The effects of ammunition price on subsistence hunting in an Amazonian village

ANDERS H. SIRÉN and DAVID S. WILKIE

Abstract Research has shown that consumers of wildlife are price sensitive and that the quantity of meat purchased is influenced by the cost of bushmeat and its substitutes. Although there is evidence that hunter-gatherers are optimal foragers whose behaviour is influenced by costs associated with foraging, there is a paucity of studies on whether the behaviour of bushmeat hunters, like that of consumers, is cost sensitive. This paper reports data on the practices of indigenous bushmeat hunters in the lowland forests of Ecuador before and after a national tax on firearms and ammunition was increased by 300%. Results show that hunters' behaviour is, as predicted by optimal foraging theory, responsive to price signals. After a substantial increase in the national tax on shotgun cartridges, hunters modified the set of species considered worth hunting, dropping smaller-bodied species from the set of species they target during a hunt and switching the technology used for hunting, increasingly using muzzle loader shotguns and thus avoiding the cost of expensive cartridges.

Keywords Amazon, ammunition price, bushmeat, Ecuador, hunting costs, optimal foraging

Introduction

People have hunted wildlife since the dawn of humankind (Cartmill, 1996). We hunt for food, for income, for religion and for prestige. What is becoming increasingly understood as a result of a growing corpus of empirical evidence is that costs matter to wildlife consumers (Auzel & Wilkie, 2000; Apaza et al., 2002; Fa et al., 2003; Wilkie et al., 2005; Bennett et al., 2007; Godoy et al., 2010; Foerster et al., 2011; Salo et al., 2013, pp. 259–279). Consumers are price sensitive and change their purchases, barter exchanges and preferences based on the price of wildlife (own-price elasticity of demand) and the price of substitutes such as chicken and fish (cross-price elasticity of demand). Price can be measured in monetary terms or in labour costs (Apaza et al., 2002). What has been less studied is how costs influence the behaviour of hunters (i.e. producers).

There is no a priori reason to believe that hunters are not as susceptible as consumers to price signals. Evidence suggests that human hunters are optimal foragers (Hames & Vickers, 1982; Hawkes et al., 1982; Hill et al., 1987; Alvard, 1995; Ohl-Schacherer et al., 2007; Koster et al., 2010; Begossi et al., 2011; Levi et al., 2011; Chacon, 2012) in that they are aware of the value of capturing large rather than small animals, and understand that large animals are sometimes more difficult to capture, depending on the weaponry they have at hand. As optimal forgers, hunters make economic decisions about what they will and will not hunt based on the cost of capturing different species and the economic value of each species when captured (Stephens & Krebs, 1986; Winterhalder, 1987). Optimally foraging hunters will ignore some animals they encounter, because if they spend time chasing and capturing them they may miss the opportunity of encountering and capturing a more valuable animal (i.e. one that is both larger and easier to catch). Thus optimally foraging hunters have a suite of preferred species, called their diet breadth, which they chase each and every time they encounter them, no matter how infrequently, and a second suite of species that they will ignore, regardless of how often they are encountered. Hunters understand that it is better to capture one 50 kg pig during 7 hours of hunting than 15 0.5 kg rodents. Optimally foraging hunters never drop valued species from their list, regardless of how scarce they become, but will progressively add the next highest valued species in the non-preferred list as the density of preferred species declines (Stephens & Krebs, 1986). Optimal foragers will also tend to expand their diet breadth during a hunt if they are unsuccessful and the time available to hunt winds down (Alvard, 1993; Levi et al., 2011). That hunters appear to be optimal foragers strongly suggests they are sensitive to costs and are likely to alter their behaviour in response to changes in the value of their labour and the costs of hunting equipment (e.g. snares, nets, firearms, ammunition).

Assuming that hunters are optimal foragers, an increase in the cost of ammunition could have various effects on hunting behaviour. Firstly, one might expect a change in the species targeted by hunters, with small-bodied species that have a low harvest-value to capture-cost ratio being dropped from their diet breadth. Secondly, there is a possibility that hunters would shift to using cheaper hunting technology, which could potentially confound the direct effect on the diet breadth. Thirdly, the time spent hunting,

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and total harvest, may change. The direction of this effect is, however, unclear and depends on the prevailing market conditions and economic objectives of the hunters (cf. Angelsen, 1999). If hunters act as profit-maximizers in an open economy they are likely to reduce the time they spend hunting as a result of the overall reduction in the profitability of hunting. This would probably cause a reduction in total harvest. If, however, their objective is to reach a fixed harvest level to feed their families, time spent hunting might, on the contrary, remain constant or even increase when some species are dropped from the diet breadth.

New legislation passed in late 2007 by the Government of Ecuador and entering into force in 2008 imposed a 300% tax on firearms and ammunition, leading to an increase in the price of a shotgun cartridge in town stores from USD 0.60 to USD 2.00 within c. 2 weeks. Similar price rises also affected the ammunition for muzzle-loaded shotguns, although this ammunition was much cheaper initially and remained relatively cheap even after the imposition of the tax. This change in taxes and prices happened when AS was conducting field work on hunting in Ecuadorian Amazonia, and provided an unexpected opportunity for an empirical study of the effects of changes in ammunition costs on hunting behaviour.

To explore how the increase in ammunition costs affected hunting effort, total harvest, choice of hunting technology, and the size distribution of hunted prey, we formulated the following hypotheses, derived from the theoretical considerations described above:

Hypothesis 1: Hunting of small prey with a low value to capture cost ratio declines

Hypothesis 2a: Hunting effort decreases as catch per unit of effort (CPUE) declines when small prey are dropped from the diet breadth, because hunters are profit-maximizers. Assumes Hypothesis 1 is true.

Hypothesis 2b: Hunting effort increases to compensate for the decrease in CPUE when small prey are dropped from the diet breadth because hunters are seeking a fixed harvest level to provide sufficient food for their families. Assumes Hypothesis 1 is true.

Hypothesis 3a: Harvest of large prey decreases. Assumes Hypotheses 1 and 2a are true.

Hypothesis 3b: Harvest of large prey increases. Assumes Hypotheses 1 and 2b are true.

Hypothesis 4a: Total harvested game biomass decreases. Assumes Hypotheses 1, 2a, and 3a are true.

Hypothesis 4b: Total harvested game biomass remains constant. Assumes Hypotheses 1, 2b, and 3b are true.

Hypothesis 5: Hunters increasingly use muzzle-loaders rather than cartridge shotguns to hunt, as the ammunition for the former is much cheaper (if this effect is strong, it may completely offset the effects predicted by Hypotheses 1–4).

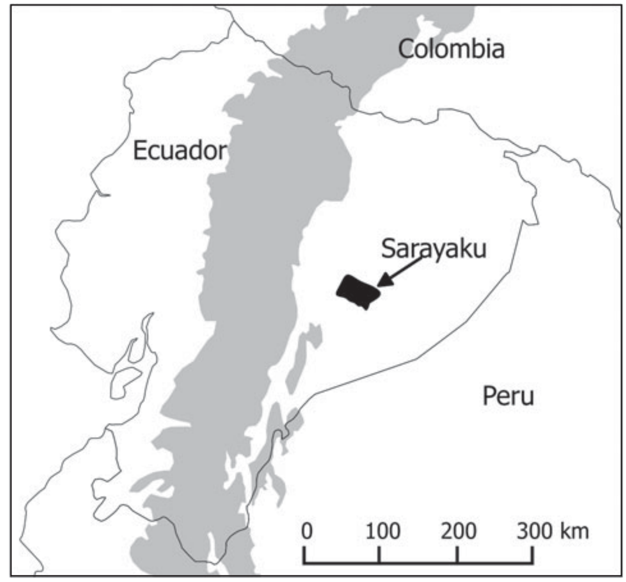

FIG. 1 The location of the study area, Sarayaku, indicated with black shading, in western Amazonia, Ecuador, near the Andes Mountains. Gray shading shows areas above 1,200 m altitude.

Study area

The study was carried out in the community of Sarayaku (at 400 m altitude) in Eastern Ecuador (Fig. 1). The community is c. 65 km south-east of the town of Puyo, on the banks of the Bobonaza River. The principal access route from Puyo to Sarayaku is by road halfway and then by canoe. There is also a small airstrip in the community. In 2001 the population of the community was 961, and the rate of population growth was estimated to be 1.65% per year (Sirén, 2004, p. 144). In 2010 Narváez (2011) reported a population of 1,223, suggesting that the rate of growth since 2001 may have been as high as 2.7%. This discrepancy, however, seems to be related to the inherent difficulty in defining who is a resident of Sarayaku at any given time. Depending on economic conditions in the community relative to towns, cities and rural estates in coastal Ecuador, many community members (mostly youth) migrate out of and back to the community over time.

The population is distributed in five hamlets, clustered within a few kilometres of each other. The hunting grounds used exclusively by the Sarayaku people cover c. 1,000 km^2. Old growth tropical rainforest covers about 96% of this area (Sirén, 2007).

For the Sarayaku, shifting cultivation, hunting and fishing form the basis of what is largely a subsistence economy (Sirén & Machoa, 2008). In the relatively recent past hunting was carried out with blowguns and poison darts but in the 1950s this technique began to be replaced by muzzle-loaded shotguns. In the last few decades almost all hunting has been done with firearms, and cartridge shotguns have become more common than muzzle-loaders (Sirén, 2004). Most shotguns in the community are made by national artisans. Few people can afford the more expensive, imported, industrially manufactured shotguns. Cartridge shotguns are more powerful than muzzle-loaders, making it somewhat easier to kill large prey even at some distance, and they are also much faster to reload. Cartridge shotguns are cheaper than muzzle-loaders but are less durable, and their ammunition is more expensive.

The Sarayaku raise chickens but these remain a minor food source. Since c. 2005 fish farming has become important as a source of food for some families. In the 1990s cattle raising, harvesting fibres from the palm *Aphandra natalia* (Balslev & Henderson, 1987), and temporary work on plantations in the coastal region of Ecuador were still important ways of providing cash for purchasing hunting and fishing equipment, agricultural tools, clothes, boots and other items. In recent years, however, there has been an increased reliance on part-time wage labour in the community, funded by government institutions, international NGOs, and the tourism industry. Several people in the community have permanent salaried jobs in the public sector, mostly as teachers. The amount of cash circulating in the community has increased markedly in recent years, and equipment such as outboard motors and chainsaws, which were rare 2 decades ago, are becoming more typical possessions for Sarayaku households.

In the last 2 decades there has been a growing concern among the Sarayaku about the increasing scarcity of wild game (Sirén, 2004). Quantitative research in the area has also confirmed that hunting has a strong impact on the populations of some animal species, particularly large-bodied species with conspicuous habits. For example, the woolly monkey (*Lagothrix* spp.) is easily seen as it moves around in the canopy, and can be heard from a long distance because of its vocalizations and the noise of branches bending and breaking. Dividing the Sarayaku hunting territory into seven zones based on their proximity to the village, a comparison between the zone closest to the village (i.e. the zone most frequently and thus intensively hunted) and the most remote zone showed that the CPUE, expressed as biomass of game killed per kilometre walked by hunters, was almost five times higher in remote compared to proximate zones (Sirén, 2004). Most noticeably, woolly monkey, tapir *Tapirus terrestris* and Salvin's curassow *Mitu salvini* were practically absent in the zone closest to the village, and collared peccary *Tayassu tajacu*, nocturnal curassow *Nothocrax urumutum* and red brocket deer *Mazama americana* were uncommon there (Sirén, 2004).

Although most wild meat is consumed directly in hunters' households, a small proportion is traded within the community (Sirén & Machoa, 2008). Prices for wildlife meat, and also for labour, are set by consensus during village assemblies, and then tend to remain constant for prolonged periods. The same price per kilogram is charged regardless of whether the traded animals have been eviscerated or not, or whether the meat is raw or smoke-dried. Such community prices thus reflect local willingness to pay but in an imprecise manner.

Methods

Data

As the ammunition price rise came suddenly and without notice, it was not possible to design in advance a true before-after-control-intervention type study to evaluate the hypotheses. Rather, the analyses relied on whatever data were available for the time before the imposition of the tax on ammunition.

The data were from three periods, of which two were before the price rise (1999–2001 and 2007–2008) and the third (2008–2009) was from after the increase in taxes and prices. These datasets differed somewhat with regards to which variables they included, and, in particular, the 2007–2008 dataset had certain limitations, which are detailed below, making it necessary to use the 1999–2001 dataset to represent the period before the price rise for some of the analyses.

Data on quotidian, non-festival, subsistence hunting, including species, hunting method, habitat type, type of equipment used and location of each hunting kill, were collected c. twice monthly at the household level through interviews with hunters from a sample of households that was changed at regular intervals. Non-hunting households, which were few, were excluded from the sample. In 1999–2001 the sample was self-selected but stratified according to hamlet. A total of 70% of the households participated in the study. To check the representativeness of the sample local field assistants categorized households into three categories based on level of hunting activity, and it was checked a posteriori that the sample was unbiased in terms of these categories. In 2007–2008 and 2008–2009 the household sample was randomly selected and few declined to participate, and thus over the two periods almost all the households were included. A form that included drawings of all (c. 60) significant prey species and a map of the community's hunting grounds divided into > 100 sub-areas was used to help hunters identify and locate each kill with a reasonable spatial resolution. The trajectories walked by hunters during each hunting bout were recorded on the map, and then measured with a ruler to obtain a measure of hunting effort in each sub-area. Data were collected from July 1999 to July 2001, and from January 2008 to March 2009. Only from January 2008 to March 2009 did data on hunting equipment distinguish between cartridge and muzzle-loader firearms. In 2000 and 2009 additional data were collected for hunting conducted exclusively for the community festivals celebrated in February. Data on such festival hunting were excluded from the analysis in this study because the factors motivating hunters during festival hunting differ in several ways from those of everyday hunting, and the biomass hunted during festivals comprises only 4% of total hunted biomass over time (Sirén, 2012).

As informant fatigue was the biggest constraint to data collection and as mapping hunter travel paths was the most time consuming element of data collection, we decided to opt out of mapping hunter travel paths when gathering additional monthly data on 14 large and preferred species (*Ateles belzebuth, Lagothrix poeppigii, Lagothrix lagotricha, Alouatta seniculus, Cebus apella, Cebus albifrons, M. americana, Mazama gouazoubira, T. terrestris, Pecari tajacu, T. pecari, Caiman crocodilus, Paleosuchus trigonatus, M. salvini*) that contributed the greatest biomass to species hunted, even though they were captured rarely. These data were collected from February 2000 to April 2001 and from May 2007 to January 2008. Hunting travel paths and species killed were recorded for a total of 16,457 household-days. An additional 22,533 household-days were recorded for the 14 large and preferred species.

Prices for ammunition, wildlife meat, and unskilled wage labour were recorded in late 1999 (Sirén et al., 2006), late 2007, February 2008, January 2009 and March 2012. The recorded cost of ammunition was based on the sale price set by shopkeepers in Sarayaku for cartridges legally obtained in Ecuador. For 2012, however, cost was also recorded for less expensive cartridges originating from Peru, which reached the community on an irregular basis through informal trade routes. Prey biomass was taken from a list of species-specific mean values originating from various sources, compiled by Sirén (2012). For some taxa, however, hunters did not always identify their hunted prey to the level of species. Some groups of species were therefore lumped together at the level of genus or family before analysis. To convert the data collected at household level to aggregated estimates for the whole community a weighting procedure was applied, weighting the raw data based on month of the year as well as place of residence (hamlet), as detailed in Sirén (2012).

Analyses

To evaluate Hypothesis 1 we (1) compared mean prey size during 1999–2001 and 2008–2009, and (2) conducted a median test on a change index that was calculated as follows. Firstly, the break-even point of biomass, where the value of the prey equals the value of a shotgun cartridge, was calculated, and the various species divided into two categories, depending on whether they were smaller or larger than this break-even point. A change index was then calculated as:

$$Index = (After - Before)/(After + Before),$$

where *Before* and *After* refer to the datasets for 1999–2001 and 2008–2009, respectively; i.e. before and after the ammunition price rise. This implies that the change index can take any value between −1 and 1, where −1 implies a decrease from a positive value to zero, 0 implies no change, and 1 implies an increase from zero to a positive value.

It is, however, not self-evident that the real break-even point should be the same as the theoretical one, because of the way meat prices are set and handled in the community and because the hunter may, at times, miss the target animal or require more than one shot to dispatch it. Similar median tests were therefore also performed for all possible placements of the dividing point between small and large species.

To test Hypothesis 2 we compared hunting effort, measured as kilometres walked by hunters per year and per square kilometre of hunting territory, during 1999–2001 and 2008–2009. To test Hypothesis 3 we compared how harvested biomass of the 14 preferred large prey species changed between 1999–2001, 2007–2008 and 2008–2009. As data for 2007–2008 were available only for May–January, to avoid any seasonal bias only data for these months were used for all datasets.

Note that, all other things being equal, one would expect the harvest to remain constant from 1999–2001 to 2007–2008, and only change after the ammunition price rise. However, as other societal changes may have occurred, the question was not about the absolute change from 2007–2008 to 2008–2009 but rather about comparing the rate of change between 2007–2008 and 2008–2009 with that between 1999–2001 and 2007–2008. Thus, other societal changes affecting hunting behaviour could affect the result of the test of these hypotheses only if they occurred abruptly between 2007–2008 and 2008–2009, but not if they occurred gradually over the whole time span from 1999 to 2009. To test Hypothesis 4 the total annual harvested game biomass was compared between 1999–2001 and 2008–2009. To test Hypothesis 5 we conducted a time-series linear regression analysis of the number of hunts per month with the different types of firearms.

Results

In village shops, where typically prices are significantly higher than in the towns, prices initially remained unchanged after the tax was imposed, until the supplies bought by shop owners before the price rise ran out. Prices then increased from USD 0.80 to USD 3.00 c. 1 month after the tax came into force, and continued to increase, reaching USD 4.00, where it remained for the next 3 years. The cost of ammunition for muzzle-loaders also increased. Muzzle-loader ammunition consists of gunpowder and lead shot bought in bulk. As the quantity of powder and shot used by

TABLE 1 Changes in daily wage, shotgun cartridge price and wild meat in the study area in western Amazonia (Fig. 1), and the resulting break-even body masses. Break-even body mass is the minimum wildlife carcass weight in kilograms that if sold would offset the opportunity cost of working as a day labourer or purchasing a single shotgun cartridge. All prices are presented in USD as Ecuador abolished its own national currency and adopted the US dollar as the official currency in 2001.

	Late 1999	Late 2007	Feb. 2008	Jan. 2009	Mar. 2012
Daily wage (USD)	1.54	10.00	10.00	10.00	10.00
1 shotgun cartridge (USD)	0.33	0.80	3.00	4.00	(2.00)*
1 kg of game biomass (USD)	0.42	2.20	2.20	2.20	4.40
Break-even body mass					
For daily wage (kg)	3.67	4.55	4.55	4.55	2.27
For shotgun cartridge (kg)	0.79	0.36	1.36	1.82	(0.45)*

*Numbers provided are for cartridges coming from Peru through informal trade routes and only intermittently available. When these were not available, cartridge price remained at a level similar to that of 2009.

TABLE 2 Mean prey biomass, hunting effort, total kills and total biomass hunted (hunting for community festivals is excluded) annually in 1999–2001 and 2008–2009. Numbers in parentheses are excluding *Tayassu pecari*.

	1999–2001	2008–2009
Mean prey biomass (kg)	2.9 (2.8)	5.7 (4.6)
Hunting effort (distance walked with a gun, km)	61,453	39,227
Number of animals hunted	11,096 (11,053)	5,571 (5,307)
Total hunted biomass (kg)	32,189 (30,948)	31,980 (24,415)

each hunter and for each load varies, it is difficult to provide exact figures for the cost per shot fired. After some time significantly cheaper cartridge ammunition from Peru became available through informal trade routes. This ammunition was, however, only intermittently available and never became common. Changes in the economic incentives affecting hunting behaviour over the study period are summarized in Table 1.

Hypothesis 1: hunting of small prey declines During most of the period after the price rise the break-even body mass, where the monetary value of a prey equalled the price of a shotgun cartridge, was 1.82 kg, and therefore species with a mean biomass larger and smaller than this were classified as large and small, respectively. As predicted by Hypothesis 1, mean prey biomass increased substantially (almost two-fold) from 1999–2001 to 2008–2009 (Table 2). Hunting of *T. pecari* increased six-fold between these two periods. Although the influence of increased ammunition costs on the behaviour of Sarayaku hunters may have played a role, we believe that the more likely explanation was that the peccary population was rebounding following a die-off from disease or other natural causes, a not uncommon occurrence (cf. Fragoso, 2004). Given this, we repeated the comparison with *T. pecari* excluded but still observed a considerable increase in mean prey size between the two periods. Visual inspection of the relationship between the change index and body mass (Fig. 2) suggests that harvest of small species declined over time and across the tax increase. Most large species show either a moderate decrease or an increase in harvest level across the same time period. A median test between the change indexes of small and large species indicated that this difference was statistically significant ($P = 0.002$ if all species were included, and $P = 0.003$ if *T. pecari* was excluded), thus confirming Hypothesis 1. This statistically significant difference ($P < 0.05$) continued when the dividing line between small and large was set at any level between 0.76 and 7.8 kg.

Hypotheses 2a and 2b: hunting effort decreases or increases The hunting effort, as measured in kilometres walked by hunters carrying a firearm, had by 2008–2009 decreased to two-thirds of its level in 1999–2001 (Table 2). The use of other hunting methods had increased only slightly, from 21% of all hunts in 1999–2001 to 25% in 2008–2009. Thus, the decrease in hunting effort using the walk-with-a-gun technique is not the result of a shift in hunting methods but rather a true reduction in overall hunting effort. This provides support for hypothesis 2a, implying that when small prey species are dropped from the diet, overall profitability of hunting declines, and hunters, behaving as profit maximizers, therefore reduce their hunting effort.

Hypotheses 3a and 3b: harvest of large prey decreases or increases The harvest of the 14 large and preferred species increased from 1999–2001 to 2007–2008 (Fig. 3) but then decreased from 2007–2008 to 2008–2009. This provides support for hypothesis 3a, and also indirectly for hypothesis 2a, as the decrease in harvest of these large species is most likely the result of a decrease in hunting effort.

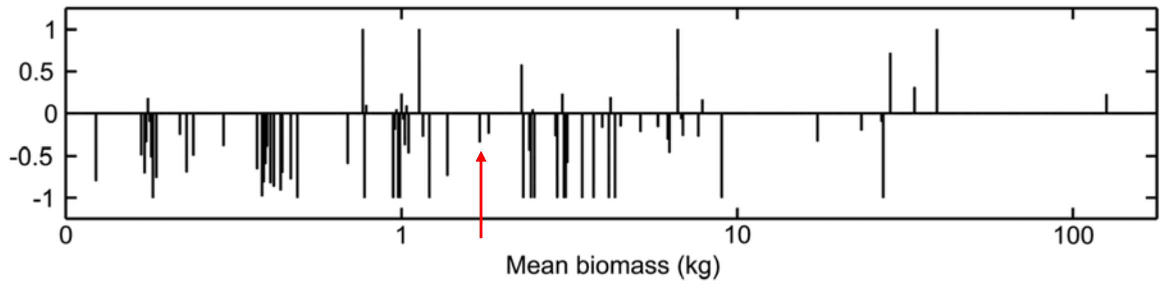

FIG. 2 The relation between the index of change (see text for details) in harvest level from 1999–2001 to 2008–2009 and mean biomass, for all species (each line represents one species). Negative values indicate a decrease and positive values indicate an increase in harvest. For example, a doubling of harvest results in a change index of 0.33, whereas a halving of harvest results in an index of −0.33. The scale of the horizontal axis is linear for masses < 1 kg and logarithmic for masses > 1 kg. The arrow indicates 1.82, which is the theoretical break-even biomass (see text for details) at which, after the ammunition price increased, small species would become unprofitable to hunt and large species would remain profitable to hunt.

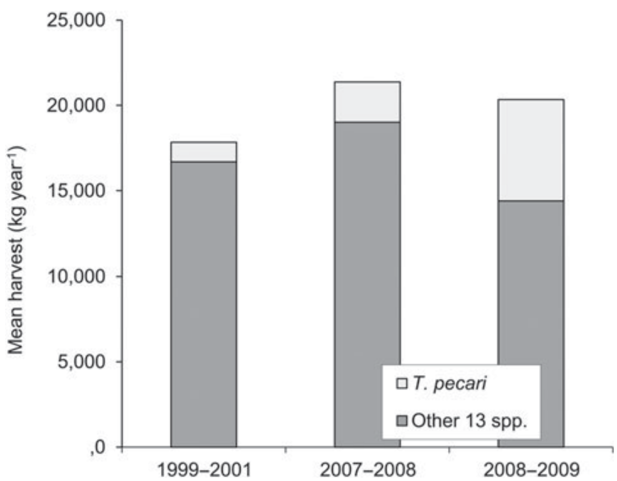

FIG. 3 Changes over time in harvested biomass of the 14 large, preferred species (see text for details). There was an increase from 1999–2001 to 2007–2008 and then a decrease to 2008–2009. This pattern is more notable if one excludes *T. pecari* from the analysis (see text for details). The numbers provided are estimates of annual harvest but, because of the limitations in the data available for 2007–2008, they are all based on data for May–January only.

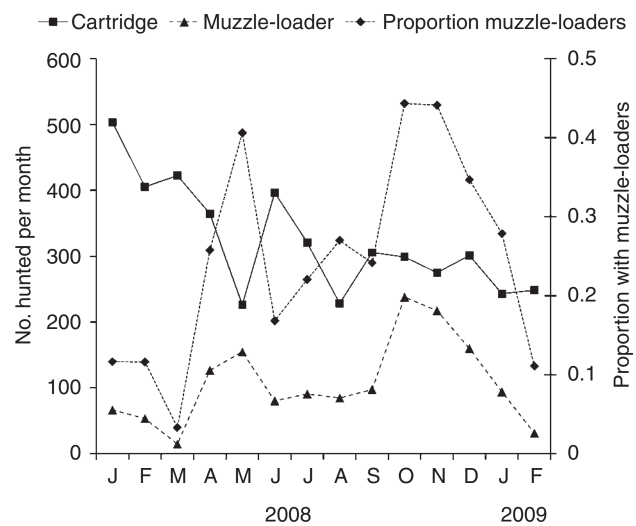

FIG. 4 Changes in the choice of hunting technology (cartridge shotgun or muzzle-loader) over the 14 months following the introduction of the tax on ammunition. Monthly numbers of prey hunted with cartridge shotguns (solid line) and muzzle-loaders (hatched line) are on the left-hand axis, and the number of hunts with muzzle-loaders as a proportion of the total number of hunts with any type of firearm (dotted line) is on the right-hand axis.

Hypotheses 4a and 4b: total harvested game biomass decreases or increases Total harvested biomass was remarkably stable from 1999–2001 to 2008–2009 (Table 2), providing support for Hypothesis 4b rather than 4a. If Sarayaku hunters are optimal foragers, theory would predict that either all a-hypotheses (hunters maximizing profit) or all b-hypotheses (hunters attempting to reach subsistence target) would be true, and therefore this result is somewhat surprising, given that the tests of Hypotheses 2 and 3 supported the a-hypotheses rather than the b-hypotheses. However, this result depends heavily on the increase in the harvest level of *T. pecari*, which increased sixfold in absolute terms as well as in terms of its share of total harvested biomass, which increased from 4 to 24%.

Hypothesis 5: hunters switch from cartridge guns to muzzle-loaders Plotting the change in monthly hunts, with different types of firearm, reveals some interesting patterns (Fig. 4). The number of hunts using cartridge shotguns dropped sharply after the ammunition price increased in late January 2008 until it more or less stabilized after c. 4 months ($P = 0.002$). The number of hunts using the cheaper muzzle-loaders began to increase after 3 months, reaching a maximum in October 2008 before falling to January 2008 levels. Thus, when analysed over the whole period, the increase in the number of hunts using muzzle-loaders was not statistically significant ($P = 0.239$). The increase in the number of hunts with muzzle-loader as a proportion of total hunts with firearms (Fig. 4), however, was significant ($P = 0.011$). Hunting with other weapons (i.e. blowguns, machetes, sticks, stones) was negligible throughout all periods of data collection. In summary, these results provide support for Hypothesis 5. A comparison of the harvest of the 14 large and preferred species between 2007–2008 and 2008–2009 indicates that the percentage of hunts of these species made with muzzle-loaders increased only modestly, from 11.8% in 2007–2008 to 13.4% in 2008–2009. Muzzle-loaders were used primarily to hunt small-bodied prey.

Discussion

The results show that hunters adapted to the ammunition price rise both by reducing hunting of small species (Hypothesis 1) and by changing to cheaper hunting technology (Hypothesis 5). Conclusions regarding the mutually exclusive Hypotheses 2a, 3a and 4a (profit-maximizing behaviour) vs 2b, 3b, and 4b (striving to reach fixed subsistence target) are, however, ambiguous. Decreased hunting effort (Hypothesis 2a) and decrease in harvest of large prey (Hypothesis 3a) suggest profit-maximizing behaviour but the near-constant total harvested biomass (Hypothesis 4b) contradicts this.

Other factors may have influenced hunter behaviour and the results observed. Demographic growth of the community was estimated to be 1.6% for the latter part of the 20th century (Sirén, 2007) but may have increased recently as socio-economic conditions have improved, reducing the incentives for emigration of youth to urban areas and agricultural estates in coastal Ecuador. Between 1999–2001 and 2008–2009 (Table 1) daily wages increased sixfold and the availability of wage work also increased. This seems to have led to increased consumption of store-bought food from < 1% of dietary intake prior to 2008 (Sirén & Machoa, 2008). A series of international donor financed projects promoting aquaculture have been implemented in the community since the mid 1990s, but it was not until after a decade of experimentation that farmed fish became a significant complement to hunting and capture fishing. Since 2003 the community has also set aside two wildlife reserves where all hunting is banned, paying local reserve guards with funds from international donors. The combined area of the reserves comprises < 10% of the community's hunting grounds, and management has been fraught with problems. Nevertheless, local inhabitants who have worked as reserve guards claim that wildlife populations within the reserves have increased markedly.

The results of the tests of Hypotheses 1, 3 and 5 are unlikely to be influenced by these factors. However, the results of the tests of Hypotheses 2 and 4 are potentially more susceptible to such effects. For Hypothesis 2 the decrease in hunting effort may have been partly caused by an increase in opportunity costs associated with a rise in the day-labour wage rate and availability of wage labour as well as by increased availability of alternative foods such as store-bought food or locally farmed fish, although such foods are still only minor contributors to family nutrition. An increased human population, however, would be expected to have led to an increase in total hunting effort, contrary to the observed results. Somewhat surprisingly the observed decline in hunting effort did not result in a decline in total harvested biomass. It is possible that spillover from the two reserves increased prey availability in the hunting area, allowing stable offtake even with reduced effort.

In addition, the results regarding Hypothesis 4 could potentially have been affected by the societal changes that occurred between 1999–2001 and 2008–2009. Moreover, the apparent support for Hypothesis 4b may also have to do with the increase in harvest of *T. pecari*, which is most likely unrelated to impacts caused by hunting. *T. pecari* is hunted differently compared to other species, which are hunted opportunistically whilst walking along a trail. Hunting of *T. pecari* typically begins with finding one of the typical trails this species leaves as it travels through the forest in large herds. Hunting activity then switches to a focused search for *T. pecari* only and, as the word spreads, other hunters join the search. The increased abundance of *T. pecari* may therefore have affected harvest level without also affecting the level of hunting effort, as would otherwise have been predicted if hunters behaved as profit-maximizers.

Overall, our results suggest that hunters behave as profit-maximizers rather than striving for a fixed subsistence target biomass, as there was support for Hypotheses 2a and 3a. Although the data contrarily supported Hypothesis 4b, there are various alternative explanations for this result.

The results also show that the behaviour of Sarayaku hunters is sensitive to price signals. We have not attempted to analyse the impacts of this on the abundance of individual species, and the data available may not be sufficient for doing this. However, some inhabitants of Sarayaku commented that within a year of the rise in the cost of ammunition, toucans (*Ramphastos* spp.) had become notably more common in the forests surrounding the community.

The results also suggest that raising ammunition prices generated conservation benefits for small-bodied species but not for large-bodied species. A much higher tax on ammunition would be required to reduce the hunting of species such as deer, peccaries, large primates and tapirs. Unfortunately, this could also potentially have negative socio-economic consequences for hunting-dependent households, at least in the short term, in the form of increased expenses for ammunition or decreased supply of bushmeat. The impacts of changes of ammunition prices may vary in different natural and socio-economic settings and thus more case studies are needed to be able to draw universally valid conclusions. Taxing ammunition is not a panacea for resolving problems of overhunting but rather one of several tools that could be used in the conservation and sustainable use of hunted wildlife species.

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