



Continuity and change in hunting behaviour among contemporary indigenous peoples



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ABSTRACT

Though subsistence hunting in tropical rainforests contributes to local food security and livelihoods, it also constitutes a major challenge to wildlife conservation. In this paper we examine different hunting practices of contemporary Tsimane', an Amazonian indigenous society native to Bolivia, and discuss their potential impact on wildlife. We also explore whether such different practices relate to greater integration into the national society and the market economy. Between 2009 and 2010, we conducted interviews with 344 Tsimane' adult men from 40 villages to collect information on their 1) hunting engagement, success, effort, offtake and prey profile and 2) their individual level of integration into the national society and the market economy. Overall, 71% of the interviewed men engaged in subsistence hunting albeit using different practices and achieving different outcomes. We used hierarchical cluster analysis to classify hunters into four groups according to their engagement and success in hunting. Two large groups of hunters had a diversified prey profile and targeted resilient species, whereas the two remaining groups were smaller, displayed high levels of offtake and efficiency, and targeted mainly ungulates and primates. We argue that the potential impact of expert hunters on wildlife is higher because they target more vulnerable species. Our results also suggest that there are no clear pathways relating hunting strategies and individual levels of integration into the national society and the market economy. However, our study provides evidence of how rapid and increasing contact with mainstream society affects hunting and subsistence livelihoods of contemporary indigenous peoples, posing severe potential impacts on biodiversity conservation.

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1. Introduction

In addition to habitat degradation and loss, overhunting is among the largest challenges to biodiversity conservation in tropical rainforests (Fa et al., 2003; Milner-Gulland et al., 2003; Peres, 2010). Overhunting

can have dramatic impacts on ecosystems, potentially contributing to alter forest composition, structure, and dynamics due to the loss of ecological interactions (Peres and Palacios, 2007), trophic meltdown (Estes et al., 2011), the decline of wildlife populations (Peres, 2000), and species extinction (Bodmer et al., 1997; Redford, 1992). Apparently undamaged tropical forests may be, in fact, heavily hunted thus resulting in vast areas of land with significantly reduced densities of game vertebrate species (Redford, 1992; Wilkie et al., 2011).

Nevertheless, overhunting is not only a major threat to biodiversity but also to the millions of people who depend on wildlife for their livelihoods (Brashares et al., 2011). Indeed, wildlife remains a vital source of protein and income for many indigenous peoples and rural populations worldwide (Brashares et al., 2011, 2004; Milner-Gulland et al., 2003; Robinson and Bennett, 2000). Due to the significant overlap between indigenous territories and the world's remaining areas of high game species abundance and diversity (Gorenflo et al., 2012), researchers have shown special interest in understanding how indigenous peoples use

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game resources (Bodmer, 1995; Constantino et al., 2008; Peres and Nascimento, 2006; Smith, 2008), with conflicting views on the topic: while some researchers have argued that indigenous and local peoples play an important role in biodiversity conservation (Alcorn, 1993; Schwartzman and Zimmerman, 2005), others have argued that biodiversity is decreasing due to local people's pressure on natural resources (Hames, 2007; Smith and Wishnie, 2000).

Irrespective of how traditional resource management has affected wildlife in the past, it is widely accepted that contemporary indigenous societies now face changes that affect their traditional livelihood strategies, including hunting. Drivers of these changes are population growth (Robinson and Bennett, 2004), access to the markets (Lu, 2007; van Vliet et al., 2015), sedentary settlement patterns (Stearman, 2000), infrastructure development (Suárez et al., 2009), access to modern technology (Dounias, 2016; Levi et al., 2009), encroachment by productive or extractive activities (Orta-Martínez and Finer, 2010; Reyes-García et al., 2012), or changes in their belief systems (Guèze et al., 2015; Luz et al., 2015). Besides local game abundance (e.g., Jerozolinski and Peres, 2003; Peres and Nascimento, 2006), hunting is also largely dependent on individual and community level factors (i.e., individual knowledge and skills, market demand, technology, or mobility (e.g., Gill et al., 2012; Morsello et al., 2015; Reyes-García et al., 2016; Vasco and Sirén, 2016)). Therefore, a shift in any of these factors, generated by the new pressures faced by indigenous peoples, may also have an impact on wildlife conservation through hunting success (Friant et al., 2015).

Here we examine the relation of one of these drivers, integration into the national society and access to markets, on hunting behaviour. Previous research has addressed how integration into the national society and access to markets change indigenous or rural people's hunting patterns and two pathways have been suggested. Some authors have argued that integration into the national society and the market economy results in increased pressure on game species (Suárez et al., 2009) because access to markets is concomitant with access to new forms of transportation and technologies (e.g., canoe motors, guns) that improve hunters' efficiency; this seems to be the case in areas where bushmeat commercialization represents an income opportunity (Nuno et al., 2013; van Vliet et al., 2014). Conversely, other authors have advocated that increased access to markets reduces the amount of time people devote to activities which do not provide cash income – including hunting in areas without or with limited access to bushmeat markets (Gill et al., 2012; Lu, 2007). In such situations, wildlife hunting may decrease, hence easing the pressure on local game populations (Gray et al., 2015; Vasco and Sirén, 2016).

As most studies on the impact of hunting on wildlife have focused on areas where hunting is both an important livelihood activity and a source of income (e.g., Kümpel et al., 2010; Brashares et al., 2011; Coad et al., 2013), the plausibility of the second argument has largely remained untested. We address this knowledge gap by providing a quantitative assessment of hunting behaviour of a contemporary indigenous society of hunter-gatherers native to the Bolivian Amazon (the Tsimane'), who do not sell the bushmeat they hunt but nonetheless are increasingly exposed to interactions with other segments of the national Bolivian society and the market economy (Luz et al., 2015; Reyes-García et al., 2014).

The goals of this study are two-fold. First, we examine Tsimane' hunting practices and their success in terms of harvest rates and offtake species composition and discuss the potential impact of different hunting behaviours on wildlife conservation. Second, we explore how different practices relate to different levels of access to the national society (e.g., schooling) and the market economy (e.g., income from the sale of agricultural or forest products, or from wage labour). We hypothesize that, in a context where hunting is not a source of cash income, increasing access to the national society and market economy may reduce the time available for hunting which would result in lower hunting effort and, consequently, offtake.

2. Methods

2.1. Study population and area

The Tsimane' are one of the largest native indigenous societies of the Bolivian Amazon, with approximately 14,000 people scattered across 125 villages south of the Department of Beni (Reyes-García et al., 2014). We conducted research in 40 villages located in two formally titled indigenous territories (known in Bolivia as *Territorios Indígenas Originarios Campesinos* or *TIOC – Territories of Native Indigenous Peasants*), the Tsimane' TIOC and the Multiethnic TIOC, as well as in a logging concession, all lying between the foothills of the Andes to the Moxos Savannas. Villages straddle the Maniqui River, two logging roads, and the main road from San Borja to Yucumo (Fig. 1). The sampled area is mostly covered by old-growth Amazonian *terra firme* forest with a highly seasonal climate, including sporadic strong cold winds from the south during the dry season (Guèze et al., 2013; Killeen et al., 1993).

The Tsimane' territory is home to >30 game vertebrate species, yet the encounter rates of large-bodied game species are lower than the rates reported in other Amazonian hunting forest sites (Luz, 2012), a situation reported by the Tsimane' themselves (Fernández-Llamazares et al., 2015; Godoy et al., 2010). Wildlife scarcity in the Tsimane' territory results from previous overhunting and habitat lost. First, the commercialization of pelts during the 1950s–1970s led to the decrease of many game species' populations, which never fully recovered (Huanca, 2008). Tsimane' hunters participated in the commercialization of pelts mainly by helping outsiders to track animals. After this period, species like the white-lipped peccary (*Tayassu pecari*) and the black caiman (*Melanosuchus niger*) were declared extinct in some areas of the Tsimane' territory (Herrera-MacBryde et al., 2000). Second, the arrival of logging companies, cattle ranchers, and highland colonists in the last quarter of the century led to severe deforestation and forest fragmentation (Paneque-Gálvez et al., 2013), affecting wildlife populations. Furthermore, these new settlers became Tsimane' direct competitors for land and natural resources, including bushmeat (Reyes-García et al., 2012).

Nowadays, most Tsimane' continue to rely on foraging and horticulture for subsistence although the production of cash-crops (e.g., rice, plantains, maize, or manioc) –which they sell in local towns or trade to itinerant merchants– has increased (Fernández-Llamazares et al., 2016). Other sources of income include the sale or barter of woven thatch palm panes and wage labour in logging camps, cattle ranches, and on homesteads of colonist farmers (Perge and McKay, 2016). At present there is no commercial hunting reported in the area, neither for bushmeat nor for pelt trade, but subsistence hunting is still a major livelihood activity for the Tsimane'. Zycherman (2013) reports that Tsimane' men enjoy hunting, an activity that –according to reports from 24-h activity recalls– occupies on average 5% of Tsimane' men's time. Furthermore, hunting also has deep cultural meanings for the Tsimane' as excellence in hunting is still a status symbol for Tsimane' men and their families and offering wild meat continues to be a way to bond with other members of the family and neighbours (Reyes-García and Huanca, 2015). Nevertheless, recent changes (e.g., access to school, jobs outside the community) seem to be altering Tsimane' hunting patterns, largely because the Tsimane' –and specially those with schooling– are increasingly allocating more time to new economic activities (e.g., wage labour) (Luz et al., 2015).

2.2. Sampling

Data were collected between March 2009 and July 2010 in 40 Tsimane' villages (out of a total of 125). Before the onset of the study we obtained Free Prior and Informed Consent from the *Gran Consejo Tsimane'*, the political organization representing the Tsimane' in the area surveyed, as well as the agreement of each village and individual participating in the study. None of the villages refused to participate

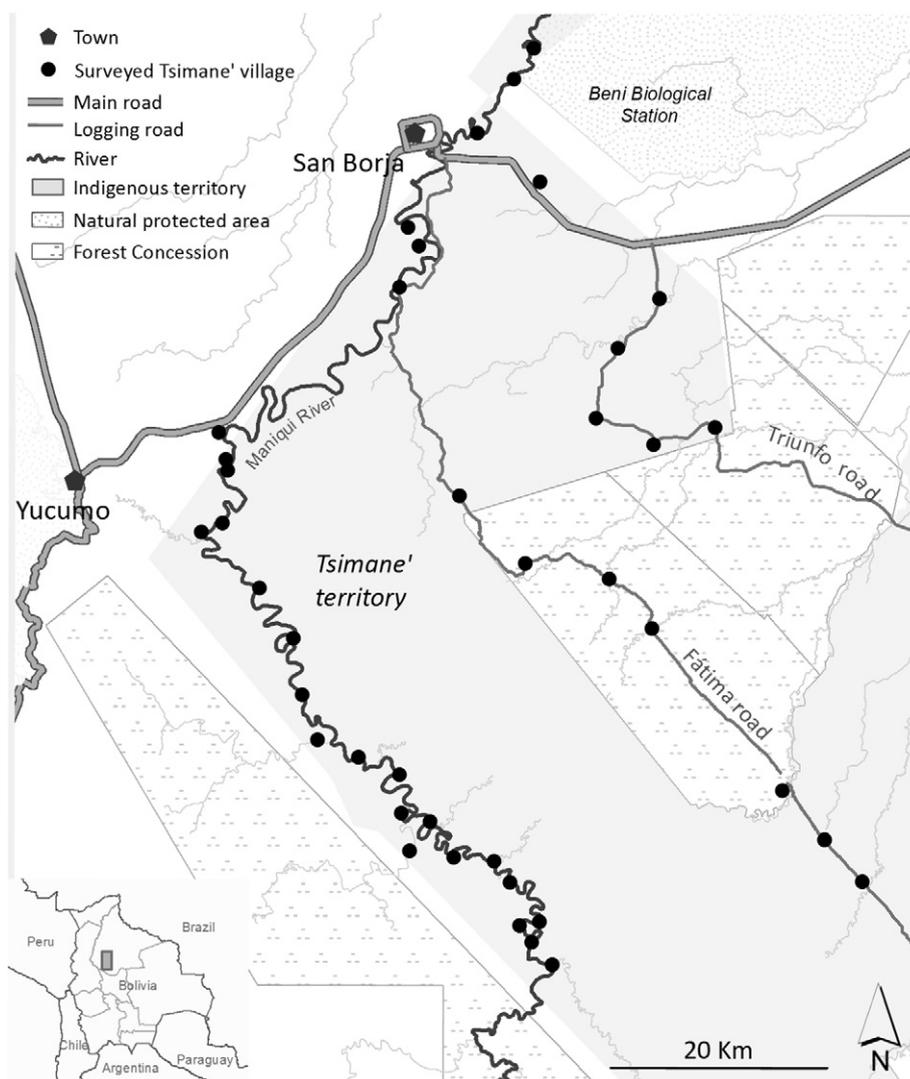


Fig. 1. Study area showing 40 Tsimane' villages where data were collected.

in the study and >95% of the hunters approached accepted to be interviewed. To select villages, we aimed at minimizing differences in villages' habitat and maximizing differences in their socio-economic characteristics. Consequently, we selected villages with 1) similar forest cover – *terra firme* rainforest and 2) similar management land tenure regimes, i.e., we included villages in indigenous territories and forest concessions, and excluded villages in protected areas and private lands, but 3) settled at different distances to the nearest market town. Within the Tsimane' territory we sampled villages in a continuum of distance to the main local town San Borja. Some villages were close to San Borja (1-hour walk) and some were far (3 canoe days). Villages also varied in size. The mean real distance of the selected villages to town was 58 km (SD = 34.81; min = 14.36 km; max = 122.87 km) and the number of households present in selected villages ranged from 3 to 95 (mean = 25.77; SD = 21.25), with household size varying from 1 to 18 members (mean = 6.07; SD = 2.92).

In each village, we randomly selected households from a list provided by the highest-ranking authority. In each household we conducted interviews with the male household head only – hereafter named hunter, because Tsimane' adult males are traditionally wild meat formal providers (Chicchon, 1992). In villages with <10 households, we interviewed all the hunters present in the village; in villages with between 10 and 40 households we interviewed 10 hunters (25%); and in villages with >40 households we selected 25% of the hunters to participate in the survey.

To capture seasonal variation in hunting, we visited 18 villages three times and 12 villages twice over the course of a year. Ten other villages were visited only once due to logistical constraints. All villages were visited during the dry season (April to November), and 12 of them were additionally visited during the rainy season (December to March). Our final survey sample includes 344 hunters, but since most hunters were interviewed more than once, the final number of observations is 1067, of which 846 were recorded during the dry season and 221 during the rainy season.

2.2.1. Hunting data

Surveys consisted in structured interviews to hunters about their hunting trips. Specifically, we asked hunters to recall their hunting trips during the two weeks prior to the day of the survey and list 1) the local name, sex, and age-class (i.e. juvenile or adult) of any vertebrate game harvested during each hunting trip reported; and 2) the number of participants involved in each hunting trip, the weapons used, and the time (in estimated hours) invested to reach the hunting location for each animal captured (i.e., the hunter's opportunity cost, in time, in tracking the preys, regardless of the direction of the trip (Sirén et al., 2013).

2.2.2. Game abundance data

To control for local game abundance in our hunting estimations, we conducted animal transect counts during the first two visits to each

village. We selected 10 two-hour transects in the vicinity of each village ($n = 400$ transects), which we sampled by walking at a slow pace (approximately 1.25 km/h) while recording information on the presence of game species. Specifically, we identified direct (i.e., calls, sightings) and indirect (i.e., tracks, faeces) signs of species presence (adapted from Carrillo et al., 2000). In each village we walked six transects in the morning (07:00–9:00 h) and four in the afternoon (17:00–19:00). To capture seasonal variation, transects were equally distributed during our first two visits. The starting point of transects was located at a minimum of 30 min walking distance from the village centre (or school), and the average transects length was 2.5 km (± 0.6). Two Tsimane' trained monitors, guided by local hunters, worked with us throughout the project. We tracked each transect and recorded the geographic location of all game observations with GPS.

2.2.3. Access to national society and the market economy data

During our first interview with a hunter, we collected information on his personal socioeconomic characteristics including: i) school level; ii) ability to speak Spanish – Bolivia's national language; iii) number of trips to the market town during the previous 12 months; iv) annual income from the sale of rice; v) annual income from the sale of thatch palm; and vi) annual income from wage labour in logging camps. We converted income data from Bolivianos (Bs) into US dollars (1US \$ = 7.1 Bs).

2.3. Data analysis

We used survey data to estimate the following variables for each hunter: i) hunting engagement, ii) hunting success, iii) hunting effort, and iv) game offtake. Individual hunting engagement was measured by the share of hunting trips made by each hunter in relation to the number of times he was enquired. Hunting success was calculated as the number of successful trips (i.e., trips in which an animal was killed) divided by the total number of trips reported. To measure hunting effort for each hunting trip – successful or not – we calculated two measures of Catch-Per-Unit-Effort (CPUE), where effort was defined as the mean walking time hunters took from the village centre to the preys killing sites. The first CPUE measure corresponds to the number of animals hunted per hour walked. The second CPUE measure corresponds to the biomass (in kg) harvested per hour walked. Both measures were calculated per hunting trip. In hunting trips with several hunters, we divided the offtake by the number of hunters involved. Biomass was calculated using published estimates of species body mass and age-class (Myers et al., 2006). Further, we also identified hunters prey profile differentiating between the number of ungulates, primates, rodents, carnivores, birds, edentates, and reptiles captured by each hunter.

To assess game abundance, we used villages transect data. Specifically, we calculated game Encounter Rates (ER) as the average number of encounters (total number of direct and indirect observations) per kilometre for two size-classes species: small- (≤ 10 kg) and medium- and large-bodied species (> 10 kg). Transects lengths were estimated with ArcGIS 9.2 using the GPS tracks recorded.

We used hierarchical cluster analysis to identify typologies of hunters according to the hunting practices reported. We used Ward's linkage method with Euclidean distances including the following variables: i) hunting engagement, ii) hunting success, iii) average hunting effort, and iv) prey profile. Individuals who did not report any hunting trip during our enquiries were excluded from this analysis. The number of groups to be retained from cluster analysis was selected using the Calinski-Harabasz criterion (Caliński and Harabasz, 2007). We then compared variables among groups using the non-parametric Kruskal–Wallis test.

To classify villages according to their game abundance, we used the same analytical technique (i.e., hierarchical cluster analysis with the Ward's linkage method with Euclidean distances and the Calinski-Harabasz criterion values to evaluate the optimal number of clusters)

and the two variables that proxy for village's game abundance (i.e., small- and large-bodied ER). We then applied a Kruskal–Wallis test to examine differences in the distribution of hunters from different typologies among the different types of villages.

To evaluate whether our proxies of access to the national society and the market economy relate to the hunting effort of the different typologies of hunters, we ran several Generalised Linear Models (GLMs). GLMs allow the use of non-normally distributed data and are recommended when the response variables are independent (Jiang, 2007). The series of GLMs we ran had a Poisson error distribution and a log link function for each hunter group and used hunting success and hunting effort clustered by hunter. Data used in the models include successful and unsuccessful hunting trips. We also ran a set of Generalised Linear Latent And Mixed Models (GLLAMMs) to test for the robustness of GLMs findings. GLLAMMs allow nesting to control whether co-variables are correlated with contextual factors (e.g., spatial distribution) represented by each level (Merlo et al., 2005). Our GLLAMMs included nesting by: 1) hunters' and villages' groups derived from hierarchical cluster analysis and by 2) hunters' groups and hunters' sampled villages. As a last step, and given that our dataset may be skewed due to the predominance of observations collected in the dry season, we repeated the analyses using only data from the dry season. All the statistical analyses were performed with STATA 11.1.

3. Results

From the 344 hunters interviewed in the 40 villages sampled, 71% reported hunting in the two weeks prior to the interview. We recorded data regarding a total of 489 hunting trips with a success rate of 85% yielding a total of 822 vertebrate animals harvested. The most commonly caught species were paca (*Cuniculus paca*), collared peccary (*Pecari tajacu*), coati (*Nasua nasua*), brown capuchin (*Sapajus apella*), red brocket deer (*Mazama americana*), spix's guan (*Penelope jacquacu*), and howler monkey (*Alouatta* spp.). These seven species accounted for 70% of the total preys hunted. Eight game species harvested are listed by the IUCN Red List of Threatened Species (IUCN, 2016) and accounted for 18% of the total game offtake. Spider monkey (*Ateles chamek*), the species of highest conservation concern listed as 'endangered', represents 2% of the preys hunted. The ungulates marsh deer (*Blastocercus dichotomus*), white-lipped peccary (*Tayassu pecari*), tapir (*Tapirus terrestris*), and the giant armadillo (*Priodontes maximusi*) and giant anteater (*Myrmecophaga tridactyla*) all appear in the category of 'vulnerable' species and accounted for 5% of the total game harvested. Collared peccary and the great tinamou (*Tinamus major*), with 11% of the total captured offtake, are listed as 'near threatened'.

Hunters mainly used shotguns or rifles (81%), but also bow and arrows (17%); <1% of the hunters went hunting with dogs or machetes only. Most hunters hunted during daytime (85%) and alone (61%). About one quarter of the hunters went accompanied by one family member or another hunter (26%), while a minority hunted in group (three to seven people) (13%). Most hunters reported having harvested adult preys (87%), and mostly males (57%) rather than females (38%). Hunters did not remember the sex of 5% of the hunted animals.

3.1. Hunters' behaviour

We identified four groups of hunters (*Groups A to D*) based on their hunting behaviour in the two weeks prior to the interviews. We found significant differences in the characteristics of all groups, including differences in the variables used to conduct the analysis (i.e., hunting engagement, hunting success, effort, and prey profile), but also in other hunting metrics (i.e., trip duration to killing site and weapon used) (Table 1).

Group A, which included 6% ($n = 14$) of the hunters, had the highest participation in hunting, the highest success rate, and high hunting yields, particularly when effort was measured in biomass harvested

Table 1

Estimates of individual hunting measures by group of hunters. Mean values and (S.D.) are presented for each variable in a sample of $n = 245$ hunters from 40 villages. Hunters who did not report any hunting trip were excluded from this analysis.

Hunting measures	Variability between groups (χ^2)	Group A	Group B	Group C	Group D	Full sample
Measures used in the hierarchical clustering						
Hunting engagement	17.44***	0.77 (0.26)	0.70 (0.26)	0.70 (0.24)	0.57 (0.25)	0.62 (0.26)
Hunting success	7.82*	0.98 (0.17)	0.94 (0.17)	0.93 (0.15)	0.82 (0.32)	0.87 (0.28)
CPUE: animals per hour walked	45.70***	0.02 (0.01)	0.03 (0.03)	0.01 (0.01)	0.01 (0.01)	0.01 (0.02)
CPUE: biomass (kg) per hour walked	37.12***	0.36 (0.25)	0.25 (0.34)	0.07 (0.11)	0.13 (0.38)	0.16 (0.35)
Other hunting measures						
Average number of animals/hunter	77.32***	2.10 (0.64)	1.91 (1.11)	1.67 (0.68)	0.88 (0.62)	1.22 (0.87)
Average biomass (kg)/hunter	33.40***	40.36 (36.70)	20.81 (20.59)	10.04 (9.66)	11.89 (15.56)	14.83 (19.08)
Distance to killing place (hours)	9.22**	2.24 (0.48)	2.73 (2.53)	3.99 (2.64)	2.62 (2.57)	2.78 (2.53)
Main weapons used (%):	14.56**					
Shotgun or rifle		80.00	78.57	83.33	76.59	78.00
Bow with arrow		20.00	17.86	16.67	21.27	20.00
Other (e.g., dog, machete)		0	3.57	0	2.12	2.00
N		14	42	28	161	245

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

per hours walked. On average, hunters from *Group A* harvested two preys per trip, which represented a total biomass of 40 kg/trip. They also reported lower trip length than hunters in the other groups (Table 1). When compared with the other groups, hunters from *Group A* captured the highest number of ungulates ($\chi^2 = 32.98$, $p \leq 0.0001$) and birds ($\chi^2 = 29.18$, $p \leq 0.0001$) per individual, targeting both large-bodied preys and very small preys (i.e., birds). Indeed, ungulates and birds composed 68% of *Group A*'s total harvest (Fig. 2). While the list of species hunted totals 83 species, the overlap of species hunted by hunters from the four groups is only of 14. Hunters from *Group A* reported harvesting 18 game species, including the largest share of collared peccary (17%) and red brocket deer (15%) across groups as well as a high percentage of spix's guans (15%) (Fig. 3). Hunters from *Group A* captured the largest share of 'vulnerable' and 'near threatened' species: 8% of the total captured offtake of *Group A* were 'vulnerable' species listed by the IUCN Red List and 21% were 'near threatened'. However, hunters from this group did not capture any spider monkey, the only 'endangered' game species present in the study area (Fig. 3). Hunters from *Group A* used shotgun or rifle in 80% of the trips and bow and arrow in 20%. None of them reported the use of dogs or machete as main weapons in a hunting trip.

Group B, comprising 17% ($n = 42$) of the hunters, was the second group in terms of hunting engagement and success rate. Similarly, to hunters in *Group A*, hunters in *Group B* presented high levels of hunting offtake and effort (Table 1). *Group B* hunters reported having harvested an average of almost two preys or about 21 kg/trip. Their prey profile

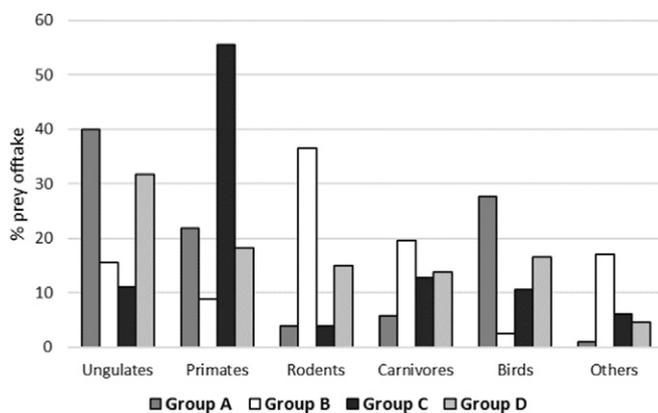


Fig. 2. Percentage of the different taxonomic classes harvested by each group of hunters (all classes presented statistically significant differences among hunter groups with $p = 0.0001$).

differs from the profile of other groups, as they mostly captured rodents (37% of the total preys), carnivores (20%) or edentates (including reptiles) (17%) (Fig. 2). Differences in groups' offtake were statistically significant for the three groups of species (i.e., rodents' $\chi^2 = 49.49$, $p < 0.001$, carnivores' $\chi^2 = 15.32$, $p < 0.001$ and edentates' ($\chi^2 = 37.07$, $p < 0.001$)). From a total of 20 different species, the species most commonly harvested by hunters in *Group B* were paca (30%), coati (13%), collared peccary (10%), and armadillos (*Dasypos* sp.) (8%) (Fig. 3). As *Group A*, hunters from this group did not capture any spider monkey. Additionally, this group had the lowest percentage of 'vulnerable' hunted game species (Fig. 3). Shotguns or rifles were used in 78% of the trips, bow and arrow in 18%, and dogs or machetes were rarely used (Table 1).

Group C included 11% ($n = 28$) of the hunters and is characterized by being the group that harvested the lowest levels of biomass (Table 1). As in *Groups A* and *B*, the average hunting offtake of hunters in *Group C* consisted of two preys; however, in contrast to *Groups A* and *B*, the average biomass hunted reached just 10 kg/trip. The prey profile for hunters from this group included mainly primates (56% of the total hunted preys) ($\chi^2 = 75.43$, $p < 0.001$) (Figs. 2 and 3). The most common preys targeted by *Group C* hunters were brown capuchin (22%), howler monkey (17%), and coati (11%). Moreover, hunters from this group had the highest records of spider monkey captured, but the lowest records of 'vulnerable' and 'near threatened' species (Fig. 3). Overall, hunters from *Group C* harvested a total of 21 different species. *Group C* hunters mostly used shotguns or rifles (Table 1).

Group D was the largest group with 66% ($n = 161$) of the hunters. This group reported the lowest level of hunting success as well as the lowest levels of hunting effort, except for CPUE biomass/h. Hunters from this group were successful in 82% of their trips, presenting a lower success rate than the hunters from the other three groups, who were successful in over 93% of hunting trips. The mean harvesting rate was below one prey/trip which represented about 12 kg/trip. *Group D* hunters walked more hours to the killing site than hunters from the other three groups, which translated into the lowest CPUE animals/h. Hunters of *Group D* targeted the widest range of species (24 species), with similar distribution of preys by taxonomic groups (Fig. 2). The most commonly harvested preys were large-bodied species such as red brocket deer (12%) and collared peccary (12%), although they also harvested smaller preys as paca (13%), coati (11%), or spix's guan (11%). Together with *Group A*, this group had the highest percentage of captured 'vulnerable' species (Fig. 3).

Our second hierarchical clustering resulted in three groups of villages which significantly differed in their game abundance (*Groups 1* to 3). *Group 1*, composed by 13 villages, displayed the lowest ER both

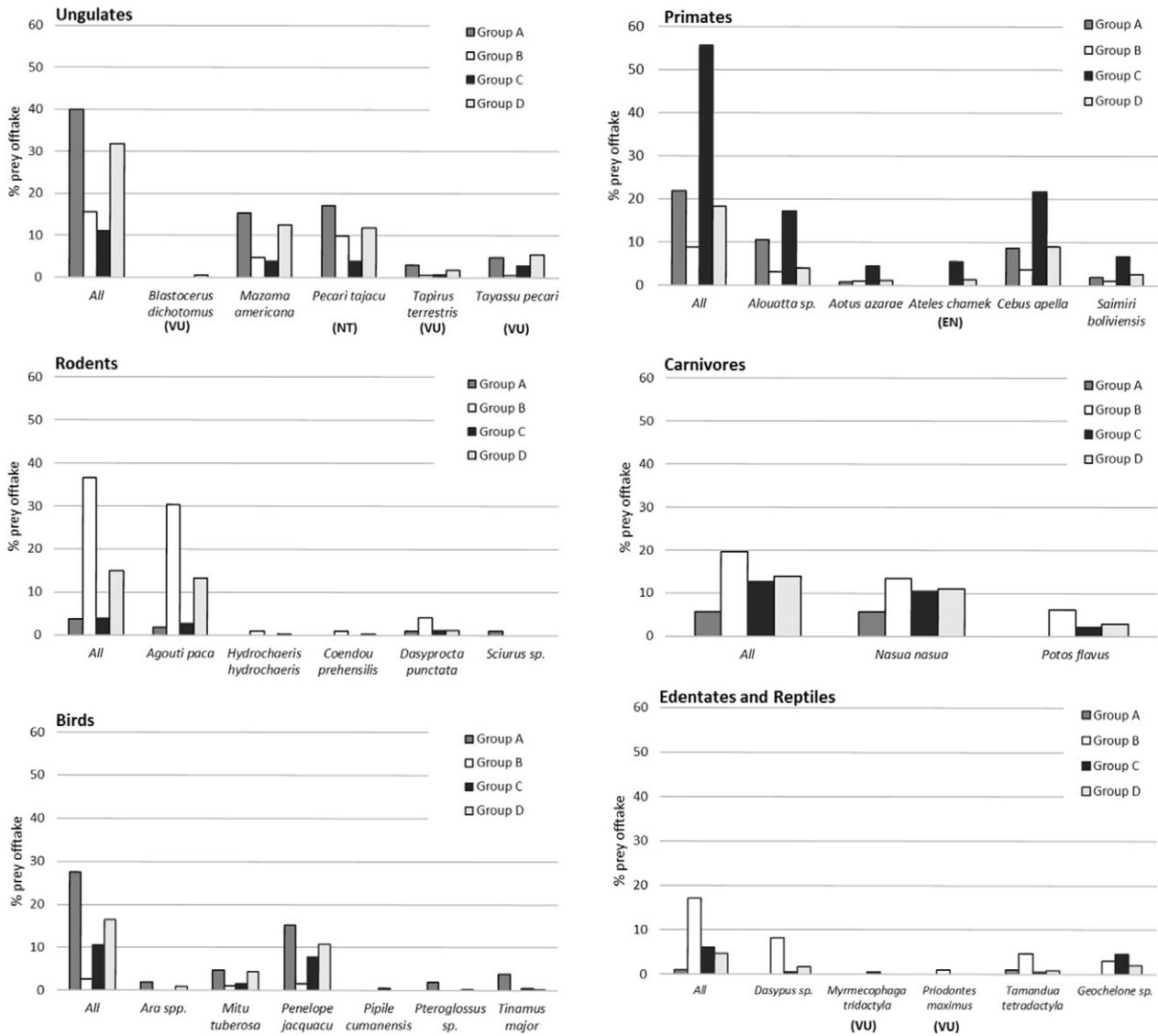


Fig. 3. Offtake percentage by species out of the total offtake recorded for each hunters' group ($n = 825$ preys). Abbreviations: EN – endangered, VU – vulnerable, and NT – near threatened species according to the IUCN Red List of Threatened Species classification (IUCN, 2016).

for small- and large-bodied game species, with the latter class having had only 1.53 individuals/km; *Group 2*, formed by 12 villages, had approximately 6 individuals/km for species ≤ 10 kg and 4 individuals/km for >10 kg; and *Group 3*, composed by 15 villages, had the highest ER for small-bodied species with an average of 8.44 individuals and intermediate values for large-bodied species (Table 2). Average village-to-town distance was lower for *Group 1*, whilst remote villages formed *Group 3*. We examined whether hunters' typologies were spread across villages with different game species abundance and found no significant differences among villages groups ($\chi^2 = 2.60$, $p = 0.27$) (Table 2). In other words, the analysis suggests that our four typologies of hunters were present in the three villages' groups in similar proportions.

3.2. Variation in hunters' strategies in relation to integration to the national society and the market economy

There were not many statistically significant differences in the socio-demographic characteristics of hunters in the different groups (Table 3). On average, *Group A* hunters were the youngest, followed by *Groups D, C* and *B*. *Group A* had also the highest percentage of individuals with

Table 2

Village characteristics and hunters distribution by villages groups created based on mean game abundance. Values correspond to means and (S.D.) for game abundance and real distance.

	Group 1	Group 2	Group 3	Full sample
Mean game abundance				
ER ≤ 10 kg	4.54 (0.83)	5.58 (1.03)	8.44 (0.86)	6.32 (1.93)
ER >10 kg	1.53 (0.67)	3.95 (1.06)	3.38 (0.72)	2.95 (1.30)
Real village distance (km)	28.19 (19.69)	62.52 (30.98)	79.84 (30.58)	57.86 (34.81)
Number of hunters	78	83	84	245
Group A (%)	2.56	6.02	8.33	5.71
Group B (%)	20.51	10.84	20.24	17.14
Group C (%)	12.82	12.05	9.52	11.43
Group D (%)	71.08	64.10	61.90	65.71
Total observations	342	332	396	1070
Dry season (%)	72.51	93.07	72.98	79.07
Rainy season (%)	27.49	6.93	27.02	20.93
Number of villages	13	12	15	40

Table 3

Socio-economic characteristics of Tsimane' with different hunters' typologies. Mean values and (S.D.) are presented for each variable in a sample of $n = 245$ hunters from 40 villages. Hunters who did not report any hunting trip were excluded.

Socio-economic measures	Variability between groups (χ^2)	Group A	Group B	Group C	Group D	Full sample
Integration to national society						
Hunters age	5.01	38.79 (15.96)	46.69 (17.54)	42.39 (13.97)	40.65 (16.05)	41.78 (16.16)
Schooling (%)	3.77***					
No schooling		71.43	59.52	39.29	46.54	49.38
Primary		14.29	26.19	57.14	44.03	40.74
Secondary		14.29	11.90	3.57	8.81	9.05
University		0	2.38	0	0.63	0.82
Spanish (%)	12.23*					
None		21.43	9.52	17.86	3.77	7.41
Some		64.29	73.81	75.00	84.91	80.66
Fluent		14.29	16.67	7.14	11.32	11.93
Integration to market						
Travels to market town	4.82	5.71 (5.99)	16.62 (18.31)	13.50 (16.69)	10.63 (12.67)	11.71 (14.20)
Annual income from rice sales (\$)	1.00	50.15 (73.64)	85.60 (183.33)	97.27 (158.85)	74.88 (119.17)	77.86 (134.70)
Annual income from thatch palms sales (\$)	6.01	151.79 (392.78)	97.69 (256.02)	38.95 (124.10)	164.26 (320.87)	137.60 (300.36)
Annual income from wage labour (\$)	10.64**	145.63 (237.41)	33.86 (86.39)	7.94 (29.14)	51.15 (147.41)	48.65 (139.18)
N		14	42	28	161	245

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

schooling in general and secondary education in particular. *Group B* hunters had the highest number of hunters with university degrees and fluent in Spanish. *Group C* had the highest average annual income from rice sales and *Group D* had the highest annual income from thatch palm sales. *Group A* hunters had an annual income from wage labour about 18 times higher than *Group C* hunters, four times higher than *Group B* hunters, and almost three times higher than *Group D* hunters. However, none of these differences, except for the annual income from wage labour ($p = 0.01$), were statistically significant.

Using GLMs with hunter's success ratio as response variable we did not find any significant association for any of the four groups of hunters' (results omitted from Table 4). However, using CPUE –in animals/h and kg/h– as outcome variables, we found several statistically significant associations, which varied from one group of hunters to another (Table 4). Thus, for *Group A* hunters age was positively associated with hunting effort, both measured as animals/h or kg/h. Hunters' age, however, was negatively associated with the number of animals harvested per hour for *Group C*. Schooling and Spanish fluency were alternatively associated

Table 4

Results from generalised linear models (GLM) of hunting effort against several socio-economic variables for the four group behavioural typologies. Mean values and (S.D.) are presented for each variable. Observations were clustered at the individual level and included 245 hunters from 40 villages.

Explanatory variables	Group A		Group B		Group C		Group D	
	CPUE, animals/h	CPUE, kg/h	CPUE, animals/h	CPUE, kg/h	CPUE, animals/h	CPUE, kg/h	CPUE, animals/h	CPUE, kg/h
Hunters age	0.19** (0.06)	1.02** (0.20)	0.03 (0.05)	0.07 (0.05)	-0.10** (0.03)	0.02 (0.08)	-0.01 (0.03)	-0.01 (0.05)
Hunters age ²	-0.00** (0.00)	-0.01** (0.00)	-0.00 (0.00)	-0.00 (0.00)	0.00* (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Schooling	-0.18** (0.05)	0.20 (0.14)	0.04 (0.06)	0.03 (0.07)	-0.33** (0.08)	-0.31 (0.21)	-0.11** (0.04)	-0.006
Spanish	0.56 (0.38)	6.59** (1.10)	0.11 (0.32)	-0.47 (0.28)	0.06 (0.14)	1.15** (0.35)	0.30 (0.22)	-0.19 (0.31)
Travels to market town	0.09 (0.06)	1.01** (0.17)	0.01 (0.01)	0.03* (0.01)	0.00 (0.01)	-0.01 (0.02)	-0.00 (0.01)	0.01 (0.01)
Log annual income from rice sales (\$)	0.05 (0.06)	-1.14** (0.18)	-0.04 (0.50)	-0.10 (0.07)	0.09* (0.04)	0.30* (0.13)	0.08* (0.04)	0.03 (0.08)
Log annual income from thatch palms sales (\$)	-0.08** (0.01)	0.16** (0.05)	0.03 (0.06)	-0.07 (0.08)	0.09** (0.02)	0.09 (0.05)	0.03 (0.03)	0.01 (0.04)
Log annual income from wage labour (\$)	-0.0105	-1.26** (0.21)	0.00 (0.05)	-0.08 (0.08)	-0.21** (0.06)	-0.64** (0.11)	0.02 (0.04)	0.10 (0.07)
Household size	0.11** (0.03)	0.40** (0.10)	-0.02 (0.04)	0.04 (0.06)	0.03 (0.02)	0.02 (0.07)	0.03 (0.05)	0.02 (0.06)
Season	0.26 (0.58)	0.78 (0.86)	-0.06 (0.30)	0.42 (0.39)	-0.01 (0.35)	0.93 (0.61)	-0.09 (0.21)	-0.35 (0.28)
ER ≤10 kg	0.23*** (0.09)	1.89** (0.35)	0.01 (0.10)	0.02 (0.11)	-0.08 (0.06)	0.16 (0.13)	0.06 (0.07)	-0.10 (0.11)
ER > 10 kg	-0.48** (0.12)	-1.35** (0.30)	0.03 (0.13)	-0.05 (0.16)	0.18* (0.09)	-0.27 (0.18)	0.21** (0.08)	0.42** (0.15)
Real village distance (km)	-0.05** (0.01)	-0.17** (0.03)	-0.01 (0.01)	0.00 (0.01)	-0.01 (0.01)	0.05 (0.01)	-0.01 (0.00)	0.00 (0.00)
Constant	-4.52** (1.60)	-26.79** (4.77)	-4.45** (1.34)	-4.6904	-2.01** (0.68)	-10.20** (2.13)	-6.00** (0.81)	-2.94 (1.56)
Observations	14	42	42	28	161	161	161	161
Log likelihood	-4.44	-37.92	-9.97	-53.5	-5.35	-24.52	-18.06	-143.51
AIC	0.56	1.64	0.36	1.01	0.36	0.73	0.13	0.62

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

with our CPUE measures for three of the four groups of hunters. Schooling had a negative association with CPUE animal/h for *Groups A, C* and *D*, whilst Spanish had a positive and statistically significant association with CPUE kg/h for *Groups A* and *C*. Economic variables showed no common patterns of association for any of the four groups. For instance, income from rice sales had a negative association with CPUE kg/h hunted by *Group A*, but a positive association with both CPUE measures for *Group C*. Moreover, the annual income provided by thatch palm sales was negatively associated with CPUE animals/h but positively associated with CPUE kg/h for *Group A*. For *Groups A* and *C* the annual income from wage labour was consistently associated in a negative and statistically significant way with both measures of hunting effort (Table 4).

When performing GLAMMs analysis as robustness tests (not shown) all the associations found in our previous analysis lost their statistical significance. In our second robustness analysis, we repeated all the previous analysis (including the hierarchical cluster analysis of the hunting groups) by using only data from the dry season. These results largely resemble results presented in Tables 1, 3 and 4 and therefore are not shown.

4. Discussion

Three main findings stem from this study. First, the Tsimane' continue to be largely dependent on subsistence hunting. Second, hunting behaviour vary across Tsimane' subsistence hunters, which might have a differential impact on local wildlife. Third, individual levels of integration into the national society and market systems are only weakly associated with hunting behaviours. Below we discuss these three findings.

Our results reveal that the Tsimane' continue to be highly dependent on the consumption of wild meat, as 71% of the hunters interviewed participated in at least one hunting trip over the two-weeks prior to the interview. This percentage seems very high considering current trends in game abundance across the study area, which is dwindling (Fernández-Llamazares et al., 2015; Godoy et al., 2010; Luz, 2012). This finding, coupled with current trends in population growth among the Tsimane' (Reyes-García et al., 2014) and in forest cover degradation across much of the study area (Paneque-Gálvez et al., 2013; Pérez-Llorente et al., 2013), evidences that both Tsimane' livelihoods and conservation of game species are increasingly vulnerable. We suggest that a key activity for the Tsimane' such as hunting should ideally become regulated by local institutions to ensure sustainability in the long term.

Our second result refers to the existence of different hunting behaviours across Tsimane' hunters. Although we could clearly identify different hunting behaviours, we could neither significantly relate them to game availability nor to individual levels of integration into the national society and the market economy. Nonetheless, these results can still be interpreted from a wildlife conservation perspective, as they help distinguish the potential impact that different types of hunters can have on wildlife populations. Hunters from *Group A* can have a severe impact on several species of high conservation concern. Despite having fewer members than other hunting groups, this group hunting offtake and effort is higher, particularly in relation to large-bodied ungulate species. Interestingly, hunters from this group had also the highest annual income from wage labour in logging camps, and a relatively high income from thatch palm sales. Previous researchers have reported that hunters in tropical forests frequently combine hunting with other extractive forest activities, either for consumption or sale, as simultaneously combining several activities in the forest reduces the time costs of gathering (Morsello et al., 2012; Parry et al., 2009). In the case of the Tsimane', hunting seems to be associated with collecting thatch palm or working on logging camps settled in old-growth forest areas, where the abundance of large-bodied mammals is usually higher (Parry et al., 2009). It is therefore plausible, that the behaviour described by *Group A* hunters is associated with the specialized extraction of forest resources for sale,

signalling one of the potential pathways through which some activities that proxy integration to the market society might also relate to hunting behaviour.

Group B hunters obtained also high hunting yields, derived mainly from harvesting pacas and coatis. However, as pacas seem to be quite resilient to hunting pressure due to high reproductive rates (Peres, 2000), it is likely that the high hunting yields reported by *Group B* hunters have a lower impact on wildlife than the specialized hunting behaviour of *Group A*.

As hunters in *Group A*, hunters in *Group C* also show a high degree of prey profile specialization, in this case targeting mainly primates. Their prey profile choice might as well be related to the hunter's economic activities. Results from bivariate analysis suggest that hunters from *Group C* had higher annual incomes from rice sales than hunters from other groups, implying that their livelihood is more dependent upon subsistence and cash-crop agriculture. As some of the primate species regularly captured by hunters from this group (e.g., brown capuchin monkey) are commonly found in secondary forests associated with scattered agricultural fields, it is possible that hunting occurs in combination with these economic activities. It is also worth mentioning that this group is also specialized in species that traditionally Tsimane' widely appreciate for their taste or recognise as having medicinal properties, such as the howler and spider monkeys (Huanca, 2008). Thus, it is also possible that the prey choice of *Group C* hunters relates to traditional cultural preferences, like in other indigenous societies (Lingard et al., 2012; Morsello et al., 2015). Although small, this group hunting behaviour may constitute a major threat for wildlife conservation, particularly for the endangered spider monkey, which is very sensitive to habitat disturbances and hunting (Link and Di Fiore, 2006).

Group D gathers the largest number of hunters. This group is characterized by the lowest levels of hunting success, a low hunting offtake but with more diversity of preys captured, including several 'vulnerable' game species. Hunters from this group have the highest level of schooling, which was negatively related to hunting effort and to the highest annual income from thatch palm sales. Schooling seems to bear a negative association with hunters proficiency, arguably because it decreases the time a person spends with skilled hunters or practices hunting, which has long-term overall effects on hunters proficiency (Luz et al., 2015). Therefore, the low hunting proficiency of *Group D* hunters might relate to a reduced time investment in hunting activities. At the same time, schooling gives them the ability to shift to new market-oriented economic activities (Reyes-García et al., 2007; Scalco and Rodrigues, 2013), which may also reduce the time investment on hunting, hunting effort and offtake (Gill et al., 2012). Further, like in *Group A*, hunting – particularly the harvest of large-bodied mammals – seems to be associated to collecting thatch palm. However, although this group shows a diverse prey profile and a lower offtake, their hunting activity can still impact vulnerable species given its large number of hunters.

Finally, we found no clear evidence of a relationship between hunting behaviour and variables that proxy for individual levels of integration into the national society and the market economy among the Tsimane'. Several studies worldwide suggest that – aside from game availability (Jerozolinski and Peres, 2003; Peres and Nascimento, 2006) – factors such as income, wealth, and household head level of education relate to the likelihood of consuming bush meat in households who primarily hunt for subsistence (e.g., Brashares et al., 2011; Foerster et al., 2012). Yet, we were not able to identify such a strong relationship. This may be related to the high dependence of Tsimane' livelihoods on forest resources, though the number of people that embrace new economic activities is growing (Reyes-García et al., 2014). In that sense, our results suggest that it might still be too early to evaluate how integration into the national society and the market system can impact wildlife in our study area.

Two main limitations may have affected our results. Ideally, to draw conclusions about the impact of the different hunting behaviours on wildlife conservation, one should rely on temporal analysis. Despite

not bringing such a diachronic perspective, our study is a first step towards understanding the significance of different hunting behaviours and possible impacts on game conservation in the Tsimane' territory. The synchronic analysis presented emphasizes the importance of understanding the possible co-occurrence of different hunting practices in societies that are rapidly changing, and elucidates about the potential effects of these changes on wildlife (Carvalho et al., 2015). Given the difficulty of assessing hunting sustainability worldwide (Shepard et al., 2010), identifying different hunting behaviours can be useful to assess the impact of hunting on different game groups. In addition, this endeavour can strengthen community awareness about the sustainability of their hunting practices and lead to improvements regarding their resource management strategies. The second limitation of this work relates to the fact that we were not able to disentangle the differential effects of the integration into the market economy and the national society in individual hunting behaviours. Although we tried to improve our estimations by controlling local game abundance and several proxies of individual integration into the market economy, hunting systems can still be highly complex making it difficult to identify common patterns (Brashares et al., 2011). Yet, we argue that game management could be more efficient with the use of guidelines that consider indigenous societies' and households' different livelihood patterns and heterogeneity. Further research should address to what extent different hunting practices are maintained or not, and their long-term effects on biodiversity conservation.

5. Conclusion

This study shows the importance of considering different hunting behaviours in an indigenous society to fully understand the diversity of hunting patterns and their differential impact on wildlife. Our results highlight the complexity of existent interacting and dynamic factors affecting hunting behaviour that can hinder the identification of general trends. We have shown that, within a large group of indigenous hunters of the Bolivian Amazon, different hunting practices coexist, potentially causing different impacts on local wildlife populations. Based on our results we argue that a small group of hunters specialized in vulnerable or endangered species, such as ungulates or primates, can have a higher negative impact on wildlife (for example through local depletion of a species), than a larger group of hunters with a less specialized prey profile.

Therefore, we posit that any effort aimed at improving conservation of game species and biodiversity in tropical forests should consider the specific impacts of different hunting behaviours on wildlife. Likewise, we argue that, in a rapidly and increasingly globalized world, understanding the links between indigenous livelihoods, their integration into the national society and the market economy is key for informing policies and drawing guidelines that are inclusive and that foster indigenous' own development pathways and biodiversity conservation. Future research and policy interventions on tropical forest conservation across indigenous territories should make a greater effort to address these issues. Indigenous peoples hold significant territorial areas world-wide, overlapping with high biodiverse regions which are places of interest to conservation (Sunderlin et al., 2005). Although there is a global recognition and effort in securing land tenure and resource rights, policies often consider indigenous peoples as a whole, disregarding differences within groups (Bennett and Sierra, 2014). Acknowledging these differences to design conservation and development policies, such as community-based management, is key to ensure wildlife populations maintenance and to strengthen the livelihood and sustainable economic development across tropical areas such as the Amazon.

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