De la Montaña, E., R. del Pilar Moreno-Sánchez, J. H. Maldonado, and D. M. Griffith. 2015. Predicting hunter behavior of indigenous communities in the Ecuadorian Amazon: insights from a household production model. *Ecology and Society* 20(4):30.
http://dx.doi.org/10.5751/ES-08032-200430

Research, part of a Special Feature on Why does hunting in tropical regions matter?

Predicting hunter behavior of indigenous communities in the Ecuadorian Amazon: insights from a household production model

Enrique de la Montaña [1], *Rocío del Pilar Moreno-Sánchez* [2], *Jorge H. Maldonado* [3] *and Daniel M. Griffith* [1]

ABSTRACT. Many indigenous communities living in the Amazon rely on hunting and fishing to meet the majority of their protein needs. Despite the importance of these practices, few studies from the region have analyzed the socioeconomic drivers of hunting and fishing at the household level. We propose a household production model to assess the effect of key economic parameters on hunting and fishing in small indigenous communities located in the Ecuadorian Amazon, whose principal source of protein is derived from hunting and fishing. The model was validated using empirical data from two communities that reflect different levels of market integration and forest conservation. Demand and supply functions were generated from household data gathered over 19 months. Elasticities were derived to determine the sensitivity of the decision to engage in hunting to exogenous parameters such as off-farm wages, hunting costs, bushmeat price, penalties for the illegal sale of bushmeat, and biological characteristics of the game species. After calibrating the model, we simulated changes in the key economic parameters. The parameter that most directly affected hunting activity in both communities was off-farm wages. Simulating a 10% wage increase resulted in a 16–20% reduction in harvested biomass, while a 50% increase diminished harvested biomass by > 50%. Model simulations revealed that bushmeat price and penalties for illegal trade also had important effects on hunter behavior in terms of amount of bushmeat sold, but not in terms of total harvest. As a tool for understanding hunters' economic decision-making, the model provides a basis for developing strategies that promote sustainable hunting and wildlife conservation while protecting indigenous livelihoods.

Key Words: *bushmeat; economic model; Ecuador; fishing; food security; hunting*

INTRODUCTION

Bushmeat constitutes the main source of protein and an important source of income for millions of inhabitants in the developing world. The harvest, sale, and consumption of bushmeat are worth billions of dollars annually (Milner-Gulland et al. 2003), and it has been suggested that these activities could make a positive contribution to development if managed sustainably and incorporated efficiently into the overall economy (Brown 2003). However, despite the importance of hunting to household economies in most areas of the tropics (Bodmer et al. 2004, de Merode et al. 2004), unsustainable bushmeat exploitation constitutes one of the principal threats to local biodiversity (Vié et al. 2009).

The current economic and social conditions that characterize most of the Amazonian region, combined with the cultural characteristics of those who provide and consume bushmeat, mean that hunting is unsustainable in the case of most species (Milner-Gulland et al. 2003). Hunting not only threatens species with extinction, but may also have serious effects on ecosystems and the goods and services they provide (Fa et al. 2002). This in turn threatens the food security and cultural integrity of indigenous populations who depend directly on the functioning of natural ecosystems for subsistence.

In the Ecuadorian Amazon, bushmeat consumption levels are high relative to other Amazonian regions (Fa and Peres 2001, de la Montaña 2013), with the result that negative effects on biodiversity, including local species extinctions, are frequent (Franzen 2006, Zapata-Ríos et al. 2009). If these effects are to be avoided, then household consumption, as well as commercial demand, must be reduced by changing habits and implementing strategies that insure sustainable wildlife management.

Despite the importance of hunting to rural populations and the dangers to local livelihoods and biodiversity imposed by overexploitation, much remains unknown about the factors affecting bushmeat consumption at the household level (Brashares et al. 2011). Most studies of bushmeat in Latin America have focused on understanding hunting practices and the sustainability of harvest levels (Robinson and Redford 1991, Peres 2000, Sirén et al. 2004, Levi et al. 2009, Shepard et al. 2012, Iwamura et al. 2014). The few studies with an economic focus have examined the relationship between bushmeat harvest and household variables based on empirical data (Wilkie and Godoy 2001, Demmer et al. 2002, Sirén et al. 2006, Godoy et al. 2010). To our knowledge, only one study from Africa explicitly models bushmeat exploitation as a component of the household economy (Damania et al. 2005). However, no previous studies have modeled the effects of household-level socioeconomic factors on hunting in Latin America.

We developed a household production model aimed at identifying the most important socioeconomic drivers of hunting and fishing activity in small indigenous communities. We validated the model with data from two communities representing different socioeconomic realities within the Amazonian context, and analyzed the effect of key economic parameters on hunting, such as off-farm wages, hunting costs, bushmeat price, and penalty for the illicit sale of bushmeat. The model results provide insights

[1]Departamento Central de Investigación, Universidad Laica "Eloy Alfaro" de Manabí, [2]Conservation Strategy Fund, [3]CEDE - Department of Economics, Universidad de los Andes

about hunters' economic decision-making and enable the identification of strategies that promote sustainable hunting and wildlife conservation while protecting indigenous livelihoods.

METHODS

Research area

The study was carried out within and adjacent to the Cuyabeno Wildlife Production Reserve, located in northeastern Ecuador (Fig. 1). The region forms part of a biodiversity hotspot (Myers et al. 2000, Brooks et al. 2006) and is a globally important ecoregion (Olson and Dinerstein 2002). The Cuyabeno Reserve contains approximately 6000 km² of tropical rain forest (Sierra 1999) and harbors > 12,000 plant and 1320 vertebrate species, including 165, 493, and 475 species of mammal, bird, and fish, respectively (Rivadeneira 2007).

Fig. 1. Location of the two indigenous communities studied with respect to the Cuyabeno Wildlife Production Reserve.

The human population living within and around the reserve numbers ~2000 individuals belonging to five distinct ethnic groups (A'i Cofán, Secoya, Siona, Kichwa, and Shuar) as well as nonindigenous colonists, who live on the periphery of the reserve (Instituto Nacional de Estadística y Censos 2010). The western half of the reserve is surrounded by secondary forests, pastures, subsistence crops, and oil palm plantations. Significant operations for oil extraction, which began in the region in 1964, have recently expanded into the reserve.

To validate the model with data that reflect the different socioeconomic contexts and hunting dynamics of indigenous communities within the region, we collected data from two indigenous communities from the A'i Cofán and Secoya ethnic groups (Table 1). Both communities are representative of the Ecuadorian Amazon with regard to size and subsistence practices (de la Montaña 2013), but differ with respect to market access and location relative to the protected area (Fig. 1).

Table 1. Social and geographic characteristics of the communities studied. The vast majority of both communities' territory consists of primary rain forest.

Community	Ethnic group	Territory (ha)	Inhabitants	Households	Households sampled
Zábalo	A'i Cofán	153,000	149	28	25
Wajosará	Secoya	9000	74	11	10

Zábalo is located within the reserve in a large area of mature primary forest and is accessible only by river. Distant from urban centers, this community is only marginally linked with the market economy. Hunting and fishing provide the main sources of protein and are practiced frequently. Subsistence crops such as cassava, banana, and other fruits, as well as commercial products such as cocoa, are grown in family plots < 1 ha in size known as *chacras.*

Wajosará is located outside the reserve and is surrounded by cultivated land, secondary forest, and a much smaller area of primary forest than is Zábalo. Located no more than one hour away from sizeable population centers, Wajosará is accessible by road and is close to small settlements where basic goods can be acquired. Similar to Zábalo, subsistence hunting and fishing constitute daily activities, and cassava and banana are grown in *chacras.* In 2010, a few Secoya families began to cultivate oil palm.

The theoretical model

To understand the effect of key economic parameters on bushmeat extraction and to simulate hunter behavior, we developed a household production model based on the bioeconomic model proposed by Damania et al. (2005) and adjusted to reflect the specific characteristics of the communities under study. The model includes the three main productive activities carried out by households in the region, i.e., hunting, fishing, and off-farm work, and assumes that the income earned from these activities is used to acquire food and other resources exclusively for the household.

We did not distinguish between game species but rather considered all species to be a single representative game species with a given population density and capture probability. We also assumed that the species is illegal to sell but can be extracted for subsistence. The model incorporated this restriction by assuming that hunting activities are monitored and some probability exists that households who sell meat obtained from hunting will be detected. In this case, bushmeat is assumed to be confiscated. Moreover, the model assumes that hunters do not use traps but rather pursue prey actively using various weapons (firearms, machetes, dogs, etc.), which is generally the case in Neotropical indigenous communities (Fa and Peres 2001). Therefore, we propose only one hunting production function, which is independent of the weapon used by hunters.

The household exhibits a Cobb-Douglas-type utility function:

$$\bar{U} = F^{\alpha_f}\gamma H^{\alpha_h}\varphi Y^{\alpha_y} \quad (1)$$

where F is household consumption of goods other than products obtained from hunting and fishing (e.g., other protein sources, foodstuffs, or consumption goods); H is the biomass of animals hunted by the household; Y is the biomass of fish caught by the household; $\alpha_f + \alpha_h + \alpha_y = 1$, a condition representing the degree to which consumption of goods (F), bushmeat (H), and fish (Y) generate utility to the household; γ_ε [0, 1] is the proportion of bushmeat consumed by the household, whereas $(1 - \gamma)$ is the proportion sold; and φ_ε [0, 1] is the proportion of fish consumed by the household, whereas $(1 - \varphi)$ is the proportion sold.

According to Eq. 1, the utility of a given household depends on the consumption of goods (F), bushmeat (H), and fish (Y). The utility of hunter-fisher-worker households exhibits a positive relationship, which decreases with increasing consumption. In other words, utility increases with consumption but at a decreasing rate. Therefore,

$$\frac{DU}{DF} \geq 0; \frac{DU}{DH} \geq 0; \frac{DU}{DY} \geq 0; \frac{D^2U}{DF^2} \leq 0; \frac{D^2U}{DH^2} \leq 0; \frac{D^2U}{DY^2} \leq 0 \quad (2)$$

.

Households also face several constraints, including budgetary constraint, hunting production constraint, fishing production constraint, and labor constraint. Budgetary constraint is determined by

$$\omega L_{off} + (1-\gamma)P_h H + (1-\varphi)P_y Y = P_f F + C_h H + C_y Y + (1-\gamma)H\Theta K \quad (3)$$

where ω is the wage received in exchange for the sale of labor, L_{off} is the labor time dedicated to off-farm work, P_r is the price of good r ($r = f, h, y$), C_h is the unit cost of hunting inputs, C_y is the unit cost of fishing inputs, θ is the probability of detection for the sale of bushmeat, and K is the penalty for the sale of bushmeat. In this case, K corresponds to the equivalent monetary value of the confiscated product obtained from hunting. A penalty was not applied in the case of selling products obtained from fishing.

Thus, the expression ωL_{off} represents household income earned from the sale of labor; $(1 - \gamma)P_h H$ is the income gained from selling bushmeat; $(1 - \varphi)P_y Y$ is the income gained from selling fish; $P_f F$ represents household spending on other consumption goods; $C_h H$ and $C_y Y$ represent the cost of inputs for hunting and fishing activities, respectively; and $(1 - \gamma)H\theta K$ represents the expected monetary value of the penalty incurred for selling bushmeat.

The hunting production function is represented according to Damania et al. (2005) as

$$H = \psi L_h^\beta \quad (4)$$

where ψ is the effect of game stock and capture probability on the biomass harvested; L_h is the labor time dedicated to hunting; and β is a technical parameter that indicates the productivity of the labor force dedicated to hunting, and $0 < \beta < 1$. We assumed a nonlinear relationship between the labor force dedicated to hunting and bushmeat harvest.

The fishing production function is defined as

$$Y = \sigma L_y^\delta \quad (5)$$

where σ is the effect of fish stock and capture probability on the biomass harvested; L_y is the labor time dedicated to fishing; and δ is a technical parameter that indicates the productivity of the labor force dedicated to fishing, and $0 < \delta < 1$. As with hunting, we assumed a nonlinear relationship between the labor force dedicated to fishing and harvest.

The labor constraint is defined as

$$\bar{L} = L_{off} + L_h + L_y \quad (6)$$

where L is the total household labor time available for hunting, fishing, and other income-generating activities. According to this constraint, the time dedicated to productive activities is distributed across off-farm work (L_{off}), labor dedicated to hunting (L_h), and labor dedicated to fishing (L_y).

The economic problem faced by hunter-fisher-worker households is to maximize utility, subject to the previously specified constraints:

$$\begin{aligned} Max\,£_{F,L_h,L_y,\gamma,\varphi} = {} & \alpha_f LnF + \alpha_h Ln\left(\gamma\psi L_h^\beta\right) \\ & + \alpha_y Ln\left(\varphi\sigma L_y^\delta\right) \\ & + \lambda\Big[\omega\left(\bar{L} - L_h - L_y\right) \\ & + \psi L_h^\beta[(1-\gamma)(P_h - \theta K) - C_h] \\ & + \sigma L_y^\delta\left[P_y(1-\varphi) - C_y\right] - P_h F\Big] \end{aligned} \quad (7)$$

.

The solution to this optimization problem yields the supply of labor for both hunting (L_h) and fishing (L_y) and the household demand for bushmeat (γH), fish (φY), and other goods (F) as a function of the parameters $H, Y, L_{off}, P_h, P_y, P_f, C_h, C_y, \omega, \alpha_f, \alpha_h, \alpha_y$, β, δ, ψ, σ, θ, and K. To carry out comparative statics, we estimated the elasticities of the variables of interest (H and Y) to changes in key economic parameters.

The empirical model

Data collection

During a period of 19 months between February 2013 and August 2014, we surveyed 35 households who agreed to participate in the study, or 90% of the total number of households between the two communities (Table 1). Nine and ten of the survey months corresponded to the dry (December–February and July–August) and rainy (March–June and October–November) season, respectively. We designed and implemented four types of surveys. First, we asked community members to complete a registration survey requesting general information about each household. Second, we conducted a weekly household survey in collaboration with 10 field assistants from the communities to gather information about demography, human resources, income, input costs, prices of bushmeat and other foodstuffs, amount of bushmeat sold, and household consumption of bushmeat and other sources of animal protein. Each field assistant was given individual training to conduct survey questionnaires. Third, field assistants interviewed households daily over the same period to minimize data loss due to memory lapses of respondents. Household members were asked to specify the numbers and

Table 2. Observed values of endogenous and exogenous variables in the model.

Variable type	Variable	Symbol	Wajosará	Zábalo
Endogenous	Bushmeat (kg household^{-1} wk^{-1})	H	14.30	16.27
	Fish (kg household^{-1} wk^{-1})	Y	5.65	7.12
	Proportion of hunting products consumed within the household (%)	γ	89	99
	Proportion of fishing products consumed within the household (%)	φ	93	99
	Time spent working off-farm (h household^{-1} wk^{-1})	L_{off}	14.08	9.66
	Time spent hunting (h household^{-1} wk^{-1})	L_h	17.07	23.16
	Time spent fishing (h household^{-1} wk^{-1})	L_y	14.64	22.82
Exogenous	Price of bushmeat (US$/kg)	P_h	5.99	3.86
	Price of fish (US$/kg)	P_y	3.02	2.20
	Food expenditures (US$ household^{-1} wk^{-1})	$P_f F$	32.92	4.89
	Cost of hunting (US$/kg)	C_h	0.44	0.62
	Cost of fishing (US$/kg)	C_y	0.35	0.49
	Off-farm wage (US$/h)	ω	2.69	2.70

species of animals caught, the time dedicated to productive activities, the final use of captured species, and amounts shared with other households. Finally, we asked hunters from both communities to complete a survey after each hunting trip. The purpose of this survey was to obtain complementary information about hunting sites, hunting effort and costs, and biological aspects of the prey. To facilitate completion by non-Spanish speakers, we provided this questionnaire in both Spanish and the relevant indigenous language. We also trained participants to weigh each animal caught using a set of scales.

Calibration of the model

To calibrate the model with the empirical data gathered from each community, we calculated the average weekly scores for the observed endogenous and exogenous variables (Table 2). Bushmeat biomass (H) was calculated as the weight of prey following preparation of the carcass, whereas fish biomass (Y) corresponded to the total catch weight as reported in the surveys because information on the weight of gutted fish was unavailable. Parameters that were not measured directly (i.e., α_f, α_h, α_y, ψ, σ, β, δ) were estimated using the equations derived from the theoretical model and numerical approximation for best adjustment (Table 3). We used these parameter estimates to calibrate the model, establishing correspondence between the observed endogenous variables and their values as predicted by the model based on estimated supply and demand functions.

Simulation

To assess the effect of changes in economic variables on hunting, we simulated different scenarios using both the estimated elasticities and the calibrated model. We constructed scenarios by modifying the key economic parameters one by one (holding all other parameters the same) and analyzing how these changes affected household behavior with regard to hunting in each of the communities under study.

RESULTS

Theoretical model

Estimation of supply and demand functions

Solving the optimization problem yielded the supplies of labor for hunting and fishing as a function of the parameters (see Appendix 1). In agreement with theoretical expectations, Eqs. A1.1 and A1.2, respectively, show that available household labor for hunting or fishing depends directly on: (1) the price of bushmeat or fish, and (2) biological factors that increase natural production of the population of game or fish species. In contrast, labor dedicated to hunting or fishing is inversely related to costs associated with hunting or fishing, wages accrued from the sale of off-farm labor, and, in the case of labor for hunting, the expected penalty for the illicit sale of bushmeat.

The theoretical model also enabled us to derive the demand for bushmeat and fish (see Appendix 1). In general terms, Eqs. A1.3 and A1.4 indicate that the demand for these products depends directly on: (1) the utility provided to the household as a result of their consumption, and (2) household income, which is the sum of expected net income gained from selling bushmeat and fish in addition to activities other than hunting and fishing. In contrast, demand for bushmeat and fish depends inversely on the expected price of these goods. It is important to note that the expected price from the sale of bushmeat reflects the implicit or shadow price of bushmeat that is consumed in the household.

Estimation of elasticities

To assess the response of supply and demand to changes in key economic parameters (wages, input costs, product prices, penalty costs for selling bushmeat, etc.), we applied comparative statics by estimating elasticities for the variables of interest: hunting (H) and fishing (Y; Appendix 2, Table A2.1). For example, the elasticities of the supply of bushmeat and fish were positive with respect to price, as predicted by theory. An increase in the price of bushmeat or fish increased the level of hunting or fishing, respectively, engaged in by the households.

Empirical model

Descriptive statistics

Hunting provided the most important source of protein for households in both communities, i.e., more than that from domestic or commercial sources. Not surprisingly, given the greater number of households, inhabitants of Zábalo hunted more animals over the course of the study than did inhabitants of Wajosará: 2128 animals representing 14,164 kg compared to 416 animals representing 3138 kg, respectively. The rate per household was also higher in Zábalo at 38.1 kg household^{-1} month^{-1} compared to 20.2 kg household^{-1} month^{-1} in Wajosará.

Table 3. Parameter values used to adjust the model.

Parameter	Symbol	Wajosará	Zábalo
Relative preference for food other than bushmeat and fish	α_f	0.28	0.06
Relative preference for bushmeat	α_h	0.54	0.65
Relative preference for fish	α_y	0.13	0.19
Technical parameter indicating labor productivity in the hunting production function	β	0.70	0.65
Technical parameter indicating labor productivity in the fishing production function	δ	0.38	0.21
Technical parameter indicating the biological productivity of game species in the hunting production function	ψ	4.29	7.70
Technical parameter indicating the biological productivity of fish stocks in the fishing production function	σ	9.42	8.06
Probability of detection for the illegal sale of bushmeat	θ	0.01	0.01
Penalty for the illegal sale of bushmeat	K	45.42	30.63

Fig. 2. Mean animal biomass obtained from hunting and fishing by 25 households in Zábalo between February 2013 and August 2014.

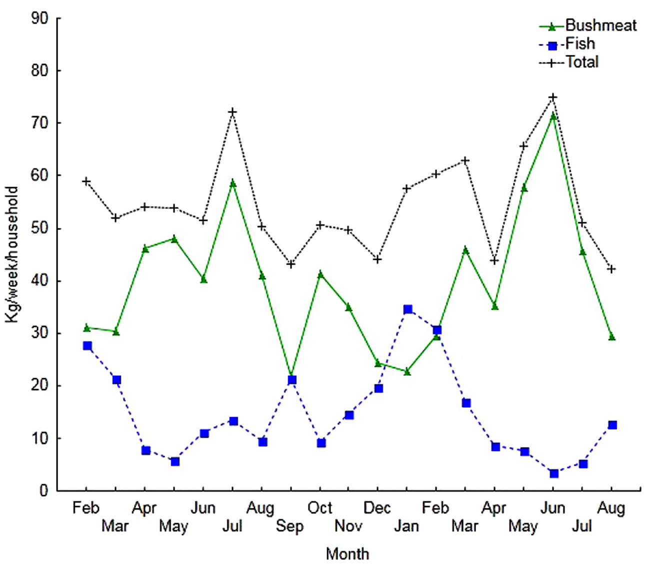
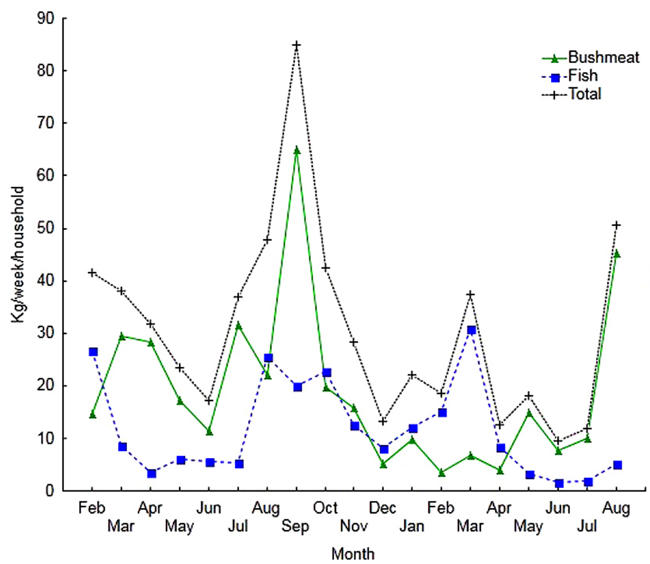


Fig. 3. Mean animal biomass obtained from hunting and fishing by 10 households in Wajosará between February 2013 and August 2014.



Fishing also played an important role in the diet of both communities. Similar to bushmeat, overall fish consumption was higher in Zábalo than in Wajosará: 5004 vs. 1963 kg, respectively. However, consumption rates per household were similar at 13.2 and 12.9 kg household^{-1} month^{-1} in Zábalo and Wajosará, respectively.

Consumption patterns of bushmeat and fish exhibited seasonality in both communities, likely as a result of species' natural cycles (Figs. 2, 3). In Zábalo, there was evidence of complementarity between fish and bushmeat consumption, whereby periods of low availability of one resource were compensated by higher exploitation of the other resource, resulting in a fairly constant rate of overall consumption (Fig. 2).

Comparison of income sources revealed that productive activities were more subsistence-based in Zábalo than in Wajosará, as indicated by the lower total income from productive and extractive activities in Zábalo (Figs. 4, 5). Earnings from off-farm work, which averaged US$26.8 per week per household, represented the nearly exclusive source (> 90%) of household income in Zábalo (Fig. 4), while the other activities were carried out mainly for subsistence purposes. However, off-farm income was unstable and depended on conditions exogenous to the community such as demand for labor by oil companies. In contrast, opportunities for earning income in Wajosará were more diversified. Approximately 96% of income was obtained from off-farm work, forestry, and agriculture, which together averaged US$118.6 per week per household. However, the proportion of total income generated by these activities was highly volatile over the period of study. As in Zábalo, sales of bushmeat and fish were minimal, and hunting and fishing were practiced to meet subsistence needs (Fig. 5).

Total bushmeat and fish harvests, the proportion of bushmeat and fish consumed within the household, labor time dedicated to hunting and fishing, and costs of these activities were greater in Zábalo than in Wajosará. In contrast, labor time dedicated to off-

Fig. 4. Mean household monetary income (US$) generated from productive and extractive activities in Zábalo between February 2013 and August 2014.

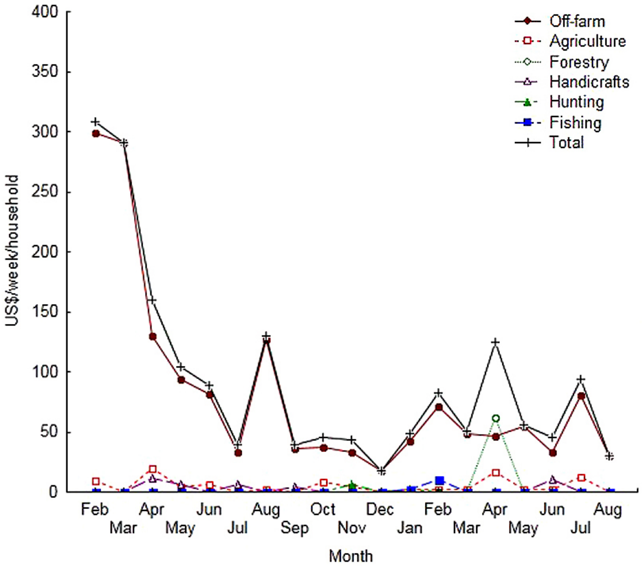
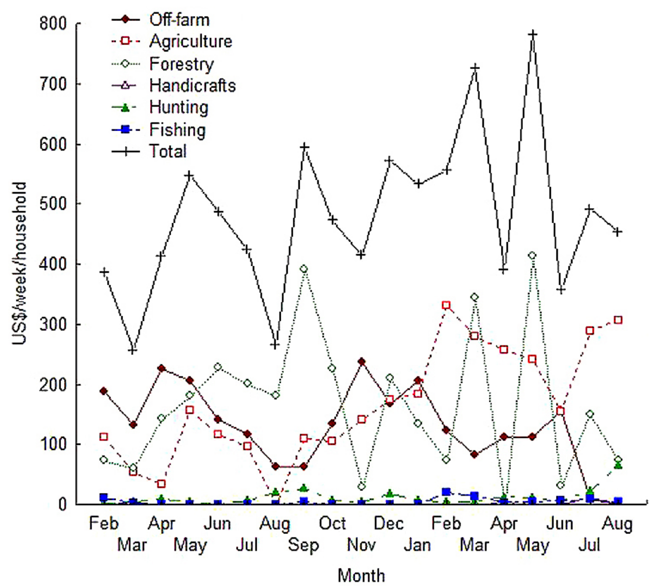


Fig. 5. Mean household monetary income (US$) generated from productive and extractive activities in Wajosará between February 2013 and August 2014.



farm work, price of bushmeat and fish, and especially food expenditures were greater in Wajosará (Table 2).

Calibration

Model calibration enabled numerical estimation of the unknown parameters to reach consistency between observed values (Table 2) and predicted values from demand and supply functions derived from the theoretical model. Table 3 shows the values of the parameters used to calibrate the model.

Elasticities

Based on elasticities calculated using equations in Appendix 2, the empirical data, and calibrated parameters, the exogenous parameters with the greatest effect on harvested biomass were bushmeat price, wages, and the game species' biological characteristics, including productivity and probability of capture (Table 4). A 1% increase in the price of bushmeat increased harvested biomass by 3.1 and 2.8% in Wajosará and Zábalo, respectively. The same increase in the species' biological productivity increased harvested biomass by 3.4 and 2.9%, while this increase in off-farm wages reduced the amount of biomass harvested by 2.4 and 1.9% in Wajosará and Zábalo, respectively. The effects of penalties as well as hunting costs were negative and inelastic. An increase of 1% in these variables reduced the amount of biomass harvested at a rate < 1.

Simulation

Incorporating the observed data collected from the communities into the calibrated model, we simulated changes in harvested biomass as a response to changes in the key economic parameters (Table 5). The parameter that exhibited the greatest effect on harvested biomass was off-farm wages. A 10% wage increase caused 20 and 16% decreases in harvested biomass in Wajosará and Zábalo, respectively. A 10% increase in hunting costs reduced harvested biomass by 2 and 4% in the respective communities.

Table 4. Cross elasticities estimated for key parameters.

Elasticity	Wajosará	Zábalo
$\eta_{H,Ph}$ (bushmeat, price)	3.101	2.789
$\eta_{Y,Py}$ (fish, price)	0.681	0.347
$\eta_{H,\omega}$ (bushmeat, wages)	−2.360	−1.857
$\eta_{Y,\omega}$ (fish, wages)	−0.602	−0.271
$\eta_{H,Ch}$ (bushmeat, cost)	−0.223	−0.444
$\eta_{Y,Cy}$ (fish, cost)	−0.080	−0.076
$\eta_{H,k}$ (bushmeat, penalty)	−0.518	−0.488
$\eta_{H,\theta}$ (bushmeat, monitoring)	−0.518	−0.488
$\eta_{H,\psi}$ (bushmeat, animal stock)	3.360	2.857
$\eta_{Y,\sigma}$ (fish, animal stock)	1.602	1.271

Table 5. Effects of changes in wages and hunting costs on estimated harvested biomass in the two communities.

Exogenous parameter	Symbol	Change in parameter	Biomass (kg [% change]) Wajosará	Zábalo
Estimated harvested biomass (kg)	H		14.3	14.6
Off-farm wages	ω	+10%	11.4 (−20%)	12.2 (−16%)
		+25%	8.4 (−41%)	9.7 (−34%)
		+50%	5.5 (−62%)	6.9 (−53%)
Costs associated with hunting	C_h	+10%	14 (−2%)	13.9 (−4%)
		+25%	13.5 (−5%)	13 (−11%)
		+50%	12.7 (−11%)	11.5 (−21%)

Table 6. Effects of changes in bushmeat price and probability of detection for the illegal sale of bushmeat on estimated bushmeat sold and total harvested biomass in Wajosará and Zábalo.

			Wajosará		Zábalo	
Exogenous parameter	Symbol	Change in parameter	Amount of bushmeat sold (kg [% change])	Change in total harvested biomass (%)	Amount of bushmeat sold (kg [% change])	Change in total harvested biomass (%)
Estimated sold bushmeat (kg)	γH		1.59		0.014	
Bushmeat price	P_h	+10%	2.10 (34%)	3.7	0.018 (30%)	0
		+25%	3.06 (96%)	10.5	0.022 (81%)	0.1
		+50%	5.16 (229%)	25.1	0.036 (183%)	0.2
		−10%	1.12 (−28%)	−3.1	0.010 (−26%)	0
		−25%	0.61 (−61%)	−6.7	0.005 (−58%)	−0.1
		−50%	0.13 (−92%)	−10.1	0.000 (−92%)	−0.1
Probability of being detected	θ	2%	0.87 (−44%)	−4.9	0.009 (−43%)	0
		3%	0.39 (−74%)	−8.2	0.004 (−75%)	−0.1
		5%	0.01 (−99%)	−10.9	0.000 (−94%)	−0.1

Two other exogenous parameters of interest were the price of bushmeat sold on the market and the probability of detection for selling bushmeat. Given that these two variables were assumed to be observed only when the hunter decides to sell bushmeat, the simulation analyzed the effect on bushmeat sold rather than the total biomass harvested. Price had an important effect on the decision to sell bushmeat. A 10% increase in the price of bushmeat induced an increase of roughly 30% in the amount of meat sold in both communities (Table 6). However, this percentage was only relevant in absolute terms in Wajosará, where the actual proportion of meat sold was approximately 11%, which implied a 3.7% reduction in total harvested biomass. In contrast, almost all bushmeat was consumed in Zábalo, so the effect on sales of bushmeat was negligible in absolute terms. On the other hand, reductions in the price of bushmeat on the order of 25% reduced commercial hunting by approximately 60%, which represents nearly 7% of the total harvested biomass at Wajosará.

Given that monitoring and regulations prohibiting commercial hunting were rare in these communities, we assumed a benchmark parameter $\theta = 0.01$, i.e., the probability of detection for selling bushmeat was set at 1%. The penalty K was estimated as the market value of the confiscated bushmeat, or the income forgone by the hunter when caught, which was calculated as the average weight of the bushmeat sold times the price per unit weight. Simulation of this relationship showed that increasing this probability to 2% would reduce commercial hunting by 44%, and increasing it to just 5% implies that commercial hunting would virtually cease altogether.

DISCUSSION

Effect of economic variables on harvested biomass

According to the model, the most important economic variable affecting indigenous hunters' behavior was off-farm wages. In the case of illegal commercial hunting, bushmeat price and probability of detection for selling bushmeat also had important effects on hunter behavior in terms of the amount of bushmeat sold, but not in terms of total harvest. Estimated elasticities exhibited signs as predicted by economic theory.

Given the economic development currently underway in the Ecuadorian Amazon, rising wage levels will likely increase indigenous residents' incentive to seek off-farm work and thereby devote less time to hunting. Simulating a 10% wage increase resulted in a 16–20% reduction in harvested biomass in the communities, while a 50% increase diminished harvested biomass by > 50%. Thus, an increase in wages would improve biodiversity conservation by reducing dependence on wildlife, although the stability of paid work has been shown to have even more of an effect on reducing bushmeat consumption (Sirén et al. 2006). However, because higher salaries also increase the opportunity cost of hunting, the theoretically positive effect of reducing the time dedicated to hunting could be canceled out if hunters employed more efficient methods that were previously unavailable due to cost. For example, higher incomes earned from activities other than hunting and fishing, such as agriculture, would be detrimental to wildlife populations if hunters used firearms more frequently (Damania et al. 2005). Our data suggest that the switch to more effective hunting technology is possible because 24% of animals in Zábalo and 10% in Wajosará are hunted with machetes or makeshift spears. The ambiguous effects of economic development on the pervasiveness of hunting have also been reported by Demmer et al. (2002). However, the model we employed does not capture this effect. In contrast, Godoy et al. (2010) maintain that no significant association exists between increased income and bushmeat consumption. Depending on the particular context, wildlife conservation policies designed to reduce hunting by increasing wages can have unintended consequences and may be less effective than direct regulation.

As expected, increased hunting and fishing costs reduced the amount of biomass harvested, although the magnitude of this elasticity was the lowest among the variables examined. Given that fuel and ammunition are essential to hunters and fishers, even relatively large increases in the cost of these inputs do little to deter hunting and fishing. A simulated 10% increase in costs caused a decline of < 5% in harvested biomass, while a 50% increase caused 11 and 21% declines in Wajosará and Zábalo, respectively. This effect could also be influenced by the fact that bushmeat is considered to be a necessary good by the indigenous communities (Wilkie and Godoy 2001).

Also in accordance with expectations, the price of game meat was positively related to the amount harvested. A 50% price rise increased the harvested biomass by nearly 25% in Wajosará. In contrast, the effect was almost null in Zábalo, where bushmeat is rarely commercialized because of the community's isolation from the market economy. Higher prices foster illegal trade by creating an incentive to sell a greater proportion of what is captured, leading to the overexploitation of game species and putting wildlife populations at risk (Damania et al. 2005). The unfortunate outcome of open-access systems with high prices is exhaustion of natural resources and deterioration of social well-being (Clark 1990). Conversely, model simulation revealed that a 50% drop in prices reduced the amount of bushmeat sold by > 90% in both communities. Although the effect on the total amount of biomass harvested was limited because of the small proportion sold, the magnitude of the elasticity suggests that in communities where bushmeat trade is important, policies that effectively reduce the price of bushmeat could promote wildlife conservation and sustainable livelihoods (Damania et al. 2005).

Given that monitoring and regulation of hunting are practically nonexistent in the study area, we conducted further simulations to evaluate the effect of improved monitoring and found that commercial hunting virtually disappears past a threshold of 5% detection probability. These results show a more effective role of monitoring than that reported by Damania et al. (2005) and indicate that a robust inspection regime would have a significant effect on the illicit bushmeat trade. Such a regime would require understanding of the patterns and mechanisms of market access and would ideally incorporate some form of community-based control. As with price reduction, the benefits of regulation in terms of wildlife conservation would be limited because the percentage of bushmeat currently sold is small, but this represents an important tool for the future if the communities become increasingly linked to markets.

Differences in wildlife harvesting between communities

Differences between the two communities with regard to market integration and location relative to the reserve help explain different levels of bushmeat harvest and fishing. The results show that foodstuffs of wildlife origin constituted the principal source of protein for most indigenous households in the research area. Hunting provided an average of 0.10 and 0.33 kg person^{-1} day^{-1} of butchered bushmeat in Wajosará and Zábalo, respectively. The latter figure is similar to the 0.44 kg person^{-1} day^{-1} of unbutchered bushmeat harvested, reported for an A'i Cofán community from Ecuador (Schel 1997). By contrast, the amount observed in Wajosará was much less than the 0.42 kg person^{-1} day^{-1} of butchered bushmeat reported for a separate Secoya indigenous community (Vickers 1980). Differences in bushmeat consumption by Secoya communities between our and earlier studies could be explained by declines in forest cover in the Wajosará territory and surrounding landscape due to advancement of the agricultural frontier, mainly by oil palm plantations, and by greater integration of these communities into goods and labor markets than in the past (Vickers 1991). Located in relative geographical and economic isolation, Zábalo, in contrast, remains highly dependent on natural supplies of protein.

Fishing appears to be less important than hunting and is markedly seasonal. This activity is more common in the dry season during September and the first months of the year, when several species swim up the Aguarico River in great numbers to spawn in the smaller tributaries (E. de la Montaña, *personal observation*). This reliable bonanza of fish is reflected in the monthly catch data during the dry season, when the biomass of fish caught is similar or even greater than the biomass captured through hunting. The complementarity between both sources of protein was more evident in Zábalo than in Wajosará, again because of the former community's higher degree of dependence on natural resources.

Insights for further research

Further iterations of the basic model that change the assumptions of household homogeneity, a representative game species, and a single hunting technique represent a promising area of research. Convergence of the results despite different levels of market integration and forest conservation in the two communities supports the idea that the model can be applied to similar groups whose subsistence depends heavily on hunting and fishing. Depending on the specific socioeconomic and hunting context, model constraints can be modified to incorporate different productive activities, labor conditions, and wildlife harvesting techniques. We propose selecting the species to be analyzed based on conservation status (i.e., nonthreatened or endangered) and socioeconomic drivers such as market price and consumer preferences for bushmeat. The production function can be adjusted to understand better the effect of particular game species' biological characteristics. The model also allows incorporation of different types of hunting techniques through the inclusion of specific production functions. Although increasing the number of species or techniques will greatly increase model complexity and require more empirical information, the model provides a powerful tool for gaining insight into hunters' economic decision-making.

A limitation of the model is the omission of agricultural activity. For most communities, subsistence agriculture is part of the daily activities that demand time from household members. Given the complexities associated with collecting too much data and modeling several decision variables, we decided to focus on fishing and hunting because they behave as close substitutes. Moreover, previous observations in the study area indicated that time devoted to agriculture tends to be fixed and inelastic relative to other activities such as hunting or fishing. Despite the omission of agricultural activity, the key implications of the model are not drastically affected. In contexts in which time dedicated to agricultural activity is affected by labor demand for hunting, the model can be adjusted to include it.

CONCLUSION

The goal of developing a simple model of the indigenous household economy is to establish a solid theoretical basis for analysis and policy development that promote sustainable bushmeat extraction and local food security. To our knowledge, this is the first study in Latin America that models the effects of conservation and development policies on hunter behavior and discusses the implications for biodiversity protection and indigenous livelihoods. Nineteen months of data collection enabled us to capture the seasonal variations that affect the biological systems and related economic activity. The results show that changes in off-farm wages have the greatest effect on harvested biomass in the communities studied. Bushmeat price and penalties for illegal trade have greater effects on harvested biomass in communities more tightly integrated with the market economy than in isolated communities. The results agree with those of similar studies and can be applied to other regions. However, because the factors that condition the consumption of bushmeat are complex and operate at a very local level, we urge caution when making broad generalizations of the results and discussing management implications. Although the results presented here are based on a simplification of reality, model constraints can be adjusted to reflect more complex socioeconomic and hunting contexts. Development of the model will enable researchers to gain further insights into hunters' economic decision-making and understand more fully the factors that impinge on the consumption of bushmeat in similar communities.

Responses to this article can be read online at:
http://www.ecologyandsociety.org/issues/responses.php/8032

Acknowledgments:

Financial support was provided by the Prometeo Project of the Secretariat of Higher Education, Science, Technology and Innovation (SENESCYT) of Ecuador, the Spanish Agency for International Development Cooperation (MAEC-AECID), the Initiative for Conservation in the Andean Amazon (ICAA) funded by the United States Agency for International Development (USAID), and the Conservation Strategy Fund (CSF). The Center for International Forestry Research (CIFOR) provided financial support for the publication of this article. We are sincerely grateful to the people of Wajosará and Zábalo, especially those who collaborated as field assistants. We also thank Lizeth Ortiz and Shirley Zurita for support with data analysis. Two anonymous reviewers provided valuable comments that improved the quality of the manuscript.

LITERATURE CITED

Bodmer, R. E., E. P. Lozano, and T. G. Fang. 2004. Economic analysis of wildlife use in the Peruvian Amazon. Pages 191-207 *in* K. M. Silvius, R. E. Bodmer, and J. M. V. Fragoso, editors. *People in nature: wildlife conservation in South and Central America.* Columbia University Press, New York, New York, USA.

Brashares, J. S., C. D. Golden, K. Z. Weinbaum, C. B. Barrett, and G. V. Okello. 2011. Economic and geographic drivers of wildlife consumption in rural Africa. *Proceedings of the National Academy of Sciences* 108(34):13931-13936. http://dx.doi.org/10.1073/pnas.1011526108

Brooks, T. M., R. A. Mittermeier, G. A. B. da Fonseca, J. Gerlach, M. Hoffmann, J. F. Lamoreux, C. G. Mittermeier, J. D. Pilgrim, and A. S. L. Rodrigues. 2006. Global biodiversity conservation priorities. *Science* 313:58-61. http://dx.doi.org/10.1126/science.1127609

Brown, D. 2003. *Bushmeat and poverty alleviation: implications for development policy.* ODI Wildlife Policy Briefing 2. Overseas Development Institute, London, UK. [online] URL: http://www.odi.org/publications/2427-bushmeat-poverty-alleviation-implications-development-policy

Clark, C. W. 1990. *Mathematical bioeconomics: the optimal management of renewable resources.* Wiley-Interscience, New York, New York, USA.

Damania, R., E. J. Milner-Gulland, and D. J. Crookes. 2005. A bioeconomic analysis of bushmeat hunting. *Proceedings of the Royal Society B* 272:259-266. http://dx.doi.org/10.1098/rspb.2004.2945

de la Montaña, E. 2013. Cacería de subsistencia de distintos grupos indígenas de la Amazonía ecuatoriana. *Ecosistemas* 22 (2):84-96. http://dx.doi.org/10.7818/ecos.2013.22-2.13

de Merode, E., K. Homewood, and G. Cowlishaw. 2004. The value of bushmeat and other wild foods to rural households living in extreme poverty in Democratic Republic of Congo. *Biological Conservation* 118(5):573-581. http://dx.doi.org/10.1016/j.biocon.2003.10.005

Demmer, J., R. Godoy, D. Wilkie, H. Overman, M. Taimur, K. Fernando, R. Gupta, K. McSweeney, N. Brokaw, S. Sriram, and T. Price. 2002. Do levels of income explain differences in game abundance? An empirical test in two Honduran villages. *Biodiversity and Conservation* 11(10):1845-1868. http://dx.doi.org/10.1023/A:1020305903156

Fa, J. E., and C. A. Peres. 2001. Game vertebrate extraction in African and Neotropical forests: an intercontinental comparison. Pages 203-241 *in* J. D. Reynolds, G. M. Mace, K. H. Redford, and J. G. Robinson, editors. *Conservation of exploited species.* Cambridge University Press, Cambridge, UK.

Fa, J. E., C. A. Peres, and J. Meeuwig. 2002. Bushmeat explotation in tropical forests: an intercontinental comparison. *Conservation Biology* 16(1):232-237. http://dx.doi.org/10.1046/j.1523-1739.2002.00275.x

Franzen, M. 2006. Evaluating the sustainability of hunting: a comparison of harvest profiles across three Huaorani communities. *Environmental Conservation* 33(1):36-45. http://dx.doi.org/10.1017/S0376892906002712

Godoy, R., E. A. Undurraga, D. Wilkie, V. Reyes-García, T. Huanca, W. R. Leonard, T. McDade, S. Tanner, V. Vadez, and TAPS Bolivia Study Team. 2010. The effect of wealth and real income on wildlife consumption among native Amazonians in Bolivia: estimates of annual trends with longitudinal household data (2002–2006). *Animal Conservation* 13(3):265-274. http://dx.doi.org/10.1111/j.1469-1795.2009.00330.x

Instituto Nacional de Estadística y Censos. 2010. *Censo de población y de vivienda: resultados.* Instituto Nacional de Estadística y Censos, Quito, Ecuador. [online] URL: http://www.inec.gob.ec/cpv/

Iwamura, T., E. F. Lambin, K. M. Silvius, J. B. Luzar, and J. M. V. Fragoso. 2014. Agent-based modeling of hunting and subsistence agriculture on indigenous lands: understanding interactions between social and ecological systems. *Environmental Modelling and Software* 58:109-127. http://dx.doi.org/10.1016/j.envsoft.2014.03.008

Levi, T., G. H. Shepard Jr., J. Ohl-Schacherer, C. A. Peres, and D. W. Yu. 2009. Modelling the long-term sustainability of indigenous hunting in Manu National Park, Peru: landscapescale management implications for Amazonia. *Journal of Applied Ecology* 46(4):804-814. http://dx.doi.org/10.1111/j.1365-2664.2009.01661.x

Milner-Gulland, E. J., E. L. Bennett, and Society for Conservation Biology 2002 Annual Meeting Wild Meat Group. 2003. Wild meat: the bigger picture. *Trends in Ecology and Evolution* 18(7):351-357. http://dx.doi.org/10.1016/S0169-5347(03)00123-X

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-858. http://dx.doi.org/10.1038/35002501

Olson, D. M., and E. Dinerstein. 2002. The global 200: priority ecoregions for global conservation. *Annals of the Missouri Botanical Garden* 89(2):199-224. http://dx.doi.org/10.2307/3298564

Peres, C. A. 2000. Evaluating the impact and sustainability of subsistence hunting at multiple Amazonian forest sites. Pages 31-56 *in* J. G. Robinson and E. L. Bennett, editors. *Hunting for sustainability in tropical forests.* Columbia University Press, New York, New York, USA.

Rivadeneira, C. 2007. Reserva de producción de fauna Cuyabeno. Pages 35-47 *in* ECOLAP and MAE, editors. *Guía del patrimonio de áreas naturales protegidas del Ecuador.* ECOFUND, FAN, DarwinNet, and IGM, Quito, Ecuador.

Robinson, J. G., and K. H. Redford. 1991. Sustainable harvest of Neotropical forest mammals. Pages 415-429 *in* J. G. Robinson and K. H. Redford, editors. *Neotropical wildlife use and conservation.* University of Chicago Press, Chicago, Illinois, USA.

Schel, L. 1997. Cacería de vertebrados terrestres y recomendaciones para organizar los esfuerzos de conservación de especies en la comunidad Cofán de Zábalo, Reserva de Producción Faunística de Cuyabeno, Amazonía Ecuatoriana. Thesis. Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

Shepard, G. H. Jr., T. Levi, E. G. Neves, C. A. Peres, and D. W. Yu. 2012. Hunting in ancient and modern Amazonia: rethinking sustainability. *American Anthropologist* 114(4):652-667. http://dx.doi.org/10.1111/j.1548-1433.2012.01514.x

Sierra, R., editor. 1999. *Propuesta preliminar de un sistema de clasificación de la vegetación para el Ecuador continental.* INEFAN-EcoCiencia, Quito, Ecuador. [online] URL: http://www.ecociencia.org/archivos/RSierra_PropVegEcuador_1999-120103.pdf

Sirén, A. H., J. C. Cardenas, and J. D. Machoa. 2006. The relation between income and hunting in tropical forests: an economic experiment in the field. *Ecology and Society* 11(1):44. [online] URL: http://www.ecologyandsociety.org/vol11/iss1/art44/

Sirén, A., P. Hambäck, and J. Machoa. 2004. Including spatial heterogeneity and animal dispersal when evaluating hunting: a model analysis and an empirical assessment in an Amazonian community. *Conservation Biology* 18(5):1315-1329. http://dx.doi.org/10.1111/j.1523-1739.2004.00024.x

Vickers, W. T. 1980. An analysis of Amazonian hunting yields as a function of settlement age. Pages 7-30 *in* R. B. Hames and K. M. Kensinger, editors. *Studies in hunting and fishing in the Neotropics 2.* Bennington College, Bennington, Vermont, USA.

Vickers, W. T. 1991. Hunting yields and game composition over ten years in an Amazon Indian territory. Pages 53-81 *in* J. G. Robinson and K. H. Redford, editors. *Neotropical wildlife use and conservation.* University of Chicago Press, Chicago, Illinois, USA.

Vié, J. C., C. Hilton-Taylor, and S. N. Stuart, editors. 2009. *Wildlife in a changing world: an analysis of the 2008 IUCN Red List of Threatened Species.* IUCN, Gland, Switzerland. [online] URL: https://portals.iucn.org/library/efiles/documents/RL-2009-001.pdf

Wilkie, D. S., and R. A. Godoy. 2001. Income and price elasticities of bushmeat demand in lowland Amerindian societies. *Conservation Biology* 15(3):761-769. http://dx.doi.org/10.1046/j.1523-1739.2001.015003761.x

Zapata-Ríos, G., C. Urgilés, and E. Suárez. 2009. Mammal hunting by the Shuar of the Ecuadorian Amazon: Is it sustainable? *Oryx* 43(3):375-385. http://dx.doi.org/10.1017/s0030605309001914

Appendix 1. Supply and demand functions.

Equation A1.1. Supply function of labor for hunting.

$$L_h = \left[\frac{\beta\psi(P_h - \theta K - C_h)}{\omega}\right]^{1/_{1-\beta}}$$

Equation A1.2. Supply function of labor for fishing.

$$L_y = \left[\frac{\delta\sigma(P_y - C_y)}{\omega}\right]^{1/_{1-\delta}}$$

Equation A1.3. Demand function for bushmeat.

$$\gamma H = \frac{\alpha_h}{P_h - \theta K}\left[H(P_h - \theta K - C_h) + Y(P_y - C_y) + \omega L_{off}\right]$$

Equation A1.4. Demand function for fish.

$$\varphi Y = \frac{\alpha_y}{P_y}\left[H(P_h - \theta K - C_h) + Y(P_y - C_y) + \omega L_{off}\right]$$

Appendix 2. Elasticities.

Table A2.1. Elasticities of hunting and fishing with respect to key exogenous variables

Variable/ parameter	Hunting (*H*)	Fishing (*Y*)
P_h	$\eta_{H,P_h} = \frac{\beta P_h}{(1-\beta)(P_h - \theta k - C_h)} > 0$	
P_y		$\eta_{Y,P_y} = \frac{\delta P_y}{(1-\delta)\left(P_y - C_y\right)} > 0$
ω	$\eta_{H,\omega} = -\frac{\beta}{1-\beta} < 0$	$\eta_{Y,\omega} = -\frac{\delta}{1-\delta} < 0$
C_h	$\eta_{H,C_h} = -\frac{\beta C_h}{(1-\beta)(P_h - \theta k - C_h)} < 0$	
C_y		$\eta_{Y,C_y} = -\frac{\delta C_y}{(1-\delta)(P_y - C_y)} < 0$
K	$\eta_{H,k} = -\frac{\beta\theta k}{(1-\beta)(P_h - \theta k - C_h)} < 0$	
θ	$\eta_{H,\theta} = -\frac{\beta\theta k}{(1-\beta)(P_h - \theta k - C_h)} < 0$	
ψ	$\eta_{H,\psi} = \frac{1}{1-\beta} > 0$	
σ		$\eta_{Y,\sigma} = \frac{1}{1-\delta} > 0$