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Allocation of hunting effort by Amazonian smallholders: Implications for conserving wildlife in mixed-use landscapes

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ABSTRACT

Most tropical forest landscapes are modified by humans, but the effects of these changes on rural hunting patterns and hunted vertebrate populations remain poorly understood. We investigated subsistence hunting patterns across a highly heterogeneous landscape mosaic in the Brazilian Amazon, where hunters from three villages had access to primary forest, active and fallow agricultural fields, and active and fallow *Eucalyptus* plantations. Landscape composition and the areas used by hunters were defined using a remote-sensing approach combined with mapping. We quantified hunting effort accounting for the availability and spatial distribution of each habitat. Overall, 71% of the kills were sourced in primary forest, but hunting in primary forest, which was often combined with other extractive activities (such as Brazil nut harvesting), yielded the lowest catch-per-unit-effort of all habitats. Hunting effort per unit area was highest in fallow fields, followed by primary forest, and both of these habitats were over-represented within village hunting catchments when compared to the composition of the available landscape. Active and fallow fields sourced a limited number of species known to be resilient to hunting, but hunting had additional benefits through crop-raider control. In contrast, hunting pressure in active and fallow plantations was low, despite a high catch-per-unit-effort, presumably because there were limited additional benefits from visiting these habitats. These results indicate that large-scale tree plantation and forest regeneration schemes have limited conservation potential for large vertebrates, as they support few forest specialists and fail to attract hunters away from primary forest.

1. Introduction

Unprecedented rates of deforestation in the tropics have led to increased coverage of agriculture, cattle pasture, plantations and regenerating native vegetation (Achard et al., 2002; Perz and Skole, 2003; Fearnside, 2005; FAO, 2006). Conservation attitudes have recently broadened to encompass this expanding acreage of anthropogenic habitats (Lindenmayer and Franklin, 2002), focusing on land-cover under production (Rice and Greenberg, 2004; Vandermeer and Perfecto, 2007), tree plantations (Brockerhoff et al., 2008) and regenerating secondary forests (Wright and Muller-Landau, 2006).

Tropical secondary forests can support a high abundance of wildlife (Fimbel, 1994; Parry et al., 2007), influencing forest dynamics and the rate of regeneration (Howe and Smallwood, 1982; Wunderle, 1997; Stoner et al., 2007). However, the conservation value of habitats in landscape mosaics could be compromised by the hunting practices of local people, because large vertebrate populations can be severely depleted by hunting, potentially disrupting forest regeneration (Peres and Palacios, 2007; Terborgh et al., 2008). Overhunting can also compromise food security (Fa et al., 2003) as large-bodied mammals and birds are a major source of dietary protein to tribal and nontribal communities in the tropics (Redford and Robinson, 1987; Jerozolimski and Peres, 2003; Robinson and Bennett, 2004). Secondary forests appear to supply significant quantities of wild meat to consumers in Africa (Wilkie, 1989), Asia (Endicott and Bellwood, 1991) and South America (Gavin, 2007). Small-scale agricultural plots can subsidize protein acquisition through "garden hunting" (Linares, 1976), which provides additional benefits in controlling local populations of crop-raiders (Smith, 2005). However, conservation scientists are yet to compare the utility of primary forest to hunters against that of adjacent active and abandoned large-scale production land-uses (recovering from clear-felling, cattle pasture or tree plantations). Our understanding of the relationship between hunting and wildlife conservation in complex landscape mosaics is thus extremely limited.

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Animal mortality in a landscape is determined by the spatial distribution of hunting effort (Winterhalder, 1997; Siren et al., 2004). In previous studies, the spatial coverage of each habitat in hunted landscapes has either been estimated from interviews with some farmers (Gavin, 2007) or from remote-sensing, but with limited reference to the distribution of the available habitat (Wilkie, 1989; Escamilla et al., 2000; Smith, 2008). This is an important omission as the spatial composition of the landscape is likely to influence hunter habitat-preferences in the same way that travel distance influences habitat choice by animal foragers (Rosenberg and McKelvey, 1999; Matthiopoulos, 2003). Hunters attempt to minimize travel costs (Haener et al., 2001) and most communities are closer to farm-fallow habitats than to primary forest (e.g. Wilkie, 1989; Naughton-Treves et al., 2003; Smith, 2008), thereby favouring a hunting bias towards disturbed habitats. In addition, hunters prefer areas where returns are highest (“rate-maximizers”; Alvard, 1995), and open anthropogenic habitats may be the most productive hunting grounds (Lovejoy, 1985; Robinson and Bennett, 2004; Wilkie and Lee, 2004) due to the high production of terrestrial browse and lower density of inedible woody biomass.

We investigate the efficiency and allocation of hunting effort in a highly heterogeneous landscape mosaic in the Brazilian Amazon. We critically assess the importance of mosaic habitats for central-place human hunters and examine implications for conserving hunted wildlife. We compare large areas of primary forest with agricultural land farmed by smallholders, industrial-scale plantation forests, small areas of agricultural regrowth (hereafter referred to as fallow fields) and large patches of secondary forest (>1000 ha) following abandonment of clear-cut plantations (hereafter referred to as fallow plantations). Specifically, we test the following hypotheses: (1) Hunters in highly heterogeneous landscape mosaics allocate their time based on the availability, distribution and foraging efficiency (mean prey size and catch-per-unit-effort, CPUE) associated with each habitat; (2) Open anthropogenic habitats are more efficient hunting grounds than closed-canopy primary forest for some large terrestrial vertebrates; and (3) Prey offtake from agricultural and non-primary habitats is less diverse than that taken from primary forest. Finally, we explore the implications of hunting patterns for the conservation of hunted mammals and birds in tropical landscape mosaics.

2. Methods

2.1. Study area

We assessed the hunting patterns of three nontribal communities in a 2500 km^2 landholding controlled by a large forestry company (Jarí Celulose) in the Rio Jarí region of north-eastern Brazilian Amazonia (00°27′00″–01°30′00″ S, 51°40′00″–53°20′00″ W; Fig. 1). There are around 5600 people belonging to 30 semi-subsistence rural communities embedded within the Jarí landscape. The principal demographic and landscape features of the three study villages – Bananal, São Militão and Vila Nova – are described in Table 1. These are “mixed activity villages” (*sensu* Coomes et al., 2004) as they pursued hunting, fishing, forest extraction, as well as small-scale agriculture (for consumption and local sale). Aside from hunting, the collection of Brazil nuts (*Bertholletia excelsa*, Lecythidaceae) was the most important extractive activity in the region.

The Jarí landscape offers a unique opportunity to compare hunting in large-scale areas of regenerating forest with relatively pristine primary forests and the farm-fallow mosaics of smallholder agriculture. All three communities had immediate access to five habitat types: primary forest, active and fallow *Eucalyptus* forestry plantations, and active and fallow agricultural fields. There were very few constraints on the use of these habitats: There were no access-right restrictions to active or fallow *Eucalyptus* plantations. Within communities, villagers would rarely hunt in the active fields of a neighbour. Hunting in primary forest was unrestricted, though interviews and observations indicate that hunters did not enter the hunting grounds of neighbouring villages. Hunting was for subsistence, and the sale of wild meat was almost non-existent in our study villages. Commercial hunting is illegal in Brazil, and these laws were enforced by Brazil’s Institute of the Environmental and Renewable Natural Resources (IBAMA) in Monte Dourado.

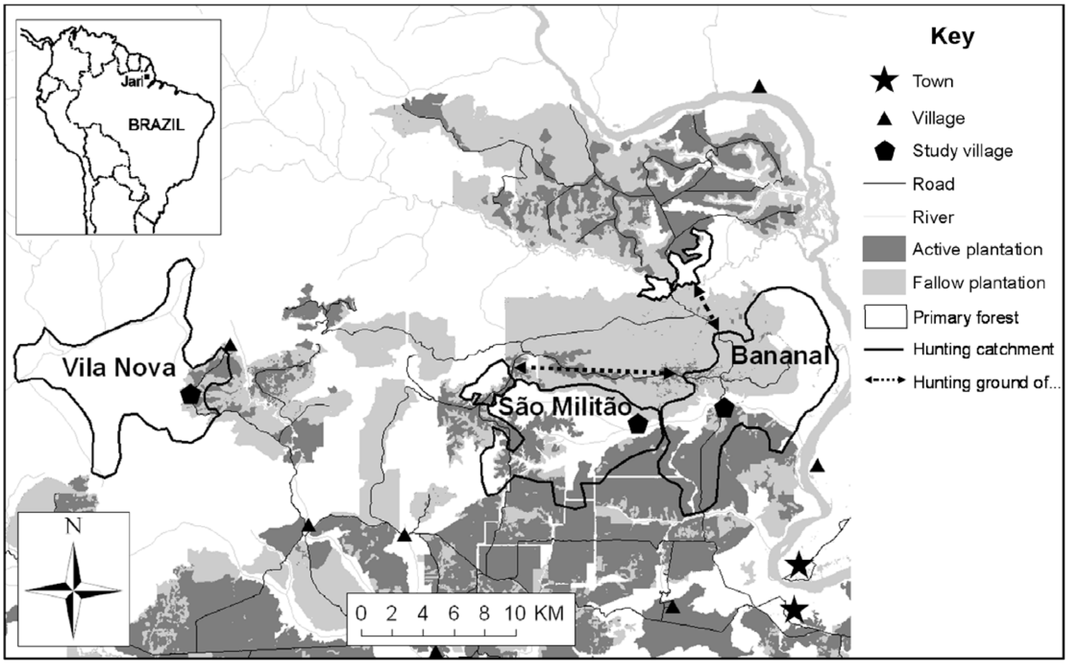

Fig. 1. Study area in the north-eastern Brazilian Amazon. Habitats are primary forest (PF); active *Eucalyptus* plantations (AP); fallow plantations (FP); active fields (AF); and fallow fields (FF).

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Table 1
Demographic characteristics of three villages in the Brazilian Amazon and habitat coverage in the surrounding landscape (LS) covering all habitat within 10 km of each village, and the actual catchment where they are known to hunt (HC). The differences of these habitat compositions are compared using *G*-tests.

	Bananal				São Militão				Vila Nova				Mean		
Community Age				43				50				50			
# Families				13				9				19			
# Hunters				14				10				14			
Estimated size of HC (km^2)				95.4				60.1				77.5			73.7
	% LS[a]	% HC[b]	HC/LS[c]	Access time (min)	% LS	% HC	HC/LS	Access time (min)	% LS	% HC	HC/LS	Access time (min)	% LS	% HC	HC/LS
Primary forest	32.9	37.1	1.1	6	17.1	46.7	2.7	2	76.1	79.8	1.1	17	42.0	52.9	1.6
Active plantation	25.9	25.0	1.0	4	40.2	28.8	0.7	18	7.2	5.5	0.8	1	24.4	20.3	0.8
Fallow plantation	33.4	30.4	0.9	12	38.5	15.0	0.4	7	9.7	4.4	0.5	5	27.2	17.8	0.6
Active field	1.3	0.9	0.7	7	0.6	1.4	2.3	3	1.0	2.4	2.4	14	1.0	1.5	1.8
Fallow field	6.6	6.6	1.0	4	3.6	8.2	2.3	3	6.0	8.0	1.3	14	5.4	7.5	1.5
	G	*df*	*p*		*G*	*df*	*p*		*G*	*df*	*p*		*G*	*df*	*p*
G tests	0.89	4	0.93		37.14	4	<0.001		4.78	4	0.31		42.79	14	<0.001

[a] % LS = Percentage of the landscape occupied by each habitat, within a 10 km radius of the village.

[b] % HC = Percentage of the actual hunting catchment occupied by each habitat.

[c] HC/LS = Hunting catchment coverage over landscape coverage.

Primary forests typically consisted of upland (terra firme) forests dominated by Lecythidaceae, Sapotaceae, Mimosaceae and Lauraceae trees. *Eucalyptus* plantations were on 5–7 year rotations and covered ~50,000 ha. Fallow plantation patches often exceeded 1000 ha, accounted for ~55,000 ha of the Jarí landscape, were typically younger than 20 years-old and were dominated by pioneer species such as *Bellucia* spp., *Cecropia* spp., *Inga* spp. and *Vismia* spp. Agricultural plots were typically small (1–3 ha), cultivated for 3–5 years, and planted with crops such as manioc, maize, and beans. Fallow fields were generally small (1–3 ha) and of variable age (5–15 years).

2.2. Harvest data

Following community meetings, we trained a local assistant in each study village to collect information on hunting trips made by members of their communities from 1 January to 31 December 2005. Assistants were chosen after consultation with elected community leaders. Prior to commencing data collection LP spent several days in each community, developing datasheets intelligible to assistants and hunters. The three villages were relatively small (⩽19 households each; total households = 41) and we were able to work with all households, each of which was visited nearly every day. Household members were interviewed by the local assistant about each hunting foray, irrespective of whether they had been successful. Questions included the hunt duration and timing, main habitat visited, local names of the areas visited, maximum distance from the village on the basis of time (all hunters carried a wristwatch) to return directly to the village, vertebrate species pursued, and whether prey items were captured or wounded but not captured.

Failing to account for collateral mortality leads to an under-estimation of prey offtake, especially for hunters using shotguns (Rist et al., 2008). Hunters presumed an animal was fatally wounded if, following a shot, they observed blood on the ground after wounded prey had fled. Whenever possible ($n = 770$), all undressed carcasses were weighed using Pesola scales (0–10 kg; and 0–50 kg). These weight data were combined with published data (Peres, 2001; Hilty, 2003) to produce mean body mass for prey species, which we used as the basis for analyses of offtake.

In addition to the daily visits by our local assistants, LP visited each village at least twice monthly to reinforce data quality control and verify information on the data sheets through discussions with both the assistant and hunters. Particular effort was taken to ensure that small-bodied species (e.g. red-rumped agouti *Dasyprocta agouti*) were not omitted from harvest records, as they are often less "memorable" than larger prey. We also visited each household in each village as a means of affirming trust, and cross-checking hunt data.

2.3. Mapping the landscape

We developed a land-cover map of our study area by combining a 2003 Landsat 7 (30 m pixel) satellite image and detailed land-use data (plantations and secondary forests) from the Jarí Celulose Spatial Planning Unit. Land cover other than *Eucalyptus* plantations was classified into primary forest, agriculture and secondary forest using a supervised classification of the Landsat image in ARC GIS 9.1 (ESRI, Redlands, California), and extensive ground-truthing around the village agricultural mosaics and the wider landscape. We used this information to assess the landscape composition within the hunting area around each village.

We complemented land-cover data with collaborative mapping because local people often retain detailed cognitive maps of their environment, and reference to geographic features and local landmarks can provide information useful to our understanding of hunting patterns (Smith, 2003; Siren et al., 2004). At least five hunters per village were accompanied (⩾10 trips per village in total); we used a GPS (Garmin 12XL) with an external antenna to ground-truth habitat classifications, map the locally-named areas of primary forest and other habitats, record area boundaries, and obtain positional data of previous kills. We used the outermost points of these data to define the cumulative area hunted (catchment) for each village, though we removed areas between these points for which we had no records of being hunted (Fig. 1). LP accompanied hunters during both the wet and dry seasons, to account for seasonal variation in the hunting areas. The locations and names of hunting areas were cross-referenced with other hunters with the aid of printed maps.

2.4. Hunting effort

For our calculations of hunting effort, based on hunter observation, we assume that hunters began hunting as soon as they entered their target habitat, and continued to hunt on the outward and return leg of their hunting foray within this habitat. We calculated the access time to habitats by estimating the distance and duration of the walk from each village to the nearest hunted patch

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of each habitat (Table 1). Our estimate of hunting effort per habitat was the duration of a hunting foray assigned to a habitat minus twice the access time (to account for outward and return journeys). We have not attempted to estimate the potential hunting effort in other habitats en route to the target habitat. It is unlikely that this biased our estimates of hunting effort in primary forest and the active and fallow plantations for Bananal or São Militão, as these habitats were not used to access other more distant forest types. However, hunts in primary forest from Vila Nova involved going through the agricultural matrix so we likely under-estimate hunting effort for these habitats around this village. Furthermore, we may slightly over-estimate hunting effort throughout, as we do not incorporate a measure of handling time (Rist et al., 2008). A meaningful estimate of handling time is difficult to attain without accompanying all hunts, which was not possible in this study. But observed preparation time was always less than 30 min per prey item (LP, pers. obs.), and so contributed a maximum of 14% of total hunting time (925 kills in 6386 h).

2.5. Data analysis

We used a likelihood-ratio (G) test to examine differences between the area of each habitat type available within a 10 km radius of each village and their actual contribution to each hunting catchment. This radial extent can be justified as 95.4% of the hunts in Jarí went no further than 10 km from a village. We predicted the amount of time hunters in each village should allocate to hunting activities in each habitat based on the relative area availability of each habitat within each village's hunting catchment (HAi), and the associated prey capture success. We calculated the relative catch-per-unit-effort of each habitat (CPUEi) based on the mean biomass of animals harvested per unit time (kg h^{-1}) in habitat i divided by the mean biomass harvested per hour in all habitats ($i \ldots j$). The expected amount of hunting time (HTi) allocated to each habitat i was then calculated as:

$$\mathrm{HT}i = \text{total time hunting} \times [(\mathrm{HA}i + \mathrm{CPUE}i) / \sum(\mathrm{HA}i \ldots j + \mathrm{CPUE}i \ldots j)]$$

We used the non-parametric Kruskal–Wallis test to compare differences in prey size across habitats. We performed Mann–Whitney U tests to compare the size of prey between habitat-pairs relevant to our hypotheses. Bonferonni adjustments were used to correct alpha levels (Mann–Whitney U; $\alpha = 0.05$, 7 tests therefore revised $\alpha = 0.0125$) in order to reduce the likelihood of Type I error as a result of multiple tests (Rice, 1989). We plotted rank-abundance plots to compare community evenness in each habitat, with the relative abundance of each species on a logarithmic scale plotted against the species rank. We analysed prey community composition using PRIMER v.5 (Clarke and Warwick, 2001). Non-metric multidimensional scaling (MDS) was used to visually explore differences in prey community structure among habitat types. Bray–Curtis was used as the coefficient for a similarity matrix as it ignores joint absences. We used analysis of similarities (ANOSIM, Clarke and Warwick, 2001) to test for significant differences in prey community composition among habitats.

3. Results

In total, we monitored 41 households for 1 year (14,965 household-days). We recorded 1105 hunting forays by 37 different hunters (from 34 households), accounting for 6386 man-hours (mean foray duration = 5 h 47 min). Hunters from the three participating villages killed at least 925 animals, with a combined weight of 14,187 kg. This overall mortality included 82 unretrieved animals (9%) that had escaped following what was reported to have been a lethal wound. All animals were killed using shotguns (16–32 gauge), with the exception of tortoises (*Geochelone* spp.) which were simply collected when sighted. Several hunters from each community occasionally hunted with dogs. Hunting from São Militão and Vila Nova was exclusively by foot. From Bananal, 61% of the hunts were on foot, though hunting sites were also reached by bicycle (38%) and very occasionally, by car (1%). Nocturnal hunts were carried out in all habitats; active plantations (79% nocturnal), fallow plantations (53%), primary forest (38%), fallow fields (30%), and active fields (15%). The strategy of waiting by flowering or fruiting trees was used by hunters in a small number of hunts during June and July, and comprised over 15% of monthly hunts from August to December. 118 (11%) of hunts recorded in this study were nocturnal waits, which were largely restricted to primary forest (107 hunts, 91%).

3.1. Prey communities

Of the 30 vertebrate species consumed, 28 were killed at least once in primary forest, 14 were killed in fallow fields and fallow plantations, nine were killed in *Eucalyptus* plantations, and seven were killed in active fields (Table 2). Prey community composition was significantly different among habitat types in the Jarí landscape (ANOSIM, $R = 0.38$, $p < 0.001$) and there was a decrease in species richness and prey community evenness from primary forest through to agricultural fields (Fig. 2).

White-lipped peccaries (*Tayassu pecari*) accounted for the highest proportion (40%, 5536 kg) of the biomass offtake (Table 2). Many species were harvested in all habitats, including white-lipped peccaries, red brocket deer, paca, agouti, and smaller armadillos (Dasypodidae). Lowland tapir (*Tapirus terrestris*) and gray brocket deer (*M. gouazoupira*) were frequently killed in primary forest, plantations and fallow plantations, but never in active or fallow fields. Four of the six primate species hunted were killed only in primary forest. Offtake rates of ungulates (kg km^{-2}) were twice as high in primary forest and fallow fields than in other habitats. The offtake of birds was low and was predominantly sourced from primary forest. Black curassow (*Crax alector*), gray-winged trumpeters (*Psophia crepitans*) and marail guans (*Penelope marail*) were only killed in primary forest. However, hunters often opportunistically harvested several species of large canopy frugivores (macaws *Ara* spp., parrots *Amazona* spp. and toucans *Ramphastos tucanus*) along the edges of fallow and active fields.

3.2. Landscape composition of hunting catchments

The hunting catchments of the three villages covered between 60 and 95 km^2 and their land-cover composition was significantly different from the landscape mosaic available within concentric buffers around each village (Table 1). In all cases, hunting catchments contained a larger area of primary forest than expected on the basis of availability (Table 1). Hunters from São Militão, for example, used nearly three times more primary forest in their catchment than the proportion of this habitat within the surrounding landscape. Fallow fields were represented in the hunting catchment according to their availability around Bananal, but were over-represented in the catchments of São Militão and Vila Nova. Active fields were over-represented in the area used by hunters of Vila Nova and São Militão, but under-represented around Bananal. It is likely that we slightly under-estimate the preference for active and fallow fields in hunting catchments as all of the active and fallow fields of a given village were incorporated into its hunting catchment whereas hunters did not access the active and fallow fields of neighbouring communities. Active and fallow plantations were under-represented in hunting catchments, with the excep-

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Table 2
Species (or groups of species not accurately distinguishable) harvested in different habitats of the Jarí landscape mosaic over a 1 year period.

		Body mass (kg)	Primary forest		Active plantation		Fallow plantation		Active field		Fallow field		Total	
			N	kg/km^2	*N*	kg/km^2	*N*	kg/km^2	*N*	kg/km^2	*N*	kg/km^2	*N*[a]	kg
Primates														
Alouatta macconnelli	Guianan howler monkey	6.5	23	1.19	0	–	0	–	0	–	0	–	23	150
Cebus apella	Brown capuchin	3.24	17	0.44	0	–	2	0.16	0	–	3	0.56	22	71.3
Ateles paniscus	Black spider monkey	9.02	8	0.58	0	–	0	–	0	–	0	–	8	72.2
Pithecia pithecia	Guianan saki monkey	2	1	0.02	0	–	0	–	0	–	0	–	1	2
Saguinus m. midas	Golden-handed tamarin	0.55	1	0.00	0	–	0	–	0	–	0	–	1	0.55
Saimiri sciureus	Squirrel monkey	0.94	0	–	0	–	0	–	0	–	1	0.05	1	0.94
				2.2		0		0.2		0		0.6		
Ungulates														
Tayassu pecari	White-lipped peccary	32	136	34.74	5	3.52	10	7.72	1	9.11	21	38.62	173	5536
Tayassu tajacu	Collared peccary	21.7	60	10.37	0	–	1	0.52	1	6.17	13	16.18	75	1625
Mazama americana	Red brocket deer	30	26	6.23	21	13.87								
	14	10.14	1	8.54	5	8.62	67	2010						
Mazama gouazoupira	Gray brocket deer	18	20	2.87	2	0.79	1	0.43	0	–	0	–	23	414
Tapirus terrestris	Brazilian tapir	150	5	5.99	1	3.30	2	7.24	0	–	0	–	8	1200
				60.1		21.5		26.1		23.8		63.3		
Rodents														
Dasyprocta agouti	Red-rumped agouti	4.2	88	2.95	7	0.65	10	1.01	24	28.70	52	12.55	181	760
Agouti paca	Paca	8.5	123	8.35	2	0.37	15	3.08	1	2.42	9	4.40	150	1275
Myoprocta acouchy	Red acouchy	0.95	1	0.01	0	–	0	–	0	–	0	–	1	0.95
				11.3		1.0		4.1		31.1		17.0		
Other mammals														
Panthera onca	Jaguar	24	1	0.19	1	0.53	2	1.16	0	–	0	–	4	96
Leopardus pardalis	Ocelot	10.3	2	0.16	1	0.23	0	–	0	–	0		3	30.8
Herpailurus yaguarundi	Jaguarundi	6.5	0	–	0	–	0	–	0	–	1	0.37	1	6.5
Coendou prehensilis	Brazilian porcupine	4.5	4	0.14	0	–	0	–	0	–	0	–	4	18
Nasua nasua	South American coati	3.1	1	0.02	0	–	1	0.07	0	–	0	–	2	6.2
Dasypodi	Armadillos	4.9	67	2.62	2	0.22	15	1.77	1	1.39	12	3.38	97	475
Pridontes maximus	Giant armadillo	43	2	0.69	0	–	0	–	0	–	0	–	2	86
				3.8		1.0		3.0		1.4		3.8		
Birds														
Tinamus major	Great tinamou	1.1	14	0.12	0	–	0	–	0	–	1	0.06	15	16.5
Crax alector	Black currassow	3.1	12	0.30	0	–	0	–	0	–	0	–	12	37.2
Psophia crepitans	Gray-winged trumpeter	1.3	8	0.08	0	–	0	–	0	–	0	–	8	10.4
Ara spp.	Macaw	1.1	5	0.04	0	–	1	0.03	0	–	1	0.06	7	7.7
Ramphastos tucanus	White-throated toucan	0.6	1	0.00	0	–	1	0.01	1	0.17	1	0.03	4	2.4
Penelope marail	Marail guan	2	2	0.03	0	–	0	–	0	–	0	–	2	4
Ortalis m. motmot	Little chachalaca	0.5	1	0.00	0	–	0	–	0	–	1	0.03	2	1
				0.59		0		0.04		0.17		0.19		
Reptiles														
Geochelone spp.	Tortoise	3.57	8	0.23	0		2	0.17	0	–	1	0.21	11	39.3
Caiman crocodilus	Common caiman	6.42	3	0.15	0		0	–	0	–	0	–	3	19.3
Total kills and kg/km^2			640	78.5	42	23	77	33.53	30	56.50	122	85.14	911	13 973.6

[a] Of the 925 kills, 10 brocket deer (*Mazama* spp.) and 4 peccaries (*Tayassu* spp.) killed were not identified to species, thus 911 kills in this table. We conservatively used the lighter species' weight for biomass calculations.

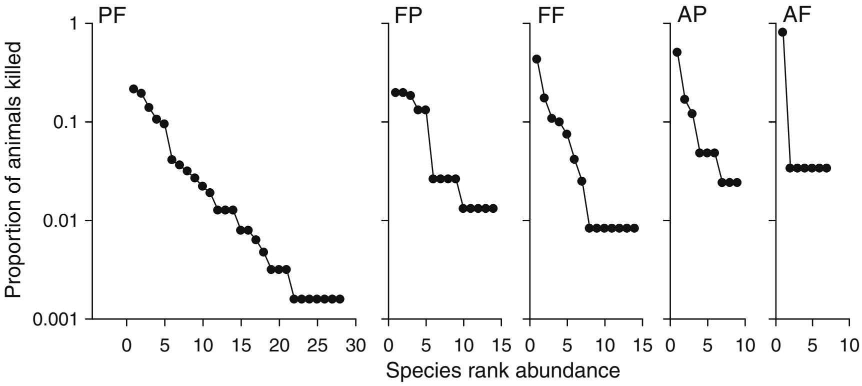

Fig. 2. Rank abundance plots of species killed by hunters in primary and anthropogenic habitats in the Jarí landscape. For each habitat we plotted the proportion of kills accounted for by each species. Habitats are primary forest (PF); fallow plantations (FP); fallow fields (FF); active *Eucalyptus* plantations (AP); and active fields (AF).

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tion of active plantations around Bananal, which were represented according to availability in the surrounding landscape.

3.3. Habitat allocation of hunting effort

Most hunting effort was allocated to primary forest and villagers spent more time hunting in fallow fields or fallow plantations than in *Eucalyptus* plantations or active fields (Table 3). Hunting effort per unit area (h km^{-2}) in active and fallow plantations was lower than that in primary forest across all three villages. Hunters allocated twice to four times more hunting time per unit area to fallow fields than to fallow plantations. Hunting pressure in active and fallow agricultural fields was highly variable among villages. In relation to their size, fallow fields received a high level of hunting effort around Bananal and São Militão, but not around Vila Nova (Table 3).

Hunting effort was similar between primary forest and other habitats within 1 km of the study villages, but despite the availability of other habitats at all distances (Fig. 3a), hunting beyond 3 km of villages shifted almost exclusively to primary forest (Fig. 3b).

3.4. Offtake and landscape structure

Hunters from all three villages killed animals in all five habitats examined (Table 3). Primary forest provided the highest numeric offtake (651 kills, 70%), whereas active fields and active plantations provided the least (30 and 44 kills, respectively). In terms of the total biomass of animals harvested or fatally wounded, 71% (10,029 kg) was sourced from primary forest (range = 48–83% per village). The vertebrate biomass harvested from habitats other than primary forest was variable. Although most animals were killed in primary forest, the offtake per unit area was highest from fallow fields (85 kg km^{-2}), followed by primary forest (79 kg km^{-2}) and active fields (57 kg km^{-2}). Fallow and active plantations, on the other hand, contributed the least offtake per unit area (34 and 23 kg km^{-2}, respectively).

3.5. Hunting efficiency

Prey body size was significantly different among habitats (Kruskal–Wallis, $\chi^2_4 = 43.8$, $p < 0.001$). On average, prey items were largest in plantations and smallest in active fields (Fig. 4). Prey obtained from fallow plantations were larger than those from fallow fields ($U_{78,122} = -2.6$, $p = 0.011$). There was no significant difference in prey size between primary forest and fallow plantations ($U_{650,78} = -0.2$, $p = 0.986$), whereas primary forest prey were larger than those of fallow fields ($U_{650,122} = -3.4$, $p = 0.001$). Animals harvested from fallow fields were significantly larger than those from active fields ($U_{122,30} = -2.7$, $p = 0.007$).

Fewer animals were killed per hour spent hunting in primary forest than in any other habitat in two of the three villages (Bananal and Vila Nova; Table 3). This measure of hunting efficiency was similar in both types of fallow. Primary forest exhibited a lower biomass return per unit of time spent hunting than at least one other habitat in all villages. Hunting efficiency in active plantations was variable between villages, yielding the highest measures of CPUE (kg h^{-1}) at Bananal, the second-highest at Vila Nova, and the lowest at São Militão (although data come from only five hunting forays for this village). For all villages, fallow plantations sustained a higher hunting efficiency in terms of biomass per unit time than fallow fields.

3.6. Distance from villages

We determined distance categories based on the centroid distance of the relevant named and mapped local hunting area polygon from villages, using a GIS. Habitat types other than primary forests provided most of the offtake per unit area (kg km^{-2}) within 1 km of the study villages (Fig. 3c). Fallow fields had the highest

Table 3
Hunting effort, animal offtake, and catch-per-unit-effort in different habitats within the Jarí landscape mosaic in the north-eastern Brazilian Amazon.

	Hunts	Hours	Hours (%)	Hrs/km^2	Kills	Kills (%)	kg	kg (%)	kills/h	kg/h
Bananal										
Primary forest	296	1665	64.4	47.0	206	55.5	2387	48.2	0.12	1.43
Active plantation	37	146	5.7	6.1	28	7.5	579	11.7	0.19	3.97
Fallow plantation	68	381	14.7	13.1	58	15.6	1125	22.7	0.15	2.95
Active field	14	41	1.6	47.8	13	3.5	99	2.0	0.32	2.41
Fallow field	84	351	13.6	55.9	66	17.8	764	15.4	0.19	2.17
Total	499	2584	100.0		371	100.0	4953	100.0	0.14	1.92
São Militão										
Primary forest	217	1215	68.2	43.3	202	79.2	2761	82.2	0.17	2.27
Active plantation	5	20	1.1	1.2	1	0.4	18	0.5	0.05	0.89
Fallow plantation	28	156	8.7	17.3	16	6.3	170	5.1	0.10	1.09
Active field	3	1	0.0	0.8	2	0.8	8	0.2	2.90	12.17
Fallow field	76	390	21.9	79.6	34	13.3	403	12.0	0.09	1.03
Total	329	1782	100.0		255	100.0	3360	100.0	0.14	1.89
Vila Nova										
Primary forest	223	1766	87.4	28.6	243	81.3	4882	83.1	0.14	2.76
Active plantation	17	92	4.5	21.6	15	5.0	505	8.6	0.16	5.51
Fallow plantation	3	20	1.0	5.9	4	1.3	112	1.9	0.20	5.60
Active field	16	67	3.3	36.6	15	5.0	92	1.6	0.23	1.37
Fallow field	18	76	3.8	12.3	22	7.4	283	4.8	0.29	3.70
Total	277	2021	100.0		299	100.0	5873	100.0	0.15	2.91
Combined										
Primary forest	736	4646	72.7	37.1	651	70.4	10 029	70.7	0.14	2.16
Active plantation	59	258	4.0	5.7	44	4.8	1102	7.8	0.17	4.27
Fallow plantation	99	556	8.7	13.4	78	8.4	1407	9.9	0.14	2.53
Active field	33	108	1.7	30.8	30	3.2	198	1.4	0.28	1.83
Fallow field	178	818	12.8	47.0	122	13.2	1449	10.2	0.15	1.77
Total	1105	6386	100.0		925	100.0	14 187	100.0	0.14	2.22

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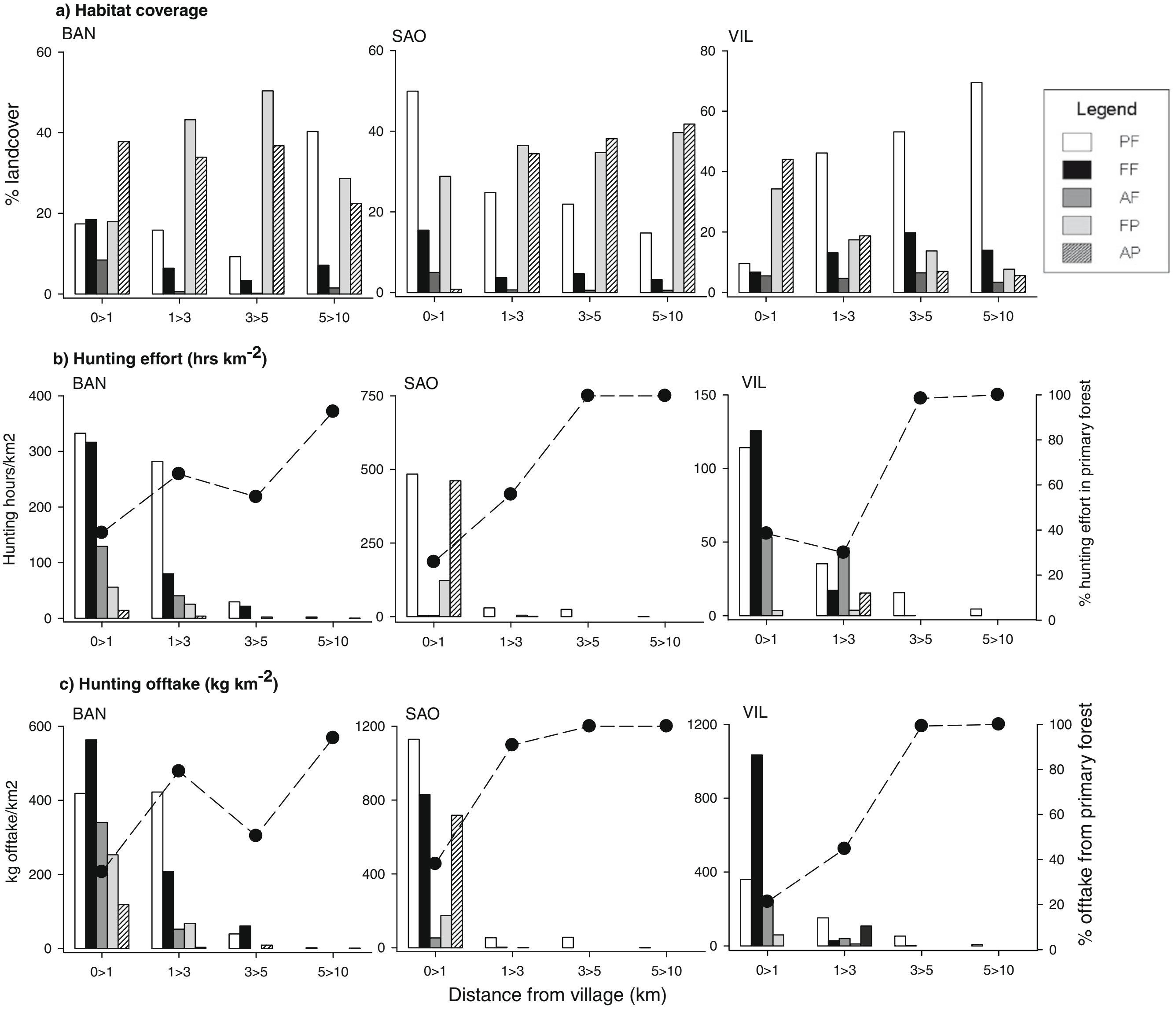

Fig. 3. (a) Habitat coverage, (b) Hunting effort (km^{-2}), and (c) Hunting offtake (km^{-2}) of each habitat, at different distance classes from the three study villages in Jarí. The percentage of hunting effort or offtake from primary forest is shown on the right-hand axis.

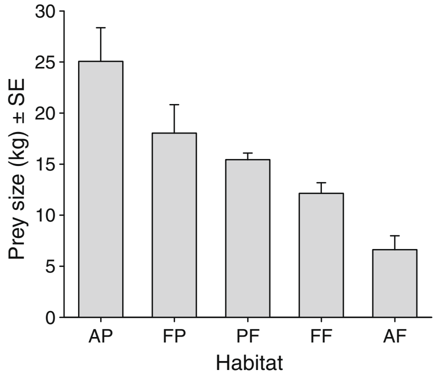

Fig. 4. Mean body mass (±SE) of animals killed by hunters in active Eucalyptus plantations (AP), fallow plantations (FP), primary forest (PF), fallow fields (FF), and active fields (AF).

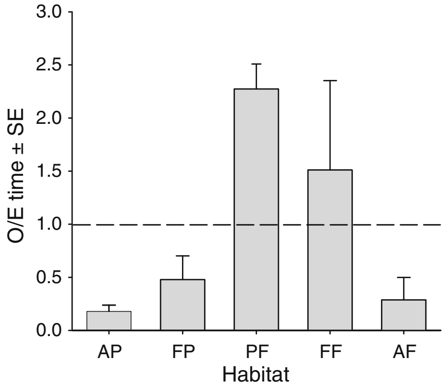

Fig. 5. Observed amount of time spent hunting in each habitat, divided by the expected time (±SE) based on the relative catch-per-unit-effort (kg per hour) and the proportion of each habitat within the hunting catchments of each study village ($n = 3$). Habitats are active *Eucalyptus* plantations (AP); fallow plantations (FP); primary forest (PF); fallow fields (FF); active fields (AF).

offtake (kg km^{-2}) in all three villages. Secondary habitats still provided 39% of biomass extracted between 1 and 3 km from Bananal,

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but only 5% and 6% for São Militão and Vila Nova, respectively. Primary forest was the sole provider of offtake between 5 and 10 km of all three villages, with the exception of 19 excursions farther into plantations by two hunters from Bananal, where the Brazil nut stands were in primary forest adjacent to a large plantation.

3.7. Predicting hunting effort

There were significant differences between the expected and observed hunting effort that was allocated to different habitats, as predicted by CPUE (kg hr^{-1}) and the area of each habitat type available within village catchments ($G = 6612$, $df = 14$, $p < 0.00001$; Fig. 5). Primary forests were hunted more intensively than expected in all villages, whereas the reverse was the case for active plantations, fallow plantations and active fields. Hunting effort in fallow fields was highly variable across villages, ranging from three-fold greater than expected in São Militão to only a third of the expected hunting effort in Vila Nova.

4. Discussion

Our findings suggest that nontribal subsistence hunters in a vast landscape mosaic of Brazilian Amazonia prefer hunting within primary forest, despite the high catch-per-unit-effort (CPUE) of some non-primary habitats. Hunters from all three study villages preferentially incorporated primary forest into their hunting territories, and spent most of their time in this habitat. Although hunters may not be optimizing their time whilst foraging in primary forest, the clumped distribution of prey and their food resources makes hunting more energetically-efficient, and they may be adopting the optimal energetic strategy by minimizing physical exertion. They also reduce their opportunity costs by collecting additional non-timber forest products. Active and fallow fields harboured an impoverished prey assemblage yet received significant attention from hunters, as a low CPUE is offset against the control of crop-raiding wildlife. Conversely, active and fallow tree plantations were rarely used by hunters, despite their high CPUE.

Our first hypothesis was not supported, as habitat coverage and foraging efficiency failed to predict the spatial allocation of hunting effort. Instead, primary forest areas were hunted more heavily than other habitats within village catchments and were consistently favoured by hunters at the landscape-scale of hunting catchment demarcation. This is in spite of the fact that, compared to other habitat types, primary forest sites were in general farther from village households, thereby incurring higher transportation costs in terms of time and energy. Consequently, most of the wild meat obtained was sourced from primary forest and hunters exploited non-native habitats during shorter hunting forays when close to home. Although hunters may avoid depleted areas and prefer those with the highest CPUE (Alvard, 1995), location choice driven by profit-maximizing rests on the implicit assumption that other factors remain equal (see Abernethy et al., 2007).

As hypothesized, our results show that anthropogenic habitats can be more efficient hunting grounds than closed-canopy primary forest for some species of large vertebrates. Primary forest yielded neither the highest CPUE nor sourced the largest average prey size. In primary forest much of the plant biomass consists of tree trunks and heavily-defended leaves (Waterman and McKey, 1989). In contrast, secondary regrowth tends to have a more open canopy and contains extensive understorey and terrestrial browse, which favours ungulates in particular (Parry et al., 2007). Species that are able to exploit seeds (e.g. agouti, Dubost and Henry, 2006) and insects (e.g. capuchin monkeys, Simmen and Sabatier, 1996) can also benefit from the food resources in secondary forest.

4.1. Why do hunters prefer primary forest?

Optimal foraging theory has informed several studies on habitat selection by wildlife users in temperate forests (Boxall and Macnab, 2000), yet this approach has received little attention in the tropics (but see Smith, 2005). We examine three alternative, but potentially complementary, reasons why hunters may prefer hunting in primary forests when they have the choice of different land-uses.

(1) *Habitat structure*: Secondary forest is much denser in the understorey than primary forest (Barlow et al., 2007b; Parry et al., 2007) and it may therefore be more difficult to locate or pursue wildlife in secondary habitats (Johns, 1985; Naughton-Treves et al., 2003). Forest management can alter the habitat-preferences of subsistence hunters (Adamowicz et al., 2004) and in our study local hunters suggested that moon phase and the herbicidal or mechanical suppression of the native understory (by the forestry company) affects hunting success in plantations. The effects of plantation management warrant further investigation.

(2) *Energetic cost*: The spatiotemporal distribution of prey may be more predictable in primary forest which allows hunting to be energetically conservative. Terrestrial vertebrates in primary forest are often seasonally attracted to large food patches such as the flowers and fruits of *Caryocar villosum* (cf. Cymerys, 2005). In primary forest, food trees are both larger and often highly dispersed, and the distribution of fruits and flowers preferred by large vertebrates is patchier than that in secondary forest (Barlow et al., 2007b; Parry et al., 2007). This has important implications for hunting as nocturnal "waits" (from raised platforms or hammocks at fruiting and flowering trees that were largely restricted to primary forest), were a major hunting strategy for five months of the year. Low-effort nocturnal hunting was especially attractive in combining night-time wild meat acquisition with day-time agricultural activities. Large terrestrial ungulates in Jarí mainly forage at night in plantations, when local hunters report that they feed on the young shoots and leaves of *Eucalyptus* and pioneer shrubs (e.g. *Manihot brachyloba* Müll. Arg.). Therefore, although plantations have a more open understorey than other forest types (Barlow et al., 2007b) hunters were rarely able to capitalize on this. Furthermore, these food resources are widely dispersed so searching for prey requires intensive searching and the use of expensive flashlight batteries (at a cost of ~US\$1 h^{-1}).

(3) *Opportunity costs*: Humans attempt to minimize risk and opportunity costs when foraging (Winterhalder, 2007) and the availability of non-timber forest products (NTFPs) may affect habitat choice in tropical landscape mosaics. Hunters in the tropics frequently combine hunting and NTFP harvesting (e.g. Rumiz and Maglianesi, 2001; Escobal and Aldana, 2003; Plowden, 2004) and hunting in primary forest in the Jarí landscape was often combined with the opportunistic or planned collection of NTFPs such as Brazil nuts, fruits (e.g. *Caryocar villosum* Aubl. and *Endopleura uchi* Cuatrec.), and fibers (e.g. *Heteropsis* spp.). These NTFPs were collected for domestic use, or for sale in the local market town. In particular, the Brazil nut harvest constitutes an important part of annual income for rural communities across Amazonia and in Jarí provides a strong incentive to be in primary forest between January and April. The opportunity costs of hunting in primary forest were therefore lower than in other habitats as these and other plant products were not collected in tree plantations and rarely collected in secondary forests (but see Gavin, 2004). Further research is required into the costs and

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benefits of hunting in different habitats, and the non-vertebrate resources that affect the profitability of time allocation to each. Avoiding arriving home empty-handed may influence habitat choice of subsistence hunters and there may be marginal valuation of prey size as the perceived value per kilogram of prey decreases in medium to large food items (Kennett et al., 2006).

4.2. Prey persistence

Our hypothesis that non-primary habitats would support less diverse prey assemblages was supported. The species richness and community evenness of prey obtained in primary forest was far greater than those of other habitats. However, although the absence of many large vertebrate species from human-dominated landscapes is thought to reflect hunting pressure, rather than habitat per se (Daily et al., 2003), it is not possible to distinguish these factors in this study. Hunting pressure was much higher in fallow fields than in fallow plantations, and this pattern may confound suggestions that anthropogenic habitats primarily support rural livelihoods, rather than wildlife (e.g. Naughton-Treves et al., 2003). Active and fallow fields around our study villages supported a depauperate suite of “weedy” species (c.f. Naughton-Treves et al., 2003), and many preferred prey species were not recorded in these habitats. Conversely, fallow plantations were used by a high abundance of large ungulates. It has been argued that large herbivores and carnivores cannot persist in multiple use zones, based on a study of farm-fallow mosaics in the Peruvian Amazon (Naughton-Treves et al., 2003). However, the agricultural plots of smallholders in the tropics are typically much smaller than the home range size of many hunted animals, which presumably require surrounding forest habitats. Therefore, harvest data from these small patches cannot be extrapolated to much larger areas of even-aged secondary forests in moderately degraded lands. Wild meat offtake from degraded lands may reflect the spatial composition of the landscape as there is generally little primary forest close to settlements and therefore hunting pressure is high in agricultural habitats. This may explain the high levels of wild meat acquisition from active and fallow fields (cf. Wilkie, 1989; Naughton-Treves et al., 2003; Smith, 2005; Gavin, 2007; this study).

4.3. Conservation implications

Nearly a third of all kills came from habitats other than primary forest. Hunting in anthropogenic habitats could potentially relieve hunting pressure in primary forest, and therefore reduce the impacts of hunting on vulnerable primary forest specialists. However, these potential benefits are offset by the low value of anthropogenic habitats for the many primary forest species, and the risks that large group-living species (e.g. white-lipped peccaries) face as they move across anthropogenic landscapes. Mammals hunted in secondary forests, agricultural fields and tree plantations in the Jarí landscape were predominantly terrestrial (cf. Robinson and Bennett, 2004), and preferred primate species were not encountered by hunters outside of primary forest. Our findings also indicate that most hunted birds do not persist in anthropogenic habitats, even in large areas of lightly-hunted second-growth.

Although conjecture that large areas of secondary forest may serve as productive hunting grounds (Lovejoy, 1985) may be correct, these habitats were not favoured by hunters who had the option of hunting in primary forests. The low hunting pressure in these abandoned and fallow areas means they may act as refugia for some matrix-tolerant large vertebrates, which could, given sufficient connectivity, replenish overhunted sink areas through immigration (Novaro et al., 2000).

4.4. Conclusions

We have shown the importance of considering the availability and spatial distribution of undisturbed and human-modified wildlife habitats in order to understand hunting patterns across structurally heterogeneous tropical landscapes. We build on recent studies showing the importance of secondary habitats as sources of hunted vertebrates (Naughton-Treves et al., 2003; Smith, 2005; Gavin, 2007) by considering the spatial distribution of hunting effort across a range of habitats. Our results highlight the complexity of decision-making by hunters, as their use of a landscape mosaic cannot necessarily be explained by the abundance of a single resource. We suggest that there is a strong interaction between hunting and the extraction of other non-timber forest products, which could have important implications for the management of forest resources (particularly in extractive reserves). This is particularly relevant given current expectations that regenerating forest habitats can provide both plant and animal resources to local people (Gavin, 2004; Robinson and Bennett, 2004) and help conserve tropical forest biodiversity (Wright and Muller-Landau, 2006; Vandermeer and Perfecto, 2007).

The spread of hunting activities across the landscape mosaic confirms the importance of anthropogenic habitat as sources of animal protein to rural peoples (Robinson and Bennett, 2004). However, under current coverage, secondary forest is likely to sustainably supply only ~2% of the required protein intake of Amazonian smallholders (Parry et al., in press). Despite optimistic predictions regarding the role of rural people in conserving Amazonian forests (Campos and Nepstad, 2006), their extensive hunting means they are unlikely to conserve many large vertebrates.

Our results suggest that the negative consequences of smallholder hunting are unlikely to be offset through large-scale forest plantation or regeneration schemes. Both secondary forests and plantations lack many primary forest species (Barlow et al., 2007a; Parry et al., 2007) and hunters in mixed-use tropical landscapes are expected to continue hunting in primary forest even when exploited populations have been depleted.

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