

How Does Cultural Change Affect Indigenous Peoples' Hunting Activity? An Empirical Study Among the Tsimane' in the Bolivian Amazon

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Abstract

Wildlife hunting is an important economic activity that contributes to the subsistence of indigenous peoples and the maintenance of their cultural identity. Changes in indigenous peoples' ways of life affect the way they manage the ecosystems and resources around them, including wildlife populations. This paper explores the relationship between cultural change, or detachment from traditional culture, and hunting behaviour among the Tsimane', an indigenous group in the Bolivian Amazon. We interviewed 344 hunters in 39 villages to estimate their hunting activity and the degree of cultural change among them. We used multilevel analyses to assess the relationships between three different proxies for cultural change at the individual level (schooling, visits to a market town, and detachment from tradition), and the following two independent variables: 1) probability of engaging in hunting (i.e., hunting activity) and 2) hunting efficiency with catch per unit effort (CPUE). We found a statistically significant negative association between schooling and hunting activity. Hunting efficiency (CPUE biomass/km) was positively associated with visits to a market town, when holding other co-variates in the model constant. Other than biophysical factors, such as game abundance, hunting is also conditioned by social factors (e.g., schooling) that shape the hunters' cultural system and impel them to engage in hunting or deter them from doing so.

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INTRODUCTION

Neotropical rainforests contain much of the world's wildlife diversity; at the same time, they home to a diversity of indigenous peoples who have used and managed these ecosystems for millennia (Redford and Stearman 1993; Redford and Sanderson 2000; Toledo 2001; Sunderlin et al. 2005). The growing concern over the loss of biodiversity in these areas has led to an intense debate about the role of indigenous peoples in wildlife conservation. Several researchers have highlighted that despite the geographic overlap between indigenous territories and areas of high biodiversity (Toledo 2001; Sunderlin et al. 2005), there is not necessarily a causal relationship between the two phenomena, because wildlife conservation by indigenous peoples may not be intentional but rather a side effect of low population density, the use of traditional hunting technologies, and the lack of external markets to impel high rates of game extraction (Smith and Wishnie 2000; Hames 2007). If so, we would expect that as the traditional lifestyles of indigenous peoples change or as their populations increase, the way in which they use and manage wildlife would also change (Gross et al. 1979; Godoy et al. 2005b; Shen et al. 2012).

Among the different processes that currently affect indigenous peoples' livelihoods, cultural change has been singled out as critical (UNESCO 2008). Indigenous peoples are increasingly in contact with external actors, which causes a progressive adoption of new values and attitudes that in turn might change their world view, social organisation, and behaviour towards nature. Several studies have shown that economic development can alter indigenous peoples' livelihoods in general and their hunting patterns in particular, although the direction of the change may vary. Sometimes, economic development might result in a decrease in hunting activity due to the demands of new forms of income generation (Gill et al. 2012); in other cases, economic growth may increase hunting activity, particularly when there is a local bushmeat market (Wilkie et al. 2005; Fa et al. 2009; Godoy et al. 2010; Brashares et al. 2011). However, with the focus on economic change, there has been less research on how cultural changes relate to indigenous peoples' hunting activity.

By cultural change, we refer to the process that occurs when individuals from different cultures come into continuous contact with one another, leading to changes in the cultural patterns of either or both the groups (Thomson and Hoffmann-Goetz 2009). For example, when a minority group with a distinct cultural background, such as an indigenous society, comes into contact with mainstream or Western society, they might adopt new behaviours, beliefs, and values; they might also embrace new social institutions and technologies or even change their language (Sam and Berry 2010). Although such interaction might also result in changes in the mainstream society, as the adoption of natural medicines in the global market exemplifies (Berry 2008), the impacts of cultural contact tend to be larger on small-scale societies, which are oftentimes overruled by the dominant narrative or setting (Gross et al. 1979; Rudmin 2009). The history of the Shuar,

an indigenous group in the Ecuadorian Amazon, can illustrate this process. Between 1950 and 1980, the Shuar dramatically changed their livelihoods, not only by adopting new social and cultural settings but also by changing the way they used resources. For instance, most people began to clear land, plant pastures, and acquire cattle, much like the dominant local society (Rudel et al. 2002).

Despite the gap in the literature on hunting and cultural change, there is enough information to hypothesise that cultural change can affect the way in which indigenous peoples use natural resources by changing their livelihoods. In a study of indigenous peoples in lowland Bolivia, schooling—a standard proxy for cultural change among indigenous societies (Sternberg et al. 2001; Zent 2001)—was associated with an increase in income from wage labour (Godoy et al. 2005a), which implied changes in indigenous peoples' traditional subsistence activities. Formal education of the male household heads of five ethnic groups in the Ecuadorian Amazon has also been associated with an increase in agricultural area, mostly of cash-crops (Gray et al. 2008). Furthermore, as indigenous people change their cultural systems, they might also abandon their traditional institutions of resource management, which potentially results in a deterioration of common pool resources (Ostrom et al. 1999; Sirén 2006; Luz 2012), or there could be a decrease in indigenous peoples' traditional knowledge, which in turn, might also affect the way indigenous people use and manage natural resources and biodiversity (Reyes-García et al. 2010, 2013).

In this article, we analyse the association between cultural change and subsistence hunting among an indigenous society of the Bolivian Amazon. Hunting is an important subsistence activity for many indigenous societies and forest-dwellers around the world, both as a primary source of protein, and in some cases, also as an income source (Robinson and Redford 1991; Milner-Gulland et al. 2003; Peres and Nascimento 2006; Gavin 2007; Ohl-Schacherer et al. 2007; Endo et al. 2010; Brashares et al. 2011). However, hunting is also one of the greatest threats to biodiversity in tropical forests (Redford 1992; Peres and Palacios 2007; Wilkie et al. 2011). When hunting overtakes the limit of sustainable harvest, it causes a decrease in animal populations and can lead to the local extinction of large-bodied wildlife species (Jerozolimski and Peres 2003). Overhunting can also affect forest dynamics and composition (Stoner et al. 2007) and ultimately threaten the livelihoods of forest-dependent people (Bennett et al. 2007).

We examine how three different proxies for cultural change (schooling, visits to the closest market town, and attachment to traditional beliefs and values) relate to hunting activity. Our analysis is conducted both at the individual and village levels, as cultural change refers both to individual and supra-individual processes (Berry 2008). This multilevel approach allows for a better understanding of the pathways through which cultural change can affect hunting patterns. Specifically, we examine the association between cultural change and; 1) the probability that a person engages in hunting trips (hereafter, hunting activity) and 2) hunting efficiency measured as catch per unit effort (CPUE) while considering village co-variates.

For the empirical analysis, we use data collected in a foraging and farming society of native Amazonians in Bolivia, the Tsimane'. Hunting is a central activity for the Tsimane', contributing to their subsistence and cultural identity (Luz 2012; Zycherman 2013). In the study area, socio-economic and cultural changes have been associated with an increase in time allocated to cash-generating economic activities (Godoy et al. 2005b; Ringhofer 2010). However, hunting is not a cash-generating activity in the area as there is no bushmeat trade in the region (Chicchon 1992; Godoy et al. 2010). In such a context, we hypothesise that: 1) individuals who are less attached to their traditional culture would engage in hunting less often than individuals who are more attached to their traditional culture as individuals less attached to their traditional culture might invest more time in cash-generating activities, and 2) individuals who are less attached to traditional Tsimane' culture would present lower hunting efficiency than the individuals who are more attached to their traditional culture as those who are less attached might have poorer hunting skills or may invest less time in hunting.

MATERIALS AND METHODS

Study area

Our study was conducted in 39 villages settled in the Tsimane' indigenous territory in the municipality of San Borja, Department of Beni, Bolivia (Figure 1). The study area is in the transition between the last foothills at the Eastern Andes, the lowland rainforest, and the Moxos wet savannahs. The mean annual temperature is 25.8 °C, and the mean annual rainfall is

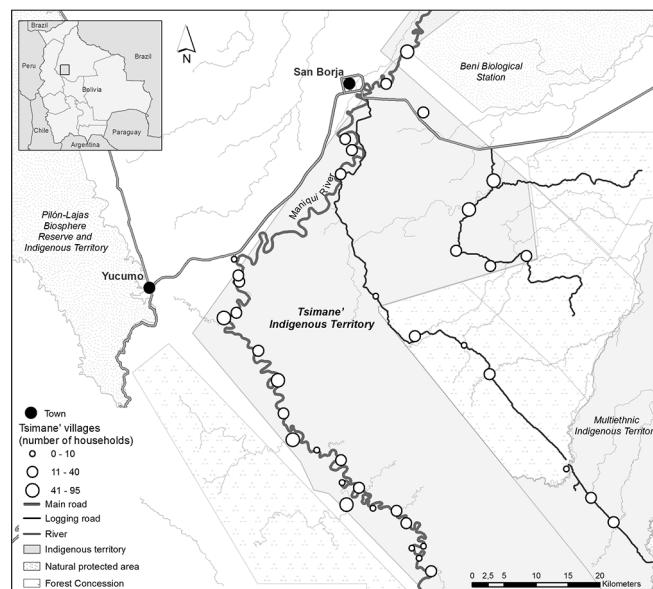


Figure 1
Distribution of the Tsimane' villages sampled along the Maniqui River and logging roads. Villages are settled in Indigenous Territory and Forest Concessions

1,743 mm, with an approximately four-month dry season with less than 100 mm rainfall per month (Guèze et al. 2013). The Tsimane' territory is covered with different types of old-growth forest. The most common type is a lowland forest lacking some typical Amazonian species due to the high seasonality of climate, including sporadic strong cold winds from the south during the dry season (Killeen et al. 1993; Guèze et al. 2013). Most forests are *terra firme* (=solid earth) forests, although some areas are covered with inundated or seasonally flooded forests due to geomorphology and highly variable topography (Killeen et al. 1993). Soils are quaternary alluvial sediments of fluvial origin, particularly Acrisols and Ferralsols (Navarro and Maldonado 2002).

The Tsimane' live in approximately 125 villages scattered along the Maniqui and Apere Rivers, the main road from Rurrenabaque to Yucumo (and to La Paz), and some villages along logging roads; the total population consists of approximately 15,000 people (Reyes-García et al. 2012a). Traditionally, semi-nomadic hunter-gatherers, who also practised small-scale slash-and-burn agriculture (Vadéz et al. 2008), the Tsimane' have maintained a distinctive cultural identity despite contacts with other sectors of the Bolivian society (Reyes-García et al. 2014a). Until the nineteenth century, they remained relatively isolated avoiding contact with the Catholic and Protestant missionaries who tried to settle them in missions (Chicchon 1992). The first significant changes in Tsimane' economic subsistence activities may have occurred during the 1930s' when cattle ranchers began to develop agricultural production in the Beni region, which relied heavily on indigenous peoples' labour (Huanca 2008). Some decades later, the development of new infrastructures (e.g., roads) facilitated the arrival and establishment of logging concessions and highland colonist farmers in the lands traditionally occupied by the Tsimane' (Reyes-García et al. 2012a). Those events brought changes to the Tsimane' socio-economic organisation. Some Tsimane' moved to more remote areas where they could continue their traditional way of life, whereas others started settling in permanent villages with schools or around working camps, progressively increasing their dependence on market-oriented economic activities. Moreover, the new situation also affected Tsimane' traditional cultural norms and values. For example, polygamous marriages were replaced by mononuclear families (Daillant 1994); some couples resisted the traditional practice of cross-cousin marriage; hierarchical structures became more accepted in a previously egalitarian organisation; and in a few villages, Christian ceremonies replaced animistic beliefs (Reyes-García et al. 2014a). Yet for most Tsimane', the most important changes have occurred in the last two decades, during which time the Bolivian national government has made a great effort to reach indigenous populations. For the Tsimane', such effort has resulted in changes in the schooling system, now with a Spanish curriculum taught by non-local teachers, and in subsidies for education and health, which impel the Tsimane' to regularly visit the local towns to benefit from them, and in

the construction of basic service infrastructures in Tsimane' villages. Altogether, such changes have intensified Tsimane' exposure to the national society (Reyes-García et al. 2014a, b).

At present, there is a large socio-economic differentiation between villages and even among people living in the same village. Some Tsimane' continue to live in small villages (with two to 10 households) without schools. Those Tsimane' are mostly monolingual, speaking the Tsimane' language. They forage and practice small-scale slash-and-burn agriculture, and have limited contact with outsiders through the barter of rice, and thatch palm for salt, sugar and some tools. Those Tsimane' still practice hunting and fishing with bow and arrow, and hold to some hunting traditions and rituals (Huanca 2008). Other Tsimane' live in large (10 to 50 or more households), more accessible, permanent villages with schools. They typically speak Spanish and have more access to cash income from the sale of crops (usually rice, manioc or bananas), forest products (especially thatch palm), and wage labour in logging camps, cattle ranches, and in colonist farmers' homesteads (Vadez et al. 2008). In these villages, people usually hunt with guns and rifles and no longer hold traditional Tsimane' beliefs and taboos (Luz 2012). Such socio-economic variation within the Tsimane' society offers a unique opportunity to evaluate the association between different levels of cultural change and hunting activities.

Sampling

Fieldwork was conducted between March 2008 and July 2010. We selected the study villages according to the following two criteria: 1) we collected data in only villages settled in *terra firme* forest to minimise variations in wildlife abundance due to the effects of different habitats; and 2) we selected villages of varying distances to the major town of San Borja to increase variation in our explanatory variable, cultural change. Our selection was based on a prior census in the study area (Reyes-García et al. 2012a). This study is part of a larger project on participatory mapping (Reyes-García et al. 2012b). The sizes of the villages we visited ranged from three to 95 households, with an average of 26.2 households (SD=21.36). To maximise the number of villages we could visit, we limited the number of interviews conducted in each village. In villages with 10 or less households (n=8), we interviewed each male household head (hereafter hunters) present in the community at the time of the visit (n=43 hunters). We interviewed the male household heads because they have traditionally been the main providers of wild meat for the entire household (Chicchon 1992). In villages with 11 to 40 households (n=22), we randomly selected 10 hunters to interview (n=193), and in villages with more than 40 households (n=9), we interviewed a 25% sample of the households (n=108). Although this approach tries to equal the proportion of enquiries among villages, we are aware that it might cause slight under-sampling in smaller villages, if some informants were absent. In other words, sampling in smaller villages is dependent of village size and/or presence of hunters during our visits, whilst in larger villages,

the sample size established can always be fulfilled due to the high number of households available for the survey. We tried to visit each village two to three times to capture seasonal variation in hunting reports; eight villages were visited twice, and nine villages were visited three times. However, due to the high mobility of the population, not all hunters interviewed during our first visit could be contacted on the follow-up visits. In sum, 20% of the hunters were interviewed three times, 32% of the hunters twice, and 48% were interviewed only once.

Assessing hunting activity

To estimate wildlife harvesting, we asked hunters about their hunting trips during the two weeks before the day of the interview. We tested different recall periods of hunting trips and observed that longer recalls provide flawed data. We asked about the characteristics of the hunting trips (duration, number of people participating, and the weapons used) and about the animals caught. For each kill, the following information was recorded: species' Tsimane' name, age class (juvenile or adult), sex (male or female), and estimated distance from the village centre to the hunting site (in hours walking). We repeated the same interview questions in the follow-up visits. To evaluate hunting activity, we first created a binary variable that reflects the inter-individual variation between hunters who participated in at least one hunting trip and hunters who did not participate in any. For each successful hunting trip, we estimated two measures of CPUE, in which, effort was defined as the total number of kilometres walked by the hunter during the trip. Distance was calculated by converting the hours spent walking to kilometres at an average rate of 2.26 km per hour (Chicchon 1992). The first CPUE measure was the number of animals hunted per kilometre walked. The second CPUE measure was the biomass harvested per kilometre walked. Biomass was calculated by using published estimates of species body mass per sex and age class (Myers et al. 2006).

Assessing game abundance

As hunting is largely dependent on local game abundance (Jerozolimski and Peres 2003; Peres and Nascimento 2006), we controlled for game abundance in our estimations. We assessed game abundance by transects. Specifically, we walked at a slow pace (approximately 1 km/hour) over 10 transects of two hours each in the vicinity of each village (n=390 transects) (adapted from Carrillo et al. 2000). The total distance covered by the transects was 987 km. Transects were set on the 10 most common hunting paths in old-growth forests in the villages' territories, with the onset at a minimum of 30 minutes walking distance from the village centre (or school). We opted for this methodology rather than using the usual line-transects approach (Peres 1999) to increase the sample size because our visits to the villages were limited to four days on average. In each village, we surveyed six hunting paths during the morning (0700-0900 hours) and four during the evening (1700-1900 hours). To capture seasonal variation

in game availability, we distributed transects equally during our first two visits, roughly corresponding to the dry and the rainy season. Two Tsimane' trained monitors, guided by local hunters, walked along hunting trails to record information on the presence of game species. Game encounters were identified, noting the Tsimane' name and the detection conditions. Tracks and other indirect signs (e.g., calls and faeces, etc.) were also recorded. We worked with the same two monitors throughout the project. We tracked each transect and recorded the geographic location of all game observations with GPS. Species observations were grouped into two size classes, taking into account their body size distribution—small species (≥ 10 kg), and medium and large-bodied species (< 10 kg). Thus, for each village, we calculated the encounter rate (ER) or the average number of encounters (total number of direct and indirect observations) per kilometre for both the species size classes). The lengths of the transects were estimated using the GPS tracks using ArcGIS 9.2 (ESRI, Redlands, California). We took into account only individual observations, which, most likely underestimated the presence of group-living species such as primates.

Assessing individual levels of cultural change

We used the following three proxies for individual levels of cultural change: 1) schooling, 2) visits to the closest market town, and 3) attachment to traditional beliefs and values (Gross et al. 1979; Sternberg et al. 2001; Reyes-García et al. 2014b). We asked informants to report the maximum grade they had completed in school and to recall the number of trips made to the nearest market town during the month before the

interview. Although the number of visits to a market town has been used as a proxy for integration into the market economy (Godoy et al. 2005b), it is also associated with the acquisition of modern human capital in indigenous societies (Morsello and Ruiz-Mallén 2013). We examined individual attachment to traditional Tsimane' values and beliefs by using a structured questionnaire on eight salient topics in traditional Tsimane' culture. We did not focus exclusively on the hunting belief system to capture a full spectrum of the cultural heritage. Questions addressed the Tsimane' traditional belief system regarding their main subsistence practices and kinship (Huancá 2008; Reyes-García et al. 2014b). For example, we asked about preferences for medicinal plants or pharmaceutical drugs or for subsistence agriculture or wage labour (Table S1). Respondents indicated their level of attachment to each topic using a visual aid, depicting a ladder with five steps. The ladder had one scene at each end, one representing a 'traditional' Tsimane' and the other a 'modern' Tsimane' (Figure S1). Answers were added to create a variable—detachment from tradition—for which, higher values indicate more closeness or the assimilation of new beliefs and values (for further details on the construction of this variable, see Reyes-García et al. 2014b).

Data analysis

We performed a reliability analysis using Cronbach's Alpha (Cronbach and Shavelson 2004) to determine the internal consistency of our three proxies for cultural variation. Moreover, before evaluating the association between our measures of hunting activity, hunting efficiency and the explanatory variables, we assessed potential overlap by

Table S1

Questions used to construct the cultural change proxy detachment from tradition. Questions were designed to capture individual variance among respondents on their traditional belief system centred on the ethnographic information collected by Huancá (2008). Respondents rated each question on a scale of 0 (attached to traditional Tsimane' cultural value) to 4 (detached from traditional Tsimane' cultural value) based on the presentation of the figure included in SMII (for further details on the construction and application of this variable see Reyes-García et al. 2014b).

Question	Description
1	Elders in upriver villages work a lot in their agricultural fields, but the Tsimane' living in the town prefer working for loggers and do not so much in their fields. How important is it for you to work in the fields? Where would you put yourself on the ladder?
2	For elders in upriver villages, it is important that their children marry their cross-cousin. For the Tsimane' living in town, it is not important that their children marry their cross-cousin. How important is it for you that your children marry their cross-cousin? Where would you put yourself on the ladder?
3	Elders in upriver villages like to fish communally with plant poison (barbasco), but Tsimane' living in town rarely fish communally with plant poison. How important is it for you to fish communally with plant poison? Where would you put yourself on the ladder?
4	When the elders in upriver villages plant manioc, they do not touch their hair to ensure the good growth of the plant, but Tsimane' living in town do not follow this custom. How important is it for you to follow this custom? Where would you put yourself on the ladder?
5	When elders in upriver villages get sick, they cure themselves with plants, but when the Tsimane' living in town get sick, they cure themselves with drugs from the pharmacy. Do you prefer to cure yourself with plants or with drugs? Where would you put yourself on the ladder?
6	For elders in upriver villages, it is important to share väij (<i>Bactris</i> sp. fruits), but the Tsimane' living in town rarely share väij. How important is it to share väij to you? Where would you put yourself on the ladder?
7	Elders in upriver villages think that if their bow breaks, they will have bad luck, but the Tsimane' living in town do not believe a broken bow brings bad luck. Do you think when your bow breaks something bad is going to happen to you? Where would you put yourself on the ladder?
8	Elders in upriver villages ask for permission to the spirit of large trees before cutting down a tree, but the Tsimane' living in town do not think it is important to ask for permission to the spirit of a tree before cutting it down. How important is it for you to ask permission to the tree spirit before cutting down a tree? Where would you put yourself on the ladder?

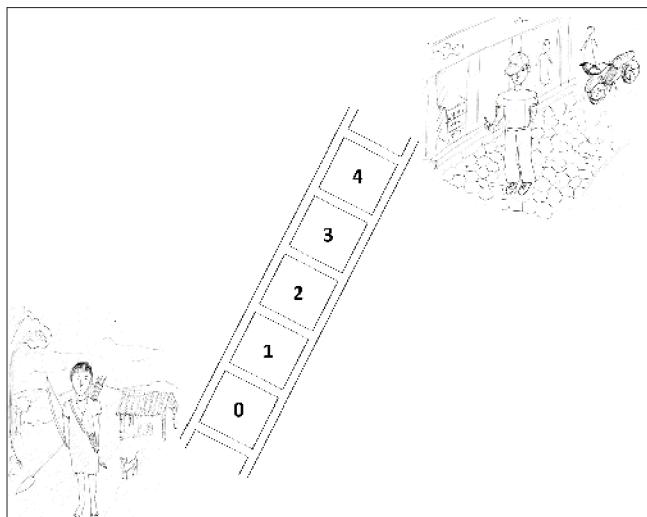


Figure S1

Ladder with five steps to estimate hunter's level of attachment to traditional Tsimane' values and beliefs. Hunters had to indicate if they were more familiar with the scene of a "traditional" Tsimane', a "modern" Tsimane', or something in between

running a series of Spearman correlations of the predictors of hunting activity at the individual and village levels. Because Spearman correlations are not suitable to estimate correlations between ordinal and binary variables, we ran linear regressions to estimate associations between the presence of the binary school variable and the other predictors of hunting activity. To explore the relationship between hunting activity and cultural change, we first ran a generalised linear latent and mixed model (GLLAMM) with a binomial family and Probit link function, using the binary variable that captures hunting activity as the outcome variable and our three proxies for cultural change as the main explanatory variables while controlling for game abundance. GLLAMM is a multilevel model that accounts for variable nesting by determining whether the co-variates are correlated with the contextual factors represented by each level (Merlo et al. 2005). In our specific analysis, we included nesting by individuals and by villages. Nesting by individuals relaxes the assumption that several observations from the same individual (e.g., during hunting trips) are independent. Nesting by villages relaxes the assumption that observations from individuals in the same village are independent as they might be conditioned by fixed-effect factors (i.e., village size or village accessibility). Random-effects are accounted in GLAMMs via introducing different levels into the model. The model included individual and village-level controls for a hunter's age (and age squared to control for possible non-linearity), household size, household income (in logarithms), average number of firearms per household, game ERs, and hunting season. Second, we examined the association between an individual's hunting efficiency, measured in CPUE in animals/km and in biomass/km, and his level of detachment from traditional culture while controlling for game abundance. To do so, we ran GLLAMMs: 1) with Poisson-distributed error terms and a logarithmical link function when analysing

CPUE in animals/km; and 2) with Gaussian-distributed error terms and an identity link function when using biomass/km. For these models, we included only observations, in which hunters reported hunting activity. Once again, we treated each hunting trip as an independent observation. Multicollinearity was checked using variance inflation factors (VIFs), which supports modelling adequacy. Except for age and age square (~38), all VIFs were <2.4 , which is below the diagnostic cut-off of 10. We included age and age square because it is known that hunting efficiency improves up to a certain age and then lessens (Gurven et al. 2006). We tested the robustness of our models by running all the prior analyses with only one of the proxies for cultural change. In this way, we controlled for the individual effect of each proxy in our outcome variables. Statistical analyses were conducted using Stata 11.1 (Stata, College Station, TX).

RESULTS

Hunting activity

Of the 344 hunters interviewed, 237 (69%) went on a hunting trip at least once during the study period. In total, we recorded 469 hunting trips, of which 398 (85%) were successful; in other words, in 85% of the cases, hunters reported game kills. Overall, 80% of the hunts lasted one day or less, whereas the remaining 20% lasted from two to nine days. In 62% of these trips, the interviewees went alone. The reported kills were mostly performed with firearms: 60% with shotguns, 21% with rifles, and just 18% with bow and arrows. Only approximately 1% of the kills were performed exclusively with dogs or machetes. On average, hunters walked almost three hours to the kill site, with a maximum estimated distance of 14 hours, corresponding to hunting incursions lasting several days. Almost 60% of the kills occurred within a range of ten minutes to three hours walking from the village centre, with only 8% of the kills occurring at a distance of more than five hours walking.

A total of 30 animal species were hunted, of which, the seven most hunted comprised 70% of all the kills (Table 1). Approximately 2% of the kills corresponded to the harvest of tapir, although this species provided the highest contribution in terms of biomass (27.5% of a total of 10,708 kg during the study period). Paca, which was the most commonly hunted species in terms of numbers, contributed only 7.9% of the total biomass. The white-lipped peccary, a vulnerable species according to the IUCN Red List (IUCN 2010), was among the ten most hunted species and represented approximately 4% of the animals killed (Table 1). Together, giant armadillo and giant anteater, also vulnerable species, represented less than 2% of the total harvests. Spider monkey, an endangered species, represented 1.5% of the total animals killed.

Considering all the hunting trips recorded (successful and unsuccessful), hunters caught an average of 1.7 (SD=1.36) animals per trip. In approximately 41% of the trips, hunters captured just one animal, and they captured three to six animals in only 10% of the trips. Unsuccessful hunting

Table 1

Number, percentage and total biomass of the animals harvested during 398 successful hunting trips with the corresponding IUCN Red List status

Vertebrate species	English common name	IUCN conservation status*	Number of killed animals	Percent of the number of killed animals	Total biomass harvested (kg)
Ungulates					
<i>Pecari tajacu</i>	Collared peccary	LC	88	11.10	1748.80
<i>Mazama americana</i>	Red brocket deer	DD	69	8.70	2817
<i>Tayassu pecari</i>	White-lipped peccary	NT	30	3.78	660
<i>Tapirus terrestris</i>	Tapir	VU	13	1.64	2950
Rodents					
<i>Agouti paca</i>	Paca	LC	103	12.99	843
<i>Dasyprocta punctata</i>	Agouti	LC	14	1.77	29.15
Primates					
<i>Cebus apella</i>	Brown capuchin	LC	84	10.59	205.50
<i>Alouatta spp.</i>	Howler monkey	-	53	6.68	342.50
<i>Aotus azarae</i>	Azara's night monkey	LC	14	1.77	16.59
<i>Saimiri boliviensis</i>	Squirrel monkey	LC	25	3.15	15.40
<i>Ateles chamek</i>	Spider monkey	EN	12	1.51	72
Edentates					
<i>Tamandua tetradactyla</i>	Collared anteater	LC	13	1.64	55.80
<i>Dasyurus sp.</i>	Armadillos	-	19	2.40	57
Carnivores					
<i>Nasua nasua</i>	Coati	LC	90	11.35	392.50
<i>Potos flavus</i>	Honey bear	LC	25	3.15	73
Cracids					
<i>Penelope jacquacu</i>	Spix's guan	LC	69	8.70	88.32
<i>Mitu tuberosa</i>	Razor-billed curassow	LC	25	3.15	76.50
Tinamus					
<i>Tinamus major</i>	Great tinamou	LC	6	0.76	6.18
Reptiles					
<i>Geochelone sp.</i>	Tortoise	-	22	2.77	139

Notes: N=793 animals recorded. Species with less than five records were excluded from these lists. *IUCN Red List categories: least concern (LC), near threatened (NT), vulnerable (VU), endangered species (EN), and data deficient (DD). Source: IUCN 2010

represented 15% of the trips. The average biomass harvested per hunting trip was 23 kg (SD=46.6). Only 3% of the trips resulted in a harvest of 100 kg or more, and these cases involved the hunting of a tapir, an incursion of several days with many captures, or both.

Game abundance

On average, we walked 2.54 km (SD=1.08) per transect. We identified a total of 26 game species, but only three—paca, agouti, and brocket deer—were observed in all the villages sampled. The mean encounter rates were higher for small-bodied game species than for medium and large-bodied vertebrates (Table 2). Overall, paca, brocket deer, and collared peccary were the most frequently encountered terrestrial mammals. The white-lipped peccary was recorded in only four villages, whereas the tapir was present in 24. Not a single specimen of spider monkey was recorded during the transect surveys.

Cultural change

The average level of schooling was low (1.9 years) (Table 2); 45% of the hunters had never attended school, 35% had completed between one and three grades, and only 2% had

completed high school. On average, Tsimane' hunters visited the market town about once a month. However, 9% of the hunters reported between two and seven visits per month. On a scale from zero to 32, the average score in our detachment index was 8.64; approximately 62% of the hunters were above this average, which suggests that most hunters have abandoned traditional practices. Nevertheless, the standard deviation was fairly high (SD=6.69), suggesting variation in the hunters' levels of cultural detachment from tradition. The Cronbach's Alpha coefficient for our three proxies for cultural variation was 0.56, indicating that each of these variables captures different aspects of the process of cultural change. In other words, these results suggest that our three one-dimensional proxies are associated with different aspects of the multi-sociocultural dimensions of an individual, providing different pathways of the complex process that is cultural change.

The relationship between hunting activity and cultural change

At the individual level, schooling was positively correlated with visits to the market town ($p<0.01$) and negatively correlated with age ($p<0.01$) (Table 3). Travel to the market town was positively correlated with household income

Table 2
Definition and descriptive statistics of variables used in the regressions

Variable	Description	N	Mean	SD	Min	Max
Hunting activity (dependent variables)						
Hunting activity	Dummy variable distinguishing between observations when hunters went in at least one hunting trip during the two weeks previous to the interview (=1) from observations without hunting activity (=0)	1002	0.47	0.5	0	1
CPUE, animals/km	Catch per unit effort estimated as the number of animals caught per kilometre walked	469	0.02	0.02	0	0.13
CPUE, biomass/km	Catch per unit effort estimated as the biomass (kg) of animals caught per kilometre walked	469	0.19	0.39	0	4.55
Cultural change (explanatory variables)						
Schooling	Maximum school grade attained (ranges from 0 to 13)	344	1.94	2.7	0	13
Visits to market	Number of monthly travels to the market-town	344	1.1	1.25	0	7
Detachment from tradition	Total score from eight questions about cultural orientation (from 0 to 32, where lower numbers indicate more closeness to traditional Tsimane' values)	344	8.64	5.69	0	32
Control variables						
Age	Hunter's age, in years	344	42.38	16.82	17	87
Household size	Number of people living in the household	344	6.1	2.94	1	18
Household income	Household income from the sale of rice since last year harvest, in US dollars	344	72.39	124.25	0	1166
Guns per household	Number of shotguns and rifles available in the village divided by the number of households	39	0.66	0.27	0.29	1.53
Village school	Dummy variable that captures the presence of a school at the village (no school=0; school established and active=1)	39	0.79	0.41	0	1
Village size	Number of households	39	26.2	21.36	3	95
Village distance	Real village distance to the nearest market-town (km)	39	56.28	33.79	14.37	122.88
ER game <10 kg	Mean encounter rate per kilometre for small-bodied (<10 kg) game vertebrates, from direct observations and indirect signs in 10 transects per village	39	6.30	1.95	3.16	10.33
ER game ≥10 kg	Mean encounter rate per kilometre for medium and large-bodied (≥10 kg) game vertebrates, from direct observations and indirect signs in 10 transects per village	39	2.96	1.3	0.34	5.38
Season	Dummy variable that captures the season in which the survey was conducted (rainy season=0; dry season=1)	1002	0.79	0.4	0	1

($p<0.01$). Detachment from tradition was also positively correlated with household income ($p<0.01$), although the correlation coefficient was low. At the village level, most variables were correlated (Table 3). Village-level variables that were not correlated were an ER game ≥ 10 kg, the presence of school and the average number of firearms per household, and these variables were not correlated among each other. As village school, village size, and village distance to the nearest market town were highly correlated with other variables, we excluded them from the GLLAMMs.

In the multivariate analysis, we found a strong negative association between the probability that a person engaged in hunting and his level of schooling (Table 4, model 1). The probabilities of Tsimane' hunters engaging in hunting within two weeks decreased with each additional school year completed, holding other variables in the model constant. The estimated coefficient indicates a probability of decrease of the hunting activity of 0.85% in a two-week period, or the equivalent of a decrease in 22% of the hunting activity per year of school attended. Our two other proxies for

cultural change, travel to the market town and detachment from tradition, also bear a negative association with hunting activity, but this association was not statistically significant. Regarding control variables, the game encounter rate for species ≥ 10 kg was significantly related to hunting activity and hunting season. Finally, our model indicates that random-effects variation among villages was higher than variation variance among individuals, suggesting that an unobserved village heterogeneity accounts for a large share of the variation in the model. The overall goodness of the model was: 1) log-likelihood = -624.35, and 2) AIC = 1,276 (Table 4).

When evaluating the correlates of CPUE in animals/km, we did not find any statistically significant association, either with our proxies for individual cultural change, with game encounter rate, or with any of the other control variables (Table 4, model 2). Individual and village random-effect variance was very low in model 2. In contrast, CPUE in biomass/km was negatively correlated with travel to the market town (Table 4, model 3). Schooling and detachment from tradition showed no significant relationship with CPUE in biomass/km. Regarding control

Table 3
Correlation coefficients r (with corresponding p values) of predictors of hunting activity at the individual and village levels

	Schooling	Travels to town	Detachment from tradition	Age	Household size	Household income	Guns per household	Village school	Village size	Village distance	ER game <10 kg	ER game ≥10 kg
Individual level (n=344)												
Schooling	1.00											
Travels to town	0.19 (<0.01)	1.00										
Detachment from tradition	0.01 (0.80)	0.06 (0.27)	1.00									
Age	-0.38 (<0.01)	0.04 (0.45)	-0.05 (0.39)	1.00								
Household size	-0.01 (0.91)	0.01 (0.86)	-0.03 (0.64)	0.17 (<0.01)	1.00							
Household income	0.08 (0.12)	0.42 (<0.01)	0.18 (<0.01)	0.11 (0.04)	0.03 (0.57)	1.00						
Village level (n=39)												
Guns per household							1.00					
Village school							-0.02 (0.94)	1.00				
Village size							-0.36 (0.03)	0.66 (0.01)	1.00			
Village distance							0.39 (0.01)	-0.19 (<0.01)	-0.53 (<0.01)	1.00		
ER game <10 kg							0.34 (0.03)	-0.20 (<0.01)	-0.37 (0.02)	0.58 (<0.01)	1.00	
ER game ≥10 kg							0.25 (0.13)	-0.01 (0.39)	-0.39 (0.01)	0.49 (<0.01)	0.40 (0.01)	1.00

variables, none of the variables selected in our model were significantly associated with CPUE in biomass/km. Finally, individual and village variances were both very low, with a higher variance being found at the individual level, which may suggest that overall, higher levels of CPUE in biomass/km are related to lower individual levels of schooling.

To test the robustness of our findings, we ran the same regression models presented in Table 4 using only one explanatory variable at a time (not shown). We found essentially the same results, namely, a statistically significant association between schooling and hunting activity, and between travel to the market town and CPUE in biomass/km, but no statistically significant association between any of our three proxies for cultural change and CPUE in animals/km.

DISCUSSION

The main result from our work is that variables that proxy individual levels of cultural change help explain engagement in hunting, even after controlling for village game abundance. Specifically, we found that schooling had a strong negative association with hunting activity, i.e., men with higher levels of formal education tend to engage less often in hunting than men with lower levels of schooling, suggesting an abandonment of subsistence hunting. Contrarily, the other two proxies used for cultural change, visits to the market town and detachment from tradition, did not seem to be associated in a statistically significant way with the probability of a man engaging in

hunting. Regarding hunting efficiency, our results indicate a positive association between travel to the market town and CPUE in biomass/km, suggesting that hunters who travel often to the market town have higher yields in terms of biomass/km. Below we discuss these two main findings.

How might schooling affect hunting activity? We advance two non-excluding potential explanations. Our first explanation relates to the potential increase in the participation in alternative economic activities that comes with schooling. Schooling allows indigenous populations to acquire new skills that might fundamentally change their behaviours, beliefs, and roles in society. In such a way, schooling provides indigenous peoples the endowments of human capital that allow them to enter modern occupations or compete for employment in the formal labour market (Godoy et al. 2005a). In highly autarchic societies such as the Tsimane', even low levels of schooling allow people to shift to new economic activities (Reyes-García et al. 2007), progressively abandoning their traditional livelihoods (Scalco and Rodrigues 2013). Thus, the ability to shift to new economic activities facilitated by schooling might explain why Tsimane' with some formal education reduce their time investments in traditional activities such as hunting. A similar result was found in a study in Equatorial Guinea (Gill et al. 2012), where a decrease in hunting seemed to be associated with employment or the desire to earn income through other activities. Although our finding dovetails with the result from that study, it also advances our knowledge of a potential correlation between subsistence hunting and cultural change.

Table 4

Results from two-level Generalised Linear Latent And Mixed Models (GLLAMM) of hunting activity and hunting efficiency against individual levels of cultural change (clustered at the individual level - n=344 hunters and at the village level - 39 villages)

	Hunting activity		Hunting efficiency			
	Model 1 ^a		Model 2 ^b		Model 3 ^c	
	Hunting (1)/No hunting (0)		CPUE in animals/km		CPUE in biomass/km	
	Coefficient ^d	p	Coefficient ^d	p	Coefficient ^d	p
Cultural change						
Schooling	-0.16 (0.04)	<0.01	-0.01 (0.04)	0.81	-0.41 (0.27)	0.12
Visits to market	-0.06 (0.09)	0.52	0.13 (0.07)	0.08	1.20 (0.57)	0.04
Detachment from tradition	-0.02 (0.02)	0.22	0.01 (0.02)	0.73	0.19 (0.11)	0.07
Control variables						
Individual level predictors						
Age	0.02 (0.03)	0.47	-0.02 (0.03)	0.57	-0.13 (0.19)	0.49
Age ²	-0.00 (0.00)	0.33	0.00 (0.00)	0.54	0.00 (0.00)	0.56
Household size	0.05 (0.03)	0.11	0.01 (0.03)	0.74	0.11 (0.18)	0.55
Household income	0.06 (0.04)	0.16	0.01 (0.04)	0.82	-0.38 (0.26)	0.14
Village level predictors						
Guns per household	0.90 (0.66)	0.17	0.49 (0.28)	0.11	0.41 (1.90)	0.82
ER game <10 kg	-0.14 (0.10)	0.17	-0.07 (0.06)	0.29	-0.32 (0.40)	0.41
ER game ≥10 kg	0.34 (0.15)	0.02	0.02 (0.07)	0.82	0.76 (0.48)	0.11
Season	-0.39 (0.20)	0.05	0.01 (0.20)	0.96	0.77 (1.35)	0.65
Constant	-0.75 (0.97)	0.44	-0.78 (0.70)	0.34	5.37 (4.88)	0.26
Random effects						
Individual level-variance (and covariance)	0.10 (0.15)		4.97e-25 (4.69e-13)		1.15e-07 (0.00)	
Village level-variance (and covariance)	0.73 (0.29)		3.90e-21 (1.37e-11)		7.72e-07 (0.00)	
Observations	1002		469		469	
Log likelihood	-624.35		-348.60		-1761.35	
AIC	1276.71		3553.83		3554.68	

Notes: ^aGLLAMM with binomial family and logit link function, include clustering by individuals and village. ^bGLLAMM with Poisson family and logarithmic link function, include clustering by individuals and village. ^cGLLAMM with Gaussian family and identity link function, include clustering by individuals and village.

^dRobust standard errors in parenthesis

Our second explanation relates to individual time investments. Several researchers have highlighted that engaging in schooling can undermine traditional culture as time and resources invested in schooling detract from time and resources invested in learning traditional activities (Sternberg et al. 2001; Zent 2001; Voeks and Leony 2004). This might be particularly true for learning complex skills such as hunting. For instance, a study among the Tsimane' suggests that even for males who have not attended school, hunting knowledge and skills peak at the age of 37 (Gurven et al. 2006). Achieving proficiency in hunting involves the consistent practice of shooting from an early age, as well as following expert hunters to learn to track and pursue animals (Kaplan et al. 2000; Blurton-Jones and Marlowe 2002). If hunting requires such a significant amount of learning to reach peak levels of performance, then it is not surprising that time spent at school decreases the time individuals spend learning and practicing their hunting abilities with expert hunters, thus affecting overall hunting performance, which ultimately also interferes with the decision to engage in hunting.

An additional finding of our work is that hunting activity is more associated with village factors than with individual factors. In other words, villages with higher hunting activity present lower average levels of schooling, which means that individual cultural traits are closely linked to

village characteristics (Sam and Berry 2010). Furthermore, hunting activity was also highly dependent on large-bodied species abundance. Tsimane' hunters—as in most Amazonian indigenous societies (Bodmer 1995; Jerozolimski and Peres 2003; Peres and Nascimento 2006)—prefer large-bodied game species, and their hunting activity is also shaped by the presence and abundance of those game species.

In contrast to schooling, we did not find any relationship between Tsimane' hunting activity and visits to town or detachment from tradition. Previous research suggests that the frequency of travel to a market town is associated with monetary income and social capital, which in turn might affect traditional economic activities such as hunting (Godoy et al. 2010; Brashares et al. 2011; Morsello and Ruiz-Mallén 2013). More specifically, according to some authors, access to a market town is associated with the ability to acquire firearms, which considerably increase hunting efficiency compared with traditional hunting technologies (Robinson and Redford 1991; Stearman 2000; Levi et al. 2009). So, we expected to find a significant positive association between hunting activity and the number of visits to town. A potential explanation for the lack of this association relates to the availability of weapons in the Tsimane' territory. In general, most of the households have a gun or rifle (Table 2), which are largely shared with

other families as long as they provide their own ammunition. Therefore, it is possible that Tsimane' travelling to town might have easier access to ammunition than Tsimane' who do not travel, a situation that does not seem to affect their engagement in hunting as much as it affects the outcome of their hunting activity, as discussed below.

We also did not find any association between hunting activity and our index of detachment from tradition. That is, attachment to traditional cultural values and beliefs did not seem to be associated with the individual choice to engage in hunting. As cultural change is a multidimensional process, some authors have argued that some values and beliefs can endure as part of the cultural heritage of a society despite changes in other values and beliefs (Inglehart and Baker 2000). In other words, it is possible that the Tsimane' have retained part of their belief system or self-identity even while adopting new values and beliefs that reflect new daily economic activities (Ryder et al. 2000). However, because our detachment-from-tradition index does not exclusively focus on hunting beliefs, we acknowledge that this index may not fully capture the relationship between cultural belief and value changes and hunting activity.

Finally, we did not find any relationship between CPUE in the number of animals killed/km and our proxies for cultural change. Variation in CPUE animals/km was low as it is closely correlated with a hunter's capacity to capture game in one hunting trip (Mysterud 2011). In contrast, CPUE in biomass/km was positively associated with the number of visits to the market town, an association that might be explained in the same way that we explained the association between hunting activity and visits to town, i.e., the CPUE in biomass caught/km increases with the number of visits to town because during such visits hunters can purchase ammunition. Research shows that when equipped with ammunition, hunters increase their effort and travel greater distances to increase their chances of capturing large-bodied animals (Levi et al. 2009; Sirén et al. 2013).

An important element to keep in mind regarding this explanation is that the association between schooling and hunting activity might also depend on contextual factors. In the case of the Tsimane', for example, there is no market for bushmeat, meaning that the Tsimane' cannot obtain cash income from the sale of game. This might generate a selective bias in who engages in hunting, i.e., those aiming at obtaining cash income might be more prone to engage in cash-generating activities such as logging or other wage labour. The context might be different in areas where there is a market for bushmeat.

CONCLUSION

In this article we have examined how individual cultural change relates to subsistence hunting in an indigenous society. Our work addresses a major gap in the literature by assessing how different individual proxies for cultural change, which measure different dimensions of the cultural adaptation process, might be associated with hunting activity and efficiency at the individual and the village levels.

Although our analysis does not allow us to conclude that there is a causal relationship between cultural change and changes in subsistence hunting, our results suggest that the Tsimane' seem to be abandoning hunting as they acquire modern human capital through schooling, most likely in response to new economic opportunities. Moreover, our results also suggest that engagement in hunting is not dependant on the individual loss of cultural beliefs and norms. Overall, our results highlight the importance of understanding the pathways through which cultural change might relate to hunting activity. Additionally, our results also signal that individual cultural traits cannot be accounted for outside of village characteristics. Understanding the hunters' behaviour is important for planning wildlife management and economic development, especially in very autarchic societies such as the Tsimane', who are rapidly changing their livelihoods and the way they manage wildlife.

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