Forest cover and social relations are more important than economic factors in driving hunting and bushmeat consumption in post-frontier Amazonia

Abstract

Identifying the economic drivers of hunting and bushmeat consumption is crucial for understanding whether economic growth in tropical forest regions can foster poverty alleviation and biodiversity conservation. However, studies investigating those drivers have drawn contrasting conclusions. Some authors attribute inconsistent findings to heterogeneous spatial and environmental contexts, yet other studies indicate that social factors may predominate over economical determinants. Here, we investigate bushmeat hunting and consumption by analyzing the relative importance of household-scale economic factors in diverse spatial and environmental contexts. We surveyed 240 households distributed across twenty diverse rural landscapes in a post-frontier region in Brazilian Amazonia. Our results show that hunting is more likely in locations with higher forest cover, where game availability is expected to be higher. In contrast, bushmeat consumption is widespread even in deforested landscapes near to urban centers. However, we find no evidence that household-scale economic factors determine variation in rural bushmeat consumption, regardless of spatial or environmental context. Consequently, we infer that future growth in income or wealth would be unlikely to significantly change patterns of bushmeat hunting and consumption. Instead, we find that eating bushmeat is mainly dependent on the hunting of relatively common species for subsistence and food sharing, rather than through market exchange. This demonstrates an important informal economy maintained by social relations. Work is needed to evaluate the sustainability of hunting these relatively small to medium-sized species given they evidently provide useful ecosystem service to poor households and are likely to support social relations in rural Amazonia.

Keywords: Income, game availability, harvest, sharing, wildlife conservation, wildmeat.

1. Introduction

Understanding the drivers of bushmeat consumption is a long-standing concern in conservation science, as bushmeat use is recognized for both its importance to human populations and its threat to biodiversity (Milner-Gulland 2003; Nielsen et al. 2018). Identifying the economic drivers is particularly important because this knowledge provides insights into how economic changes (e.g. market expansion, market integration, projects and policies aimed at increasing household income) can affect bushmeat use. Researchers have been particularly interested in determining whether poverty alleviation and wealth creation strategies are likely to decrease bushmeat hunting and consumption. This so-called win-win scenario for development and biodiversity conservation would not occur if, instead, economic growth leads to increased bushmeat demand and more hunting (Milner-Gulland et al. 2003; Brashares et al. 2011). Resolving the economic basis of wildlife use is important in rural areas of the forested tropics because of high but changing rates of multi-dimensional poverty (Sunderlin et al. 2008).

Economic theory commonly used for explaining variation in bushmeat consumption offers divergent predictions about what happens with wealth grow (being asset-wealth or monetary income) (Milner-Gulland et al. 2003), depending on preferences for bushmeat relative to other forms of animal protein. Where bushmeat is relatively cheap and accessible and people would rather replace it with other available meat types (i.e. bushmeat is an inferior good), bushmeat consumption would decline with wealth rise (Wilkie & Godoy 2001). Alternatively, if considered largely equivalent to other forms of animal protein (i.e. a normal good), then increased wealth should translate into a proportional increase in bushmeat consumption. Finally, if bushmeat is a preferred source of animal protein (i.e. a superior good) then we would expect rising wealth to lead to a disproportionately high increase in consumption (Wilkie & Godoy 2001; Wilkie et al. 2005; Fa et al. 2009; Godoy et al. 2010).

Because we do not know whether bushmeat is an inferior, normal or superior good, it is unclear whether wealth creation is likely to decrease or increase pressure on wildlife. In fact, empirical assessments of the economic drivers of bushmeat consumption have provided contrasting conclusions about the direction of the relationship between wealth and consumption (e.g. Wilkie & Godoy 2001; Fa et al. 2009; Godoy et al. 2010).

Evidence from Africa and Amazonia suggests these divergences may reflect spatial and environmental contexts (e.g. proximity to urban centers and local forest cover), which affect bushmeat demand and supply. Remoteness from urban centers can decrease the availability of domestic sources of protein, resulting in high prices and high bushmeat demand (Chaves et al. 2017a). Bushmeat may therefore be a necessity (i.e. an inferior good) in remote places, which is substituted by other meats when they become available or wealth increases. Such localities are also less deforested, according to a von Thunian model of higher transport costs and lower land rents with distance from cities (Angelsen 1994). Hence, the abundance of many game species should be higher, increasing their supply. This situation would offer greater net benefits of hunting and bushmeat consumption, especially for poorer households with less access to traded domesticated meats. Indeed, when harvestable wildlife populations are more easily available (e.g. near to protected areas, large forest patches), bushmeat prices tend to be lower and its consumption rate higher (Brashares et al. 2011; Foerster et al. 2012; Torres et al. 2018). In contrast, nearer to urban centers, domestic sources of protein are cheaper and bushmeat can be relatively expensive due to distance and transport costs from high-forest cover hunting areas. There, Brashares et al. (2011) found that wealthier households consume more bushmeat than poorer ones, indicating bushmeat as a normal or superior good. Summarizing, increasing wealth appears to impact game populations differently, depending on the spatial and environmental context.

It is problematic that only one study has formally addressed how economic drivers of bushmeat consumption interact with spatial and environmental factors. To our knowledge, Brashares et al.'s (2011) African study provides the only insights. Indeed, most bushmeat research is based on work in West and Central Africa, where there is intense, large-scale trade in bushmeat markets (Dupain et al. 2012; Petrozzi et al. 2016). Market exchange may be less important for determining bushmeat consumption in other places. In Latin America, studies evaluating this relationship have focused on urban areas (Parry et al. 2014; Morsello et al. 2015; Chaves et al. 2019) or in semi-autarkic indigenous groups (Wilkie & Godoy 2001; Godoy et al. 2010; Vasco & Sirén 2016). Moreover, analysis of consumption has tended not to distinguish whether bushmeat was hunted by household members or acquired through exchange, purchase, or sharing. Clearly, prices of bushmeat and domestic meat are likely to affect bushmeat consumption more through trade than through subsistence hunting.

In this paper, we investigate bushmeat hunting and consumption from the novel perspective of analyzing the relative importance of household-level economic factors in diverse spatial and environmental contexts. We did so by surveying households across twenty rural landscapes with varied urban-remoteness and local forest cover. We addressed five interrelated questions: Are economic factors associated with (i) hunting and (ii) bushmeat consumption? If so, is the relationship between economic factors and (iii) hunting, or (iv) bushmeat consumption, dependent on spatial and environmental factors? (v) Does the relationship between economic factors and bushmeat consumption differ between households that hunted and those that acquired bushmeat by alternative ways (i.e. purchase or gift)?

2. Methods

2.1. Study region

Our study was carried out at a meso-scale in eastern Brazilian Amazonia, in rural areas of three municipalities: Santarém (78 790 rural inhabitants from 294 580 in total); Belterra (6 852 of 16 318); and Mojuí dos Campos, a recently established municipality with no data on rural population (combined rural and urban population of 15 232) (IBGE 2010). The two smaller towns are c.30-45 km by paved road from Santarém. Bordered by the Amazon, Tapajós and Curuá-Una Rivers, our study region encompasses approximately 1 million ha (Fig. 1) of a diverse mosaic evolved over decades of government policies and economic cycles. Although above half of the region is still covered by primary/secondary forests (Fig. 1), there is a gradient in forest cover (correlated with distance to urban areas), and a diversity of socioeconomic contexts (e.g. rural population density, property sizes, wealth and market access) (details in Appendix A.1).

In Brazil, commercial hunting is illegal in any circumstances, although it still occurs and may involve large volumes in urban settings of remote Amazonian towns (van Vliet et al. 2015; El-Bizri et al. 2020; Chaves et al. 2019). Subsistence hunting has an uncertain legal status. The Brazilian Wildlife Protection Act (1967) made hunting wildlife illegal, although subsequent laws allowed hunting by traditional and rural populations only in a “state of necessity” or “to quench hunger” (Antunes et al. 2019).

2.2. Sampling design

We used a hierarchical sampling design. We first selected twenty 7 850-ha areas (circular with a 5km radius), hereafter landscapes, that captured variability in forest cover (33% to 93%) and road distance from Santarém (10-140km). Within each landscape, we randomly selected 12 households (n=240) (Fig. 1) by randomly drawing 12 points along the paved, unpaved roads or rivers, using ArcGIS 9.3, ensuring ≥400m between them to avoid spatial clustering. The selected household was the nearest from the point drawn. We skipped households when household heads declined to participate (n=3), or if after three visits no resident was encountered (n=4) (Appendix A.2).

2.3. Data collection

To collect data on hunting and bushmeat consumption, as well as demographic and socioeconomic characteristics of households, we conducted an interview-based survey with household heads (when possible, both heads) between July and November 2013. Beforehand, we pilot-tested the interview protocol for clarity, resolving any inconsistencies, and establishing a reliable recall period based on respondents' answers. The survey was conducted by P.C.T and three trained assistants (two from the region).

2.3.1. Hunting and bushmeat consumption variables

We considered hunting and bushmeat consumption as count variables. Values were defined as the number of times anyone in the household had gone hunting in the previous 30 days - hereafter hunting frequency - and the number of times bushmeat was consumed in the household in the previous 15 days - hereafter bushmeat consumption frequency. Bushmeat consumption data was restricted to the previous 15 days based on the pilot study (Appendix A.3.1). For each hunting trip and meal containing bushmeat, we asked which species were hunted or consumed.

2.3.2. Economic variables

We estimated two economic variables - *per capita* monetary income (previous 30 days) and *per capita* asset-wealth. We used both indicators because they reflect different aspects of the household's economic condition. Monetary income measures transitory income, which may sharply fluctuate especially in rural areas, whereas asset-wealth reflects long-term economic conditions (Wilkie et al. 2005). Economic variables were measured in Brazilian *Reais* (1 Real = 0.45 US$, in December 2013) (Appendix A.3.2).

We winsorized the values of monetary income at the 97th percentile to limit extreme values and reduce their possible spurious effect (Van Kerm 2007). Households above this percentile were either the few much richer households in the sample (both in terms of monetary income and wealth) or those that had an atypical high monetary income the previous month (earning from 2.5 to 25 times more income than those below the 97th percentile). For the same purpose we winsorized the highest wealth value to the second highest value, as their difference was twofold (Fig. A.1). Monetary income and wealth were weakly correlated (Pearson=0.26, $p<0.001$).

2.3.3. Spatial and environmental variables

We considered one spatial and one environmental variable: the time (in minutes) that household members took to reach the largest city, Santarém (collected through interviews) - hereafter 'remoteness' -, and the amount of forest cover surrounding the household - hereafter 'forest cover'. We considered time rather than distance because the former was less correlated with forest cover (Pearson=0.64, $p<0.001$, against Pearson=0.88, $p<0.001$ for distance [km]) and more appropriate for understanding urban accessibility and decision-making (Kwan 2013). We calculated forest cover (a proxy of game availability) as total forest cover (km^2), including primary forest (non-degraded and degraded) plus mature secondary forest (>10 years) within a 10-km radius (31,400-ha) from the household (Appendix A.3.3).

2.3.4. Control variables

We used two additional variables as controls in our analyses, proxies of culture and education attainment, because they had been linked to hunting and bushmeat consumption (Poulsen et al. 2009; Foerster et al. 2012; Mgawe et al. 2012). For culture, we used the origin of the household male head as a binary variable indicating whether he was born in the Legal Amazon (see Appendix A.3.4). Education attainment was accessed by the number of schooling years of the male household head. We used data of the male head because only men reported hunting. For hunting, we used data of the woman head only when there was no male head. For bushmeat consumption, we explored using also the maximum number of schooling years between the male and female heads and whether at least one of the heads was born in Legal Amazon, but the results did not change.

2.4. Data analysis

We first tested and found no multicollinearity among independent variables (low values of variance inflation factor; highest VIF=1.77). There was considerable variation in economic and control variables within all landscapes (Table A.1).

To investigate the association between hunting and bushmeat consumption and the economic, spatial and environmental variables, we ran different sets of generalized linear mixed-effects models (GLMM) for each of the two dependent variables. We used GLMM to account for the hierarchical nature of the sampling design, with landscapes as random factors (Zuur et al. 2009). Alternative models in each set were compared using the difference in their AICc values in relation to the first-ranked model (ΔAICc) (Burnham & Anderson 2002). We considered that a value of $\Delta AICc \leq 2$ indicates equally plausible models.

To answer questions (i) to (iv) we modeled both hunting and bushmeat consumption frequencies using zero-inflated Poisson models, because approximately two thirds of the data for both dependent variables were zeros. These models treat the zero-count outcomes as a mixture of structural and sampling zeros, which allows us to analyze both the variables associated with performing the behavior (hunted/did not hunt and consumed/did not consume bushmeat) and their frequencies (from zero on).

Both sets of candidate models (i.e. one set for hunting, another for bushmeat consumption) contained: an intercept-only model for reference (that did not include any fixed factors), a control model with only the two control variables as fixed effects, and additive and interaction models. Additive and interaction models always contained the two control variables and combinations of economic, spatial and environmental variables as fixed effects. We included only two-way interaction terms between economic variables and spatial or environmental variables (Table A.2).

To answer question (v) we considered only those households that consumed bushmeat. Therefore, we modeled bushmeat consumption frequency using zero-truncated Poisson models. We used the Conway-Maxwell Poisson model to account for the underdispersed nature of our data, and included a binary variable - whether the bushmeat consumed in the household was hunted by a household member or not. We added two-way and three-way interactions with this binary variable to each model to investigate whether any association between bushmeat consumption and the variables and interactions previously tested differed between hunters and non-hunters' households (Table A.3).

We standardized all non-categorical fixed factors so that each had a mean of zero and a standard deviation of one to improve convergence of the fitting algorithm (Zuur et al. 2009). We also tested the effect of the three continuous independent variables as quadratic terms, to account for possible U-shaped associations with hunting and bushmeat consumption (Wilkie & Godoy 2001), but model fit was not improved. All analyses were implemented in *R* 3.5.1 (R Core Team 2014) and all model selections were run using the *glmmTMB package* (Brooks et al. 2017). Selected models were tested for misspecification problems (e.g. uniformity, under or over dispersion and zero-inflation) using *DHARMa* package for residual diagnostics (Hartig 2019), and no such problems were found.

2.5. Ethics statement

Our study protocol was evaluated and approved by a Research Ethics Committee from the Brazilian National Commission for Research Ethics (CAAE 16766413.4.0000.5464 *Plataforma Brasil)*. Prior to interviews, we contacted representatives of nearby rural communities, explaining the research. We later obtained their written voluntary and informed consent. Then, we obtained written and informed consent from each participant before beginning the interview. At the interview onset, we explained the research aims, guaranteed the information anonymity and assured their participation was voluntary and they could withdraw at any time.

3. Results

Members of 31% of the surveyed households had hunted during the previous 30 days. In total, respondents declared 189 hunting events (mean=0.8, SD=1.5 across all households; mean=2.6, SD=1.6 across households that hunted), of which 47% were successful (≥1 animal caught), and 106 individuals caught. In 26% of households that hunted, animals were never caught, while in 84% of successful hunting events, only one individual was caught (mean=1.2 animals, SD=0.5).

Bushmeat consumption, not necessarily from their own hunting, was relatively more common; 45% of the households had consumed it within the previous 30 days and 33% within the previous 15 days. Respondents declared 208 meals containing bushmeat in the previous 15 days (mean=0.9 meals, SD=1.9 across all households; mean=2.6, SD=2.5 across households where bushmeat was consumed). The mean number of meals in households with a hunter was higher than in those that acquired bushmeat by other means (mean=3.2, SD=2.9 and mean=1.8, SD=1.4, respectively). Perhaps surprisingly, our data indicate very low levels of bushmeat trade in our rural study area. For 59% of the meals, bushmeat was hunted by a household member, in 40% bushmeat was a gift from relatives, friends or neighbors, and for only two meals (1%) bushmeat was purchased.

Paca (*Cuniculus paca*) and nine-banded armadillo (*Dasypus novemcinctus*) were the most frequently hunted and consumed species, accounting for nearly 80% of successful hunting trips and meals (Fig. 2).

3.1. Hunting correlates

Hunting frequency was not associated with any factor investigated (Table 1). However, having hunted was strongly and positively associated with forest cover in the surroundings and with origin of the household head. Higher forest cover and Amazonian origin of the household head were associated with increased probability of hunting, with hunting occurring in 37.7% of Amazonian origin households but only in 20.2% of those non-Amazonian (Table 1, Fig. 3). People in households with non-

Amazonian origin were three times less likely to hunt than those with Amazonian origin (odds-ratio=0.32, CI=0.16–0.65, for the first selected model). Education had a U-shaped relationship with hunting probability, increasing through elementary education and decreasing with high-school education and beyond (Fig. 3). We found no association of having hunted with household monetary income and wealth in any spatial or environmental context.

3.2. Bushmeat consumption correlates

When considering all households sampled (n=240), bushmeat consumption within the past 15 days (both binary and frequency variables) was not strongly associated with any of the tested factors. We found weak evidence that people in households where the male had was non-Amazonian are two times less-likely to consume bushmeat than those where the male head had Amazonian origin (odds-ratio=0.45, CI=0.21–0.97, for the first selected model), although the upper confidence interval approaches 1, meaning the two groups might have similar probabilities (Table B.1). However, we did not find this effect when we considered the origin of both household heads that is, whether at least one of them was Amazonian.

Considering only households that consumed bushmeat within the past 15 days (n=80), we also found no evidence that consumption frequency is associated with any of the tested factors and neither that it is associated with different factors for hunting households compared to non-hunting households. However, consumption frequency in hunting households was 2.7 times higher (CI=1.5–4.8) compared to non-hunting households, when controlling for other variables (Table B.2).

4. Discussion

Hunting and bushmeat consumption in our study region were mainly driven by game availability and social relations and not market exchange. Wealth did not play an important role in in shaping neither hunting not bushmeat consumption, irrespective of the environmental and spatial context. This evidence contrasts with what has been suggested elsewhere (Fa et al. 2009; Brashares et al. 2011). As such, differences in spatial and environmental contexts between regions investigated in previous studies may not explain all the contrasting findings of those studies about the association of economic factors and bushmeat consumption. Overall, our findings suggest that the way bushmeat is acquired is crucial in defining the drivers of hunting and bushmeat consumption.

Conventionally, access to bushmeat is conceptualized as playing out through market exchange involving rational economic actors, with markets then responding predictably to spatiotemporal variation in supply and demand (e.g. Wilkie & Godoy 2001). Yet, buying bushmeat was rare in our rural study area. Instead, households tended to acquire it directly through hunting, or through an 'economy of affection' within social networks. We found no evidence that economic factors are key in determining hunting or bushmeat consumption, irrespective of spatial and environmental factors. As such, variations in income or wealth levels would unlikely lead to major changes in hunting and bushmeat consumption in our study region and similar post-frontier Amazonian regions.

Moreover, by investigating hunting, we tested whether the economic determinants of consumption are conditional on how bushmeat is acquired. We found no evidence of this between hunting and sharing, which were the prevalent ways in our study area. Hunting was more likely in locations with higher forest cover, where game availability is likely higher. Instead, bushmeat consumption was widespread.

4.1. Hunting in a post-frontier region

We found that hunting is more likely in less-deforested landscapes, confirmatory of other studies identifying that hunting is more likely when living closer to game sources (i.e. large forest patches or protected areas) or areas with high forest cover (as proxies of game availability) (Shively 1997; Brashares et al. 2011; Torres et al. 2018). We also found that hunting was more prevalent among 'Amazonian' (as opposed to in-migrants from elsewhere in Brazil) headed households. This may result from culturally-based differences (Mgawe et al. 2012) or hunting expertise passed across generations. Yet, hunting frequency was not associated with any factor investigated, which may result from limited variation in our sample, as most households (60%) reported hunting just once or twice in the last 30 days. Those species most frequently hunted were smaller and classified as least concern (IUCN Red List), which seems consistent with more deforested and overhunted tropical forests, where hunters catch commonly occurring species instead of preferred ones (e.g. Southeast Asia - Rao et al. 2010). Nonetheless, even in highly forested regions of the Amazon, *C. paca* is widely hunted and a preferred species (Parry et al. 2014; Valsecchi et al. 2014; Nunes et al. 2019). Low occurrence of large-bodied species (i.e. deer, peccaries, tapir) catches is likely to indicate their depressed populations in our post-frontier study region. Local depletion and extinction of large-bodied species has already been suggested by another study in the region (Sampaio et al. 2010).

4.2. Rural bushmeat consumption outside of market exchange

Our results differ from previous work, in diverse contexts, which found that monetary income or asset-wealth were important in explaining bushmeat consumption (e.g. Wilkie & Godoy 2001; Wilkie et al. 2005; Fa et al. 2009; Godoy et al. 2010; Brashares et al. 2011; Foerster et al. 2012). Notably, almost none of the surveyed households in our study reported they had purchased bushmeat. Instead, most rural consumers had obtained bushmeat directly from the surrounding forest or farm-fallow matrix or received as a gift. Because bushmeat trade is illegal in Brazil and only one household reported purchasing bushmeat, we might have underestimated trade. Nonetheless, the lack of association between consumption and micro-economic factors suggests trade is relatively unimportant in the rural zone of our study region. Although we report almost no trade within rural areas, we cannot discard that rural hunters may be selling meat directly in the urban area or to traders and therefore, supplying local urban markets with these relatively common 'post-depletion' mammal species. Rural-urban bushmeat networks are found elsewhere in Amazonia, although even urban consumers often obtain bushmeat through gifting instead of trade (Morsello et al. 2015; van Vliet et al. 2015, Chaves et al. 2019).

Elsewhere, the lack of correlation between bushmeat consumption and wealth has been explained by high prevalence of consumption together with harvest being consumed mostly within hunting households (Schulte-Herbrüggen et al. 2013). Likewise, here, in all but three hunting events, at least part of the catch was consumed in the hunter's household. In 43% of all successful catches, bushmeat was also shared, and in 13% of those cases it was shared with relatives or friends that lived far away (>50-km). That might explain why bushmeat consumption was so widespread in the region, even in more deforested landscapes and in less-remote places with greater access to other meat types. Sharing often involves reciprocity and is considered very important in rural areas (e.g. Nunes et al. 2019). Consequently, bushmeat gifting belongs to the informal economy and is still critical to people whose economic lives sit somewhere between subsistence peasantry and market economy. This informal economy has been termed 'economy of affection' to describe kin-based networks of exchange in East Africa (Hyden 1983). In rural Amazonia, continued reliance on this informal system of production and exchange helps maintain bonds between households, enhances social cohesion and contributes to survival, with bushmeat being a very frequent gift (WinkerPrins & Souza 2005; Minzenberg & Wallace 2011; Nunes et al. 2019).

Although we did not find an association between economic factors and overall consumption, this linkage might exist for particular species, as found in rural Africa and Asia (Foerster et al. 2012; Shively 1997) and urban Amazonia (Parry et al. 2014). In our study region, there were mainly two species consumed (*C. paca* and *D. novemcinctus*) (80% of bushmeat meals, combined), the only ones we had enough consumption events to rigorously test such association. Again, we failed to find any association of economic factors and the consumption of these animals in any spatial and environmental context (Table S6).

Geographical origins, used as a proxy for culture, was not a strong driver of bushmeat consumption. This finding echoes Morsello et al.'s (2015) findings from Amazonian towns. Interestingly, their urban study also found social relations were stronger predictors of bushmeat consumption than economic factors. Those who believed that sharing bushmeat strengthens social bonds (with family and friends) were more likely to consume and to prefer it over other animal proteins. Gifts were the second most important source of bushmeat in our sample and hunters often shared their catch, which both suggest that social relations play important roles in our study region, consistent with work elsewhere in Amazonia, and in Africa (Morsello et al. 2015; van Vliet et al. 2015; Bachmann et al. 2019; Chaves et al. 2019; Nunes et al. 2019).

4.3. Implications for conservation and rural livelihoods

As relatively self-sufficient rural populations experience changing economic conditions through market integration, government-led development projects and cash transfer programs, it becomes increasingly important to understand how these changes affect livelihood strategies, resource use and biodiversity conservation (Billé et al. 2012). Our results suggest neither hunting nor bushmeat consumption in our study region is likely to be affected by changes in levels of households' monetary income or wealth. Hence, public policies aimed at increasing monetary income in rural households are unlikely to impact hunted wildlife.

Hunting seems instead driven by environmental factors associated with wildlife availability and cultural preferences or experience. Bushmeat consumption, on the other hand, seems strongly linked to social relations, through an 'economy of affection' based on small to medium-bodied size common species. Nevertheless, the scale of the any urban trade supplied by rural hunters is unclear. The apparent scarcity of the larger-bodied or sensitive Amazonian game species suggests these are probably severely depleted or even locally extinct in our study region. In fact, other studies in the region, using interviews and line-transects, have found higher abundance of small-bodied species such as nine-banded armadillo (*Dasypus novemcinctus*) and agouti (*Dasyprocta* *leporina*) and very low abundance or evidence of local extinction of medium and large-bodied species, such as tapir (*Tapirus terrestris*) and white-lipped peccary (*Tayassu pecari*) (Sampaio et al. 2010; Ravetta 2015). Collared peccary (*Pecari tajacu*) and brocket deer (*Mazama spp.*) may persist in fragmented landscapes, although red brocket deer (*Mazama americana*) had lower abundance in such landscapes than in locations with continuous forest. The same was observed for agouti (Sampaio et al. 2010). This may explain the higher hunting frequency of agouti we found in more forested landscapes and some of those adjacent to a protect area (Tapajós National Forest) (Fig. 2).

Although bushmeat is probably consumed not only for necessity, bushmeat consumption is widespread, suggesting the remnant hunted mammal species provide critical sources of macro- and micro-nutrients for more deprived households, particularly in rural areas far from rivers. In addition, bushmeat gifting contribute to support social bonds (Minzenberg & Wallace 2011) that may provide both hunting and non-hunting households with nutrients in times of need, favoring food security (Nunes et al. 2019).

Regarding wildlife conservation, there is evidence from other Amazonian regions that species associated with agricultural areas (crop-raiding species) (e.g. lowland paca, agouti, collared peccary, brocket deer) are more frequently hunted (Nunes et al. 2020) and frequently detected in early successional forests (Abrahams et al. 2018). Hunters in larger villages use smaller catchment areas and harvest more game per unit time than hunters in smaller villages, suggesting that forests around agricultural areas can sustain hunting of crop-raiding species (Nunes et al. 2020). However, ~~evaluating~~ monitoring the sustainability of hunting even common species is key, as there is also evidence that ~~even~~ populations of such species (e.g. *C. paca*) may be susceptible to overhunting (Valsecchi et al. 2014). In our study region, red brocket deer has been found to be absent from some locations where forest is fragment (Sampaio et al. 2010). Therefore, interventions that reduce hunting and consumption of species that are already depleted in some locations is important. Research shows that awareness of overhunting (Morsello et al. 2015; Bachmann et al. 2019; Kouassi et al. 2019), and community engagement activities (Steinmetz et al. 2014; Chaves et al. 2017b) can reduce trade and consumption in rural and urban areas. However, these mechanisms may not work everywhere (e.g. Chausson et al. 2019, in an urban African context). Interventions aimed at decreasing overall levels of hunting by rural populations may constrain access to an important ecosystem service, disturb social relations and lack popular support. Therefore, campaigns to avoid hunting locally-scarce species could be more successful if rural Amazonians in post-frontier regions are allowed to hunt more resilient species sustainably.

Acknowledgements

We are grateful to: P.C.R de Araújo and E.R. da Silva for assistance in data collection; K.S. Gonçalves for assistance in mapping roads and households and pilot-testing interviews; J.V. Siqueira for mapping forest cover; and all interviewees and community representatives in Santarém, Mojuí dos Campos and Belterra.

Funding sources

This work was supported by the Fundação de Amparo à Pesquisa do Estado de São Paulo-FAPESP [grant numbers 2011/19108-0, 2011/19606-0]; the Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq [grant numbers 306715/2011-2, 308205/2014-6, 311051/2018-9]; the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – CAPES.

Appendix A and B. Supplementary material

Supplementary data to this article can be found online.

References

Abrahams MI, Peres CA, Costa HCM. 2018. Cassava loss by terrestrial vertebrates in western Brazilian Amazonia. Journal of Wildlife Management 82: 734–746.

Angelsen A. 1994. Shifting Cultivation Expansion and Intensity of Production: The Open Economy Case. Chr. Michelsen Institute for Development Studies and Human Rights. Working Paper 1994:3. Bergen. Available from http://bora.cmi.no/dspace/bitstream/10202/355/1/WP1994.3%20Arild-07192007_7.pdf

Antunes AP, et al. 2019. A conspiracy of silence: Subsistence hunting rights in the Brazilian Amazon. Land Use Policy 84: 1-11.

Bachmann ME, Junker J, Mundry R, Nielsen MR, Haase D, Cohen H, Kouassi JAK, Kühl HS. 2019. Disentangling economic, cultural, and nutritional motives to identify entry points for regulating a wildlife commodity chain. Biological Conservation 238 DOI: 10.1016/j.biocon.2019.07.022.

Billé R, Lapeyre R, Pirard R. 2012. Biodiversity conservation and poverty alleviation: a way out of the deadlock? SAPIENS 5: 1-15.

Brashares J S, Golden CD, Weinbaum KZ, Barret CB, Okello GV. 2011. Economic and geographic drivers of wildlife consumption in rural Africa. Proceedings of the National Academy of Sciences of the United States of America 108: 13931–13936.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9: 378–400. https://journal.r-project.org/archive/2017/RJ-2017-066/index. html.

Burnhan KP, Anderson D. 2002. Model selection and multi-model inference: A practical information-theoretic approach. 2nd edition. Springer-Verlag, New York.

Chausson AM, Rowcliffe JM, Escouflaire L, Wieland M, Wright JH. 2019. Understanding the Sociocultural Drivers of Urban Bushmeat Consumption for Behavior Change Interventions in Pointe Noire, Republic of Congo. Human Ecology 47: 179-191.

Chaves WA, Wilkie DS, Monroe MC, Sieving KE. 2017a. Market access and wild meat consumption in the central Amazon, Brazil. Biological Conservation 212: 240-248.

Chaves WA, Valle DR, Monroe MC, Wilkie DS, Sieving KE. 2017b. Changing wild meat consumption: an experiment in the central Amazon, Brazil. Conservation Letters 11: 1-10.

Chaves WA, Monroe MC, Sieving KE. 2019. Wild meat trade and consumption in the central Amazon, Brazil. Human Ecology 47: 733 – 746.

Dupain J, Nackoney J, Vargas JM, Johnson PJ, Farfán MA, Bofaso M, Fa JE. 2012. Bushmeat characteristics vary with catchment conditions in a Congo market. Biological Conservation 146: 32-40.

El-Bizri HR, et al. 2020. Urban wild meat consumption and trade in central Amazonia. Conservation Biology 34: 438-448.

Fa JE, Albrechtsen L, Johnson PJ, Macdonald DW. 2009. Linkages between household wealth, bushmeat and other animal protein consumption are not invariant: evidence from Rio Muni, Equatorial Guinea. Animal Conservation 12: 599-610.

Foerster S, Wilkie DS, Morelli GA, Demmer J, Starkey M, Telfer P, Steil M, Lewbel A. 2012. Correlates of bushmeat hunting among remote rural households in Gabon, Central Africa. Conservation Biology 26: 335–344.

Godoy R, et al. 2010. The effect of wealth and real income on wildlife consumption among native Amazonians in Bolivia: estimates of annual trends with longitudinal household data (2002–2006). Animal Conservation 13: 265–274.

Hartig F. 2019. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.2.4. https://CRAN.R-project.org/package=DHARMa.

Hyden G. 1983. No Shortcuts to Progress: African Development Management in Perspective. Heinemann, London.

Instituto Brasileiro de Geografia e Estatística (IBGE) 2010. Censo Demográfico 2010. IBGE, Rio de Janeiro, Rio de Janeiro.

Kouassi JAK, Normand E, Koné I, Boesch C. 2019. Bushmeat consumption and environmental awareness in rural households: a case study around Taï National Park, Côte d'Ivoire. Oryx 53: 293-299.

Kwan M-P. 2013. Beyond space (as we knew it): Toward temporally integrated geographies of segregation, health, and accessibility. Annals of the Association of American Geographers 103: 1078–86.

Mgawe P, Mulder MB, Caro T, Martin A, Kiffner C. 2012. Factors affecting bushmeat consumption in the Katavi-Rukwa ecosystem of Tanzania. Tropical Conservation Science 5: 446-462.

Milner-Gulland E.J, Bennet EL, SCB 2002 Annual Meeting Wild Meat Group. 2003. Wild meat: the bigger picture. Trends in Ecology and Evolution 18: 351-357.

Minzenberg E, Wallace R. 2011. Amazonian agriculturalists bound by subsistence hunting. Journal of Cultural Geography 28: 99-121.

Morsello C, Yague B, Beltreschi L, van Vliet N, Adams C, Schor T, Quiceno-Mesa MP, Cruz D. 2015. Cultural attitudes are stronger predictors of bushmeat consumption and preference than economic factors among urban Amazonians from Brazil and Colombia. Ecology and Society 20: 21. DOI: 10.5751/ES-07771-200421.

Nielsen MR, Meilby H, Smith-Hall C, Pouliot M, Treue T. 2018. The importance of wild meat in the Global South. Ecological Economics 146: 696-705.

Nunes VA, Guariento RD, Santos BA, Fischer E. 2019. Wild meat sharing among non-indigenous people in the southwestern Amazon. Behavioral Ecology and Sociobiology 73: 26 DOI: 10.1007/s00265-018-2628-x.

Nunes AV, Oliveira-Santos LGR, Santos BA, Peres CA, Fischer E. 2020. Socioeconomic drivers of hunting efficiency and use of space by traditional Amazonians. Human Ecology DOI: 10.1007/s10745-020-00152-6.

Parry L, Barlow J, Pereira H. 2014. Wildlife Harvest and Consumption in Amazonia's Urbanized Wilderness. Conservation Letters 7: 565-574.

Petrozzi F, Amori G, Franco D, Gaubert P, Pacini N, Eniang EA, Akani GC, Politano E, Luiselli L. 2016. Ecology of bushmeat trade in west and central Africa. Tropical Ecology 57: 545-557.

Poulsen JR, Clark CJ, Mavah G, Elkan PW. 2009. Bushmeat supply and consumption in a tropical logging concession in northern Congo. Conservation Biology 23: 1597-1608.

R Core Team 2015. R: The R Project for Statistical Computing. Available at https://www.r-project.org/.

Rao M, Htun S, Zaw T, Myint T. 2010. Hunting, Livelihoods and Declining Wildlife in the Hponkanrazi Wildlife Sanctuary, North Myanmar. Environmental Management 46: 143-153.

Ravetta AL. 2015. Distribuição e abundância de médios e grandes mamíferos na Amazônia Central. PhD Thesis. Universidade Federal do Pará, Belém, Brazil.

Sampaio R, Lima AP, Magnusson WE, Peres CA. 2010. Long-term persistence of midsized to large-bodied mammals in Amazonian landscapes under varying contexts of forest cover. Biodiversity and Conservation 19: 2421–2439.

Shively GE. 1997. Poverty, technology, and wildlife hunting in Palawan. Environmental Conservation 24: 57-63.

Schulte-Herbrüggen B, Cowlishaw G, Homewood K, Rowcliffe JM. 2013. The importance of bushmeat in the livelihoods of West African cash-crop farmers living in a faunally-depleted landscape. PLoS ONE 8 DOI: 10.1371/journal.pone.0072807.

Steinmetz R, Srirattanaporn S, Mor-Tip J, Seuaturien N. 2014. Can community outreach alleviate poaching pressure and recover wildlife in South-East Asian protected areas? Journal of Applied Ecology 51: 1469–1478.

Sunderlin WD, Dewi S, Puntodewo A, Müller D, Angelsen A, Epprecht M. 2008. Why forests are important for global poverty alleviation: a spatial explanation. Ecology and Society 13: 24.

Torres PC, Morsello C, Parry L, Barlow J, Ferreira J, Gardner T, Pardini R. 2018. Landscape correlates of bushmeat consumption and hunting in a post-frontier Amazonian region. Environmental Conservation 45: 315-323.

Van Kerm P. 2007. Extreme incomes and the estimation of poverty and inequality indicators from EU-SILC. IRISS Working Paper Series. Centre d'Etudes de Populations, de Pauvreté et de Politiques Socio-Economiques, Luxembourg.

Van Vliet N, Quiceno MP, Cruz D, Neves de Aquino LJ, Yagüe B, Schor T, Hernandez S, Nasi R. 2015. Bushmeat networks link the forest to urban areas in the trifrontier region between Brazil, Colombia, and Peru. Ecology and Society 20: 21 DOI:10.5751/ES-07782-200321.

Valsecchi J, El-Bizri HR, Figueira JEC. 2014. Subsistence hunting of *Cuniculus paca* in the middle of the Solimões River, Amazonas, Brazil. Brazilian Journal of Biology 74: 560-568.

Vasco C, Sirén A. 2016. Correlates of wildlife hunting in indigenous communities in the Pastaza province, Ecuatorian Amazonia. Animal Conservation 19: 422-429.

Wilkie DS, Godoy RA. 2001. Income and price elasticities of bushmeat demand in lowland Amerindian societies. Conservation Biology 15: 761-769.

Wilkie DS, Starkey M, Abernethy K, Effa EN, Telfer P, Godoy R. 2005. Role of prices and wealth in consumer demand for bushmeat in Gabon, Central Africa. Conservation Biology 19: 268-274.

WinklerPrins AMGA, Souza PS. 2005. Surviving the City: Urban Home Gardens and the Economy of Affection in the Brazilian Amazon. Journal of Latin American Geography 4: 107-126.

Zuur AF, Ieno EN, Wlaker NJ, Saveliev AA, Smith GM. 2009. Mixed Effects Models and Extensions in Ecology with R. 1st edition. Springer, New York.

Table 1. GLMM model selection results for hunting (n=240) showing only models with ΔAICc≤ 3 and the intercept-only model for reference.

	Zero-inflation Model									Conditional Model					
Model	Intercept	orig	edu	edu^2	for	wea	for:wea	inc	rem	Intercept	logLik	AICc	ΔAICc	K	weight
Intcpt+orig+edu+edu^2+for	1.01 (0.36)	-0.94 (0.37)	-0.59 (0.22)	0.31 (0.16)	-0.53 (0.18)					0.81 (0.10)	-261.3	539.3	0.0	8	0.18
Intcpt+orig+edu+for	1.42 (0.29)	-1.13 0.36)	-0.34 0.16)		-0.55 0.18)					0.81 (0.10)	-263.1	540.7	1.4	7	0.09
Intcpt+orig+edu+ edu^2+for+wea+ for:wea	0.99 (0.36)	-0.89 (0.38)	-0.61 (0.22)	0.31 (0.17)	-0.50 (0.18)	0.20 (0.20)	0.31 (0.21)			0.81 (0.10)	-259.9	540.8	1.5	10	0.08
Intcpt+orig+edu+ edu^2+for+ inc	1.00 (0.36)	-0.90 (0.38)	-0.59 (0.22)	0.29 (0.17)	-0.53 (0.18)			0.12 (0.18)		0.81 (0.10)	-261.1	541.0	1.7	9	0.08
Intcpt+orig+edu+ edu^2+for+wea	1.01 (0.36)	-0.92 (0.38)	-0.59 (0.22)	0.30 (0.17)	-0.52 (0.18)	0.12 (0.18)				0.81 (0.10)	-262.7	541.1	1.8	9	0.07
Intcpt+orig+edu+ edu^2+for+rem	1.01 (0.36)	-0.94 (0.38)	-0.59 (0.22)	0.31 (0.17)	-0.51 (0.22)				0.02 (0.20)	0.81 (0.10)	-263.1	541.5	2.1	9	0.06
Intercept-only	0.63 (0.16)									0.80 (0.11)	-274.1	556.3	17.0	4	<0.001

Intcpt=Intercept, orig=Amazonian origin, edu=years of formal education of the male household head, for=forest cover, rem=remoteness, inc=monetary income, wea=asset-wealth; K: number of parameters; logLik: log-Likelihood of the model; AICc: AICc value; ΔAICc: difference in AICc value compared to the first-ranked model; ωi: Akaike weight; coefficients for each variable of the model. In parenthesis = SE. Zero-inflation Model – estimates the probability of not have hunted (binary variable). Conditional Model – frequency variable.

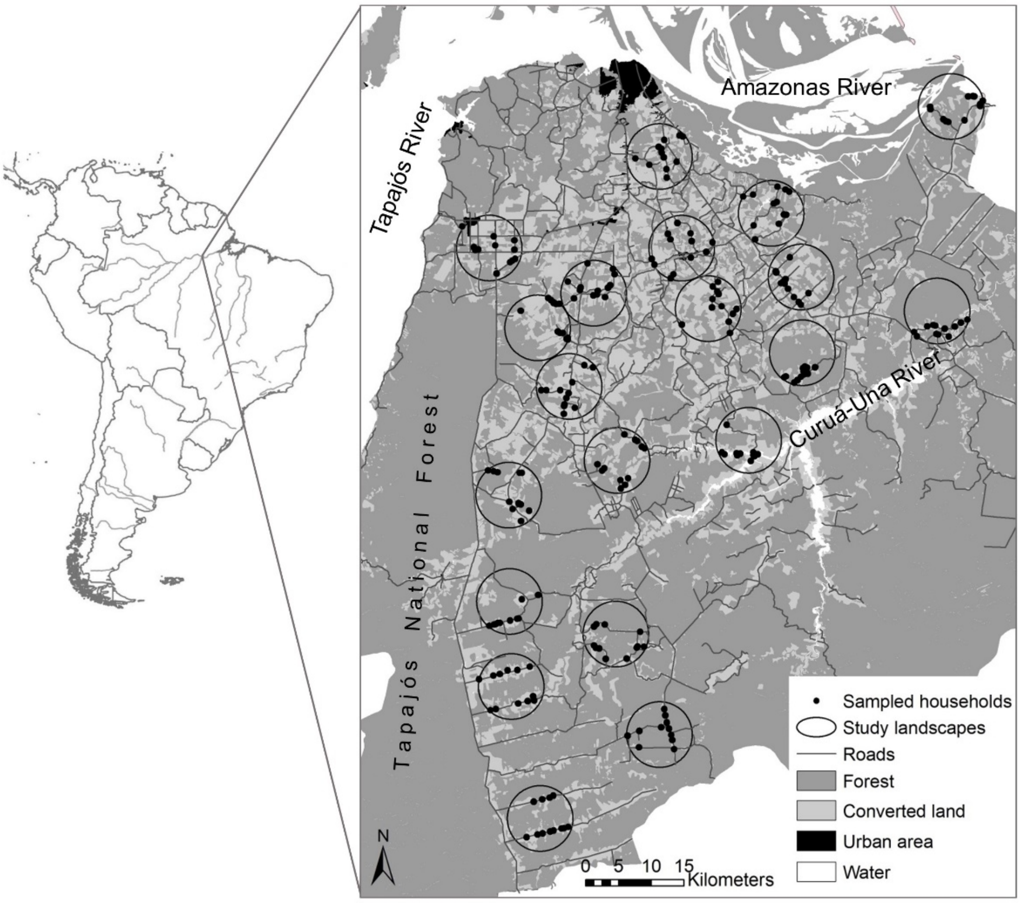

Figure 1. Location of the study region in South America and land-cover map of the study region, indicating the location of the 20 study landscapes and the 240 sampled households.

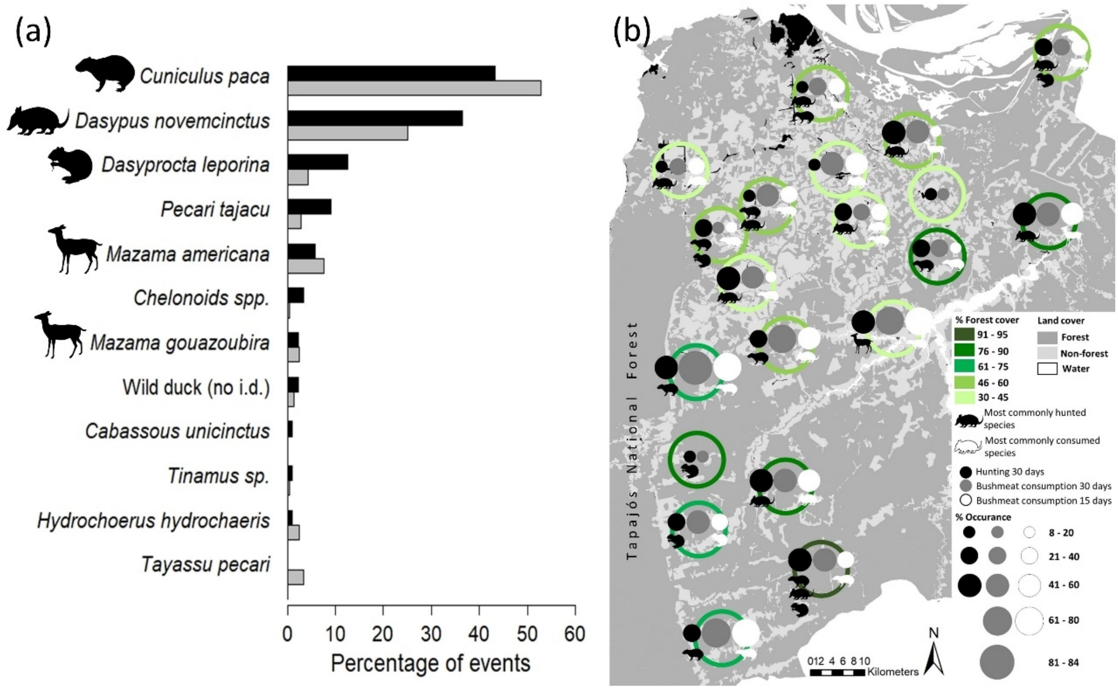

Figure 2. Species hunted and consumed in the study region. (a) Percentage of hunting (n=88) and meal (n=208) events where the species was hunted (black) or consumed (grey). Totals sum to more than 100% because more than one species could have been hunted or consumed in the same event. (b) Percentage of households that hunted and consumed bushmeat and species most commonly hunted and consumed in each landscape. More than one species could me hunted or consumed in the same number of events or no species could have been hunted or consumed in a given landscape.

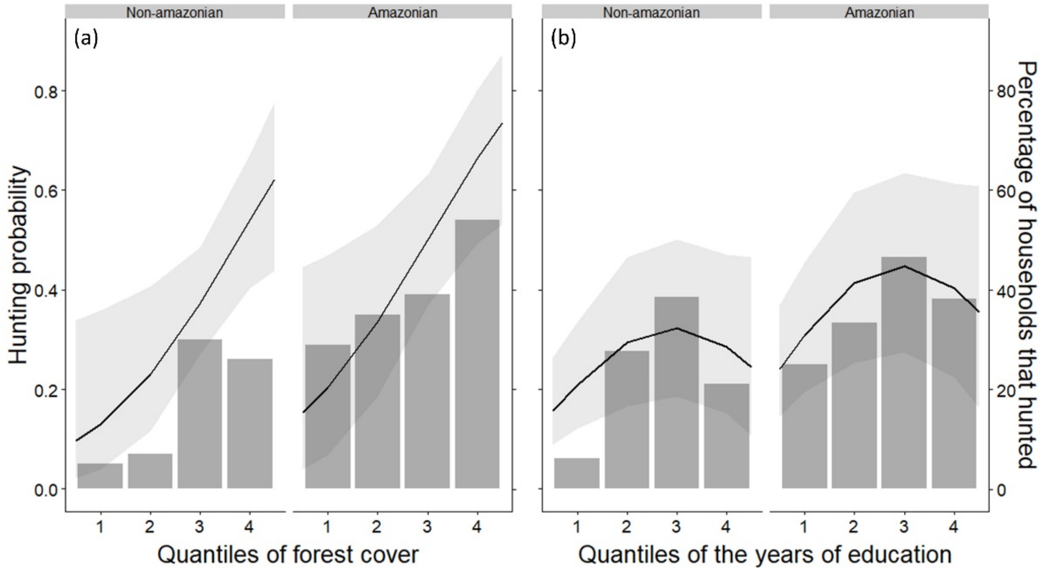

Figure 3. Relationships between hunting activity and (a) origin and forest cover; (b) origin and reliance on non-monetary income. Bars represent raw data. Curves represent hunting probability predicted by the first model selected (95% CI).