



Final Report to the Rufford Foundation

The need to feed: hunting in second-growth forests of the Brazilian Amazon

Luke Parry^{1,2}

October 2006

Please note that parts of the following Report have been taken from an unpublished manuscript (submission forthcoming; L Parry, J Barlow & CA Peres). These data and their interpretation remain copyright of L Parry and no part of the report should be copied or reproduced without the express permission (in writing) of the L Parry

¹ School of Environmental Sciences, University of East Anglia, Norwich NR47TJ United Kingdom. Email: l.parry@uea.ac.uk

² Center for International Forestry Research (CIFOR), EMBRAPA, Trav. Dr. Enéas Pinheiro, S/N, Belém, CEP 66.095-100, Pará, Brazil

Contributions

We are pleased with the outputs of the project to-date and anticipate on-going outputs (in the form of publications and landscape management decisions by the landowner) over the next few years. We believe that we have shed new light on anthropogenic habitats in the Amazon, and demonstrated that they serve as important areas for both nature conservation and protein acquisition for the rural poor.

Local outputs

The community assistants played crucial roles in making a success of the project. In all cases it was the first research they had been involved in, yet they were extremely competent and interested participants in the research. The training process for game harvest monitoring took several months and a high degree of energy and commitment from all concerned. The assistants all recall that they learnt a lot from the work and have assumed roles of considerable responsibility within their communities as a result. One community, Vila Nova, is particularly interested in continuing the research, and working more as a community to sustainably harvest their forest resources. L Parry is in discussion with CIFOR to bring planning and conservation workshops to the community (and any other community in the Jari landscape that wishes). The landowner, Jarí Celulose SA, has been very supportive of our work, and have taken an active interest in our findings. We have worked with their community liaison team and they are considering adopting a long-term monitoring plan for hunting in the vast landscape under their control. We have also recommended that certain secondary forests in the Jarí landscape are preserved and taken out of the production cycle, due the extremely high densities of large vertebrates in certain areas of secondary forest. These recommendations are being considered by the Board of Directors.

Regional outputs

We have clearly demonstrated that anthropogenic habitats in the Amazon host a range of species important to nature conservation and play an important role in supplying the rural poor with animal protein. More specifically, our project has demonstrated that both large-scale industrial landuse and smallholder rural agricultural habitats serve dual roles as wildlife habitats and hunting grounds. However, there are distinct differences in hunting pressure between industrial- and smallholder habitats. The South American regional office of CIFOR (Center for International Forestry Research) has taken a strong interest

in the results of our project, and have already included selected results into a forthcoming handbook on Managing Secondary Forests (Portuguese).

Global outputs

Two manuscripts have already been written from the work. These are in the process of submission to high-ranking conservation biology journals. L Parry presented very early provisional results and a summary of the project to two major international conferences in 2005 - the annual conference of the *Society of Conservation Biology* in Brasilia, and the annual conference of the *Association of Tropical Biology and Conservation* in Uberlandia, Brazil, in the July 2005. All feedback received was very positive and encouraging.

L Parry also presented a talk (13 February 2006) to the *Zoological Society of London* in which provisional results and conservation implications of this study were presented and discussed with a range of bushmeat experts such as Dr Marcus Rowcliffe and Dr Guy Cowlshaw. Feedback received was very positive. L Parry also presented the findings again to the *Centre for Ecology, Evolution and Conservation* at the University of East Anglia in March 2006. The support and role of the Rufford Foundation has been (and will continue to be) acknowledged in all talks and articles.

Summary of results

Please note that parts of the following Research Report have been taken from an unpublished manuscript (submission forthcoming; L Parry, J Barlow & CA Peres). These data and their interpretation remain copyright of L Parry and no part of the report should be copied or reproduced without the express permission (in writing) of the L Parry

Human-dominated tropical forest landscapes are increasingly ubiquitous. Although these habitats are used by a range of game species, their role in sustaining game populations and game harvest remains poorly understood. We investigated subsistence hunting patterns across a large landscape mosaic in the Brazilian Amazon, where hunters from three colonist villages had access to primary forest, active and fallow agricultural fields, and active and fallow *Eucalyptus* plantations. We accounted for the availability and spatial distribution of each habitat, and the hunting effort allocated to them. Landscape composition and the area used by hunters was mapped using remote-sensing combined with participatory mapping. Primary forest was over-represented within village hunting catchments compared to the habitat composition of the wider landscape. Hunting effort per unit area was highest in fallow fields, followed by primary forest. Overall, 71% of the kills were from primary forest. Hunting in primary forest was often combined with other extractive activities (such as Brazil nut harvest) and yielded the lowest catch-per-unit-effort of all habitats. Active and fallow agricultural fields were hunted more than expected by their coverage, and provided 16% of the kills and 12% of the total biomass of game killed, consisting primarily of mammals known to be resilient to hunting. Hunting pressure in nearby plantations and large areas of secondary forests was low, despite a high catch per unit effort. Consequently, large mammals such as tapir (*Tapirus terrestris*) appeared to persist in active and fallow plantations though not in active or fallow agricultural fields. We show that habitats typical of mixed agricultural landscapes are highly variable in their role of supplying game to local communities. Our results suggest that large areas of secondary regeneration following agri- or silvi-culture hold some potential as wildlife refuges in hunted tropical landscape mosaics.

Introduction

Unprecedented rates of deforestation in the tropics have led to increased coverage of agriculture, cattle pasture, plantations and regenerating native vegetation (FAO 2001; Achard et al. 2002; Perz & Skole 2003; Fearnside 2005). Conservation attitudes have recently broadened to encompass this expanding acreage of anthropogenic habitats (Lindenmayer & Franklin 2002), focusing on land-cover under production (e.g. Rice & Greenberg 2004, Vandermeer & Perfecto in press) and regenerating secondary forests (Wright & Muller-Landau 2006, but see also Gardner et al. 2007). Large vertebrates are particularly important in secondary forests because they exert a major impact on tropical forest dynamics and the rate of forest regeneration (e.g. Howe & Smallwood 1982; Wunderlé 1997, Stoner et al. 2007). Yet large mammals and gamebirds are also a major source of dietary protein to tribal and nontribal communities in the tropics (Redford & Robinson 1987; Jerozolinski & Peres 2003; Robinson & Bennett 2004). Large vertebrate populations are therefore often severely depleted by subsistence or commercial game hunting, thereby potentially disrupting forest regeneration (Peres & Palacios 2007).

Secondary forests can support high densities of game species (Fimbel 1994; Parry et al. in review) and appear to supply significant quantities of wild meat to consumers in Africa (Wilkie 1989) and South America (Gavin 2007). Small-scale agricultural plots also subsidize protein acquisition through “garden hunting” (Smith 2005), which may compensate for crop losses to herbivores (Naughton-Treves 2003). The potential of plantation forests as hunting grounds in areas formerly covered by native habitat has not yet been addressed, though anthropogenic habitats could serve as productive grounds (Lovejoy 1985; Wilkie & Lee 2004; FAO 2005). However, tropical hunting studies are yet to compare the profitability of primary forest against that of adjacent anthropogenic habitats, so our understanding of wildlife conservation and wildmeat hunting in landscape mosaics remains poor.

Furthermore, wildmeat obtained across a landscape reflects the use of space and time by hunters (Winterhalder 1997; Siren et al. 2004), both of which are likely to differ among habitats (Boxall & Macnab 2000). No landscape hunting study has yet considered hunting effort across habitats, and the spatial coverage of each habitat has either been estimated from interviews with some farmers (Gavin 2007) or from remote sensing without reference to the distribution of the available habitat (Wilkie 1989; Escamilla et al. 2000). The spatial composition of the landscape is likely to

influence hunter habitat-preference as distance to habitats influences habitat choice by animal foragers (Rosenberg & McKelvey 1999; Matthiopoulos 2003).

We investigate hunting patterns across a human-dominated landscape matrix in the Brazilian Amazon and critically assess the importance of primary habitat compared to a range of alternative land uses for both human hunters and large vertebrates. We predict that large herbivores and carnivores can persist in multiple-use zones when subjected to low hunting pressure. Studies that report the hunting of a degraded fauna in anthropogenic habitats use agricultural fields and small patches of fallow second-growth (e.g. Naughton-Treves 2003). However, the fields of smallholders in the tropics are typically much smaller than the home range size of many game animals, and do not reflect the large areas of secondary forests growing on moderately degraded lands. Our study landscape incorporates large areas of primary forest, agricultural land, and plantation forests, in addition to small areas of agricultural regrowth and large secondary forests following clear-cut plantations. We also consider the use of space (habitat area and distance from villages) and time (hunting effort) in primary forests and other habitats. Specifically, we test the hypothesis that hunters in highly heterogeneous landscape mosaics partition their time based on the availability, distribution and the foraging efficiency (catch-per-unit-effort, CPUE) associated with each habitat.

Methods

Study Area

We assessed the hunting patterns of three colonist communities in a 1.7Mha landholding controlled by a large forestry company (Jari Celulose) in the Rio Jari region of the northeastern Brazilian Amazon (00°27'00" - 01°30'00" S, 51°40'00" - 53°20'00" W; Fig. 1). There are around 6000 people belonging to 30 semi-subsistence rural communities embedded within the Jari 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 food crops. Aside from hunting, the collection of the wild seed crop of Brazil nut trees (*Bertholletia excelsa*, Lecythidaceae) was the most important extractive activity in the region.

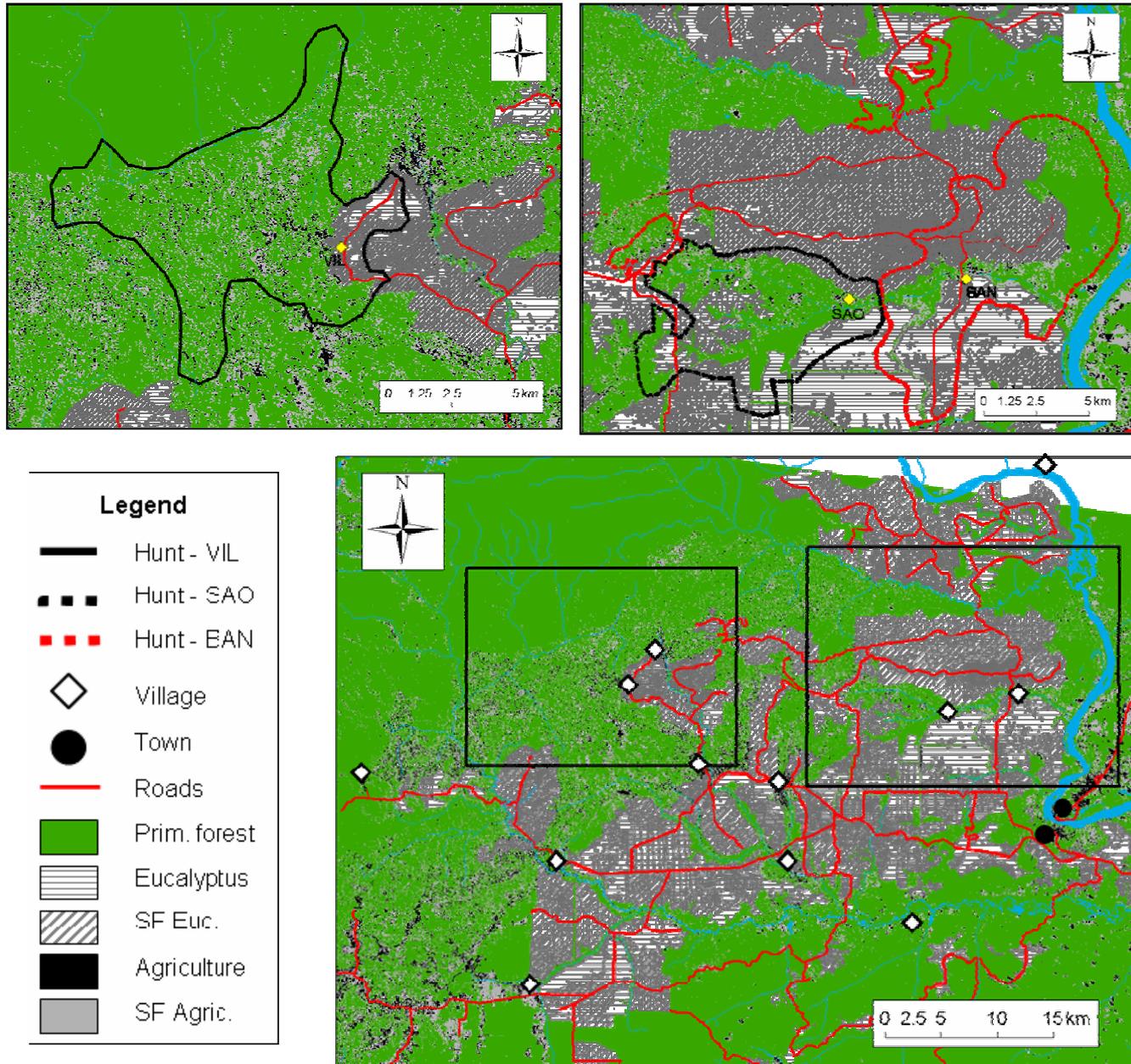


Figure 1. The study area in the northeastern Brazilian Amazon. Inset rectangles indicate the three study villages (Bananal; São Militão; Vila Nova). Areas hunted by each community are indicated by a black line (Vila Nova) and light and dark dotted lines (Bananal and São Militão, respectively).

All three communities had immediate access to five habitat types: primary forest, *Eucalyptus* plantations, post-plantation secondary forest, active agricultural plots, and fallow plots that had been abandoned. 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. Post-plantation secondary forest patches often exceeded 1,000 ha, accounted for 55,000 ha of the Jari landscape, were typically younger than 20 years old and were dominated by pioneer species such as *Cecropia* spp, *Inga* spp., *Bellucia* spp. and *Vismia* spp. Secondary forest within fallow agricultural plots were generally small (1-3 ha) and of variable age (5-15 years). Agricultural plots were typically small (1-3 ha), cultivated for 3-5 years, and were planted with manioc, maize, and beans

Game 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 January to December 2005. The three villages were relatively small (<15 households; total households = 39) 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 were successful. Questions included the hunt duration and timing, main habitat visited, local name for the area visited, maximum distance from the village on the basis of time (all hunters carried a wristwatch) to return directly to the village, and the game species pursued, and whether the prey was captured or wounded but not captured. Hunters presumed an animal was fatally wounded if they observed significant bleeding following a shot (which was confirmed by verifying blood on the ground after wounded prey fled). Whenever possible, all undressed carcasses were weighed using Pesola scales (0-10 kg; and 0-50 kg). These weight data were combined with data from the literature (Peres 2001) 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, one of us (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 species (e.g. 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.

Mapping the landscape

We developed a land-cover map of our study area by combining a 2003 Landsat 7 (30m pixel) satellite image and detailed land-use data (plantations and secondary forests) from Jari Celulose. 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, and extensive ground-truthing around the village agricultural mosaics and the wider landscape. We used this information to assess the landscape composition around each village.

Local villagers often have 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). We therefore complemented our land-cover data through participatory mapping with hunters. Hunters were accompanied on at least ten hunts in each village, in which we used a GPS (Garmin[®] 12XL) to map the locally-named areas of primary forest and other habitats, record area boundaries, and obtain positional data of previous kills. From these data we defined the area hunted (catchment) for each village.

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 the actual contribution of each habitat to each hunting catchment. 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, and the prey capture success associated with, each habitat (HA_i) within each village catchment. We calculated the relative catch per unit effort of each habitat ($CPUE_i$) based on the kg of wildlife shot per hour in habitat i divided by the mean kg shot per hour in all habitats ($i\dots j$). The expected amount of hunting time (HT_i) allocated to each habitat i was then calculated as:

$$HT_i = \text{total time hunting} \times [(HA_i + CPUE_i) / \sum(HA_{i\dots j} + CPUE_{i\dots j})]$$

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 ($\alpha = 0.05, 7 = 0.0125$) in order to reduce the likelihood of Type

I error as a result of multiple tests (Rice 1989). We plotted rank-abundance curves to compare community evenness in each habitat, with the relative abundance of each species on a logarithmic scale plotted against species' rank. We analyzed prey community composition using PRIMER v.5 (Clarke & Warwick 2001). Nonmetric 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 & Warwick 2001) to test for significant differences in prey community composition among habitats.

Results

In total, we recorded 1,105 hunting forays by 37 different hunters from 34 households, accounting for 6,001 man-hours (mean foray duration = 5 h 26 min). Hunters from the three participating villages killed at least 925 animals, accounting for a combined weight of 14,187 kg. These included 82 unretrieved animals (8.9%) that had escaped following what was thought to have been a lethal wound. All animals were killed using shotguns (0.16 to 0.32 calibre), with the exception of tortoises (*Geochelone* spp.) which were simply picked up when sighted. Several hunters from each community occasionally hunted with dogs. Diurnal and nocturnal hunts were carried out in all habitats, and nocturnal hunts comprised 79%, 53%, 38%, 30%, and 15% of all hunts in plantations, secondary forests of plantations, primary forest, fallow and active agricultural fields, respectively. The strategy of waiting by flowering and fruiting trees was used by hunters in a small number of hunts during June and July, and made over 15% of all hunts monthly from August through December. 10.7% (118) of the 1,105 hunts recorded in this study were nocturnal waits, mostly (107 or 91%) in primary forest.

Game species harvested in different habitat

Game species harvest in the Jari landscape included at least 21 mammal, seven bird, and two reptile species. There was a decrease in species richness and prey community evenness from primary forest to agricultural fields (Fig. 2). Of the 30 species killed, 28 were killed at least once in primary forest, 14 were killed in secondary forests following either agriculture or plantations, nine were killed in *Eucalyptus* plantations,

and seven were killed in agricultural plots (Table 2). Prey community composition was significantly different among habitats (ANOSIM, $R = 0.38$, $p < 0.001$).

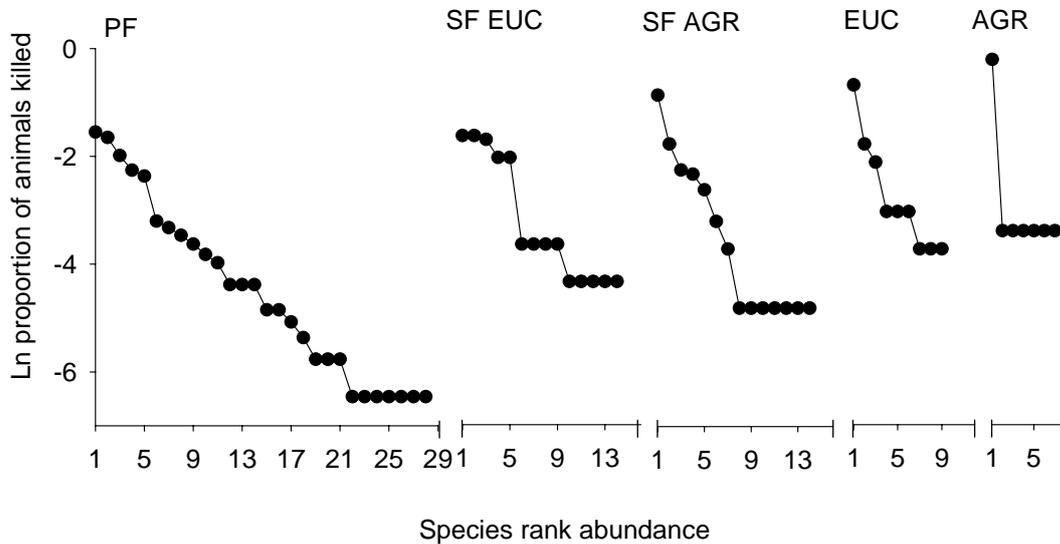


Figure 2. Rank abundance plots of game species killed by hunters in native and non-native habitats in the Jarí region of the northeastern Brazilian Amazon. For each habitat we plotted the proportion of animals killed accounted for by each species, on a logarithmic scale.

White-lipped peccaries (*Tayassu pecari*) accounted for the highest proportion (40%, 5,536 kg) of the biomass offtake (Table 2). Red-rumped agouti accounted for the largest number of 181 kills, 20% of the total. Four of the six primates hunted were killed only in primary forest, including the two largest species — Guianan howler monkey (*Alouatta macconnelli*), and black spider monkey (*Ateles paniscus*). Ungulates were widely hunted across the landscape, though offtake rates (kg per km²) were twice as high in primary forest and agricultural second-growth than in other habitats. White-lipped peccaries and red brocket deer (*Mazama americana*) were harvested from all habitats. (*Tapirus terrestris*) and grey brocket deer (*M. gouazoubira*) were frequently killed in primary forest, plantations and secondary

Table 1. Demographic characteristics of the three study villages and habitat coverage in landscapes around the study villages (LS) covering all habitat within 10km of each village, and the actual catchment where they are known to hunt (HC).

	<i>Bananal</i>			<i>São Militão</i>			<i>Vila Nova</i>			<i>Mean</i>		
Community Age	43			50			50					
# Families	13			9			19					
# Hunters	14			10			14					
Catchment size (km ²)	95.4			60.1			77.5			73.7		
	% LS ^a	% HC ^b	LS/HC ^c	% LS	% HC	LS/HC	% LS	% HC	LS/HC	% LS	% HC	LS/HC
Primary forest	32.9	37.1	1.1	17.1	46.7	2.7	76.1	79.8	1.1	42.0	52.9	1.6
Eucalyptus	25.9	25.0	1.0	40.2	28.8	0.7	7.2	5.5	0.8	24.4	20.3	0.8
SF Eucalyptus	33.4	30.4	0.9	38.5	15.0	0.4	9.7	4.4	0.5	27.2	17.8	0.6
Agricultural	1.3	0.9	0.7	0.6	1.4	2.3	1.0	2.4	2.4	1.0	1.5	1.8
SF Agriculture	6.6	6.6	1.0	3.6	8.2	2.3	6.0	8.0	1.3	5.4	7.5	1.5
G tests	<i>G</i>	<i>df</i>	<i>p</i>	<i>G</i>	<i>df</i>	<i>p</i>	<i>G</i>	<i>df</i>	<i>p</i>	<i>G</i>	<i>df</i>	<i>p</i>
	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 the habitat, within a 10 km radius of the village

^b% HC = Percentage of the actual hunting catchment occupied by each habitat

^cLS/HC = Landscape coverage over hunting catchment coverage

Need to Feed: Final Report

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

		Body mass [*]	N	kg/km ²	N	kg/km ²	N	kg/km ²	N	kg/km ²	N	kg/km ²	N**	kg
		(kg)	Primary forest	Eucalyptus	SF Eucalyptus	Agricultural fields	SF Agriculture	Total						
Primates														
<i>Alouatta macconnelli</i>	Guianan howler monkey	6.5	23	1.19	0	-	0	-	0	-	0	-	23	150
<i>Cebus apella</i>	Brown capuchin	3.24	17	0.44	0	-	2	0.16	0	-	3	0.56	22	71.3
<i>Ateles paniscus</i>	Black spider monkey	9.02	8	0.58	0	-	0	-	0	-	0	-	8	72.2
<i>Pithecia pithecia</i>	Guianan saki monkey	2	1	0.02	0	-	0	-	0	-	0	-	1	2
<i>Saguinus m. midas</i>	Golden-handed tamarin	0.55	1	0.00	0	-	0	-	0	-	0	-	1	0.55
<i>Saimiri sciureus</i>	Squirrel monkey	0.94	0	-	0	-	0	-	0	-	1	0.05	1	0.94
				2.2		0		0.2		0		0.6		
Ungulates														
<i>Tayassa pecari</i>	White-lipped peccary	32	136	34.74	5	3.52	10	7.72	1	9.11	21	38.62	173	5536
<i>Tayassa tajacu</i>	Collared peccary	21.7	60	10.37	0	-	1	0.52	1	6.17	13	16.18	75	1625
<i>Mazama americana</i>	Red brocket deer	30	26	6.23	21	13.87	14	10.14	1	8.54	5	8.62	67	2010
<i>Mazama gouazoubira</i>	Gray brocket deer	18	20	2.87	2	0.79	1	0.43	0	-	0	-	23	414
<i>Tapirus terrestris</i>	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														
<i>Dasyprocta agouti</i>	Red-rumped agouti	4.2	88	2.95	7	0.65	10	1.01	24	28.70	52	12.55	181	760
<i>Agouti paca</i>	Paca	8.5	123	8.35	2	0.37	15	3.08	1	2.42	9	4.40	150	1275
<i>Myoprocta acouchy</i>	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														
<i>Panthera onca</i>	Jaguar	24	1	0.19	1	0.53	2	1.16	0	-	0	-	4	96
<i>Leopardus pardalis</i>	Ocelot	10.3	2	0.16	1	0.23	0	-	0	-	0	-	3	30.8
<i>Herpailurus yaguarundi</i>	Jaguarundi	6.5	0	-	0	-	0	-	0	-	1	0.37	1	6.5
<i>Coendou prehensilis</i>	Brazilian porcupine	4.5	4	0.14	0	-	0	-	0	-	0	-	4	18
<i>Nasua nasua</i>	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
<i>Pridontes maximus</i>	Giant armadillo	43	2	0.69	0	-	0	-	0	-	0	-	2	86
				3.8		1.0		3.0		1.4		3.8		
Birds														
<i>Tinamus major</i>	Great tinamou	1.1	14	0.12	0	-	0	-	0	-	1	0.06	15	16.5
<i>Crax alector</i>	Black curassow	3.1	12	0.30	0	-	0	-	0	-	0	-	12	37.2
<i>Psophia crepitans</i>	Gray-winged trumpeter	1.3	8	0.08	0	-	0	-	0	-	0	-	8	10.4
<i>Ara spp.</i>	Macaw	1.1	5	0.04	0	-	1	0.03	0	-	1	0.06	7	7.7
<i>Ramphastos tucanus</i>	White-throated toucan	0.6	1	0.00	0	-	1	0.01	1	0.17	1	0.03	4	2.4
<i>Penelope marail</i>	Marail guan	2	2	0.03	0	-	0	-	0	-	0	-	2	4
<i>Ortalis m. motmot</i>	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														
<i>Geochelone spp.</i>	Tortoise	3.57	8	0.23	0	-	2	0.17	0	-	1	0.21	11	39.3
<i>Caiman crocodilus</i>	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	13973.6

* Body mass estimates are taken from Hilty; Peres 2001 and our own data from Jarí (undressed) using Pesola 0-10 kg and 0-50 kg scales.

** 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.

forest of plantations, but never in active or fallow fields. Jaguars (*Panthera onca*) were killed in primary forest, and both active and fallow plantations. They were not killed in active or fallow agricultural fields. Paca (*Agouti paca*), agouti, and smaller armadillos (*Dasyposidi*) were harvested from all habitats. The highest number of agouti (both crude and per km²) were harvested from fallow and active agricultural fields.

The offtake of birds was generally low, and came predominantly from primary forest. Black currasow (*Crax alector*), grey-winged trumpeters (*Psophia crepitans*) and marail (*Penelope marail*) guans were only killed in primary forest areas. However, hunters often shot large canopy frugivores (macaws *Ara* spp., parrots *Amazona* spp. and toucans *Ramphastos tucanus*) at the edges of fallow and active fields.

Landscape composition of hunting catchments

The hunting catchments of the three villages covered between 60 and 95 km² and their land-cover composition was significantly different from the landscape mosaic available within a circumcentric buffers around each village (Table 1). Hunting catchments contained more primary forest than expected on the basis of availability (Table 1). The hunters of one village, São Militão, had nearly three times more primary forest in their catchment than in the surrounding landscape. Secondary forest on fallow fields was represented in the hunting catchment according to its availability at Bananal, but was over-represented in the hunting catchments of São Militão and Vila Nova. *Eucalyptus* plantations and post-plantation secondary forests were under-represented in hunting catchments, with the exception of plantations around Bananal, the area of which was equally represented in the surrounding landscape. Agricultural plots were over-represented in the area used by hunters of Vila Nova and São Militão, but under-represented around Bananal.

Spatial structure of hunting effort

Most hunts took place in primary forest. The hunters of Vila Nova spent 86% of their total hunting time in primary forest and those of Bananal and São Militão spent approximately two thirds of their hunting time in this forest type (Table 3).

Considering other habitats, villagers spent more time hunting in secondary forest recovering from either agricultural plots or plantations than in *Eucalyptus* plantations or active fields.

Table 3. Hunting effort, offtake of game, and catch per unit effort in different habitats within the Jarí landscape mosaic.

	<i>Hunts</i>	<i>Hours</i>	<i>% hrs</i>	<i>Hrs/km²</i>	<i>Kills</i>	<i>% kills</i>	<i>kg</i>	<i>% kg</i>	<i>Kills / hr</i>	<i>kg / hr</i>
<i>Bananal</i>										
Primary forest	296	1661	65.2	46.9	206	55.5	2387	48.2	0.12	1.44
Eucalyptus	37	139	5.4	5.8	28	7.5	580	11.7	0.20	4.18
SF Eucalyptus	68	359	14.1	12.4	58	15.6	1125	22.7	0.16	3.13
Agriculture	14	44	1.7	51.6	13	3.5	99	2.0	0.29	2.23
SF Agriculture	84	344	13.5	54.7	66	17.8	764	15.4	0.19	2.22
Total	499	2547	100.0	26.9	371	100.0	4953	100.0	0.15	1.95
<i>Sao Militão</i>										
Primary forest	217	1067	65.3	38.0	202	79.2	2761	82.2	0.19	2.59
Eucalyptus	5	23	1.4	1.3	1	0.4	18	0.5	0.04	0.78
SF Eucalyptus	28	153	9.4	17.0	16	6.3	170	5.1	0.10	1.11
Agriculture	3	1	0.1	1.2	2	0.8	8	0.2	2.02	8.48
SF Agriculture	76	390	23.9	79.6	34	13.3	403	12.0	0.09	1.03
Total	329	1634	100.0	27.2	255	100.0	3360	100.0	0.16	2.06
<i>Vila Nova</i>										
Primary forest	223	1572	86.4	25.4	243	81.3	4882	83.1	0.15	3.10
Eucalyptus	17	85	4.7	20.1	15	5.0	505	8.6	0.18	5.94
SF Eucalyptus	3	19	1.0	5.4	4	1.3	112	1.9	0.22	6.05
Agriculture	16	74	4.1	40.7	15	5.0	92	1.6	0.20	1.23
SF Agriculture	18	70	3.9	11.3	22	7.4	283	4.8	0.31	4.03
Total	277	1820	100.0	23.6	299	100.0	5873	100.0	0.16	3.23
<i>Combined</i>										
Primary forest	736	4300	71.7	34.3	651	70.4	10029	70.7	0.15	2.33
Eucalyptus	59	247	4.1	5.4	44	4.8	1103	7.8	0.18	4.46
SF Eucalyptus	99	531	8.8	12.8	78	8.4	1407	9.9	0.15	2.65
Agriculture	33	119	2.0	34.0	30	3.2	199	1.4	0.25	1.66
SF Agriculture	178	804	13.4	46.2	122	13.2	1449	10.2	0.15	1.80
Total	1105	6001	100.0		925	100.0	14187	100.0	0.15	2.36

Hunting effort per unit area (hours per km²) in plantations and post-plantation secondary forests was lower than that in primary forest across all three villages. Hunters allocated twice to four times more hunting time per unit area to secondary forests of fallow fields than to secondary forests of cleared plantations. Hunting pressure in active and fallow agricultural fields was highly variable among villages. Fallow agricultural plots received a high hunting effort per km² 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 shifted almost exclusively to primary forest further away from the villages (Fig 3a).

Game offtake and landscape structure

Hunters of all three villages killed animals in all of the five habitats examined (Table 3). Considering all kills, primary forest provided the most numeric offtake (651 kills, 70%), and agricultural plots and *Eucalyptus* 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 biomass of game killed from habitats other than primary forests was variable. Although most game were killed in primary forest, offtake per unit area was actually highest from fallow agricultural plots (85 kg/km²), and primary forest had only the second-highest offtake (79 kg/km², Table 2). Less than half this biomass density was extracted from fallow plantations (34 kg/km²), and active *Eucalyptus* plantations contributed the least game per unit area (23 kg/km²).

Hunting efficiency in different habitat types

Prey size was significantly different among habitats (Kruskal-Wallis, $X^2_4 = 43.8$, $p < 0.001$). On average, prey were largest in plantations and smallest in agricultural fields (Figure 4). Prey killed in post-plantation secondary forests were larger than prey killed in fallow fields ($U_{78,122} = -2.556$, $p = 0.011$). There was no significant difference in prey size between primary forest and post-plantation secondary forest ($U_{650,78} = -0.18$, $p = 0.986$) whereas prey killed in primary forest tended to be larger than that of fallow fields ($U_{650,122} = -3.352$, $p = 0.001$). Animals shot in fallow fields were significantly smaller than animals shot in active fields ($U_{122,30} = -2.697$, $p = 0.007$).

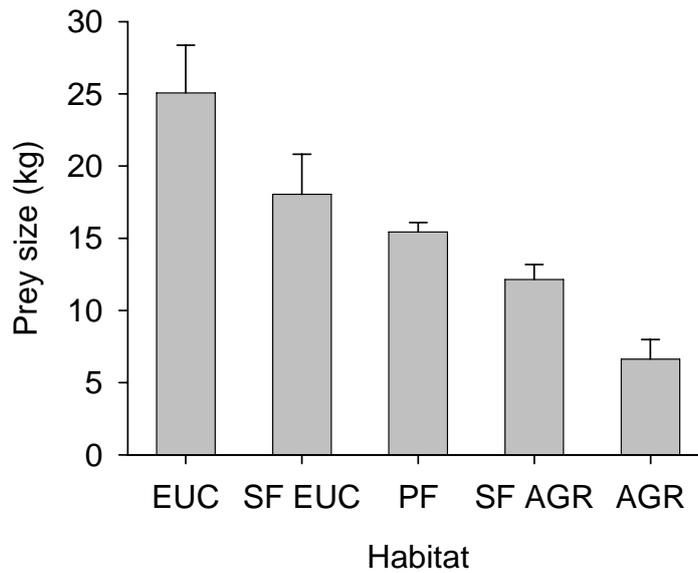


Figure 4. Mean size (\pm SE) of animals killed by hunters in primary and anthropogenic habitats of Jarí, northeastern Brazilian Amazon.

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 second-growth. However, primary forest exhibited a lower biomass return per unit of time spent hunting than at least one other habitat in all villages. Hunting in plantations was variable between villages, yielding the highest measures of CPUE (both in terms of number of kills and biomass returned) for Bananal and Vila Nova, and the lowest in São Militão (although data from only five hunting forays were available from this village). For all villages, secondary forests following plantations sustained a higher hunting efficiency in terms of biomass per unit time than secondary forests following agriculture.

Distance from villages

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. 3b), which is not surprising given that these areas were highly disturbed. Fallow agricultural plots had the highest offtake per km^2 in all three villages. Secondary habitats still contributed with game extracted between 1 and 3 km from the villages of Bananal and Vila Nova. For São Militão, however, primary forest remained the exclusive source of game beyond 1 km of the

village. Primary forest remained the sole provider of game between 5 and 10 km of all three villages, with the exception of a small number of excursions farther into *Eucalyptus* plantations by hunters from Bananal.

Predicting hunting effort

There were significant differences between the observed and the expected amount of hunting effort (kg per hour) allocated to different habitats, as predicted by CPUE and the area of each habitat available within village catchments (Fig. 5). Primary forests were allocated a higher hunting effort than expected in all cases, whereas the reverse was the case for plantations, post-plantation second-growth and agricultural plots. Hunting effort in fallow fields was highly variable between villages, ranging from three-fold greater than expected in São Militão to only a third of the expected hunting effort in Vila Nova.

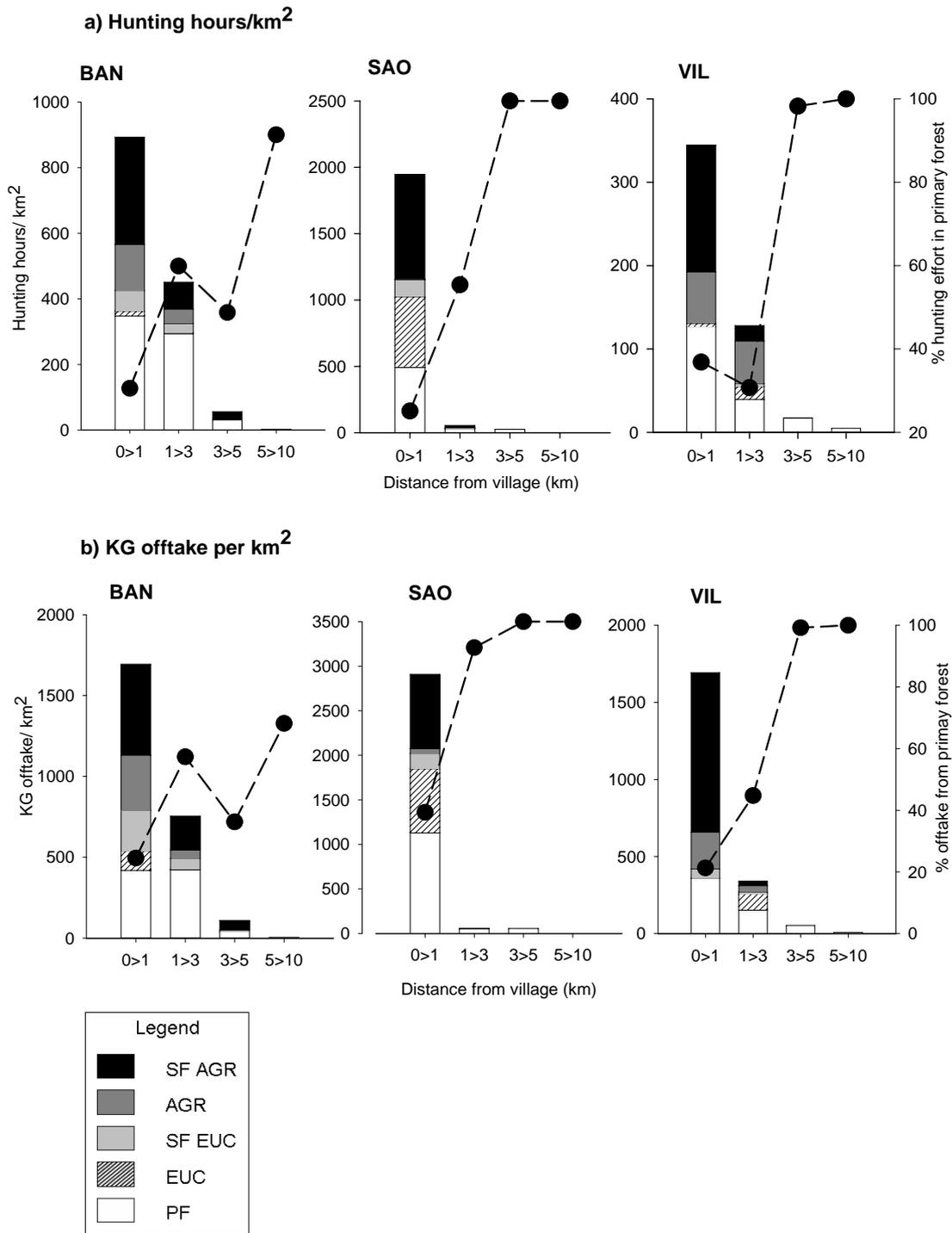


Figure 3. a) Hunting effort per km² of habitat coverage, and b) Bushmeat offtake per km² of each habitat, at different distance classes from the three study villages in Jarí. The percentage of hunting effort or offtake from primary forest is shown on the right-hand y axis.

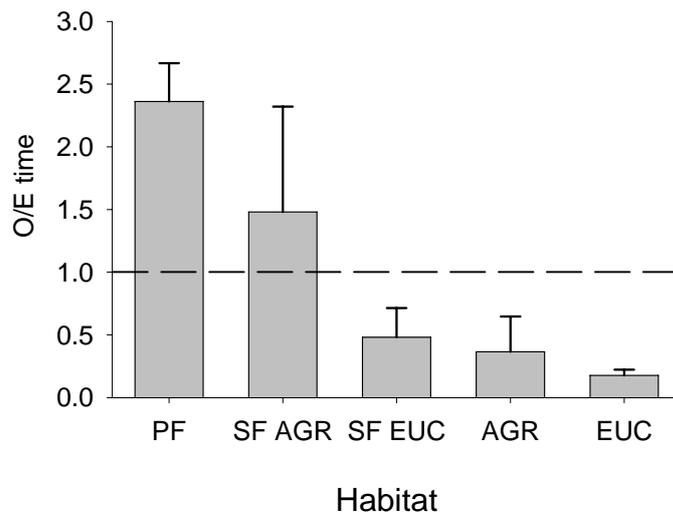


Figure 5. Observed hunting time in each habitat, divided by the expected time (\pm SE) based on the relative catch per unit effort (kg per hour) and the proportion of each habitat within the hunting catchments of each study village ($n = 3$). There was a significant difference between observed and expected hunting effort across habitats ($G = 6524$, $df = 14$, $p < 0.00001$).

Discussion

Anthropogenic habitats are increasingly widespread in tropical forested regions and there is a growing wildlife conservation interest in game hunting within human-dominated landscapes (Robinson & Bennett 2004). We discuss the importance of accounting for habitat availability and habitat-specific hunting effort when documenting game offtake from heterogeneous landscape mosaics. We present potential explanations for hunter preference for primary forest, using evidence from optimal foraging theory. Finally, we compare the prey communities of different habitats and consider the implications of our results for the conservation of herbivores and carnivores in industrial- and smallholder-dominated landscapes in the humid tropics.

Primary forest

Primary forest was consistently favoured by hunters at the landscape-level, and primary forests were hunted more heavily than other habitats within village hunting

catchments. As a result, primary forest supplied most of the game meat to the three communities in our study. However, primary forests were not the most efficient hunting grounds, and our prediction that habitat availability and CPUE would explain allocation of hunting effort was not supported. So why did hunters prefer primary forest? Research in temperate forests has examined habitat selection based on optimal foraging (Boxall & Macnab 2000), yet this approach has been given little attention in the tropics (but see Smith 2005). We examine three alternative, but potentially complementary, explanations for the preference for primary forests.

(1) Habitat structure: Hunters' preference for primary habitats may simply be a function of habitat structure, as it may be more difficult to locate or pursue game in secondary habitats, which are generally much denser in the understorey (Johns 1985, Naughton-Treves 2003). Tree plantations also have limitations as hunting grounds (see Boxall & Macnab 2000). Large terrestrial ungulates in Jarí mainly use plantations at night, where on the basis of reports from local hunters they feed on the young shoots and leaves of *Eucalyptus* and pioneer plants (e.g. *Manihot brachyloba* Müll. Arg.). Food plants are widely dispersed so searching for prey requires intensive searching and the concomitant use of expensive flashlight batteries. Local hunters also suggest that moon phase and the herbicidal or mechanical suppression of the native understorey (by the forestry company) affects hunting success in plantations. The effect of large-scale management on the suitability of plantation forests as either wildlife areas or hunting grounds warrants further investigation.

(2) Energetic cost: Hunting techniques in primary forest were more energetically conservative because terrestrial vertebrates were often attracted to the seasonal flowering and fruiting of food trees such as *Caryocar villosum* (cf. Cymerys, 2005). Nocturnal "waits" at fruiting and flowering trees was a major hunting strategy for five months of the year and was largely restricted to primary forest, where fruiting trees were larger. Low-effort nocturnal hunting was especially attractive in combining wildmeat acquisition with day-time agricultural activities.

(3) Opportunity costs: 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. Escobal & Aldana 2003; Plowden 2004). Hunting in primary forest in our study was often combined with the opportunistic or planned collection of NTFPs such as Brazil nuts, vines (*Heteropsis* sp.), and fruits. The opportunity costs of hunting in primary forest were therefore

lower than in other habitats. However, further work is required on the costs and benefits of hunting in different habitats, and the non-game resources that affect the profitability of spending time in each.

Secondary habitats

Active and fallow agricultural areas around our study villages supported a depauperate suite of “weedy” species (c.f. Naughton-Treves 2003), and many preferred game species were not recorded in these habitats. Large ungulates (e.g. tapirs) and carnivores (e.g. jaguars) were apparently unable to persist in the smallholder agricultural components of landscape mosaics. Despite the limited range of species in these habitats, levels of wildmeat acquisition from agricultural fields and their fallow forests are often high (Table 3, cf. Wilkie 1989, Naughton-Treves 2003; Smith 2005; Gavin 2007). We attribute this to the high hunting pressure within these habitats, as hunters were often able to combine opportunistic hunting with the cultivation of their fields.

The area of plantation forestry is increasing in Latin America and elsewhere (FAO 2001), and an increasing proportion of forest dwellers are therefore likely to inhabit landscapes incorporating this land cover. Our results show the potential importance of plantations, as hunters obtained a wide range of large mammal species from plantations, including those of conservation concern such as white-lipped peccary, tapir and jaguar.

As predicted, the large areas of second-growth in the Jari landscape supported species of greater conservation interest than the agricultural secondary forests. Post-plantation secondary forests were used by a high abundance of large herbivores including ungulates and large rodents (Parry et al. in review). Although conjecture that large areas of degraded secondary forest may be productive hunting grounds (Lovejoy 1985) may be correct, these habitats were not preferred by hunters in this study. In this respect, abandoned or fallow areas following land clearance in the tropics (e.g. cattle ranching; clear-cut logging; plantation forestry) may offer greater potential for large vertebrates than smallholder agricultural areas.

White-lipped peccaries were shot in all forest and agricultural habitats. However, for a large herd-living species using home ranges in excess of 10,000 ha (Fragoso 1998), they are clearly transient visitors in anthropogenic habitats. In fact, habitats other than primary forests, where species of conservation concern were shot,

were more likely operating as population sinks than “breeding grounds”. More research is required on animal movements across tropical landscapes (Law & Dickman 1998), especially for other area-demanding mammals such as jaguar. Nonetheless, even the occasional presence of these species in plantations and other habitats demands that greater consideration is given during project planning and management.

Although consistent hunting patterns emerge from our study, there were also clear differences among communities. The hunters from São Militão rarely hunted in plantations, in contrast to the two other villages. This may be due to the young age of the plantations accessible to this village. Villagers at Vila Nova, who had access to largest areas of intact primary forest and harvested the largest amounts of Brazil nuts, hunted almost exclusively in this forest type. While our results reveal some strong landscape-level hunting patterns, the variability between villages also highlights the importance of taking specific local factors into account.

Conservation implications

The absence of many mammal species from human-dominated landscapes is thought to reflect hunting pressure, rather than habitat *per se* (cf. Daily et al. 2003), and in our study hunting pressure was much higher in agricultural second-growth than in post-plantation secondary forests. This may have confounded recent suggestions that anthropogenic habitats support primarily rural livelihoods, rather than wildlife (e.g. Naughton-Treves 2003). Wildmeat offtake from degraded lands may reflect the spatial composition of the landscape as inevitably there is little primary forest close to settlements and therefore hunting pressure high in agricultural habitats.

Hunting in secondary habitats could potentially relieve hunting pressure in primary forest, and therefore reduce the impacts of hunting on vulnerable primary forest specialists. However, the value of any such effect may be diminished by the unsuitability of anthropogenic habitats for many primary forest species, and the vulnerability to hunting of highly conspicuous and mobile species (e.g. white-lipped peccaries) as they move across the landscape. Mammals hunted in secondary forests, agricultural plots and plantations at Jari were predominantly terrestrial (cf. Robinson & Bennett 2004) and most primates were not encountered by hunters outside of primary forest. Our findings also indicate that most game birds do not persist in anthropogenic habitats, even in large lightly-hunted areas of second-growth.

Conclusions

This study demonstrates the importance of considering the availability and spatial distribution of different habitats to understand hunting patterns in tropical landscapes. We build on progress made by recent studies investigating the habitats supplying game by considering hunting effort and the spatial distribution of habitats. Our results also highlight the complexity of hunter decision-making, as the use of mosaic habitats by hunters cannot necessarily be explained by the abundance of a single resource. They suggest 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 anthropogenic habitats can provide both plant and animal resources to local people (Gavin 2004; Robinson & Bennett 2004) *and* serve as a theatre for biodiversity conservation (Wright & Muller-Landau 2006; Vandemeer & Perfecto in press). That hunting activities were widespread across the landscape mosaic confirms the importance of anthropogenic habitat as sources of meat to rural peoples (Robinson & Bennett 2004). However, the sustainability of hunting bushmeat across different habitats remains unknown (but see Wilkie & Lee 2004). Despite optimistic predictions regarding the role of smallholders in conserving Amazonian forests (Campos & Nepstad 2006), the heavy toll of hunting in agricultural areas makes them unlikely conservationists of preferred game species. Sensitive management of large-scale regrowth areas may offer more congruence with conservation objectives.

Literature Cited

- Achard, F., H. D. Eva, H.-J. Stibig, P. Mayaux, J. Gallego, T. Richards, and J.-P. Malingreau. 2002. Determination of deforestation rates of the world's humid tropical forests. *Science* **297**:999-1002.
- Boxall, P. C., and B. Macnab. 2000. Exploring the preferences of wildlife recreationists for features of boreal forest management: a choice experiment approach. *Canadian Journal of Forest Research* **30**:1931-1941.
- Campos, M. T., and D. C. Nepstad. 2006. Smallholders, the Amazon's new conservationists. *Conservation Biology* **20**:1553-1556.

- Clarke, K. R., and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation. Primer-E Ltd, Plymouth. 172 pp.
- Coomes, O. T., B. L. Barham, and Y. Takasaki. 2004. Targeting conservation-development initiatives in tropical forests: insights from analyses of rain forest use and economic reliance among Amazonian peasants. *Ecological Economics* **51**:47-64.
- Cymerys, M. 2005. Chamando a caça: as frutíferas favoritas. Page 129 in P. Shanley, and G. Medina, editors. *Frutíferas e plantas úteis na vida Amazonica*. CIFOR, Imazon, Belém, Brazil.
- Daily, G. C., G. Ceballos, J. Pacheco, G. Suzan, and A. Sanchez-Azofeifa. 2003. Countryside biogeography of Neotropical mammals: Conservation opportunities in agricultural landscapes of Costa Rica. *Conservation Biology* **17**:1814-1826.
- Escamilla, A., M. Sanvicente, M. Sosa, and C. Galindo-Leal. 2000. Habitat mosaic, wildlife availability, and hunting in the tropical forest of Calakmul, Mexico. *Conservation Biology* **14**:1592-1601.
- Escobal, J., and U. Aldana. 2003. Are nontimber forest products the antidote to rainforest degradation? Brazil nut extraction in Madre De Dios, Peru. *World Development* **31**:1873-1887.
- Fearnside, P. M. 2005. Deforestation in the Brazilian Amazon: history, rates, and consequences. *Conservation Biology* **19**:680-688.
- Food and Agriculture Organization (FAO). 2001. Global Forest Resources Assessment 2000. Available from www.fao.org, Rome (accessed September 2006).
- Food and Agriculture Organization (FAO). 2005. State of the world's forests. Rome
- Fimbel, C. 1994. The Relative Use of Abandoned Farm Clearings and Old Forest Habitats by Primates and a Forest Antelope at Tiwai, Sierra-Leone, West-Africa. *Biological Conservation* **70**:277-286.
- Fragoso, J. M. V. 1998. Home range and movement patterns of white-lipped peccary (*Tayassu pecari*) herds in the northern Brazilian Amazon. *Biotropica* **30**:458-469.
- Gardner, T. A., J. Barlow, L. Parry, and C. A. Peres. 2007. Predicting the uncertain future of tropical forest species in a data vacuum. *Biotropica*

- Gavin, M. C. 2004. Changes in forest use value through ecological succession and their implications for land management in the Peruvian Amazon. *Conservation Biology* **18**:1562-1570.
- Gavin, M. C. 2007. Foraging in the fallows: Hunting patterns across a successional continuum in the Peruvian Amazon. *Biological Conservation* **134**:64-72.
- Hilty, S. L. 2003. *Birds of Venezuela*. Christopher Helm, London.
- Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* **13**:201-228.
- Jerozolimski, A., and C. A. Peres. 2003. Bringing home the biggest bacon: a cross-site analysis of the structure of hunter-kill profiles in Neotropical forests. *Biological Conservation* **111**:415-425.
- Johns, A. D. 1985. Differential detectability of primates between primary and selectively logged habitats and implications for population surveys. *American Journal of Primatology* **8**:31-36.
- Law, B. S., and C. R. Dickman. 1998. The use of habitat mosaics by terrestrial fauna: implications for conservation and management. *Biodiversity & Conservation* **7**:323-333.
- Lindenmayer, D. B., and J. F. Franklin 2002. *Conserving forest biodiversity: a comprehensive multiscaled approach*. Island Press, Washington DC.
- Lovejoy, T. A. 1985. Rehabilitation of degraded tropical forest lands. *The Environmentalist* **5**:13-20.
- Matthiopoulos, J. 2003. The use of space by animals as a function of accessibility and preference. *Ecological Modelling* **159**:239-268.
- Naughton-Treves, L., J. L. Mena, A. Treves, N. Alvarez, and V. C. Radeloff. 2003. Wildlife survival beyond park boundaries: the impact of slash-and-burn agriculture and hunting on mammals in Tambopata, Peru. *Conservation Biology* **17**:1106-1117.
- Parry, L., J. Barlow, and C. A. Peres. in review. Large-vertebrate assemblages of primary and secondary forests in the Brazilian Amazon. *Journal of Tropical Ecology*.
- Peres, C. A. 2001. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. *Conservation Biology* **15**:1490-1505.

- Peres, C. A., and E. Palacios. 2007. Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal-mediated seed dispersal. *Biotropica* **39**.
- Perz, S. G., and D. L. Skole. 2003. Secondary forest expansion in the Brazilian Amazon and the refinement of forest transition theory. *Society & Natural Resources* **16**:277-294.
- Plowden, C. 2004. The ecology and harvest of andiroba seeds for oil production in the Brazilian Amazon. *Conservation & Society* **2**:251-272.
- Redford, K. H., and J. G. Robinson. 1987. The game of choice: patterns of Indian and colonist hunting in the Neotropics. *American Anthropologist* **89**:650–667.
- Rice, W. R. 1989. Analyzing tables of statistical test. *Evolution* **43**:223-225
- Rice, R. A. and R. Greenberg. 2004. Silvopastoral systems: ecological and socioeconomic benefits and migratory bird conservation. Pages 453-472 in G. Schroth, A. B. da Fonseca, C. A. Harvey, C. Gascon, H. L. Vasconcelos, and A-M. N. Izac, editors. *Agroforestry and biodiversity conservation in tropical landscapes*. Island Press, Washington DC.
- Robinson, J. G., and E. L. Bennett. 2004. Having your wildlife and eating it too: an analysis of hunting sustainability across tropical ecosystems. *Animal Conservation* **7**:397-408.
- Rosenberg, D. K., and K. S. McKelvey. 1999. Estimation of habitat selection for central-place foraging animals. *Journal of Wildlife Management* **63**:1028-1038.
- Siren, A., P. Hamback, and E. Machoa. 2004. Including spatial heterogeneity and animal dispersal when evaluating hunting: a model analysis and an empirical assessment in an Amazonian community. *Conservation Biology* **18**:1315-1329.
- Smith, D. A. 2003. Participatory mapping of community lands and hunting yields among the Buglé of western Panama. *Human Organization* **62**:332-343.
- Smith, D. A. 2005. Garden game: Shifting cultivation, indigenous hunting and wildlife ecology in western Panama. *Human Ecology* **33**:505-537.
- Stoner, K.E., K. Vulinec, S.J. Wright, and C.A. Peres. 2007. Hunting and plant community dynamics in tropical forests: a synthesis and future directions. *Biotropica*.

- Vandermeer, J., and I. Perfecto. in press. The agricultural matrix and a future paradigm for conservation. *Conservation Biology*.
- Wilkie, D. S. 1989. Impact of Roadside Agriculture on Subsistence Hunting in the Ituri Forest of Northeastern Zaire. *American Journal of Physical Anthropology* **78**:485-494.
- Wilkie, D. S., and R. J. Lee. 2004. Hunting in agroforestry systems and landscapes: conservation implications in West-Central Africa and Southeast Asia. Pages 346-370 in G. Schroth, A. B. da Fonseca, C. A. Harvey, C. Gascon, H. L. Vasconcelos, and A-M. N. Izac, editors. *Agroforestry and biodiversity conservation in tropical landscapes* Island Press, Washington DC.
- Winterhalder, B. 1997. A forager-resource population ecology model and implications for indigenous conservation. *Conservation Biology* **11**:1354-1364.
- Wright, S. J., and H. C. Muller-Landau. 2006. The future of tropical forest species. *Biotropica* **38**:287-301
- Wunderle, J. M. J. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecology & Management* **99**:223-235.