Age structure of the Vulnerable white-lipped peccary *Tayassu pecari* in areas under different levels of hunting pressure in the Amazon Forest

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Abstract Subsistence hunting can change the demographic structure of wild mammal populations, increasing the proportion of young animals, inducing females to reproduce early and increasing litter sizes. We examined the relationship between hunting pressure and age structure in the Vulnerable white-lipped peccary *Tayassu pecari*, analysing the distribution of age classes at seven sites in the region Terra do Meio in the Brazilian Amazon. These sites differ in the number of human inhabitants and hence were subject to differing hunting pressures. We completed semi-structured interviews with local people to assess the importance of hunting and of the white-lipped peccary as food. We also estimated the age of hunted white-lipped peccaries by assessing tooth eruption and tooth wear in skulls of hunted individuals. Our results indicated that the white-lipped peccary was the most frequently hunted terrestrial animal in the region. Fishing, followed by hunting, provided the main sources of animal protein. Our data suggest there is no relationship between age structure and hunting at the study sites. The social structure and mobility of white-lipped peccaries seem to minimize the effects of hunting on age structure. Our results, similar to previous studies, show that the age structure of the white-lipped peccary is robust to hunting impacts. Other factors may have stronger effects on age structure than subsistence hunting. We suggest that deforestation may explain the prevalence of older individuals in peccary populations to the north of our study sites.

Keywords Age structure, Amazon Forest, Brazil, hunting, *Tayassu pecari*, Terra do Meio, white-lipped peccary

Introduction

The exploitation of wild animals through hunting or fishing creates selective pressures that affect the life history of natural populations (Allendorf et al., 2008). These impacts may affect the reproductive capacity of the exploited populations and compromise their resistance to the increased mortality caused by exploitation. Hence such impacts on the life history of hunted populations should be considered, together with identified changes in density and biomass of exploited populations (e.g. Redford, 1992; Peres & Palacios, 2007), when planning conservation and management.

Hunting can change the demographic structure of wild populations, increasing the proportion of young animals, inducing the females to reproduce early and increasing litter sizes (Servanty et al., 2011). Changes in the age structure of such populations are frequently related to the density-dependent effects of the decrease in population density as a result of hunting. This increases the recruitment rate by relaxing intraspecific competition (Bodmer et al., 1997; White & Bartmann, 1998). Another factor related to the increase in the proportion of young individuals in hunted populations is immigration, usually of young animals from non-hunted neighbouring areas (Bodmer & Robinson, 2004; Naranjo & Bodmer, 2007; Cooley et al., 2009).

Collection of information from hunters (Bodmer & Robinson, 2004; Naranjo et al., 2004) facilitates the gathering of a large volume of data on the age structure of hunted populations at relatively low cost (Bodmer & Puertas, 2000). Despite this, little is known about how the age structure of the most commonly hunted mammals in the Neotropics is affected by hunting (Bodmer & Robinson, 2004). In the Amazon one of the targets is the white-lipped peccary *Tayassu pecari* (Vickers, 1984; Redford & Robinson, 1987; Bodmer, 1995; Peres, 2000), which is sensitive to hunting, with its population density strongly reduced in exploited areas (Peres & Palacios, 2007). The white-lipped peccary is categorized as Vulnerable on the IUCN Red list (IUCN 2013) and hunting has affected c. 30% of the species' distribution. In addition to deforestation and habitat transformation, hunting is considered to a major threat to this species (Altrichter et al., 2012).

Knowledge of how hunting affects the age structure of the white-lipped peccary is required to elucidate the factors that contribute to its vulnerability. This species has some unique characteristics, such as forming large, complex social groups (up to several hundred) and using large areas (Kiltie & Terborgh, 1983; Fragoso, 1998; Keuroghlian et al.,

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Received 26 December 2013. Revision requested 10 February 2014. Accepted 30 April 2014. First published online 10 October 2014.

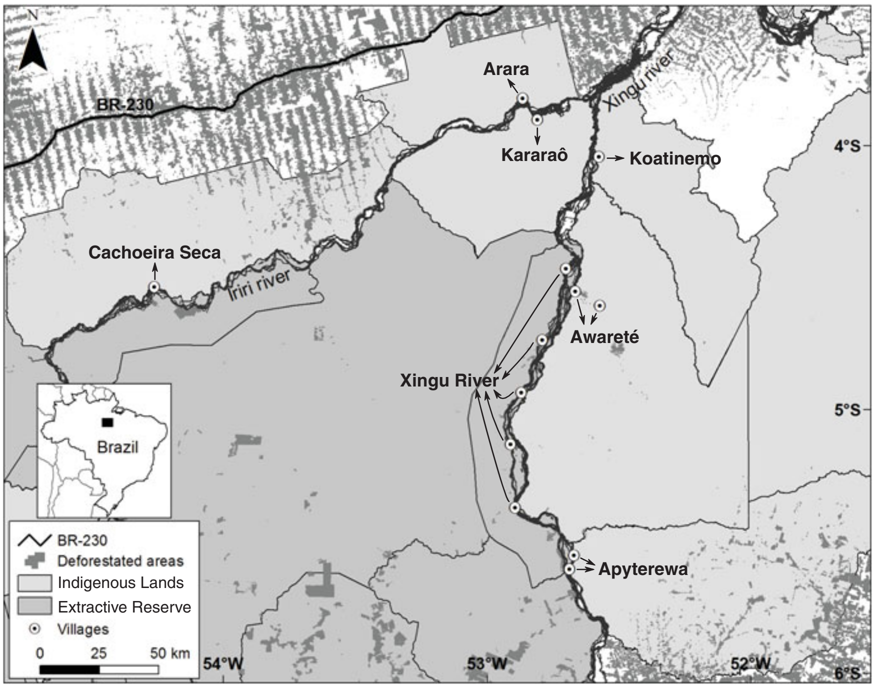

FIG. 1 Locations of the seven study sites (Table 1), with the delimitations of Indigenous Lands and the Xingu River Extractive Reserve in the Brazilian Amazon Forest. Skulls obtained in neighbouring villages were grouped, and each group was considered as one site in the analyses. Arrows indicate to which site each village was allocated. The black rectangle on the inset indicates the location of the main map in Brazil.

2004; Reyna-Hurtado et al., 2009b, 2012). These characteristics may alter the way age structure is affected by hunting. Although previous studies have not identified a relationship between age structure and subsistence hunting (Bodmer et al., 1997; Naranjo & Bodmer, 2007; Reyna-Hurtado et al., 2009a), these studies did not focus specifically on how age structure is affected by hunting pressure. A better understanding of this issue is needed to facilitate the conservation of hunted populations (Bodmer & Robinson, 2004).

In this study we investigated the age structure of the white-lipped peccary at seven sites that differ in the number of human inhabitants. We expected that at sites with larger human populations there would be greater hunting pressure on the white-lipped peccary and thus a skewed age structure, with more young individuals. This could result from an increase in the population growth rate (or a decrease in the mortality of juveniles) caused by a decrease in intraspecific competition and by immigration of young individuals from non-hunted areas. A secondary objective was to assess the relevance of this species and other animal protein sources in the diet of these seven local communities.

Study area

We surveyed the age structure of white-lipped peccary populations and consumption of wildlife at seven sites: the Xingu River Extractive Reserve and six Indigenous Lands (Arara, Cachoeira Seca, Kararaô, Koatinemo, Araweté and Apyterewa; Fig. 1). Mean annual temperature is 24–28 °C and total annual rainfall is c. 2,000 mm, with 80% falling in the Austral summer (hereafter the rainy season), and with little rainfall in the winter (the dry season) from June to September (Lucas et al., 2009). Vegetation is dominated by open rainforests, with some patches of dense rainforest along rivers and streams and sparse patches of submontane dense rainforest (IBGE, 2006),

The study sites are located on the margins of the Xingu River and one confluent, the Iriri River. The area between these rivers is known as Terra do Meio (middle land). This vast mosaic lies within Indigenous Lands and protected areas in the south-east Brazilian Amazon Forest. The Terra do Meio forms a continuum of protected areas along the Xingu River Basin and surrounding areas, covering c. 28 million ha (Carneiro Filho & Souza, 2009).

Terra do Meio is faced by a growing agricultural frontier and is subject to pressures such as deforestation, fire, establishment of unofficial roads for resource exploitation, the growth of urban and agricultural areas, and the expansion of livestock holdings (Carneiro Filho & Souza, 2009). Deforestation is most severe to the north of this mosaic, into which official and unofficial roads penetrate from the Trans-Amazonian Highway, BR-230. To the south-east deforestation is associated with the roads emanating from São Félix do Xingu.

The study sites are inhabited by culturally diverse groups, with riverine populations in the Xingu River Extractive Reserve and various indigenous groups: Arara (Cachoeira Seca and Arara), Kararaô, Assurini (Koatinemo), Araweté and Apyterewa. Although culturally diverse, these groups are similar in their economic and productive systems, with low levels of economic development and strong dependence on activities such as fishing, hunting and small-scale agriculture.

Methods

In the Indigenous Lands we collected data on the diet of people and the age structure of peccaries during the 2010 dry season (July–September), spending about 5 days in each village. In the Xingu River Extractive Reserve we collected data six times, between May 2011 and April 2012, covering both rainy and dry seasons. In each of two of the Indigenous Lands (Araweté and Apyterewa) we surveyed two villages close to each other ($<$ 10 km) and pooled their data. In the Xingu River Extractive Reserve we pooled the data collected in five localities. The distances between neighbouring pairs of these five villages were 22–32 km (the distance between the two most distant villages is c. 100 km).

We inferred the level of hunting pressure based on the number of inhabitants at each site and the spatial distribution of the villages. This premise has been used in other studies (e.g. Peres & Dolman, 2000; Jerozolimski & Peres, 2003). There were 22.4–445.0 inhabitants per site (Table 1). We categorized sites as being under moderate or high hunting pressure (Table 1). We defined the hunting pressure in the Xingu River Extractive Reserve as moderate based on the total number of inhabitants and the dispersion of the households. Although there are $>$ 200 inhabitants in the Reserve the people live in 10 communities along $>$ 100 km of the Xingu River, with 8–30 people per community. and as hunting practices were similar, data for the five sampled communities were pooled and hunting pressure was considered moderate.

To assess the relative importance of game in the diet we gathered data on animal food sources through questionnaire-based interviews focused on meals eaten in the previous 24 hours and on our observations (Dufour & Teufel, 1995). We carried out these interviews with randomly selected heads of households, to whom we also applied a questionnaire focused on the last hunting activity. We thus constructed a profile of the most frequently consumed animal products (fish, game or other source of protein) and the most hunted animal species. For comparison of the consumption data for the Xingu River Extractive Reserve with data for the Indigenous Lands we considered only the data from 30 interviews that took place in July 2011 in the Xingu River Extractive Reserve. We used all available data, however, to compare hunting patterns between rainy and dry seasons.

The age of white-lipped peccaries was estimated based on tooth eruption and tooth wear in skulls kept by hunters, at our request, and found on trails and close to residences. We considered the age of peccaries hunted at each site as a sample of the age structure of the population, assuming that hunters do not select particular age classes. In the Amazon Forest visibility is low, precluding selection of specific individuals by hunters, and therefore the skulls can be considered a sample of the population (Bodmer et al., 1997). The estimation of age structure using animals killed by hunters has been commonly used (Caughley, 1966; Bodmer & Robinson, 2004). We categorized the skulls following Kirkpatrick (1962) and Bodmer et al. (1997), considering four age classes: 1, incomplete dentition; 2, complete dentition with slight wear; 3, complete dentition with mild wear; 4, complete dentition with excessive wear.

We tested for a possible relation between human population size and the age structure of peccaries in two ways. Firstly, we tested for independence of age classes and study areas with a χ^2 test. We expected that, if there was a relationship, the sites with greater hunting pressure would have more individuals of younger classes than expected by chance. We tested for such differences by analysing the standardized residuals to identify the particular cells that contribute most to the overall χ^2. Additionally, we used the odds ratio to assess the results of the χ^2 test. This measure allows estimation of the effect size in the association between two or more variables, and is suitable for distinguishing which age classes are associated with each other. For this calculation we pooled Classes 1–3, and considered Class 4 separately (based on the residuals of the χ^2 test, which were greater in this class; see Results).

Secondly, we examined the relationship between age structure and hunting pressure using a linear regression,

Table 1 Hunting pressure inferred from the total number of inhabitants in each of the seven study sites (see Fig. 1 for locations). Data for the Indigenous Lands are from the Fundação Nacional de Saúde (2010) and those for the Xingu River Extractive Reserve were collected during this study.

Site	Inhabitants	Villages	Hunting pressure
Apyterewa Indigenous Land	445[1]	2	High
Araweté Indigenous Land	413[1]	2	High
Arara Indigenous Land	253	1	High
Koatinemo Indigenous Land	155	1	Moderate
Cachoeira Seca Indigenous Land	86	1	Moderate
Xingu River Extractive Reserve	224[2]	10	Moderate
Kararaô Indigenous Land	48	1	Moderate

[1]Sum of the two villages because of their proximity
[2]Sum of inhabitants in the 10 villages

ranking the variables to meet the assumptions of the test. The independent variable is the human population size at each site, and the dependent variable is the proportion of individuals of Class 4 hunted at each site. In the Araweté and Apyterewa Indigenous Lands we grouped both sites sampled at each and pooled their human population sizes and the number of peccary skulls. In the Xingu River Extractive Reserve, as the villages were distant from each other, the sum of the number of inhabitants would not be a good proxy of local hunting impact. We therefore used the mean number of inhabitants in the five sampled villages as a proxy of density. *R v. 2.15.1* (R Development Core Team, 2012) was used for all statistical tests.

Based on the distances between pairs of sites (median 84 km, range 10–210 km), we assumed that the skulls collected at each site came from different populations. The two pairs of sites separated by < 25 km (Arara and Kararaô Indigenous Lands, 11 km, and the northernmost village of the Xingu River Extractive Reserve to the nearest village in the Araweté Indigenous Land, 10 km) are separated by a large river (the Xingu or Iriri; Fig. 1). These rivers limit the dispersion of peccaries. In addition, these communities have local agreements that delimit their hunting areas and minimize overlap (R.M. Ramos, pers. obs.). Thus the separation between these sites, and the local rules that define hunting areas, reduce the probabilities of consumption of the same peccary populations by these distinct ethnic groups. We thus considered the seven study sites as independent samples, assuming that each site was hunting a different peccary population.

Results

We completed 200 interviews about hunting (154 in the Xingu River Extractive Reserve and 5–13 in each of the Indigenous Lands) and recorded 168 meals in 76 interviews (5–28 interviews per site). For animal protein, fish was the most frequently consumed, present in 59% of all meals recorded and in 29–100% of meals at each site. Hunted species were the second-most frequently consumed animal protein, consumed in 33% of meals (7–100% per site). Locally bred animals or items purchased in towns contributed little to the diet (in 0–5% of meals).

The white-lipped peccary was the most frequently hunted terrestrial species, with a mean of 35 ± SD 27% of all animals hunted (0–78% of all animals hunted at each site) and was the most frequently hunted animal at four sites (Arara, Araweté, and Apyterewa Indigenous Lands, and Xingu River Extractive Reserve) and the second-most hunted species at Kararaô Indigenous Land. The occurrence of peccaries in the diet may have been underestimated, as the data used for this comparison were collected during the dry season, when the species was less frequently hunted in the Xingu River Extractive Reserve. At this site we found a marked between-season difference in the importance of the white-lipped peccary, which comprised 31% of animals hunted in the dry season and 64% in the wet season. Considering the whole year, c. 50% of the animals hunted in the Reserve were white-lipped peccaries.

We obtained the skulls of 486 peccaries (23–177 per site), of which c. 9% were of Class 1, 47% of Class 2, 32% of Class 3 and 12% of Class 4. The distribution of age classes differed significantly between sites ($\chi^2 = 37.3$, df = 18, P = 0.005). The analysis of the standardized residuals (Table 2) indicated that the differences were concentrated in Class 4 (i.e. the oldest individuals) and were not related to hunting pressure. In terms of age structure the sites formed two groups: those to the north of the Iriri River and the sites along the Xingu River. At the sites to the north of the Iriri River (the Cachoeira Seca and Arara Indigenous Lands), there were proportionally more individuals in Class 4 (Table 3).

The analysis using the odds ratio showed a similar pattern (Fig. 2). The chance of an individual in Class 4 being hunted (i.e. its skull being found) in the Cachoeira Seca and Arara Indigenous Lands was 4–10 times higher than at the sites in the Xingu River Extractive Reserve. The Kararaô Indigenous Land, however, to the south of the Iriri River, between the northern sites and the River, did not differ from them. Likewise, the regression did not indicate a relationship between the proportion of individuals in Class 4 and the proxy of hunting pressure (the number of inhabitants; $r^2 = 0.03$, $F = 0.17$, df = 1.5, P = 0.70).

Discussion

We did not find evidence of a direct effect of hunting on the age structure of populations of white-lipped peccaries at

TABLE 2 Standardized residuals of the χ^2 test of independence between age structure of the white-lipped peccary *Tayassu pecari* (age classes were inferred based on tooth condition; see text for further details) and the seven survey sites (Fig. 1, Table 1).

	Indigenous Lands						Xingu River
Age class	Cachoeira Seca	Arara	Koatinemo	Kararaô	Araweté	Apyterewa	Extractive Reserve
1	−1.05	−1.02	−0.64	0.60	1.13	0.32	1.07
2	0.26	−2.05	0.69	−0.53	0.25	0.75	0.53
3	−1.64	−0.08	0.33	0.13	0.61	0.44	−0.28
4	2.89	4.19	−0.98	0.09	−2.26	−2.07	−1.36

TABLE 3 Age structure (age classes were inferred based on tooth condition; see text for further details) of the white-lipped peccary in relation to hunting pressure (high or moderate; Table 1) in the seven study sites (Fig. 1). Total number of skulls collected = 486 (Apyterewa = 177, Araweté = 62, Arara = 82, Koatinemo = 71, Cachoeira Seca = 43, Xingu River = 27, Kararaô = 24). Values are percentages of the total number of skulls.

Site	Class 1	Class 2	Class 3	Class 4
High hunting pressure				
Apyterewa	9.6	49.2	33.3	7.9
Araweté	12.9	48.4	35.5	3.2
Arara	6.1	36.6	31.7	25.6
Mean	9.5	44.7	33.5	12.2
Moderate hunting pressure				
Koatinemo	7	50.7	33.8	8.5
Cachoeira Seca	4.7	48.8	20.9	25.6
Xingu River	14.8	51.9	29.6	3.7
Kararaô	12.5	41.7	33.3	12.5
Mean	9.8	48.3	29.4	12.6

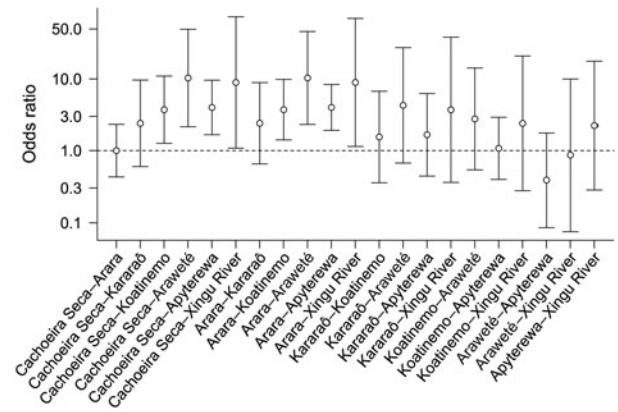

FIG. 2 Pairwise comparisons between sites of the odds ratios of an individual belonging to Class 4 (in relation to Classes 1–3). Age classes were inferred based on tooth condition (see text for further details). The whiskers indicate the 95% confidence interval. Paired comparisons that do not cross the dotted line (at 1.0) are statistically different (at $P = 0.05$).

seven sites in the Amazon Forest subjected to differing hunting pressures. Nevertheless, our data indicate the importance of the species in the diet of the inhabitants.

One of the potential explanations for the apparent absence of relationship between the age structure of hunted white-lipped peccaries and human population size is the relatively small difference in the number of inhabitants between sites. The effect of hunting on the populations of the white-lipped peccary may thus not have been sufficiently strong to lead to differences in age structure between sites. Little is known about how the survival and birth rate of the white-lipped peccary respond to changes in density and to stochastic effects. As it is a short-lived species, Robinson & Redford (1991) suggested that its birth rate reaches its maximum value when the population density reaches 60% of the carrying capacity. Hence, a large decrease in population density would be needed for the birth rate reach its theoretical maximum value.

Alternatively, the high mobility (Reyna-Hurtado et al., 2012) and relatively high reproductive rates of this species compared to other ungulates (Robinson & Redford, 1991) may mitigate any potential effects of density changes on the hunted populations. In addition, immigration of juveniles from neighbouring areas may not have a strong effect on age structure. This species usually forms large groups, with home ranges that may exceed 100 km^2 (Fragoso, 1998; Reyna-Hurtado et al, 2009b). These large areas are used by distinct groups in a patchy way (Reyna-Hurtado et al, 2012), as areas with high food availability are also used by adjacent herds (Bodmer, 1990). Hence it is possible that the dispersion of a group to underexploited neighbouring areas may be a more important factor in peccary population dynamics than the movement of individuals between source and sink populations. The lack of non-hunted populations was not the case in the study sites because hunting occurs only near the major rivers, where the villages are located (R.M. Ramos, pers. obs.).

Other studies in the Neotropics have not indicated a clear effect of subsistence hunting on the age structure of white-lipped peccaries (Bodmer & Robinson, 2004; Naranjo & Bodmer, 2007). However, Reyna-Hurtado et al. (2009a) found a non-significant tendency towards a decrease in the number of juveniles caused by hunting (the opposite of our expectation) and a decrease in the size of white-lipped peccary groups. Even considering the sensitivity of this species to hunting (its populations are markedly smaller in hunted areas of Amazonia; Peres & Palacios, 2007) and that sometimes the survival of populations in hunted areas depends on the immigration of animals from source areas (Naranjo & Bodmer, 2007), the effects of hunting on age structure does not seem to be strong. This inference is corroborated by other studies (Bodmer & Robinson, 2004; Naranjo & Bodmer, 2007; Reyna-Hurtado, 2009a).

Knowledge of how hunting affects the age structure of Neotropical mammals is incipient (Bodmer & Robinson, 2004) and the current theoretical framework does not explain differences between species. Some species, such as tapirs (*Tapirus* spp.), have a higher proportion of juveniles in intensively hunted areas (Bodmer & Robinson, 2004; Naranjo & Bodmer, 2007). Other species, such as the white-tailed deer *Odocoileus virginianus*, has a higher proportion of old individuals in areas under higher hunting pressure (Naranjo & Bodmer, 2007). A better understanding of these relationships is required for the management of hunted species.

Comparing our results with other studies (Table 4), the age structure of the white-lipped peccary in the sites north of the Iriri River are similar to the age structure recorded in

TABLE 4 Age structure (age classes were inferred based on tooth condition; see text for further details) of the white-lipped peccary from various studies. Values are percentages of the total number of skulls at each site. Sources: Pacaya-Samiria, Tahuayo and Yavari-Miri (Bodmer et al, 1997); Nhumirim (Desbiez, 2007); Acurizal (Schaller, 1983); north of the Iriri River, Kararaô and Xingu River sites (this study).

Site	Class 1+2	Class 3	Class 4
Pacaya-Samiria	43.1	41.2	15.7
Tahuayo	44.4	42.4	13.2
Yavari-Miri	46.5	39.5	14.00
Nhumirim	21.1	36.8	42.1
Acurizal	23.3	39.5	37.2
N. of Iriri River	46.4	28.0	25.6
Kararaô	54.2	33.3	12.5
Xingu River	59.6	33.6	6.8

Peru (Bodmer et al., 1997). On the other hand, the age structure at sites on the Xingu River differs from these Peruvian sites and from the Brazilian Pantanal (Schaller, 1983; Desbiez, 2007).

As the observed differences in age structure between sites in the Terra do Meio did not appear to be related to hunting pressure, the greater proportion of younger individuals on sites along Xingu River may have other causes. We suggest that this distinct age structure, with a prevalence of older animals north of the Iriri River, may be a result of differences in land use. Although the region has a continuous vegetation cover, in the north there is a concentration of deforested areas along the Trans-Amazonian Highway (Fig. 1). The habitat loss, and the potential increase in hunting pressure associated with this deforestation, was outside but close to the area used by hunters from the Indigenous Lands to the north of the Iriri River. This may have caused a decrease in population growth and immigration rates in these areas compared to the sites on the Xingu River.

The residents of the Xingu River Extractive Reserve believe that the white-lipped peccary is more abundant and more important in their diet than a decade earlier (Ramos, 2013). The hunting pressure at the study sites, mainly those located along the Xingu River, is probably now much lower than it was a few decades ago. There may be two causes of this: the emigration of a significant number of inhabitants when the Brazilian government suspended the allowance for native rubber extraction in 1986, and conservation actions in the region, which culminated in the creation during 2004–2008 of eight conservation units (totalling > 6.8 million ha) in the Terra do Meio (Ramos, 2013). The hypothesis that populations of the white-lipped peccary are recovering is consistent with the patterns of age structure that we observed in the Terra do Meio. But the impacts caused by deforestation along Trans-Amazonian Highway may have hindered full recovery of populations to the north of the Iriri River.

In conclusion, our results indicate that differences in hunting pressure may not affect the age structure of white-lipped peccary populations. The age structure of this species appears to be robust to the effects of hunting, in agreement with previous studies. Other factors that have yet to be assessed may have stronger effects on age structure than subsistence hunting. Deforestation may explain the prevalence of older individuals in peccary populations in our northern study sites.

Acknowledgements

We are grateful to the Fundação O Boticário de Proteção à Natureza and WWF for their financial support, and to Instituto Vida Verde, especially Anthony Brandão. EMV received a Research Productivity Grant (Number 308153/2007–3) from the Brazilian National Council for Scientific and Technological Development (CNPq). We thank three anonymous reviewers for providing valuable suggestions and the inhabitants of the study sites for their collaboration.

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