ^a	No. of kills	% of kills	Total biomass (kg)	% of biomass
Mammals						
Primates						
Cebus apella	Brown capuchin monkey	2711	203	14.9	550.24	4.0
Chiropotes satanas utahicki	Bearded saki monkey	2412	66	7.3	238.75	1.7
Alouatta belzebul	Red-handed howler monkey	6533	ю	0.2	19.60	0.1
Perissodactyls						
Tapirus terrestris	Lowland tapir	139,600	33	2.4	4606.80	33.4
Artiodactyls						
Tayassu pecari	White-lipped peccary	31,400	72	5.3	2260.80	16.4
Pecari tajacu	Collared peccary	16,237	54	4.0	876.83	6.4
Mazama americana	Red brocket deer	36,000	10	0.7	360.00	2.6
Mazama gouazoupira	Gray brocket deer	14,500	9	0.4	87.00	0.6
Odoicoleus virginianus	White-tailed deer	30,000	1	0.1	30.00	0.2
Xenarthrans						
Dasypus kappleri	Great long-nosed armadillo	10,907	126	9.3	1374.30	10.0
Dasypus novemcinctus	Nine-banded armadillo	3140	14	1.0	439.60	3.2
Pridodontes maximus	Giant armadillo	31,500	5	0.4	157.50	1.1
Myrmecophaga tridactyla	Giant anteater	30,500	6	0.7	274.50	2.0
Tamandua tetradactyla	Collared anteater	3100	-	0.1	3.10	0.0
Rodents						
Agouti paca	Paca	6820	54	4.0	368.28	2.7
Dasyprocta agouti	Red-rumped agouti	2875	7	0.5	20.13	0.1
Hydrochaeris hydrochaeris	Capybara	50,000	1	0.1	50.00	0.4
Lagomorphs						
Sylvilagus brasiliensis	Brazilian rabbit	1200	1	0.1	1.20	0.0
Carnivores						
Nasua nasua	South American coati	3047	39	2.9	118.82	0.9
Potos flavus	Kinkajou	2600	4	0.3	10.40	0.1

Panthera onca	Jaguar	35,000	1	0.1	35.00	0.3
Total (mammals) Birds Craoids			743	54.6	11,882.85	86.3
Mitu tuberosa	Razor-billed Curassow	2611	26	1.9	62.89	0.5
Crax fasciolata	Bare-faced Curassow	2678	13	1.0	34.81	0.3
Penelope superciliaris and P. pileata	Rusty-margined and White-crested Guan	1097	52	3.8	57.02	0.4
Pipile cujubi	Red-throated Piping-Guan	1222	32	2.4	39.11	0.3
Trumpeters						
Psophia viridis	Dark-winged Trumpeter	1167	2	0.5	8.17	0.1
r suudoius						
Ara ararana	Blue-and-yellow Macaw	1233	8	0.6	9.87	0.1
Ara chloroptera	Red-and-green Macaw	1218	18	1.3	21.93	0.2
Ara macao	Scarlet Macaw	1187	14	1.0	16.62	0.1
Anodorhynchus hyacinthinus	Hyacinth Macaw	1500	9	0.4	9.00	0.1
Aratinga spp., Pyrrhura spp. and Amazona spp. Ramphastids	Parakeets and parrots	I	57	4.2	30.75	0.2
Ramphastos vitellinus and R. tucanus Icterids	Channel-billed and Red-billed Toucan	400	S	0.4	2.00	0.0
Psarocolius decumanus and Gymmostinops bifasciatus Anatids	Crested and Amazonian Oropendula	267	12	0.9	3.20	0.0
Cairina moschata	Milscovy Diick	2067	9	0 4	12 40	0.1
Total (birds)			256	18.8	312.77	2.3
Reptiles Testudines						
Geochelone carbonaria	Red-footed tortoise	4913	201	14.8	987.51	7.2
Geochelone denticulata	Yellow-footed tortoise	3698	160	11.8	591.88	4.3
Total (reptiles)			361	26.5	1579.39	11.5
Overall total		Ι	1360	100.0	13,775.01	100.0
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'Mean body mass (g) of all carcasses (or live captures in the case of tortoises) weighed at A'Ukre.

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Species	No. of events	detection	Mean grc	oup size	ESW (m)		Group de (Groups	ensity km ⁻²)	Populatic density (ind. km ⁻	п -2)	Populatio mass ^a (kg	n bio- km ⁻²)	% Change ^b
	Pinkaití	A'Ukre	Pinkaití	A'Ukre	Pinkaití	A'Ukre	Pinkaití	A'Ukre	Pinkaití	A'Ukre	Pinkaití	A'Ukre	
Cebus apella	99	18	7.3	5.2	24.0	20.0	5.0	2.3	36.6	11.7	99.2	31.7	-68.1
Chiropotes s. utahicki	16	ю	23.5	6.3	35.0	35.0	0.92	0.21	16.5	1.3	39.8	3.2	-91.9
Alouatta belzebul	18	0	7.8	3.0	35.0	35.0	1.03	0.14	8.0	0.4	52.3	2.7	-94.8
Tapirus terrestris	6	0	1.0	1.0	38.0	I	0.62	0.00	0.62	0.0	86.6	0.0	-100.0
Tayarsu pecari	1	0	150	Ι	45.0	I	0.04	0.00	5.9	0.0	185.3	0.0	-100.0
Pecari tajacu	10	0	4.0	3.0	14.0	14.0	1.2	0.36	8.5	1.1	137.7	17.5	-87.3
Mazama spp.	37	6	1.0	1.0	20.0	13.0	3.2	1.7	4.5	1.7	129.7	50.2	-61.3
Nasua nasua	0	6	12.5	3.5	9.0	9.0	0.45	2.5	5.7	8.9	17.4	27.2	56.8
Dasyprocta agouti	274	68	1.05	1.0	13.0	13.6	41.2	12.5	43.3	12.5	124.5	35.9	-71.2
Agouti paca ^c	7	1	1.0	1.0	1.0	1.0	4.5	0.5	4.5	0.5	30.7	3.4	-88.9
Priodontes maximus ^d	5	0	1.0	Ι	5.0	I	1.6	Ι	1.6	0.0	50.4	0.0	-100.0
Crax fasciolata and	55	5	2.0	1.8	15.6	15.6	7.1	0.8	9.0	1.44	23.8	3.8	-84.0
Mitu tuberosa													
Penelope spp.	64	36	2.8	1.7	17.4	10.3	8.0	8.3	22.3	14.2	24.5	15.6	-36.3
Pipile cujubi	18	б	2.0	1.6	24.6	24.6	1.5	0.31	2.8	0.52	3.4	0.6	-81.4
Psophia viridis	40	12	6.4	4.7	14.8	12.0	4.4	2.5	33.1	11.8	38.6	13.8	-64.4
Tinamus spp.	61	20	1.05	1.07	23.5	23.5	14.4	10.8	15.1	11.6	18.1	13.9	-23.2
Crypturellus spp.	34	19	1.06	1.2	12.5	12.5	9.8	14.6	10.4	17.5	4.0	6.7	68.3
Geochelone spp.	6	7	1.0	1.0	3.5	3.5	7.5	1.4	7.5	1.43	32.3	6.2	-80.9
Total	I	I	I	I	I	I	I	I	223.3	93.6	1098.1	232.4	-58.1
^a Population biomass (lensity wa	is calculated	d on the ba	asis of me	an (male a	nd female) weights o	of carcases	obtained	at A'Ukre			

^bRelative shift in population density (or biomass) from Pinkaití to A'Ukre. ^cDensity estimate based on the number of fresh tracks (<24 h) recorded within 5 m of all transects. ^dDensity estimate based on the number of recently dug holes (<24 h) recorded within 5 m of all transects.



Figure 5. Population density estimates $(\log_{10} x + 1)$ for game species in an unhunted (Pinkaití) and a persistently hunted forest site (A'Ukre). Species are ranked from the most negative to the most positive abundance differences (open circles) between the unhunted and hunted sites. Only 2 of the 18 game vertebrate taxa censused were more abundant in the A'Ukre catchment area.

harvested at A'Ukre, which suggests that populations of most target species had been moderately to severely reduced by hunting in the A'Ukre catchment area. Furthermore, body size of game species (expressed as \log_{10} mean body mass) explained most of the variation in the direction and magnitude of differences in both population density ($r^2 = 0.53$, $F_{1,22} = 24.8$, p < 0.001) and biomass between Pinkaití and A'Ukre ($r^2 = 0.59$, $F_{1,22} = 31.9$, p < 0.001). The intrinsic rates of natural increase (r_{max}), on the other hand, had no apparent effect on these differences in abundance (density shifts: $r^2 = 0.001$, $F_{1,22} = 0.02$, p = 0.878; biomass shifts: $r^2 = 0.003$, $F_{1,22} = 0.08$, p = 0.784).

Game yield in relation to distance from A'Ukre

On the basis of 822 carcasses obtained during day-hunts and hunting treks for which the location of the kill was known, we estimate that game vertebrates consumed at A'Ukre were brought down at an average distance of 10.2 km (SD = 8.6 km; range = 1–25 km) from the village, and for many important species, game yields were substantially higher in hunting zones that were increasingly farther from the village. This is illustrated for four desirable and





Figure 6. Relationship between prey capture efficiency (expressed as kills obtained per day spent hunting) and physical accessibility to different hunting zones, defined as their straight-line distance from the village of A'Ukre, for (a) brown capuchin monkey, (b) bearded saki monkey, (c) lowland tapir, (d) both species of forest tortoises, and (e) all game species combined. The total prey biomass captured (f) as a function of distance from the village is also shown using the same metric.

frequently harvested species by the variation in prey capture success (defined as the number or biomass of kills obtained per unit of hunting time) as a function of the straight-line distance between kill sites and the village. In these terms, locally depleted prey species such as brown capuchin monkey, bearded saki monkey, tapir, and *Geochelone* tortoises—which contributed with 50.6% of the total game biomass harvested—were most cost-effectively harvested in the most distant hunting sites (Figure 6a–d). The same relationship applies to most target species for which we have data on kill location, whether we consider the total number of kills retrieved (Figure 6e) or the aggregate biomass they represented (Figure 6f). Furthermore, prey body size explained a significant proportion of the species variance in mean linear distance between A'Ukre and kill sites ($r^2 = 15.4\%$, $F_{1,26} = 4.75$, p = 0.039, N = 28). In other words, largebodied species were more likely to be captured by these central-foragers far away from the village, presumably because stocks in the immediate vicinity of A'Ukre had already been heavily depleted.

Sustainability of game harvest

To evaluate the degree to which Kayapó hunting practices could be defined as sustainable, observed annualized harvest rates (per km²) for frequently

harvested target species were compared with estimates of maximum production (P_{max}) and MSH within the core hunting catchment of 117 km². Of the 16 species listed in Table 3, 9 were harvested well below their MSH, 3 were harvested at levels approaching their MSH, and harvests of 4 clearly exceeded their MSH. Only tapirs were harvested at levels far greater than the MSH calculated for this species (11.2 times), whereas both tortoise species, brown capuchin monkeys and piping guans were overhunted at levels 18–31% above their respective MSH. Harvest rates could be interpreted as sustainable for most species for which it was possible to estimate the MSH, but due to limitations of the harvest model we applied these results must be interpreted with caution (see below).

Comparisons between the observed and sustainable harvest rates were poor predictors of the marked differences in independent estimates of game population densities at A'Ukre and Pinkaití, which clearly suggest that most stocks of key target species had been moderately to severely depleted in the village catchment. For example, the OH/MSH ratio, which describes the proportion of a sustainable offtake that was actually removed, explained only 14% of the variation across target species in the population density ratios between A'Ukre and Pinkaití ($F_{1,22} = 3.57$, p = 0.072, N = 24). Moreover, although there was a wide variation in population density differentials for species that could not be defined as overharvested, 14 of the 19 species harvested at levels below their MSH were still far less abundant in the hunted site.

Discussion

Game vertebrates are the most valuable non-timber products in Amazonian forests (Peres 2000a), raising serious concerns over the long-term subsistence needs of tribal and non-tribal communities as game stocks become depleted due to longer village persistence times, greater consumer pressure and greater access to more efficient hunting and transportation technology (Jerozolimski and Peres 2003). The Kayapó of A'Ukre are in a state of economic flux, with wage labor and an increasingly diverse portfolio of household income gradually replacing traditional subsistence activities. The mean aggregate annual household income in 2000 was highly variable but relatively high for an Amazonian Indian group (US 3253 ± 2560 ; Morsello 2002), compared to the average annual per capita income in Brazil of US\$2850. This can be seen as either good or bad news depending on the long-term wisdom and resource management stewardship of the Kayapó as they maintain sovereignty rights and control access over a large territory. But despite an increasing degree of market integration and reliance on external commodities, all but one of the 15 Kayapó Indian villages of southeastern Amazonia can still rely heavily on forest wildlife to meet their daily protein requirements. For the time being, this is clearly tied to the low density of village catchments and resource users $(\sim 0.035 \text{ km}^{-2})$ across the entire the Kayapó Reserve.

consumed by the regard of f	CMC.								
Species	BM (kg)	Density (ind. $\rm km^{-2}$)	$\lambda_{ m max}{}^{ m a}$	$P_{ m max}$	Numeri (ind. kn	c harvest n^{-2})	Biomass (kg km ⁻²	harvest)	% removed ^b
					НО	MSH	НО	HSM	
Mammals									
Cebus apella	2.7	29.2	1.15	2.63	0.65	0.53	1.75	1.42	122.7
Chiropotes satanas utahicki	2.4	16.5	1.19	1.83	0.27	0.37	0.65	0.88	73.6
Tapirus terrestris	139.6	0.6	1.22	0.08	0.18	0.02	25.55	2.29	1117.7
Tayassu pecari	31.4	5.9	2.32	4.67	0.29	0.93	9.07	29.35	30.9
Pecari tajacu	16.2	8.5	3.49	12.67	0.15	2.53	2.50	41.14	6.1
Mazama americana	36.0	3.0	1.49	0.89	0.05	0.35	1.73	12.74	13.6
Mazama gouazoupira	14.5	1.5	1.63	0.57	0.01	0.23	0.15	3.31	4.4
Dasypus kappleri	10.9	8.0	1.86	4.12	0.24	1.65	2.63	17.98	14.6
Dasypus novemcinctus	3.1	21.8	1.99	13.03	0.07	5.21	0.21	16.36	1.3
Nasua nasua	3.0	5.7	1.26	0.89	0.15	0.18	0.47	0.54	86.6
Dasyprocta agouti	2.9	43.3	3.00	52.01	0.06	20.80	0.17	59.81	0.3
Agouti paca	6.8	4.5	1.95	2.56	0.50	0.51	3.42	3.50	97.7
Gamebirds									
Crax/Mitu ^c	2.6	9.0	1.46	2.48	0.21	0.50	0.56	1.31	42.7
Penelope spp. ^d	1.1	22.3	1.49	6.54	0.38	1.31	0.41	1.44	28.7
Pipile cujubi	1.2	2.8	1.54	0.90	0.21	0.18	0.26	0.22	118.1
Testudine reptiles									
Geochelone spp.	4.4	7.5	1.73	3.30	0.86	0.66	3.78	2.89	130.9
^a Values taken from Robinson ^b Percentage of the MSH rate i	and Redford (1 that was consun	991) and Begazo and and A'ukre; valu	nd Bodmer (es >100% ii	1998). ndicate overl	hunting.				

Table 3. Estimates of annual production (P_{max}), observed harvest (OH) and maximum sustainable harvest (MSH) for the 16 most important prev taxa

^cIncludes Bare-faced curassow (*Crax fascicolata*)and Razor-billed curassow (*Mitu tuberosa*). ^dIncludes both sympatric congeners, Rusty-margined guan (*Penelope superciliaris*) and White-crested guan *Penelope pileata*.

Terrestrial vertebrates were undoubtedly the most important subsistence resources extracted from the forest by the Kayapó of A'Ukre, although the transaction value of broadleaf mahogany roundlogs and cold-pressed Brazil nut oil was more significant (Zimmerman et al. 2001; Morsello 2002). During this study, the Kayapó of A'Ukre harvested some 9.6 tons of game meat per year from a minimum of 42 forest vertebrate species, although the eight most important species - belonging to five vertebrate genera (Tapirus, Tayassu, Dasypus, Cebus and Geochelone) – accounted for 84.8% of the total biomass offtake. Kayapó hunters were able to specialize on large-bodied prey items, with ungulates alone comprising 60% of the overall game biomass harvested (Figure 2). This was possible despite a small amount of time spent hunting; hunters allocated only 4% of their overall time budget to hunting activities, corresponding to about a third of the 11% of time invested in all subsistence activities (Morsello 2002). The highly skewed kill profile towards large mammals, Geochelone tortoises, and large gamebirds at A'Ukre corroborates previous studies showing that neotropical hunters prefer large-bodied species wherever these are still available (e.g. Peres 1990; Bodmer 1995; Mena et al. 2000), but switch to smaller-bodied prey of higher reproductive productivity, once preferred game species have been depleted (Jerozolimski and Peres 2003). This considerable degree of prey size selectivity is all the more remarkable considering that the overall size structure and relative abundance of Amazonian large vertebrate communities are heavily skewed towards small-bodied game species (Fa and Peres 2001).

The sheer importance of large ungulates, large armadillos and forest tortoises for the Kayapó can be partly explained by the relatively high biomass density of large terrestrial vertebrates in the A'Ukre territory compared to central-western Amazonian forests censused to date using the same methods (Peres 1996, 2000a, b). This is probably a reflection of the highly seasonal rainfall and highly heterogeneous landscape mosaic consisting of different vegetation types, and high levels of discontinuity in canopy structure even in high terra firme forests, all of which can favor large terrestrial browsers and/or frugivores. Large terrestrial frugivore/granivores at Pinkaití and A'Ukre will also benefit from relatively high levels of soil nutrient availability and a high abundance of large arborescent palms (Baider 2000), which provide clumped but super-abundant fruit resources during several months of the year. For example, 63 of the 72 white-lipped peccary kills were recorded from November to April (Figure 2), a period coinciding with, or immediately following, the extended fruiting season of inajá palms, Attalea maripa (Salm 2002). Undoubtedly, the spatial distribution of large concentrations on the ground of mature Attalea fruits affected both the landscape-wide movements of the large, highly mobile herds of this species, and the probability of hunters encountering them (Peres 1996).

Meat consumption was highly seasonal throughout the year, peaking during the wet season. However, there was a strong compensatory effect of aquatic sources of animal protein, such as key species of fish (e.g. tucunaré, *Cichla*

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ocellaris) and aquatic turtles (*Podocnemis* spp.), which were consumed by villagers all year-round but became particularly important during the dry season when the low river water level facilitated catches (Figure 2). For example, the mean water level (a good predictor of fishing efficiency) was positively correlated with the number of terrestrial previtems harvested at A'Ukre (r = 0.428). p = 0.06, N = 20) on a monthly basis, indicating that availability of aquatic prey effectively relieved local demand for forest wildlife. The overall game offtake resulted in a mean per capita rate of daily protein intake from forest wildlife of 27.6-34.5 g, assuming that (i) the wild game meat harvested was shared equally among all villagers older than 3 years, and (ii) a range of 20-25% of protein content in fresh wild meat (Leung and Flores 1961). This clearly underestimates the total amount of animal protein consumed because it fails to consider offtakes of aquatic fauna which was beyond the scope of this study. Moreover, a socio-economic survey showed that most of the 23 A'Ukre households made monthly purchases of frozen chicken (80%), bovine meat (60%) or tinned fish (20%) from traders in Redenção (Morsello 2002), which undoubtedly also alleviated protein demand and hunting pressure on wild game. In any case, game meat consumption comfortably exceeded the minimum daily per capita intake of 20 g of protein from high-quality sources as recommended by the World Health Organization (WHO 1973).

Brown capuchin monkeys accounted for the greatest numeric contribution from a single species to the A'Ukre wildlife harvest, although tapirs and whitelipped peccaries, followed by armadillos and tortoises, yielded the largest amount of meat consumed. The heavy reliance on large ungulates and primates is consistent with other studies on patterns of subsistence hunting in Amazonian forest, which show that large mammals often account for over 60% of the kills and over 90% of the meat biomass consumed by different indigenous groups (Vickers 1984; Redford and Robinson 1987; Jerozolimski and Peres 2003).

Successful prey acquisition for this group of central-place foragers, rather than taking place in conveniently accessible sites near the village, appears to be heavily skewed to distant areas near the catchment boundaries between frequently hunted zones visited during day-hunts, and infrequently hunted zones visited during multi-day hunting treks. This is entirely consistent with other Amazonian hunting studies that have considered the spatial structure of the harvest (e.g. Hames and Vickers 1982; Alvard 1994; Souza-Mazurek et al. 2000). However, game yields as a function of radial distance from the village was significantly affected by prey body mass, with smaller, higher-fecundity species more likely to be harvested nearer the settlement.

Yet the heavy reliance on some harvest-sensitive species is at odds with predictions from the sustainable harvest model applied to closed populations and the relatively long settlement history at A'Ukre. Having persisted at their current location and exploited roughly the same catchment area for over 23 years, A'Ukre villagers continue to frequently harvest primates and the two largest ungulate species. These are often severely depleted by hunting at other

Amazonian forests (Peres 1996, 2000a, b) due to their low reproductive rates. low densities, relatively long life span, and ease of capture (Peres 1990; Bodmer 1994; Bodmer et al. 1997). For example, the tapir harvest around A'Ukre $(19.54 \text{ kg km}^{-2} \text{ year}^{-1})$ has been sustained at levels 14 times greater than the MSH predicted for this species (1.40 kg km⁻² year⁻¹). Under the same conditions. A'Ukre hunters would require a catchment area of 1630 km² to maintain a sustainable offtake. However, tapirs continue to be harvested at very high levels although they have become extremely rare in the vicinities of A'Ukre. This suggests that most of the tapirs killed in the core catchment were immigrants drawn from surrounding underharvested (or unhunted) areas as predicted by healthy patterns of landscape scale dispersal across a range of exploitation levels (Novaro et al. 2000; Salas and Kim 2002). This is only possible because of the vast area of uninhabited primary forest surrounding the village catchment, which serves as a year-round source of immigrants. However, this source-sink dynamic would be expected to break-down in other landscape contexts under conditions of considerably larger villages and higher village densities should neighboring village catchments ever coalesce to the point of eliminating interstitial source areas (Peres 2001).

In addition to tapir, 3 of the 24 game species evaluated using the Robinson and Redford (1999) model were unsustainably harvested: brown capuchins, bearded saki monkeys and piping guan. These were frequently killed by Kayapó hunters and their populations were also heavily reduced in the persistently hunted area. Platyrrhine primates typically have low annual birth rates, long periods of infant development, long inter-birth intervals and long, socially mediated delays of first reproduction (Robinson and Redford 1986), which combined with their easily detectable groups, makes them particularly prone to overhunting (Peres 1990). Both the harvest model and field censuses thus indicate that these species had been overhunted.

Nevertheless, the proportion of the sustainable harvest estimates known to be removed by hunters (OH/MSH) was a generally poor predictor of the density differentials between the hunted and unhunted sites surveyed. There are several reasons why model predictions from village kill profiles could be at odds with such density estimates. First, any two forest sites are bound to support slightly different baseline vertebrate abundances even if they are comparable in terms of structure and floristic composition and only 12–16 km apart. Second, the low observed harvest rates of some species simply reflected low local availability – resulting from small residual populations that had already been depleted prior to this study – rather than hunter preference. This appears to be the case of at least giant armadillos and both species of curassow. Finally, the number of fatally wounded individuals that could not be retrieved by hunters (and therefore missing from village samples) was not taken into account in this study and this can range from 10% (Townsend 2000) to over 40% of all retrieved kills (C. Peres, unpubl. data).

The collection of *Geochelone* tortoises, which is a crucial part of ceremonial feasts at A'Ukre, is an additional issue of concern. Because of their low

metabolic rates and ease of capture once they are detected, these heterotherms can be conveniently brought into the village and kept alive for up to several months until they were roasted in large numbers in an open bonfire marking the 'tortoise feast'. Such ritual events are an integral part of Kayapó village culture and provide the motivation for long hunting treks into rarely exploited parts of the village territory, Yet *Geochelone* populations appear to be declining even in distant hunting grounds accessed from seasonal camps used during hunting treks. For example, Jerozolimski (2004, unpubl. Thesis) monitored the rate of tortoise captures per unit effort (CPUE) during hunting expeditions by A'Ukre hunters in four consecutive years and estimated a decline in successful captures from 3.37 to 2.20 tortoises per 100 h of hunter search time between 1999 and 2002. Assuming a negative linear slope for the annual CPUE rate over this period ($\beta = -0.384$, $r^2 = 96.8\%$, N = 4), we conclude that an additional search time of 38 h and 24 min is required each year in order to capture every additional tortoise.

Tortoises collected near A'Ukre were also considerably smaller (mean = 2.8 kg) than those collected during hunting treks into more remote areas (mean = 5.0 kg; Nascimento 1999), suggesting directional change of body size in a heavily harvested population resulting from greater adult mortality in the severely depleted inner catchment. This illustrates the rather severe local depletion rates for game species in the peripheral A'Ukre catchment even for wide ranging species such as forest tortoises which exhibit high dispersal rates and little site-fidelity in terms of their year-round home range (A. Jerozolimski, pers. comm.).

Although several studies have concluded that large neotropical forest gamebirds such as cracids are easily overhunted because of their slow rate of population recovery (Silva and Strahl, 1991; Begazo and Bodmer 1998), cracids accounted for 68.7% of the total avian biomass harvested and only one of the five genera occurring in the Kayapó Reserve appeared to be overexploited (although chachalacas, Ortalis motmot, were never taken). The offtake rate of red-throated piping guans (Aburria pipile) was slightly higher than the maximum sustainable harvest estimated for this species on the basis of observed densities, but those of both sympatric common guans (Penelope superciliaris and P. pileata) and both curassow species (Mitu tuberosa and Crax fasciolata) were considerably lower. The model indication that curassows had not been harvested unsustainably should, however, be interpreted with caution. These large cracids can serve as good indicators of hunting pressure (Silva and Strahl 1991; Strahl and Grajal 1991), and the small number of kills recorded can also mean that curassows had already been severely depleted. This is consistent with the fact that hunters rarely bypassed an opportunity to kill a curassow, whereas this was often the case with smaller cracids and other gamebirds.

The Robinson and Redford model showed some limitations in evaluating hunting sustainability but successfully pinpointed those species that had been overharvested. In any case, widely extrapolated density and r_{max} estimates based on populations in optimal habitat conditions or captive animals can

result in severe overestimates of potential game production. Even when local density estimates of game species can be incorporated into the model, it is difficult to evaluate the impact of hunting on those species that were not diagnosed as unsustainably harvested (Slade et al. 1998). The short-term nature of this study accounts for further limitations in that residual game stocks may be a legacy of the history of hunting in the recent past when the number of villagers at A'Ukre was 250 strong, or almost twice the village size during the study. In fact, although the proximate cause of the village sub-division in 1995 was an acrimonious dispute between two influential, kinship-based groups of households, it could be argued that this fission - which resulted in the resettlement of approximately half of the village - was instigated by local game scarcity resulting from excessive numbers of consumers (B. Zimmerman, pers. comm.). The harvest rate is also not a static constant and is expected to fluctuate over time as a result of changes in prey availability and consumer population size (Vickers 1988; Winterhalder et al. 1988; Robinson and Redford 1994). Harvest models should thus be refined with considerations of such spatial and temporal dimensions.

Conclusions

The contiguous area 13 million ha of the Kayapó reserve of southeastern Pará, and the upper Xingú Indian reserves of northern Mato Grosso (Figure 1) is larger than that of any strictly protected area in the humid tropics, and has become the main deterrent to frontier expansion in the southeastern Amazon (Peres and Zimmerman 2001). The aspirations of different Kayapó villages have been strengthened through collaborative projects with conservation organizations seeking to safeguard the long-term integrity of their natural resources (Zimmerman et al. 2001). However, it remains unclear to what extent extractive practices such as game hunting will be sustainable in the long run if the village size and village density increases, and the cost-benefit ratio of resettling a village increases and villages become increasingly sedentary due to investments in local infrastructure, and access to schools and medical services.

Subsistence hunting by the Kayapó of A'Ukre has already depressed local game stocks, although observed landscape-scale patterns of game acquisition can be considered to be sustainable for the time being provided that village catchment areas do not overlap and can be expanded (cf. Hill et al. 1997; Emídio-Silva 1998). The severe local depletion of tapirs and white-lipped peccaries is perhaps the most serious subsistence problem currently faced by A'Ukre villagers, but for now this is compensated by the vast extent of pristine forest ecosystems around the village catchment, most of which remains unhunted and faunally intact. A possible solution to dilute local hunting pressure at A'Ukre would be to increase the village catchment area by increasing the length and utilization of hunting trails on the western bank of the river, a forest area that was rarely hunted. Another solution would be to increase the harvest

of locally undesirable species (if their poor acceptance can be overcome) such as brocket deer (*Mazama* spp.), collared peccaries and agoutis, which were harvested at levels well below those predicted to be sustainable. The importance of a source-sink population structure for key target species can be illustrated by the high yields sustained under conditions of low village density, which may be the best available option in the absence of enforceable game management policy.

Measuring the regional scale sustainability of subsistence hunting is critical to wildlife conservation in Amazonian forests. Indian reserves represent over one fifth of the Brazilian Amazon or 52% of the total area under any form of non-private protection, and comprise large and often strategically placed wildlands containing relatively undisturbed forests (Peres 1994). Natural resources management can only link biodiversity conservation to the needs of local people if crucial resources are not overexploited to the point of collapse. The perceived value of the forest to indigenous people can therefore become considerably reduced as game populations are overexploited if not eventually driven to local extinction. This will also strengthen the joint cause of conservationists and aborigine-rights advocacy groups for maintaining large Indian Lands in Amazonian forests against encroachment by more insidious agricultural interests that often see this alliance as a conspiracy to thwart development. Further studies on the impacts of extractive activities are required to implement appropriate wildlife management programs to ensure the preservation of both biological and cultural diversity in Amazonia.

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