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Diversity, abundance and the impact of hunting on large mammals in two contrasting forest sites in northern amazon

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A variety of Amazonian mammals serve as sources of food for its human inhabitants, but hunting can have a strong negative impact on them. Diversity, abundance, biomass, and average group size of medium-sized and large mammals are compared across two forest areas of the northern Amazon: the Viruá National Park (protected) and the Novo Paraíso settlement (a human settlement where hunting is permitted). Hunting pressure was also characterized in Novo Paraíso. A total of 33 mammal species were recorded. There were no significant differences in the sighting rates, relative abundance and biomass, and mammal group sizes between the two areas, although the totals of all these variables were higher in Viruá due to the higher abundance of *Tayassu pecari*, which was not recorded at Novo Paraíso. It is suggested that *T. pecari* may be on the verge of local extinction, as it was the most hunted species in the settlement area. Through interviews with 50 hunters, we estimate that 541 mammals of 20 species were hunted during the study year, resulting in an estimated biomass take of 8517 kg. While the hunting intensity in Novo Paraíso may be sustainable in the short term, the reported decline of hunting efficiency, combined with the extirpation of *T. pecari*, suggests that mammal abundance may decline there in the near future. In the study year, 849 hunts were carried out in a hunting effort of 4575 hours, with a maximum distance travelled of 5.4 km. There was an average of 4.82 consumers for each hunt, and a per capita harvest rate of 2.24 individuals/consumer year. Hunting was not only for subsistence, but also for retaliation, although some species may not be hunted due to cultural taboos. The need for quantification of harvesting rates to maintain hunting at sustainable levels is highlighted.

The Brazilian Amazon represents over a third of all tropical forest on Earth (Peres 2000), but vast tracts of primary forest are being degraded by deforestation and fragmentation (Laurance and Peres 2006). As a result, much of the remaining primary forest is surrounded by human modified habitats (Stone et al. 2009).

While secondary tropical forests can sustain a high abundance of wildlife, in many tropical forest landscapes the conservation value of habitat mosaics have often been severely compromised by the hunting practices of local people (Parry et al. 2007, Peres and Palacios 2007). Wild animals are an important part of the diet of many inhabitants of the Amazon forest, but hunting can have serious negative impacts on vertebrate populations (Peres 1990, Alvard et al. 1997). In addition, Amazonian peoples have become more sedentary over the last decades (Vickers 1991), and the increasing availability of firearms and more efficient transport continues to intensify hunting pressure (Souza-Mazurek et al. 2000). In this context, large mammals are among the

most hunted species (Redford and Robinson 1987, Bodmer 1995, Peres 2000).

The animal mortality rate in an anthropogenic landscape is strongly related to the spatial distribution of the hunting effort (Sirén et al. 2004). Overall, hunting areas located near villages and settlements in Amazonia are more frequent than more distant hunting areas (Vickers 1984, Alvard 1992, Peres and Nascimento 2006, Ohl-Schacherer et al. 2007, Parry et al. 2009). According to Alvard et al. (1997), about 87% of the animals eaten by a native community are hunted within a 10-km radius of the village, which seems to be the standard in the Neotropics (Vickers 1984, Alvard 1992, Ohl-Schacherer et al. 2007, Parry et al. 2009). As a result, the abundance of game species in areas surrounding humanoccupied sites becomes gradually less, and hunters have to travel further to capture target species (Ohl-Schacherer et al. 2007).

In continuous forest areas, where the persistence of populations in the sink habitat depends on their migration

from high quality source-habitats (Pulliam 1988), the establishment of reserve areas may serve as refuges for prey populations (Fragoso et al. 2000, Bodmer and Robinson 2004), which is vital for the persistence of the hunted species (Peres 2001). Additionally, primary forests far from human settlements are highly effective in maintaining biodiversity, even if not officially protected (Souza-Mazurek et al. 2000, Peres et al. 2003, Peres and Palacios 2007).

Hunters usually target larger prey (Emlen 1966, MacArthur and Pianka 1966), although when the preferred species are exhausted the range of hunted species increases as hunters are forced to target less valuable prey (Alvard 1994, Jerozolimski and Peres 2003). Hunting pressure, nevertheless, may be moderated by taboos and prey preferences (McDonald 1977, Colding 1998). In this sense, the different cultural aspects of each human population can affect wildlife on different scales. It is necessary to know the species chosen or avoided (and why), hunting techniques used, number of animals harvested, and motivation or purpose for hunting in order to both determine the impact of this activity, and promote conservation and sustainable management (Trinca and Ferrari 2006).

Studies of large and medium-sized mammals in the State of Roraima are relatively recent and the focus has been mainly on the mammals of Maracá Ecological Station (Fragoso 1998, Mendes Pontes 1997, 1999, Mendes Pontes et al. 2007) and the Waimiri-Atroari (Souza-Mazurek et al. 2000), Yanomami and Macuxi Indian reserves (Fragoso 2004); whereas studies in recently colonized settlement areas are virtually absent. Given the limited number of studies, the diversity of mammals, the impact of hunting and the types of wildlife used in these settlements of Roraima remain virtually unknown. The aim in this study was, therefore, to compare the diversity of medium and large-sized mammals in two areas of the State of Roraima, one protected (Viruá National Park) and one impacted by hunting (Novo Paraíso settlement), and to characterize and quantify hunting pressure to determine the impact of hunting on the mammalian community.

Methods

Study area

This study took place in two study sites some 100 km apart, in the northernmost part of the Brazilian Amazon, where the annual mean and maximum temperatures are approx. 26°C and 40°C, respectively (Sombroek 2001). The average annual rainfall is 1500 mm, with the rainy season occurring between April and August. During the seven months of the dry season, rainfall is less than 100 mm (Sombroek 2001). The studied region in the south of the State of Roraima is formed by pristine highly heterogeneous vegetation mosaics formed by open forest formations ('Campina' and 'Campinarana') and closedcanopy ombrophilous forests. Although serving as a source forest to the impacted areas, most of these pristine forests are not legally protected and are totally accessible, the only factor preventing the human presence being remoteness (Fig. 1).

Novo Paraíso settlement (impacted area)

The Novo Paraíso settlement (01°13′24.59″N; 60°23′6.27″W) (Fig. 1) is a fish-bone human settlement (forest clearings that appear in satellite images in a fishbone pattern, with forest clearance extending along secondary roads from the main road). The settlement was founded in 1982 by the Government of the State of Roraima in what was once pristine forests (Governo do Estado de Roraima 2005). It is primarily populated by non-indigenous settlers from the north and northeast of Brazil, who were attracted by the free land offered by the Federal Government as part of an Amazon colonization program initiated in the late 1970s.

Located at km 500 on the BR-174 highway, the settlement has an area of 92.84 km² (Governo do Estado de Roraima 2005) and approximately 120 families living in its urban center, the Novo Paraíso village. Dozens of families, however, living on plots of land along the BR-432, BR-210 and BR-174 highways and adjacent side roads depend on this village for the purchase of supplies and access to health and education services.

The population has a low income, the main source of which is livestock and smallholder farming. As a result, frequent deforestation and forest fires occur both inside and outside their plots to clear the land for pasture and planting crops. Because these plots are demarcated within the forest, it is easily accessed and hunting is facilitated (E. R. A. Melo unpubl.), which is practiced indiscriminately and without any control by the local government. Additionally, settlers are entitled to 'subsistence hunter's permits' granted on request by the local office of the Federal Police.

Viruá National Park (protected)

Located 70 km to the northeast of the Novo Paraíso settlement, the Viruá National Park (headquarters: 01°42′25″N; 61°10′24″W) (Fig. 1) is a federal conservation area created in 1998. With a total area of 2 270.11 km² (ICMBio 2011), the Park is located in a region of relatively flat terrain, with altitudes between 45 and 326 m a.s.l. (Governo do Estado de Roraima 2005).

Viruá contains one of the 25 km² RAPELD (long-term ecological research) grids of the PPBio (Biodiversity Research Program), consisting of 12 trails each 5 km in length. Six of the trails run north–south and six run east–west (grid: 01°28′13.75″N; 61°0′16.63″W) (Fig. 1); all of the trails are maintained by the park administration, which also patrols the area full time. The park and its surroundings are formed of untouched tracts of forest that were little used by former Amerindian inhabitants and virtually unknown to colonists. The RAPELD grid opened areas that had no human tracks and were equally unknown to local people. There are no residents within 10 km of the grid, a distance much greater than that found by this study to be the effective distance around habitations to be impacted by hunting(≤ six km).

Both study areas Novo Paraíso and Viruá are formed by the typical vegetation mosaic of 'Campina' and 'Campinarana' and closed-canopy ombrophilous forest, in this case, on relatively flat land with altitudes ranging between 89 and 122 m a.s.l. (IBGE 2005a, b, Mendes Pontes et al. 2012).

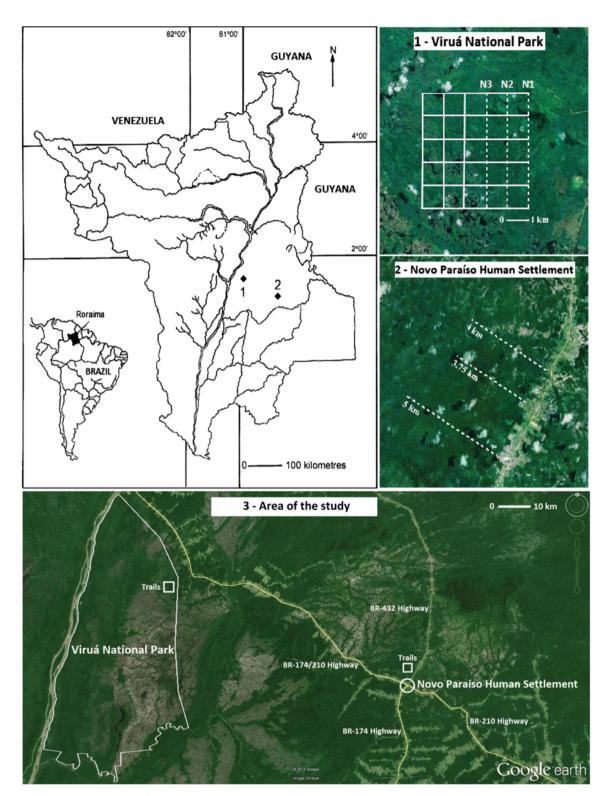


Figure 1. Location of the two study areas in Roraima, northern Brazilian Amazon is shown as follows: (1) Viruá National Park (PARNA Viruá) (showing the grid of the Biodiversity Research Program - PPBio), (2) Novo Paraíso settlement, and (3) the area of study, formed by the continuous non-protected recolonization source area. Transects where the study was conducted are represented by dotted lines. The images of the areas were obtained using Google Earth ver. 6.1.

Surveys of medium- and large-sized mammals

The surveys of medium- and large-sized mammals were performed using the line transect method (Burnham et al. 1980, Buckland et al. 1993, Mendes Pontes et al. 2008). At Novo Paraíso (impacted), three parallel trails some 3 km apart were opened behind and perpendicular to three inhabited settlement plots (Fig. 1). The trails were alphanumerically marked every 50 m, and measured 5 km (trail 1), 3.75 km (trail 2) and 4 km (trail 3). At Viruá (protected), three of those 12 PPBio grid trails were chosen for the surveys (N1, N2, N3; Fig. 1), which are parallel and contained the same types of vegetation as the Novo Paraíso area. This prevented vegetation type from becoming a source of variation in mammal abundance.

The diurnal surveys were conducted between 07:00 and 17:30. An average of 10 km was walked each day at a mean speed of 1 km h⁻¹. The nocturnal surveys were conducted between 18:30 and 04:30, travelling on average 8 km each night at an average speed of 1.25 km h⁻¹. During the nocturnal surveys, headlamps were used to illuminate the trail and adjacent vegetation, and long-range flashlights were used to view the animals.

At Novo Paraíso (impacted), mammal surveys were conducted from December 2009 to January 2010, totalling a sample of 100 km for each trail during the day, and 40 km at night – a sum total of 420 km walked in the area. At Viruá (protected), surveys were carried out in March and October 2011, and the sampling effort was also 420 km.

For each animal or group of animals seen during the survey, the following data were recorded: species, group size, time and location along the trail, and type of vegetation. To compose a list of mammal species for each area, sightings outside of the survey times were also considered, including animals observed on roads, in open areas, as well as those sighted during the opening of trails, plus carcasses, skins, and bones of animals found in the forest or shot by hunters. No footprints or burrows were considered due to the degree of uncertainty inherent to this type of record.

Hunter interviews and hunting impact

To characterize and quantify the hunting pressure exerted on the mammal community, 50 hunters residing in the Novo Paraíso settlement (impacted) were interviewed during January and February 2011. The hunters interviewed were chosen with the aid of a local resident, who served as a mediator and witness for the interviews.

A semi-structured questionnaire was used to obtain the following information regarding the hunting activity of each respondent: hunting time (years), number of consumers, duration of each hunt (hours), frequency (hunts month⁻¹), maximum distance (km), strategies used (type of weapon, type of hunting, use of dogs), reasons for hunting, number of animals hunted, the importance of hunting for their livelihood, and the possible existence of taboos or cultural factors that influence the activity of hunting. The hunters identified the species using an illustrated guide based on images derived from Emmons and Feer (1997), Reid (1997) and Eisenberg and Redford (1999). The respondents signed a consent agreement, and had their anonymity guaranteed.

The Committee for Ethics on Research – CER, CCS – UFPE approved the interviews; a written consent was read to those interviewees who were illiterate, or given to them to read and subsequently sign.

From the data collected in the interviews, the following were calculated for each hunter and for the settlement as a whole: hunting range (km) – the average maximum distance walked per hunt; hunting effort (h) – the sum of the average duration of all hunting; capture per unit of effort (CPUE) (kg h⁻¹) – the biomass of hunted animals per time unit (Souza-Mazurek et al. 2000, Fleck 2004, Sirén et al. 2004, Parry et al. 2009); and per capita harvest rate (HR) (individuals/consumer year) – the number of individuals of each species hunted divided by the number of consumers multiplied by the study period (one year) (Redford and Robinson 1987, Souza-Mazurek et al. 2000, Sirén et al. 2004, Gavin 2007).

Data analysis

From the data collected during the surveys, the following were calculated for each species in each area: sighting rate (sightings/10 km walked) (Chiarello 1999), relative abundance (individuals/10 km walked) (Silva Júnior and Mendes Pontes 2008, Galetti et al. 2009), and mean group size (individuals group⁻¹). For these calculations, only the total number of kilometers walked that corresponded to the activity period of each species was considered. The species activity periods (diurnal, nocturnal or cathemeral) were obtained from the literature (Emmons and Feer 1997, Reid 1997, Reis et al. 2011). Furthermore, the relative biomass (kg/10 km walked) of each species per unit area was calculated by multiplying the body weight by their relative abundance, as in Galetti et al. (2009). The body weight of each species was considered as the arithmetic mean of the values reported by Eisenberg and Redford (1999), Emmons and Feer (1997), Reid (1997) and Reis et al. (2011). A Shapiro-Wilk (W) statistic showed that the variables had a nonparametric distribution. Statistical analyses were performed using Statistica 10.0 software.

To assess whether the population variables differed between the impacted and protected areas, the data were compared using the Wilcoxon t-test (Z) (significance level 0.05) by pairing the values of each species in both areas and assigning '0' to the species absent in one area. Additionally, abundance ratios (Rd) were calculated to analyze the individual variation in the abundance of each species between the two areas, which consisted of paired comparisons of species-specific estimates of relative abundance between two populations exposed to different levels of hunting pressure (Peres and Palacios 2007).

Results

Sampling of medium and large-sized mammals

After a sampling effort of 840 km, 29 species were registered in both studied sites, in addition to four species whose occurrence was confirmed by records outside of the surveys, providing a total of 33 species from seven orders (Table 1).

Table 1. Medium- and large-sized mammal species (following Mendes Pontes et al. 2010) expected to be present at the Novo Paraíso settlement and the Viruá National Park, Roraima, northern Brazilian Amazon, and the forms of detection during the present study. ^aS = sighted during survey; ^bI = interviews; ^cC = carcass, skin or bones; ^dN = sighting not during survey.

Species	Novo Paraíso settlement	Viruá National Park	
Artiodactyla			
Cervidae	- h		
Mazama americana	Salp		
Mazama nemorivaga	SC ^c I		
Tayassuidae			
Pecari tajacu	SN^dCI	SN	
Tayassu pecari	CI	SN	
Carnivora			
Canidae	NI	S	
Cerdocyon thous			
Speothos venaticus	SI		
Felidae			
Leopardus pardalis	CI		
Leopardus tigrinus	I .		
Leopardus wiedii	I		
Panthera onca	SCI	SN	
Puma concolor	CI		
Puma yagouaroundi	I		
Mustelidae			
Eira barbara	SCI	S	
Galictis vittata			
Lontra longicaudis	I		
Pteronura brasiliensis	SI		
Procyonidae			
Bassaricyon beddardi	CI		
Nasua nasua	SNI	SN	
Potos flavus	SI		
Procyon cancrivorus	I		
Cingulata			
Dasypodidae			
Cabassous unicinctus	1		
Dasypus kappleri	SI		
Dasypus novemcinctus	SI	S	
Priodontes maximus	NI		
Lagomorpha			
Leporidae			
Sylvilagus brasiliensis	I		
Perissodactyla			
Tapiridae	0.01		
Tapirus terrestris	SCI	S	
Pilosa			
Bradypodidae			
Bradypus tridactylus			
Cyclopedidae			
Cyclopes didactylus			
Megalonychidae			
Choloepus didactylus	SNI		
Myrmecophagidae			
Myrmecophaga tridactyla	<u> </u>		
Tamanduate tradactyla	I	S	
Primates			
Callitrichidae	61.1	2	
Saguinus midas	SN	S	
Cebidae			
Alouatta macconnelli	SI	SN	
Aotus trivirgatus	SI	SN	
Ateles paniscus	SCI	SN	
Cebus apella	SNI	SN	
Cebus olivaceus	1		
Saimiri sciureus	SI	S	

(Continued)

Table 1. Continued.

Species	Novo Paraíso settlement	Viruá National Park
Pitheciidae		
Chiropotes chiropotes	SI	SN
Pithecia pithecia	SI	S
Rodentia		
Agoutidae		
Cuniculus paca	CI	SN
Dasyprocta cristata	SI	
Dasyprocta leporina	SNI	SN
Myoprocta acouchy	SCI	S
Erethizontidae		
Coendou prehensilis	1	
Hydrochaeridae		
Hydrochoeris hydrochaeris	I	
Sciuridae		
Sciurus aestuans	SI	S
Sciurus igniventris		

At Novo Paraíso (impacted), 209 records were made of 25 medium- and large-sized mammal species, and seven other species were recorded from indirect records (Table 1). The total sighting rate in Novo Paraíso was 7.07 sightings/10 km, while the total relative abundance was 22.72 individuals/ 10 km (Table 2). The relative biomass at Novo Paraíso was 126.08 kg/10 km (Table 2).

The species that showed the highest sighting rate and relative abundance in Novo Paraíso (impacted) was *Cebus apella*, with 1.77 sightings/10 km and 8.7 individuals/10 km, respectively. The species that showed the lowest values for both variables were *Panthera onca*, *Speothos venaticus*, *Dasypus novemcinctus* and *Dasypus kappleri* (0.02 sightings/10 km and 0.02 individuals/10 km, respectively). The species with the highest relative biomass was *Tapirus terrestris* (39.4 kg/10 km), while *Sciurus aestuans* had the lowest biomass (0.04 kg/10 km). *Saimiri sciureus* had the largest mean group size (10.5 individuals/group) (Table 2).

At Viruá (protected), 21 species of medium- and large-sized mammals were sighted over 231 records (Table 1). The total sighting rate at Viruá was 7.62 sightings/10 km, while the total relative abundance was 54.05 individuals/10 km, and the total relative biomass was 490.54 kg/10 km (Table 2).

Similar to Novo Paraíso (impacted), *C. apella* was the most-frequently observed species (2.68 sightings/10 km) at Viruá, and also had the greatest relative abundance (18.5 individuals/10 km) in Viruá (protected). The species with the lowest values for both variables were *Cerdocyon thous*, *P. onca*, *D. novemcinctus* and *T. terrestris* (0.02 sightings/10 km and 0.02 individuals/10 km, respectively). *Tayassu pecari* exhibited the highest value for both relative biomass (350.1 kg/10 km) and average group size (34.54 individuals/group), while *S. aestuans* had the lowest relative biomass (0.07 kg/10 km) (Table 2).

Comparison between areas

There was no significant difference between the two areas for sighting rates (n = 27; Z = 0.4204; p = 0.6742), relative abundance (n = 27; Z = 1.75; p = 0.0799), relative biomass (n = 27; Z = 0.00; p = 1.00), and average group size (n = 26; Z = 0.91; p = 0.3624). Similarly, for the 10 mosthunted species (*D. novemcinctus, Cuniculus paca, Pecari*

Table 2. Abundance of medium- and large-sized mammals detected during surveys at the Novo Paraíso settlement (NP) and Viruá National Park (V), Roraima, northern Brazilian Amazon.

Species	Sightings		Sighting rate (sightings/10 km)		Relative abundance (ind/10 km)		Relative biomass (kg/10 km)		Mean group size (ind/group)	
	NP	V	NP	V	NP	V	NP	V	NP	V
Artiodactyla										
Mazama americana	4	_	0.09		0.09	_	2.66	_	1	_
Mazama nemorivaga	3	_	0.07		0.07	_	1.25	_	1	_
Pecari tajacu	15	5	0.36	0.12	0.88	0.95	19.99	21.58	2.47	8
Tayassu pecari	_	13	_	0.31	_	10.69	_	350.1	_	34.54
Carnivora										
Cerdocyon thous	_	1	_	0.02	_	0.02	_	0.13	_	1
Eira barbara	5	2	0.17	0.07	0.23	0.1	1.4	0.61	1.4	1.5
Nasua nasua	1	2	0.07	0.03	0.17	0.33	0.97	1.89	2.5	10
Panthera onca	1	1	0.02	0.02	0.02	0.02	1.93	1.93	1	1
Potos flavus	1	_	0.08	_	0.08	_	0.24	_	1	1
Pteronura brasiliensis	2	_	0.07	_	0.1	_	3.08	_	1.5	_
Speothos venaticus	1	_	0.02	_	0.02	_	0.12	_	1	_
Cingulata										
Dasypus kappleri	1	_	0.02	_	0.02	_	0.19	_	1	_
Dasypus novemcinctus	1	1	0.02	0.02	0.02	0.02	0.08	0.08	1	1
Peryssodactyla										
Tapirus terrestris	6	1	0.14	0.02	0.17	0.02	39.4	4.64	1.17	1
Pilosa										
Choloepus didactylus	2	_	0.04	_	0.04	_	0.25	_	1	_
Tamandua tetradactyla	_	2	_	0.05	_	0.05	_	0.315	_	1
Primates										
Alouatta macconnelli	13	10	0.43	0.33	1.3	1.05	8.81	7.11	3	3.2
Aotus trivirgatus	8	4	0.67	0.35	0.75	0.61	0.73	0.59	1.13	1.75
Ateles paniscus	6	12	0.2	0.39	0.67	1.08	6.2	9.99	3.33	2.75
Cebus apella	53	82	1.77	2.68	8.7	18.5	25.67	54.58	4.92	6.9
Chiropotes chiropotes	5	18	0.17	0.59	0.9	6.86	2.7	20.58	5.4	11.67
Pithecia pithecia	13	6	0.43	0.2	1.43	0.49	2.75	0.94	3.31	2.5
Saguinus midas	25	15	0.83	0.49	4.9	2.94	2.4	1.44	5.88	6
Saimiri sciureus	2	11	0.07	0.36	0.7	8.69	0.68	8.43	10.5	24.18
Rodentia										
Cuniculus paca	_	1	_	0.09	_	0.09	_	0.77	-	1
Dasyprocta cristata	3	_	0.1	-	0.1	_	0.27	-	1	-
Dasyprocta leporina	28	33	0.93	1.08	0.93	1.08	4.03	4.69	1	1
Myoprocta acouchy	4	2	0.13	0.07	0.2	0.07	0.24	0.08	1.5	1
Sciurus aestuans	5	10	0.17	0.28	0.23	0.28	0.04	0.07	1.4	1.2
Total	209	231	7.07	7.62	22.72	54.05	126.08	490.54		

tajacu, Dasyprocta leporina, T. pecari, D. kappleri, Mazama americana, Mazama nemorivaga, Dasyprocta cristata and Eira barbara), there was no significant difference between the areas in the sighting rates (n = 9; Z = 0.3554; p = 0.7223), relative abundance (n = 9; Z = 0.0592; p = 0.9528), relative biomass (n = 9; Z = 0.0592; p = 0.9528), and average group size (n = 8; Z = 0.14; p = 0.8886).

The population-abundance ratio analysis revealed that 10 species had significantly-higher abundances at Novo Paraíso (impacted), and nine species at Viruá (protected), with 10 species showing almost equal relative abundance in both areas (Table 3). The species that showed the greatest variation in relative abundance between the two areas was *T. pecari*, which was more abundant at Viruá ($R_d = -2.0330$), and *Pithecia pithecia*, which was more abundant at Novo Paraíso ($R_d = 0.4138$) (Table 3).

Characterization and quantification of hunting at the Novo Paraíso settlement

Interviews with 50 hunters at the Novo Paraíso settlement revealed that 20 species of mammals were hunted within one year (Table 4), with a total of 541 (SD \pm 41.54) individuals killed, and an estimated biomass of 8517 kg (SD \pm 739 kg) taken. The most-hunted species was *D. novemcinctus*, with 122 (SD \pm 5.61) individuals taken; consequently, this species also had the highest harvest rate (0.506 individuals/consumers year). In this one-year period, there were 849 (SD \pm 21.24) hunts resulting in a hunting effort of 4575 (SD \pm 127) hours. The average duration of each hunt was 6.48 (SD \pm 4.08) hours, and the average distance travelled in each hunt was 3.21 km (SD \pm 2.96), with a maximum of 5.4 km (SD \pm 4.5).

Considering the biomass and hunting effort, hunting efficiency (CPUE) was $1.87~{\rm kg~h^{-1}}$. The number of hunts conducted each month averaged $1.41~({\rm SD}\pm1.75)$. The total number of hunting consumers for the 50 hunters interviewed was 241 people, resulting in an average of $4.82~({\rm SD}\pm2.84)$ consumers for each hunter and a per capita harvest rate (HR) of $2.24~{\rm individuals/consumer}$ year.

Hunting at Novo Paraíso was always performed with firearms, namely 16 (n = 12), 20 (n = 28), 28 (n = 7), 32 (n = 1), and 36 (n = 4) gauge shotguns, and 22 caliber rifles (n = 1), except in the rarely-reported cases of the use

Table 3. Population abundance ratios (R_d) of mammal species detected at the Novo Paraíso settlement and Viruá National Park, Roraima, northern Brazilian Amazon.

Species	R_d	Species	R_d
Artiodactyla		Pilosa	
Mazama americana	0.2788	Choloepus didactylus	0.1461
Mazama nemorivaga	0.2304	Tamandua tetradactyla	-0.1761
Pecari tajacu	-0.0300	Primates	
Tayassu pecari	-2.0330	Alouatta macconnelli	0.0854
Carnivora		Aotus trivirgatus	0.0782
Cerdocyon thous	-0.0792	Ateles paniscus	-0.1854
Eira barbara	0.2175	Cebus apella	-0.3250
Nasua nasua	-0.2021	Chiropotes chiropotes	-0.8426
Panthera onca	0.0000	Pithecia pithecia	0.4138
Potos flavus	0.2553	Saguinus midas	0.2161
Pteronura brasiliensis	0.3010	Saimiri sciureus	-1.0409
Speothos venaticus	0.0792	Rodentia	
Cingulata		Cuniculus paca	-0.2788
Dasypus kappleri	0.0792	Dasyprocta cristata	0.3010
Dasypus novemcinctus	0.0000	Dasyprocta leporina	-0.0590
Peryssodactyla		Myoprocta acouchy	0.2467
Tapirus terrestris	0.3010	Sciurus aestuans	-0.1717

 $R_d \le -0.15$: more abundant in the non-hunted area; $-0.15 < R_d < 0.15$: equal abundances; $R_d \ge 0.15$: more abundant in the hunted area.

of traps (n = 1), snares (n = 2), or knives (n = 2). Waiting without bait (n = 36) was the most frequent hunting technique, while the snare/trap method was used the least (n = 3) (Fig. 2). Waiting and the snare and trap methods were performed at night, while hunting by walking and using dogs took place during the day.

Table 4. Number of mammals hunted during the study year (2010) and per capita harvest rate (individuals/consumer year) in Novo Paraíso, Roraima, northern Brazilian Amazon.

Species	Quantity	HR
Dasypus novemcinctus	122	0.5062
Cuniculus paca	98	0.4066
Pecari tajacu	94	0.39
Dasyprocta leporina	85	0.3527
Tayassu pecari	80	0.332
Dasypus kappleri	14	0.0581
Mazama americana	10	0.0415
Mazama nemorivaga	8	0.0332
Dasyprocta cristata	6	0.0249
Eira barbara	6	0.0249
Tapirus terrestris	5	0.0207
Alouatta macconnelli	2	0.0083
Ateles paniscus	2	0.0083
Leopardus pardalis	2	0.0083
Puma concolor	2	0.0083
Myoprocta acouchy	1	0.0041
Procyon cancrivorus	1	0.0041
Bassaricyon beddardi	1	0.0041
Panthera onca	1	0.0041
Nasua nasua	1	0.0041
Total	541	2.2445
Standard deviation	41.54	

All of the hunters said that obtaining food is the main reason for hunting (n = 50), but only 6% (n = 3) of them considered game meat as the main source of animal protein for their family. The other 94% (n = 47) reported that the meat of domestic animals (cattle, pig, goat, chicken, duck, and turkey) formed a greater proportion of the family diet. The second most-cited reason for hunting was to protect property against predators (n = 19). Such hunting targeted members of the order Carnivora, namely *P. onca* (n = 50 individuals killed), *Puma concolor* (n = 37), *C. thous* (n = 71), *E. barbara* (n = 32), and small felids (*Leopardus* spp.) (n = 55). The least-reported reason for hunting was for use of body parts (skin and fat) (n = 1), allegedly due to more access to allopathic medicine (Fig. 3).

Cultural taboos and hunting preferences

The hunting activity at Novo Paraíso was influenced by cultural taboos and hunting preferences, which were mentioned by all of the respondents (n = 50) (Fig. 4). For some species, the influence of these taboos is positive, as hunters avoid hunting them because they believe that killing these animals "brings bad luck". In this case, the species most frequently mentioned was *Priodontes maximus* (n = 36) and, as an example, several hunters reported cases of serious illness, accident or death in their families after someone killed an individual of this species. The order Primates (n = 6), and the species *Myrmecophaga tridactyla* (n = 2), *Choloepus didactylus*, and *Bradypus tridactylus* (n = 1) also fell into this category, although they were less frequently mentioned.

There were also hunters who avoided killing certain species, because they were considered to have a bad taste, as in the case of T. terrestris (n=1), C. didactylus (n=1), and B. tridactylus (n=1). Small mammals were also avoided (n=14), because of the low energetic return. Primates were also avoided by some hunters (n=5) due to empathy or superstition based on this group's "similarity to humans". The hunting of pregnant females (n=48), young (n=48) or females accompanied by young (n=47) was also avoided due both to the small size of these individuals and empathy or awareness that the death of these individuals is more likely to impact negatively the species or the future availability of prey (Fig. 4).

Conversely, there were cases where cultural factors have acted negatively, with hunters targeting predators to defend domestic animals. The following species were cited as examples: $P.\ onca\ (n=12),\ P.\ concolor\ (n=10),\ C.\ thous\ (n=12),\ E.\ barbara\ (n=6),\ and\ small\ cats\ (Leopardus\ spp.)\ (n=23).$ There were even reports of hunters who were paid by ranchers to kill jaguars ($P.\ onca$) that were attacking or even just patrolling around their herds, which we classified as retaliatory hunts. Such actions, which could also be classified as predatory since it is not for subsistence, are deeply rooted in the culture of the settler's families, who argue that it aims at protecting their livestock.

Discussion

Diversity of medium and large-sized mammals

A total of 32 mammal species were recorded at Novo Paraíso settlement (impacted), whereas 21 species were found in

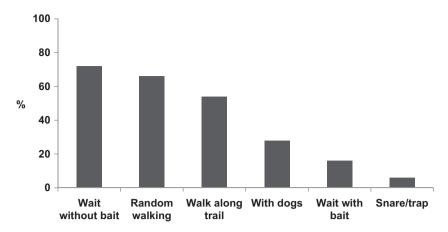


Figure 2. The hunting types and strategies used by 50 hunters at the Novo Paraíso settlement, Roraima, northern Brazilian Amazon.

Viruá National Park (protected). Thus, the area richest in mammal species was that which has been subject to hunting and impacted by the fish-bone forest clearance and regional development. This result has a direct relation with Tayassu pecari, as this species was the most hunted and was not recorded in the Novo Paraíso survey. Accordingly, its absence (or, more likely, very low abundance) may have favored the proliferation of more resilient species that exploit similar resources (e.g. Mazama americana, M. nemorivaga, Dasyprocta cristata) in a likely process of density compensation (Peres and Dolman 2000, Endo et al. 2010). Furthermore, the persistence of M. americana and M. nemorivaga in disturbed areas may also be linked to the fact that these species use secondary forests, natural or artificial clearings, agricultural fields, and areas of pioneer vegetation for feeding (Vogliotti 2008); whereas *T. pecari* depends on intact forests for survival (Keuroghlian et al. 2012).

Our data suggests that *Pecari tajacu* may proximately benefit from the considerable decline of their competitor, *T. pecari*, since *P. tajacu* sightings rates at Novo Paraíso settlement (impacted) were higher than in Viruá (protected). However, the complete (or, perhaps, effective) extirpation of the latter, has led hunters to shift their focus towards *P. tajacu*, already among the third most hunted species. Ultimately, this may also cause their extirpation.

Although there was no significant difference between the relative abundances and biomasses in the study areas, the total values of these variables were significantly higher in Viruá (protected). This result is also due to the relatively higher abundance of *T. pecari* in this area than at Novo Paraíso (impacted), given that it is known to be extremely sensitive to hunting and often disappears quickly from hunted areas (Peres 2001, Altrichter et al. 2012).

Of the total relative biomass calculated for Viruá (protected), *T. pecari* represented 71.37%. This proportion is much higher than that recorded in other conservation units in Amazonia, such as others reported by Lopes and Ferrari (2000) (18.45%), Mendes Pontes (2004) (43.99%), Peres and Nascimento (2006) (19.4%), and Endo et al. (2010) (40.55%), and also higher than presented by Cullen Jr. et al. (2001) in the Brazilian Atlantic forest (between 20% and 34%). This suggests that the population of this species at Viruá is above the expected ecological equilibrium. We do not believe that it could be a methodological artifact since in another strictly protected area in the same region, white-lipped peccary biomasses are even higher and the highest in the Amazon (Mendes Pontes 2000, 2004, Mendes Pontes and Chivers 2007).

Primates were another group that also showed relatively high abundance and biomass at Viruá (protected). Although species of this order are rarely hunted in the settlement area, their lower abundances and biomasses at Novo Paraíso (impacted) suggests that larger species that are more sensitive to the effects of hunting (e.g. *Ateles paniscus*) may be impacted (Peres and Dolman 2000).

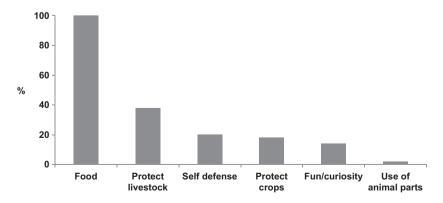


Figure 3. The hunting reasons cited by 50 hunters at the Novo Paraíso settlement, Roraima, northern Brazilian Amazon.

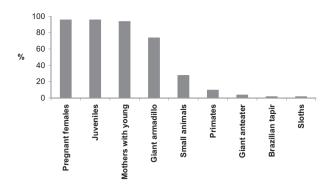


Figure 4. The species and groups of mammals avoided by hunters at the Novo Paraíso settlement, Roraima, northern Brazilian Amazon.

Hunting at the Novo Paraíso settlement (impacted)

The mammal community in adjacent forests have probably been subjected to the effects of hunting since the settlement was created (some 37 years prior to the study). During the study period, the demand for hunting by the human population (HR) was 2.24 individuals/consumer year, a value below that found by Redford and Robinson (1987) (7.5), Peres (2000) (~7.0), Souza-Mazurek et al. (2000) (5.77), Fleck (2004) (2.57), and Parry et al. (2009) (4.75). This shows that the Novo Paraíso settlement (impacted) has one of the lowest per capita consumption rates (HR) when compared with similar studies. This, coupled with the fact that the abundance found at Novo Paraíso was quite similar to those at Viruá (protected), indicates that hunting has probably not caused major losses to the local mammal assemblage.

At Novo Paraíso, hunting has lost its importance as a source of animal protein, as evidenced by the reduction in the average monthly number of hunts and in hunting efficiency. This is a result of the improved socio-economic conditions of the settlers and greater access to meat from domestic animals. Additionally, the number of preferred prey is diminishing because, according to the hunters, it has been necessary to increase the hunting effort to find the larger species, which reduces hunting efficiency and discourages hunters.

The hunting range at Novo Paraíso (about 5.4 km) is one of the lowest ever recorded in hunted areas (e.g. Vickers 1984 [8.5 km], Alvard 1992 [9.5 km], Peres and Nascimento 2006 [25 km], Ohl-Schacherer et al. 2007 [10 km], Parry et al. 2009 [10 km]). This relatively limited spatial range of hunting may have positive or negative implications for conservation. A limited hunting range impacts only a small area, preserving more distant areas. However, species with extensive ranges using such an area as part of their range can be completely eliminated. In such an instance, the area impacted by hunting would be larger (Alvard 1994). This is probably the case for white-lipped peccaries.

When hunting has a greater radius of action, its effects are more diluted, and the risk of local extinction may be reduced. Thus, for hunting in restricted areas to be sustainable, an efficient source-sink balance is required in order to ensure the constant restocking of hunted areas (Alvard 1994). This seems to be the case with Novo Paraíso, as the low hunting rates and the relatively-high abundance of mammals are strong indications that the source areas surrounding the

settlement are fulfilling the role as a recolonization source for the human-impacted sink area.

The importance of Viruá National Park for mammal conservation in northern Amazonia

The Guyana Shield has one of the lowest mammal diversities and abundances in the Brazilian Amazon, and within this region, Roraima is one of the poorest (Sombroek 2001, Hoorn et al. 2010, Mendes Pontes et al. 2010). Though Roraima has an extensive protected areas network that covers almost two million hectares (Governo do Estado de Roraima 2012), none of these is located in the dense ombrophilous non-floodable terra firme forests of the southeast of the state, where forest biomass is one of the highest (Barbosa et al. 2010).

Very little is known of the biological value of these extensive forested areas surrounding the fish-bone human settlements (impacted), which, nevertheless, have systematically been colonised and destroyed since the 1970s. However, the extent of information lack is such that, on the official World Bank/WWF/Government-defined Amazon Region Protected Areas (ARPA) map (MMA 2007), which illustrates the importance and priority areas of Roraima for protection of biological resources and creation of protected areas, the southeast of the state consists only of blank space.

In these highly impacted fish-bone human settlements most large mammals will ultimately be locally and regionally extirpated, as will the dense ombrophilous forests of the comparatively flatter and richer soils of the region. This already appears to be the case for the highly sensitive *T. pecari*, which had the highest biomass of any of the surveyed mammals at Viruá (protected), but is almost completely absent from the forested areas surrounding the settlement. Viruá therefore plays a crucial role in the maintenance of a highly representative sample of the original mammalian fauna of the region, as well functioning as a repository for its invaluable biological diversity.

Conservation implications

Hunters reported that, in the past, T. pecari was the most hunted mammal at Novo Paraíso. However, by 2010 this species has become only the fifth most-hunted species, suggesting a reduction from its historical abundance. The R_d for T. pecari (-2.033) indicates a relative abundance of around 100 times greater in the protected area, suggesting that this species has been hunted beyond a sustainable level in forests around the settlement.

Due to the extreme sensitivity of *T. pecari* to hunting, this species is often locally or regionally extirpated in areas close to human settlements (Peres 1996, Naranjo and Bodmer 2007, Reyna-Hurtado and Tanner 2007). Peres (2001) found the local extinction of *T. pecari* in six areas to be a result of hunting. In the case of Novo Paraíso (impacted), although we observed an individual killed by a hunter, showing that the species still remains in the area, our data suggest that local extinction will certainly occur, since a few individuals left in a remnant subherd cannot maintain a viable population (Biondo et al. 2011). What seems to be happening is that the source population has probably been

depleted, which is highlighted in the differences in abundance between protected and hunted sites.

Urgent measures are needed to recover the population of *T. pecari* at Novo Paraíso and reverse the process of local extinction. The first and ideal step towards this recovery would be to suspend *T. pecari* hunting long enough to allow its population to recover, but this proposal tends to encounter resistance from the population, because *T. pecari* is one of the species most prized by consumers (Leeuwenberg 1997, Fragoso et al. 2000).

A second alternative proposed by previous authors was the establishment of non-hunting refuges by dividing the space into hunting zones. Thus, the most hunted areas (those closest to the settlement – sink areas) would be free of hunting for some years, with hunting activities only being allowed in more remote (source) areas. After the recovery of *T. pecari* populations, hunting would again be allowed in the sink areas, but with the establishment of maximum extraction quotas per hunter, thus ensuring the sustainability of hunting and the population viability of the species in the long term. Although the source areas surrounding the settlement are fulfilling the role as a recolonization source for the sink area, without sustainable hunting practices, the source fauna that replenishes this area near the settlements will eventually be depleted.

For a more accurate control, however, this evaluation should be done at least once annually, and individually for each species. A tool for assessing the sustainability of hunting is the CPUE, which allows the local population themselves to analyze the abundance of hunted species and indicate whether they are being over-exploited (Sirén et al. 2004). This could be a viable alternative that could be implemented in the Roraima settlements through conservation projects, which both involve the local community and generate income.

In places where there is a low availability of meat from domestic animals, hunting pressure is much higher and tends to lose selectivity, leading to notable reductions in the densities of various vertebrate species (Lourival and Fonseca 1997). At Novo Paraíso, however, meat from domestic animals is widely available for consumption, which has a positive effect on the conservation of mammals and the sustainability of hunting, as it reduces the harvest of wild animals.

Despite the present hunting levels being considered sustainable, hunters reported that the abundance of game mammals has decreased. In this sense, measures aimed at controlling the effects of hunting are necessary, even if they are only preventive. These measures must come from environmental authorities and should be accompanied by educational actions and intense scrutiny to ensure that the existing environmental legislation is followed. Finally, it is essential that any measures occur with the involvement of local inhabitants to make clear the benefits that conservation will bring.

Conclusions

Relatively high mammal abundances, the existence of extensive contiguous source forests and the low hunting levels detected during this study suggest that hunting at the Novo Paraíso settlement (impacted) as currently practiced is sustainable. The progressive decrease in hunting efficiency

reported, and the absence of *T. pecari*, demands the immediate implementation of sustainable alternatives of wildlife harvest, the immediate suppression of *T. pecari* hunting and population monitoring.

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