Revisiting Optimal Foraging Theory (OFT) in a Changing Amazon: Implications for Conservation and Management

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Abstract

Hunter decision-making influences prey selection and is key to understanding the impacts of hunting on biodiversity. Optimal foraging theory (OFT) is often used to describe the decision-making and prey selection of subsistence hunters. We examined the behavior and game meat use of hunters in an indigenous Amazonian community and used free listing and generalized linear mixed-effects models under the framework of OFT to assess the decision-making of individuals who hunt for economic gain and subsistence. We found that prey selection generally followed OFT, and was influenced by hunters' skills, patch choice, and characteristics of the prey encountered. Hunters preferred paca (*Cuniculus paca*), collared peccary (*Pecari tajacu*), and brocket deer (*Mazama americana*), and only partially preferred tapir (*Tapirus terrestris*) and large-bodied primates likely due to economic influences such as access to markets and prices, contrary to OFT predictions.

Keywords Subsistence hunting · Decision-making · Game meat · Mammals · Prey selection · Wild game · Optimal foraging theory · Maijuna (Orejón) · Northeastern Amazon · Peru

Introduction

Tropical forests support an estimated 50% of the world's described species and many more not described to date (Groombridge & Jenkins, 2002). Logging and overhunting are frequently cited as drivers of biodiversity loss, particularly in the Amazon Basin of South America (Benítez-López et al., 2017; Brancalion et al., 2018; Milner-Gulland

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& Bennett, 2003; Redford, 1992; Schipper et al., 2008). Overhunting often results from commercial hunting by local hunters who sell game meat to local markets in urban centers throughout the Amazon Basin (El Bizri et al., 2020; Lozano & Fang, 2004; Mayor et al., n.d.). While the effects of intensive hunting pressure are well studied (Benítez-López et al., 2017), the impacts of small-scale hunting on mammalian populations are often confounded by other disturbances, such as habitat degradation (Peres, 2001; Redford, 1992; Remis & Jost Robinson, 2012). Even in the absence of other disturbances, variability can still be introduced due to differences among hunting practices and behavior of individual hunters and communities. Optimal foraging theory (OFT) (Charnov, 1976) is often used to describe the decision-making behavior of hunter-gatherers. OFT is a set of models that dictate the breadth and proportion of prey items a predator should take (diet breadth model) as well as where those prey should be taken (patch choice model) (Hames & Vickers, 1982).

Under the diet breadth model (Emlen, 1966), prey are ranked according to the return rate afforded to the hunter, often calculated as the caloric intake gained per hour spent pursuing, killing, and processing the animal (Alvard, 1993; Bettinger et al., 2015; Smith et al., 1983; Winterhalder, 1981). As such, OFT focuses mainly on hunting for subsistence, not

economic gain. A prey item is included in the diet breadth if the return rate of pursuing and killing the animal is higher than the expected mean return rate of ignoring the species and continuing to search for a higher ranked species, thereby maximizing the hunter's short-term harvesting rate (Alvard, 1993; Bettinger et al., 2015; Hawkes & O'Connell, 1992; Smith et al., 1983; Stephens & Krebs, 1986). A key prediction of the diet breadth model is the zero–one rule, which states that hunters should always pursue species within the diet breadth and never pursue species outside, thereby never exhibiting "partial preferences" for prey (Bettinger et al., 2015; Levi et al., 2011a; Stephens & Krebs, 1986). However, studies have shown that partial preferences could be introduced by conservation behaviors, taboos, and economic influences (Alvard, 1993; Hames, 2007). In the case where hunting causes declines of high-ranked species and the search time for those species increases, new, more abundant species may be added to the diet breadth (Bettinger et al., 2015; Hames & Vickers, 1982; Pyke et al., 1977). Erosion of traditional taboos and technologies may also allow new species to be introduced to the diet breadth (Hames, 2007; Hames & Vickers, 1982; Hill & Hawkes, 1983; Vickers, 1980). Frequently, the species that provide the highest return rate are the largest bodied species, which are also vulnerable to extirpation due to low reproductive rates (Mayor et al., 2017; Redford, 1992; Vickers, 1991).

The patch choice model (Charnov, 1976) assumes that hunters are central place foragers who exploit resources nearby the community first, eventually producing a gradient of game availability (Venkataraman et al., 2017; Winterhalder, 2001). The model states that hunters will choose to hunt in patches where resource availability is highest, and therefore the return rate is highest (Bettinger et al., 2015). However, species that become rare in depleted patches are still pursued when encountered and are not dropped from the diet breadth (Bettinger et al., 2015; Hames & Vickers, 1982; Winterhalder & Lu, 1997). Hunters who do not change their patch choice in response to game depletion are forced to expand their diet breadth to include more abundant, less preferred species (Charnov, 1976; Hames & Vickers, 1982; Levi et al., 2011a).

The choices and characteristics of individual hunters or hunts may influence the effectiveness of OFT in predicting hunter behavior, including the hunter's skill (Hill et al., 1987), beliefs (Lemos et al., 2021), food preferences (Chaves et al., 2020) and cultural taboos (Hames, 2007), the conditions of the hunt (Levi et al., 2011a, b), the characteristics of the animal encountered, and the available technology (Bettinger, 2009; Hames & Vickers, 1982). Individuals may also have different goals and currencies and therefore return rates (Mithen, 1989). For example, a hunter may want meat for subsistence to feed his family, for gifting to neighbors to further his social standing (Bird & Bird, 1997; Hawkes et al., 2001), or for market sales for economic gain (Ayres

et al., 1991). Previous studies on the applications of OFT to human hunters have aggregated data from individual hunters to be analyzed on a community level (e.g., Hill et al., 1985; Hurtado et al., 1985); however, the variation due to these individual influences is then lost (Asmhyr et al., 2013; Chaves et al., 2020; Mithen, 1989).

We use OFT to examine hunting behavior, partial preferences, patch choice, and game meat economics in an indigenous Amazonian community that has access to the regional market. We use free-listing of hunter preferences and generalized linear mixed-effects models to assess whether OFT applies and accurately describes individual hunter behavior where economic considerations influence hunter decision-making alongside subsistence pressures. Specifically, we address the following questions:

1. Which species hunters sell and how much are they worth?
2. Which species hunters prefer, and do those preferences align with what would be predicted by OFT?
3. Does OFT accurately predict individual hunter decision-making upon encountering prey?

Methods

Study Site

Fieldwork was conducted in collaboration with the Maijuna (Orejón) indigenous group of the northeastern Peruvian Amazon. The Maijuna are a Western Tucanoan people with a population of approximately 600 individuals (Gilmore, 2010). There are four Maijuna communities: Puerto Huamán and Nueva Vida along the Yanayacu River, Sucusari along the Sucusari River, and San Pablo de Totolla (Totoya) along the Algodón River (Fig. 1). These three river basins are part of the ancestral territory of the Maijuna and no other communities are located within this area (Gilmore, 2010). The Maijuna traditionally lived in the area between these three rivers until the early 1900s when they began to slowly migrate downriver due to influence from missionaries and *patrones* (colonists and their descendants who exploited indigenous labor to harvest forest resources) to where they eventually formed their current communities (Bellier, 1993, 1994; see also Gilmore, 2010 for greater ethnographic context).

We conducted fieldwork in the Maijuna community of Sucusari (72.92995° W, 3.24373° S) (Fig. 1). Sucusari is approximately 126 km by river from the city of Iquitos, the commercial and political center of Loreto. However, the trip can be shortened to 70 km by crossing the narrow isthmus between the Napo and Amazon Rivers by road at Mazán, a small town. The titled land of the community encompasses 4,771 hectares and adjoins the
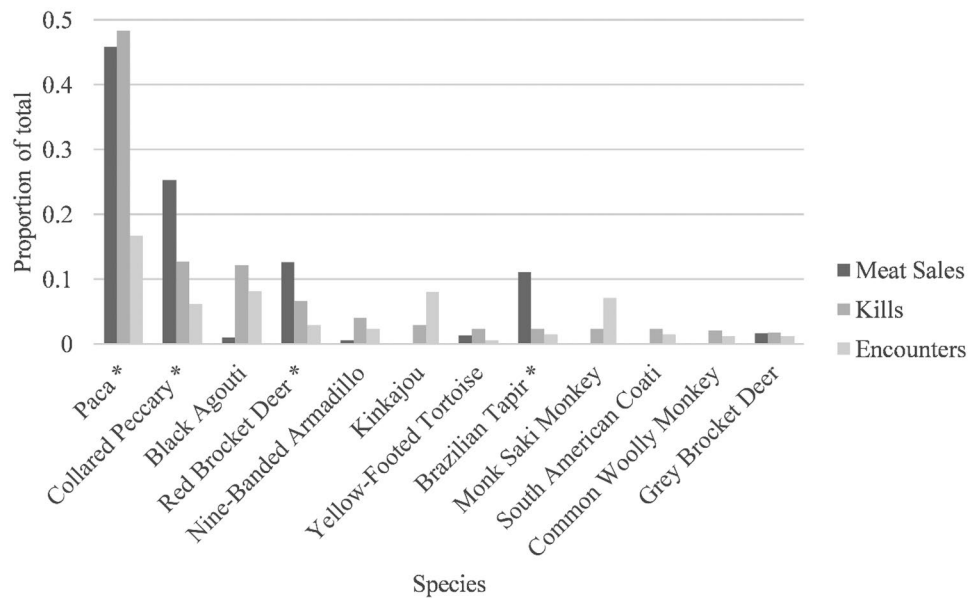
Fig. 1 Study area, including the Maijuna community of Sucusari and the Maijuna-Kichwa Regional Conservation Area (MKRCA)
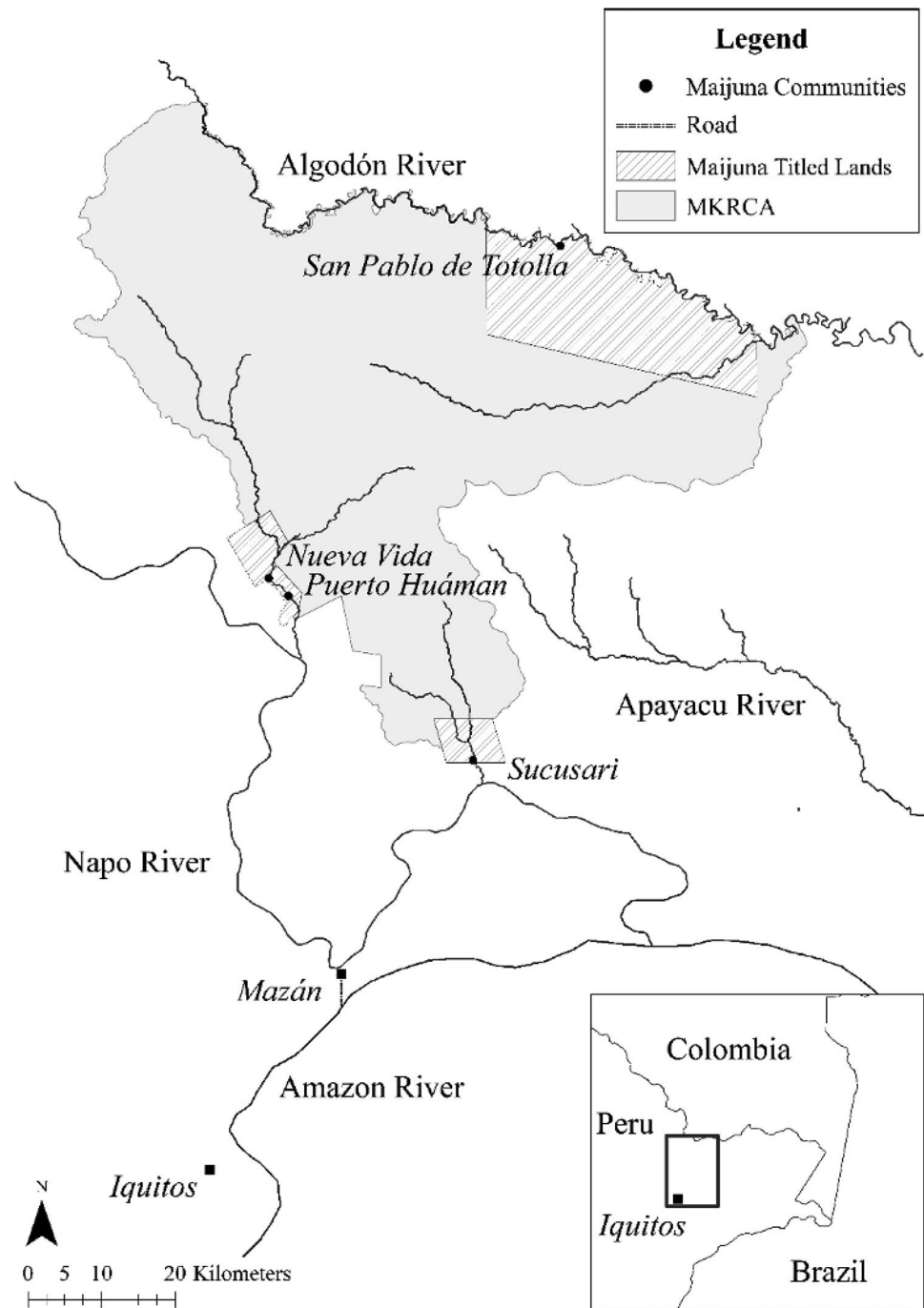
Maijuna-Kichwa Regional Conservation Area (MKRCA), a 391,040-hectare protected area that is made up of Maijuna ancestral lands and collaboratively managed by Maijuna and Kichwa indigenous communities and the regional government (El Peruano, 2015). The community has a population of 166 residents made up of both single and multifamily households, of whom 59% are ethnically Maijuna, 35% are mestizos (individuals of mixed Amerindian and Iberian descent; Coomes & Ban, 2004), and 6% are indigenous Kichwa (Roncal et al., 2018).

Subsistence and income generating strategies of community members include hunting, fishing, swidden-fallow agriculture, and the gathering of various non-timber forest products (NFTPs) (Gilmore, 2010). Community members sell game meat in the city of Iquitos, in towns surrounding their communities on the Napo River, and in the market of Mazán (Gilmore et al., 2020). Mean household income of Maijuna families averages about 505 USD annually (Horn et al., 2012; Fig. 2). Game meat is also traditionally gifted to neighbors, family, and friends within the community. Only

Fig. 2 Proportions of total meat by mass that was sold, number of animals killed, and number of animals encountered broken down by species and ordered by number of kills. Only species that were killed more than five times during the study period are shown. Note: *indicates a preferred game species, as determined by salience indices

Data Collection and Analysis

We conducted weekly semi-structured interviews in Spanish (Berg & Lune, 2014) with 19 hunters (90.48% of all active hunters) to capture decision-making processes on prey selection and the economics of hunting for a ten-month period from September 2018 to June 2019. The mean age of hunters interviewed was 41 years old, with a range of 22 to 68. Of the 19 hunters interviewed, ten were ethnically Maijuna, eight were mestizo, and one was Kichwa. If a hunter was not home when we visited his house, we made at least two more attempts during the days immediately following the initial visit. If a hunter was still not at home after three visits, we gathered the data for that week during the following week's interview. During the interview, for each hunt, we first asked hunters what time they went hunting, how long the hunt lasted, and the mode(s) of travel they used (i.e., by boat, canoe, or on foot). We then asked which animals they encountered during each hunt and where, asking them to indicate the location on a base map of locally relevant points, and if they had attempted to kill the animal. If they did not try to kill the animal, we asked why they chose not to. We digitized all encounter and kill locations, extracting

coordinates using ArcGIS (ESRI, 2018). We coded interview responses focused on decision-making (Berg & Lune, 2014), where reasons for not shooting an animal were coded and then grouped into overall themes. These themes were "Killed," "Escaped," "Low Return," "Attack-Limited," and "Conservation," following classifications of behavior informed by Alvard (1993) and OFT (Table 1). We used these codes to calculate partial preferences based on pursuit rate, or the proportion of encounters in which the animal was killed, shot at, or pursued until it escaped.

When a hunter reported that he killed an animal, we asked how many kg of meat he sold, to whom he sold it, and at what price. Each hunter was also asked how many kg of meat he had consumed with his family and how many kg he had gifted and to whom. All hunters in the community have spring scales that they use to measure the mass of a carcass and portions to sell or gift.

We conducted separate semi-structured interviews in Spanish (Berg & Lune, 2014) with 17 of the 19 hunters at the end of the study period to provide context to observed pursuit rates and relative species-specific preferences. Two hunters were not interviewed because they moved away from the community for an extended period while the survey was conducted. We asked hunters to list three species they preferred to kill while hunting (a) by canoe, (b) by land, (c) at a mineral lick, and (d) for game meat to sell. These different hunting methods (a-c) were chosen because hunters noted that they look for different species using each technique. Freelisting is an interview method that can be used to determine the salience of named species (Quinlan, 2005; Roncal et al., 2018). In this case, it allowed us to rank species in relation to individual hunter preferences. Following Quinlan (2005), we used the following formula to determine

men hunt in Sucusari (Roncal et al., 2018), hunting opportunistically from canoes, on foot, and at mineral licks (Gilmore et al., 2020). All hunters use shotguns or machetes for slow-moving game species. Two hunters in the community use dogs to hunt. Only community members from Sucusari have hunting rights in the Sucusari titled lands and MKRCA. Our research team has been working in the Sucusari community since 1999, which has allowed us to foster strong and close relationships with hunters in the community.

Table 1 Themes of reasons hunters gave for not shooting at an animal during an encounter, grouped according to Alvard (1993) and OFT, in an indigenous community in the Peruvian Amazon

Code	Explanation	Sample Interview Responses
Killed	The animal was killed without the use of a shotgun	I chased it into its hole and killed it with my machete
Escaped	The hunter intended to kill the animal and may have pursued it, but the animal escaped	It ran away and left me behind It escaped from me
Low Return	Killing the animal would have been too much effort for the return it gave	It was too small It was too hard to get to
Attack-Limited	The hunter is restricted in the number of kills he can make, and a shot would have precluded a later kill	I did not want to make any noise I did not have enough cartridges
Conservation	The hunter gave up a short-term gain to avoid killing certain species/sexes/age groups	It had young with it I don't eat monkeys

the salience of an individual species in a hunter's list of preferences:

$$\text{Salience} = (1 + \text{length}_i - \text{position}_i)/\text{length}_i$$

where length is the total number of species listed by the hunter, and position is the numbered position at which species *i* appears in the hunter's list. We calculated the total salience of each species named at least three times for hunters in Sucusari as the mean of all salience values for that species. Species listed in free lists as preferred are considered those which hunters perceive as having the highest return rates, under OFT. Species which hunters did not list as preferred but pursued sometimes are considered species that are partially preferred (Alvard, 1993).

Mixed-Effects Modeling

We used generalized linear mixed-effects models to assess hunter decision-making using encounter data. Species that were encountered by hunters were aggregated into species groups because of a lack of data for some species (Table S1). Paca (*Cuniculus paca*), collared peccary (*Pecari tajacu*), tapir (*Tapirus terrestris*), and brocket deer (*Mazama americana* and *Mazama gouazoubira*) formed their own separate groups, since these were preferred species of hunters. Game birds were grouped together, as were large-bodied (> 1.5 kg, those which are pursued by hunters) and small-bodied primates. All other species, which were hunted but not listed as preferred (such as the agouti (*Dasyprocta fuliginosa*) and kinkajou (*Potos flavus*), were grouped into "Other Species". Encounters with carnivores (e.g. the jaguar (*Panthera onca*), puma (*Puma concolor*), and giant river otter (*Pteronura brasiliensis*)) were excluded from analyses because they were not killed during the study period. The yellow-footed tortoise (*Chelonoidis denticulata*) was also excluded from analyses because they were not killed with a shotgun.

As our primary, overarching model to evaluate hunter decision-making, we constructed a generalized linear mixed-effects model with a binomial distribution to assess the factors that contributed to whether a hunter decided to pursue an animal he encountered (Model 1). Each encounter was a sample ($n = 1,012$), and the response variable was a 0/1 based on whether the hunter pursued the animal (animal was killed, hunter took a shot at the animal unsuccessfully, or hunter pursued the animal and it escaped). We included a series of covariates formed under the framework of OFT (Table 2) and the hunter's name as a random effect to account for pseudoreplication caused by repeated samples from the same set of hunters. Only hunters who went hunting at least ten times during the study period were included in modeling ($n = 17$).

To add context to our primary model's results, we constructed three more models. The second model was created to evaluate the factors that contributed to a hunter deciding not to pursue an animal because its return rate was perceived to be too low and was therefore outside the diet breadth (Model 2). This was a generalized linear mixed-effects model with a binomial distribution. Each encounter was considered a sample ($n = 1,012$) and the response variable was a 0/1, based on whether the animal was ignored because of a reason coded as "low return." Covariates included were the same as the previous model (Table 2), with the exception of species groups that were excluded due to a lack of sufficient data in each group.

Since an assumption of OFT is that species are never partially pursued, we constructed a third generalized linear mixed-effects model with a binomial distribution to assess the factors that influence when hunters choose to pursue partially preferred species and test this assumption (species in the "Other Species," "Small Primate," "Large Primate," and "Game Birds" groups, see Table S1, which were not always pursued when encountered) (Model 3). Each encounter with a partially preferred species was a sample ($n = 652$)

Table 2 Hypotheses for inclusion of covariates in generalized linear mixed-effects models, formed under the framework of the optimal foraging theory, a description of how metrics were calculated, and mean and standard deviation of continuous covariates

Fixed Effects	Hypothesis for Model 1	Reference	Calculation	Mean	SD
Distance from Community (km)	Hunters may seek patches farther from the community for a greater return rate (patch choice theory)	(Charnov, 1976; Alvard, 1995)	Euclidean distance from encounter to community center	9.13	7.70
Hunt Duration (hr)	When a hunt lasts longer unsuccessfully, hunters may be more apt to shoot less preferred species so they do not come home empty handed	(Alvard, 1993; Levi et al., 2011a, b)	Total duration of hunt in which hunter was actively searching for or pursuing prey	6.85	4.48
Group Size (# individuals)	Hunters may be more likely to shoot at larger groups, when the chances of success are higher	(Alvard, 1993)	Estimated group size of animals	4.65	9.13
Hunter's Overall Return Rate (kg/hr)	Variation in hunter skill may drive variation in diet breadth	(Hill et al., 1987)	Total kg harvested over entire study period / total hours spent actively hunting	0.85	0.54
Hunter's Household Consumer/Producer Ratio	Hunters with larger households may have a wider diet breadth since food is needed more often	(Alvard, 1993)	Total number of people in hunter's household / total number of hunters in the household	0.29	0.12
Body Size (kg)	Larger species may be more likely to be in the diet breadth of hunters because they provide a greater return rate	(Alvard, 1993)	Estimated body size of species, from the literature, in kg	10.59	23.26
Species Group	Hunters may prefer some species over others due to factors such as taste	(Alvard, 1993)	-	-	-
Distance from Community: Mean Price	Hunters may seek patches farther from the community specifically to target species that are more economically valuable (patch choice theory)	(Charnov, 1976; Alvard, 1995)	Mean price calculated as the mean number of Peruvian soles received per kg for all sales within that species group during the study period	-	-
Hunter's Overall Return Rate: Mean Price	Hunters that are more successful may be more likely to sell game meat, and less skilled hunters may be more willing to accept less valuable species	-	-	-	-

and the response variable was a 0/1 based on whether the hunter pursued the animal (the animal was shot at, killed, or escaped before an intended shot was taken). Covariates included were the group size and mean body size of the animal, the Euclidean distance from the community, the total duration of the hunt, the hunter's overall return rate, and the consumer/producer ratio of the hunter's household, with the hunter's name as a random effect to account for pseudoreplication (Table 2).

Under the hypothesis that a partial preference for a species could be a result of increased wariness of hunters close to the community, requiring greater effort on the part of the hunter to pursue species, we constructed a final generalized linear mixed-effects model with a binomial distribution to assess the factors which contributed to preferred, major game species (paca, tapir, collared peccary, and brocket deer) escaping hunters during an encounter (Model 4). Each encounter with one of these species was a sample ($n = 361$) and the response was a 0/1 based on whether or not the animal escaped while the hunter intended to kill it (i.e., the reason for not shooting the animal was that it escaped pursuit or a shot taken was unsuccessful). Covariates in the model included the species group, the hunter's overall return rate, as a measure of the hunter's prowess, and the Euclidean distance from the community.

For all models, continuous covariates were scaled and checked for collinearity before including them in the model, with a correlation cutoff of 0.60 for inclusion (Dormann et al., 2013) before proceeding with model selection. We used a model-averaging approach to determine the optimal model, forming a candidate set of all possible combinations of relevant covariates then weighting the coefficient estimates of each model by that model's Akaike weight (Burnham & Anderson, 2002). All mixed-effects models were calculated using the *lme4* (Bates et al., 2015) package and model averaging conducted using the MuMIn package (Barton, 2009) in R (version 4.0.3) (R Core Team, 2019). Model fit was assessed using the theoretical pseudo-R^2 for mixed-effects models for the top-ranked models in each averaged candidate set (Nakagawa et al., 2017) and by visually examining residuals.

Results

General Hunting Behavior

We collected data on 671 hunting trips during the study period. Overall, 38.6% of hunts ($n = 256$) were conducted over land, 31.9% ($n = 214$) by canoe, 27.0% ($n = 181$) opportunistically from motorboats, and 3.0% ($n = 20$) included both a canoe and land component. During 14.3% of hunts,

a hunter visited a mineral lick. However, only 1.2% of these visits to a mineral lick lasted longer than 15 min. Overall, 66.9% of hunts ($n = 449$) were conducted during the day, 20.3% of hunts ($n = 136$) took place at night, and 12.8% of hunts ($n = 86$) spanned both night (20.00 h – 06.00 h) and daylight hours (06.00 h – 20.00 h). On average, hunts were 6.85 h (median 6 h) in length, with a range of ten minutes to 27 h.

Of all game meat harvested during the study period, by weight, hunters sold 58.2%, gifted 10.6%, and kept 31.2%. The species that were killed most frequently were paca, collared peccary, and red brocket deer (Fig. 2). There were no white-lipped peccary (*Tayassu pecari*) encountered by any hunters during the study period because the local population had experienced a crash (e.g., see Fragoso, 2004). The highest proportion of meat sold was paca, collared peccary, red brocket deer, and Brazilian tapir (Fig. 2).

Hunters had highly variable overall return rates, with a mean of 0.85 (SD = 0.54) kg meat harvested/hr spent hunting and a range of 0.19 to 1.94 kg meat harvested/hr spent hunting. All hunters sold meat during the study period and return rates from sales had a mean of 5.03 soles (1.51 USD) earned/hr spent hunting and a range of 0.51 to 16.77 soles (0.15 to 5.04 USD) earned/hr spent hunting (Table S2). Overall, paca was the most frequently reported species with 212 encounters, followed by agouti (103 encounters) and kinkajou (98 encounters). Hunters reported encountering animals from 0.10 km from the community to 30.82 km from the community (mean = 9.20 km, SD = 7.73 km) (Fig S1). When broken down by species group, there was some variation in the distribution of encounters by distance from the community (Fig S2). Primates in particular, both large and small-bodied, were encountered more frequently nearby the community, whereas paca were generally found farther from the community compared to other groups.

Game Meat Economics

Game meat was frequently sold within the community to neighbors and friends, to communities near Sucusari on the Napo River (labeled as "Napo" in Fig. 3), and to the regional market in the town of Mazán or the city of Iquitos. Game meat was typically sold salted or salted and then smoked. Four species made up 63.2% of total meat sales by mass: paca, collared peccary, red brocket deer, and tapir. On average, meat from each of the most commonly sold species sold for the most money at the regional market, at S/. 12.12 (3.64 USD) for paca meat, S/. 11.94 (3.59 USD) for collared peccary, S/. 8.92 (2.68 USD) for red brocket deer, and S/. 9.80 (2.94 USD) for tapir per kg (Fig. 3). Meat sold for less in nearby communities along the Napo River and for even lower prices in the community itself (Fig. 3).

Hunters also frequently gifted game meat that they harvested to extended family, friends, and neighbors (10.6% of

Fig. 3 Average price per kilogram of meat sold of the four most frequently sold species for sales within the community of Sucusari, Peru, to other communities nearby on the Napo River, and to the regional markets in either Mazán or Iquitos. Only species for which more than 30 kg were sold during the study period are shown. Species are shown in descending order of frequency of kills. Descriptive error bars show ranges
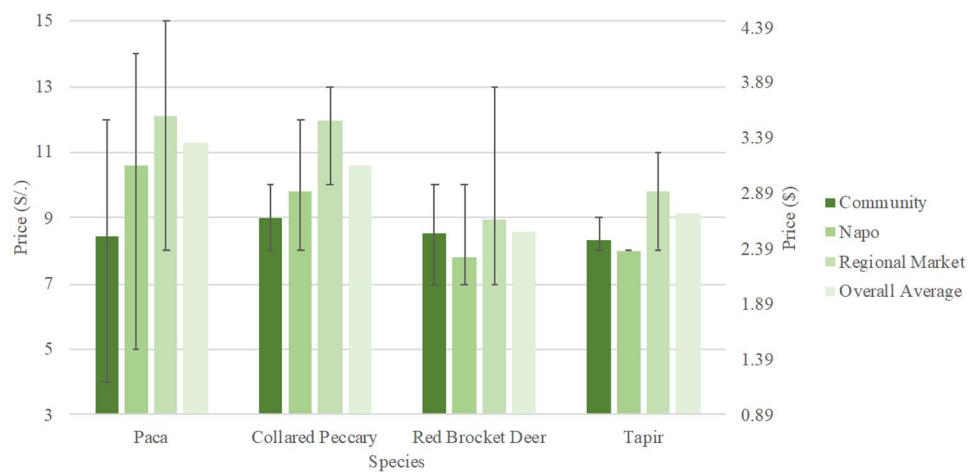
all meat harvested, by mass). The most commonly gifted species were the yellow-footed tortoise (36.36% by mass), grey brocket deer (29.55% by mass), South American coati (*Nasua nasua*) (18.60% by mass), and common woolly monkey (*Lagothrix lagotricha*) (17.65% by mass) (Fig. S3). All of these species were sold relatively infrequently (Fig. 2).

Hunter Preferences

During interviews at the end of the study period, we asked hunters to list three species they prefer to kill while hunting on trails, by canoe, and at mineral licks and three species they prefer to kill when hunting for economic gain. The collared peccary and the paca were the most preferred species, with overall salience indices of 0.80 and 0.76, respectively (Table 3). The collared peccary was the most preferred species targeted on land with an index of 0.95 but was less preferred than other species by canoe or at mineral licks. Paca was the most preferred species targeted from canoes, with an index of 0.99, but was also less preferred than other species on land and at mineral licks. The white-lipped peccary and Brazilian tapir were the most preferred species targeted in mineral licks, with indices of 0.83 and 0.79 respectively, but

were not preferred prey on land or in canoes. The collared peccary and paca were also the most highly preferred species when hunting for meat to sell, with salience indices of 0.88 and 0.72 respectively while the white-lipped peccary and red brocket deer were similarly ranked at 0.42 and 0.43 respectively. The tapir was never listed as a species that was targeted for sale. While red brocket deer was listed repeatedly by hunters, it was the least preferred species overall compared to the other four species (Table 3).

Partial Preferences of Species

We used hunter-reported encounter data and the reasons the hunter gave for not shooting an animal during an encounter to assess partial preferences of species groups. The paca, collared peccary, and brocket deer were almost always pursued upon encounter, each with a pursuit rate of over 96.0% (Table 4). The tapir and game birds were usually pursued when encountered, at a rate of 76.2% and 73.5%, respectively. However, when the tapir was not pursued it was typically for an attack-limited reason (14.3% of encounters), while the reason game birds were not pursued was typically for a perceived low return rate (23.5% of encounters). The species in the "Other Species" category, which were species not listed as preferred species by hunters, were killed at least once during the study period, and were not encountered frequently enough to form their own group, were also partially preferred at a pursuit rate of 52.5% of encounters (Table 4). Large primates were also partially preferred at a pursuit rate of 42.8% of encounters, but were often ignored for a perceived low return rate (33.1% of encounters) and for attack-limited (13.8% of encounters) and conservation reasons (10.3% of encounters). Small primates were almost never pursued (3.50% of encounters), typically for a perceived low return rate (65.9% of encounters) or for conservation reasons (22.0% of encounters) (Table 4).

Table 3 Salience indices showing preferred species from semi-structured interviews with hunters in Sucusari, Peru. Only species listed more than ten times by hunters are shown

| | Hunting Method | | | | |
Species	Land	Canoe	Mineral Lick	Sale	Overall Mean
P. tajacu	0.95	0.89	0.48	0.88	0.80
C. paca	0.56	0.99	0.77	0.72	0.76
T. terrestris	0.53	0.50	0.79	-	0.60
T. pecari	0.63	0.25	0.83	0.42	0.53
M. americana	0.62	0.49	0.56	0.43	0.52

Table 4 Proportions of encounters resulting in pursuit or not shooting an animal because of a perceived low return rate, attack-limited reasons, or conservation reasons by species group. Species killed, shot at unsuccessfully, or escaped are classified as pursued

Species Group	Number of Encounters	Proportion Pursued*	Proportion Killed	Proportion Shot At Unsuccessfully	"Escaped"	Proportion of Encounters: Reasons for No Pursuit		
						"Low Return"	"Attack-Limited"	"Conservation"
Paca	212	0.972	0.726	0.042	0.203	0.009	0.019	0.000
Collared Peccary	78	0.962	0.526	0.038	0.397	0.000	0.038	0.000
Deer	50	0.960	0.540	0.040	0.380	0.020	0.020	0.000
Tapir	21	0.762	0.381	0.286	0.095	0.095	0.143	0.000
Game Birds	34	0.735	0.353	0.088	0.294	0.235	0.029	0.000
Other Species	304	0.526	0.234	0.056	0.237	0.280	0.069	0.125
Large Primate	143	0.420	0.119	0.105	0.196	0.336	0.140	0.105
Small Primate	171	0.035	0.012	0.012	0.012	0.661	0.088	0.216

*Proportion pursued is the sum of proportions killed, shot at unsuccessfully, and "escaped"

Mixed-Effects Modeling

We used generalized linear mixed-effects models to assess the factors that influenced whether hunters decided to pursue an animal that they encountered while hunting (Model 1). The averaged model of hunter decision-making included species group and body size of the animal as significant covariates (Table 5). In general, predicted probabilities of pursuit followed stated pursuit rates (Table 4), with paca, deer, and collared peccary almost always pursued (Fig. 4). Model results showed that as the hunter's overall return rate increased, the probability of pursuit decreased (Fig. 4). Probability of pursuit increased with the body size of the animal and group size, and decreased with distance from the community and consumer/producer ratio (Table 5).

Model results for Model 2 showed that mean price was the most important factor in determining whether a hunter did not pursue a species because of a perceived low return rate (Table 5). As distance from the community increases, hunters are more likely to ignore species with cheaper meat prices, particularly species worth less than about S/. 6 (1.81 USD) per kg (Fig. 5). Model results for Model 3 showed that species body size and mean price were the most important covariates (Table 5). Hunters were more likely to shoot at larger partially preferred species and those that were worth more economically (Table 5). Model results for the probability of a preferred species group (paca, collared peccary, tapir, and deer) escaping during an encounter (Model 4) showed that both the hunter's overall return rate (a measure of hunter prowess) and the distance from the community were important factors (Table 5). As distance from the community and the hunter's overall return rate increased, the probability of an animal escaping decreased (Fig. 6, Table 5). There was no correlation between the hunter's overall return rate and the distance from the community (0.048). See Table S3 for parameters of model subsets for all averaged models (Models 1–4).

Discussion

Diet Breadth Model

Results from hunter preference data indicated clear preferences for some species over others. Interestingly, the white-lipped peccary and tapir had lower preference indices in comparison to paca and collared peccary, even though these species are reported to be among the most commonly hunted species in Amazonia (de Andrade Melo et al., 2015; El Bizri et al., 2020; Mayor et al., n.d.). These results match game meat prices, where paca and collared peccary are the species most likely to be sold and the most valuable. Accordingly, paca and collared peccary were the most commonly sold species by proportion of total meat sales. Some hunters remarked that the tapir was often not killed because of its large body size, with monetary rewards not matching the effort required to process and carry the meat to market. These results indicate that hunters consider both economic and subsistence return rates when they are hunting, challenging the theory that the largest species provide the highest return rates to hunters (Alvard, 1993; Bettinger et al., 2015). The relatively low salience for paca from land-based hunting can likely be partially attributed to the nocturnal nature of the species (Griffiths et al., 2020) or differential habitat preferences (El Bizri et al., 2018). Several hunters noted that they did not like to hunt by land at night because they were afraid of being bitten by snakes. It is also possible that paca is more commonly found in riparian areas at night, leading hunters to target them by canoe rather than by land.

Hunter preferences found here did not line up with previously reported results from other communities, such as those reported by Bodmer (1995), where tapirs and white-lipped peccaries were the most preferred species. It is possible that since white-lipped peccary was not encountered by hunters during the study period, hunters' listed preferences were

Table 5 Generalized linear mixed–effects model results of hunter decision–making. Coefficient estimates of averaged models shown with standard error in parentheses. NA indicates that fixed effect was not tested in the model due to convergence issues, and a dash indicates that fixed effect was not tested because of the hypotheses of the model. Reference species group for species group fixed effect is the collared peccary. Statistically significant estimates in bold

	Model 1	Model 2	Model 3	Model 4
Response Variable (0/1)	Whether an animal is pursued	Whether an animal is not pursued for perceived low return rate	Whether a partially preferred species is pursued	Whether an animal escapes pursuit by a hunter
Sample of encounters	All	All	Partially preferred species	Preferred species
Sample Size (n)	1,012	1,012	651	361
Fixed Effects				
Group Size	0.022 (0.074)	–0.005 (0.043)	–0.142 (0.134)	-
Body Size	**1.948 (0.775)**	–0.071 (0.166)	**3.062 (1.036)**	-
Distance from Community	–0.073 (0.113)	–0.067 (0.122)	–0.164 (0.198)	**–0.635 (0.146)**
Hunt Duration	–0.122 (0.131)	0.003 (0.056)	–0.166 (0.153)	
Hunter's Overall Return Rate	–0.144 (0.188)	–0.021 (0.128)	–0.283 (0.267)	**–1.019 (0.260)**
Hunter's Consumer/Producer Ratio	–0.021 (0.109)	0.005 (0.111)	0.024 (0.124)	-
Species Group (Paca)	**2.057 (0.909)**	NA	NA	–0.256 (0.367)
Species Group (Deer)	–0.134 (0.945)	NA	NA	0.110 (0.326)
Species Group (Tapir)	**13.100 (4.563)**	NA	NA	0.111 (0.410)
Species Group (Game Birds)	–0.331 (1.064)	NA	NA	-
Species Group (Other Species)	–1.403 (0.915)	NA	NA	-
Species Group (Large Primate)	**–2.082 (0.955)**	NA	NA	-
Species Group (Small Primate)	**–4.750 (1.100)**	NA	NA	-
Mean Price	NA	**–1.631 (0.142)**	**1.002 (0.246)**	-
Mean Price:Distance from Community	NA	–0.203 (0.180)	–0.171 (0.236)	-
Mean Price:Hunter's Overall Return Rate	NA	–0.012 (0.056)	–0.170 (0.218)	-
Random Effect	Hunter Name	Hunter Name	Hunter Name	Hunter Name
Marginal R^{2*}	0.630	0.444	0.248	0.278
Conditional R^{2*}	0.670	0.534	0.360	0.397

$^{*}R^2$ values calculated based on the top–ranked model of each averaged model by Akaike weight
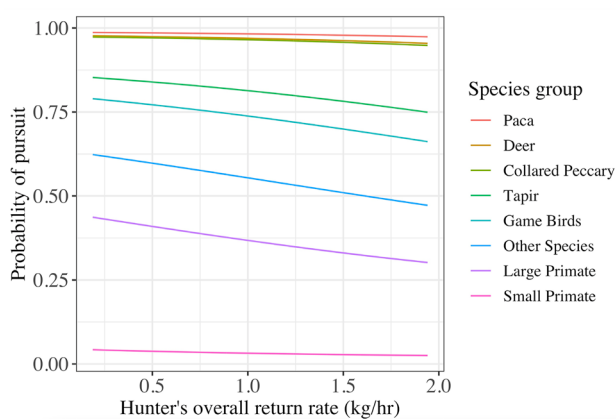

Fig. 4 Generalized linear mixed-effects model results predicting the probability of a hunter pursuing an animal that is encountered versus the hunter's overall return rate and species group of the encountered animal. Other covariates held at the mean value for display, and hunter chosen for display represents the median intercept of the random effects of the optimal model

conflated, placing white-lipped peccary lower on the preference list than it would be if it were still abundant.

Evaluation of hunter pursuit rates for species groups revealed that hunters in Sucusari do not follow the predicted zero–one rule of the diet breadth model (Bettinger et al., 2015; Stephens & Krebs, 1986), similar to Alvard (1993) who reported that Piro hunters frequently exhibited only partial preferences for some species. The measured pursuit rates we present showed that paca, collared peccary, and brocket deer were in the optimal diet breadth of all hunters, and were almost always pursued, a result that is directly in line with free-listed preferences. Since these species were almost always pursued, it is likely that these species yield the highest return rate for hunters. The currency of the return rate (Winterhalder, 1981) in this case is likely a mixture of economic gain and subsistence, where the most preferred species are not only relatively large-bodied but also economically valuable.

Tapir was only a partially preferred species, pursued only on 76.2% of encounters, even though it is the largest game
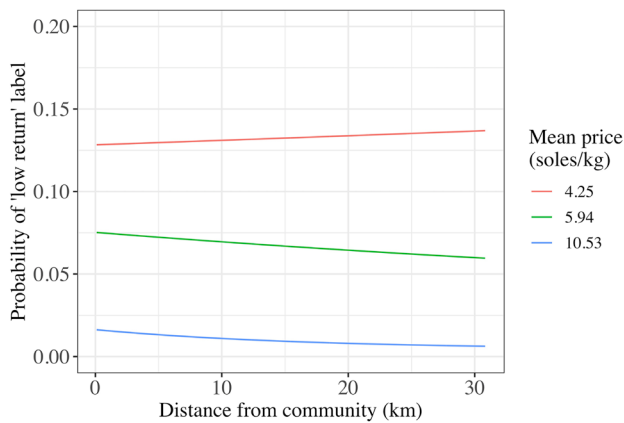
Fig. 5 Generalized linear mixed-effects model results of the predicted probability of a hunter not pursuing an animal upon encounter versus distance from the community and the mean price per kg of the meat of the species encountered. Hunter chosen for display represents the median intercept of the random effects of the optimal model. Mean price values chosen for display represent quartiles and mean of mean price

species. Given the reasons for not pursuing tapirs on some occasions (9.5% low return, 14.3% attack-limited), it is possible that hunters are not willing to invest the time needed to transport and process tapir, significant tasks given its size, since that handling time precludes time that could be spent searching for other smaller and more economically profitable species (Bettinger et al., 2015; Chaves et al., 2020; Smith et al., 1983; Winterhalder & Lu, 1997). It also should be noted that tapir often could not be effectively killed with a shotgun without getting close or using a special lead slug that some hunters carry. In some cases, hunters may have encountered tapir without having a slug with them,
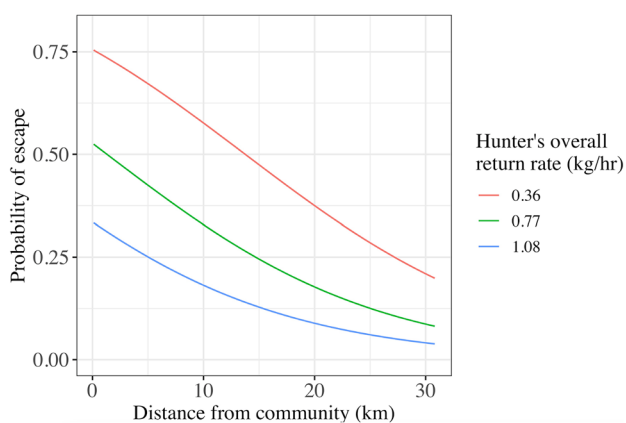

Fig. 6 Generalized linear mixed-effects model results of the predicted probability of a preferred species escaping a hunter during an encounter versus distance from the community and the hunter's overall return rate (a measure of hunter prowess). Hunter chosen for display represents the median intercept of the random effects of the optimal model

increasing the probability of attack limitation (Levi et al., 2011a, b). Tapir also had a high preference index (0.79) to be hunted at mineral licks, but only 14.31% of hunts during the study period included a visit to a mineral lick. This result lends evidence to the idea that while hunters know where to find tapir, which frequently visit mineral licks in the region (Griffiths et al., 2020), they choose not to hunt them in favor of other species. Large-bodied primates were also partially preferred and were frequently ignored because of a perceived low return rate (33.1% of encounters) or for conservation reasons (10.3% of encounters). Our finding of the prevalence of conservation-based reasons for ignoring primates while hunting contrasts with Alvard (1993, 1995), who showed that Piro hunters targeted species only with short-term maximization of harvest in mind and not long-term conservation. Levi et al. (2009, 2011b) estimated a kill rate for another large-bodied primate, the spider monkey (*Ateles chamek*) at 0.90, much larger than the 0.119 we report here. Tapir and large primates perform key ecosystem functions, including seed dispersal (Brodie et al., 2009; Effiom et al., 2014; Galetti et al., 2001; Tobler, 2008) and are crucial to the health of the broader ecosystem. The partial preference results indicate that hunters were not going to the forest to look for these species specifically, which may result in lower off-take levels and a lower risk of overexploitation of those species in our study area than others across the region (Peres, 1990) if the population of the community stays low (Alvard et al., 1997). In contrast, the relatively high pursuit rate and preference for paca compared to tapir has conservation implications since paca is a rodent with a much higher reproductive rate than tapir and is therefore more resistant to population decline (Bodmer et al., 1997; El Bizri et al., 2018). However, our data did show fewer encounters with paca nearby the community, suggesting that some local population decline or behavioral avoidance may be occurring.

Our decision-making model and partial preference results indicated that species were pursued based on hunter and species-specific characteristics, showing that individual hunters have different diet breadths that are influenced by their own beliefs (e.g., propensity to ignore primates for conservation reasons) (Lemos et al., 2021), and their own skill at hunting (Hill et al., 1987). These results support arguments made by Hames and Vickers (1982) and Mithen (1989), who stated that individuals vary in their behavior and return rates and therefore their diet breadths, and studies assessing hunter behavior should examine individual choices rather than aggregating data for analysis at the group level.

Patch Choice Model

The importance of distance from the community in all decision-making models indicated that hunters are making decisions

about potential return rates based upon the patch that they enter, consistent with the patch choice model (Charnov, 1976) and Hames and Vickers' (1982) results showing where hunters will choose to enter patches further from the community for preferred species or will accept a wider variety of species closer to the community. Levi et al. (2011a) also showed an effect of distance from the community on diet breadth, where hunters expanded their diet breadth as distance increased to avoid the risk of returning empty-handed. Our model results indicate preferred species were more likely to escape encounters closer to the community, indicating that those animals are more wary of hunters closer to the community and exhibit a behavioral response to humans that enables them to escape more often. The probability of escape was much lower farther from the community and when facing a more skilled hunter. Since there was no correlation between hunter skill and distance from the community of encounter locations, it can be assumed that this result is not due to more skilled hunters choosing patches farther from the community. The wariness of species closer to the community likely has a large effect on hunter return rate, since hunters would need to spend more time pursuing preferred species when they are encountered close to the community. This result supports the patch choice theory, where hunters who are hunting closer to the community likely have to accept a wider range of species than those hunting farther away (Hames & Vickers, 1982). However, the patch choice theory has focused on depletion of game following the central place foraging theory causing a decline in return rate in patches closer to the community, not a behavioral response by animals (Charnov, 1976; Pyke et al., 1977; Winterhalder, 2001). Our results for increased wariness nearby the community add greater context to the expansion of diet breadth predicted by the patch choice model.

Conclusions

We suggest that the behavior of Amazonian hunters who have access to markets but still depend on hunting for subsistence is still largely explained by OFT and its applications, the diet breadth model, and the patch choice model. With greater access to technology and markets, it is likely that other Amazonian communities that previously hunted only for subsistence now hunt for both subsistence and economic gain, and that these results of prey selection can be generalized to those communities. Our results indicate that the influence of the market may drive preference towards valuable species such as paca and collared peccary, and away from tapir and large primates that have been shown to be well within the diet breadth of subsistence hunters in other communities (Alvard, 1993). The partial preference for these keystone (Paine, 1995) seed dispersers compared to species such as paca suggests that indigenous communities engaged in small-scale commercial and subsistence

hunting may have a lesser effect on biodiversity than has been previously suggested by other studies showing tapir and primates as preferred species (Alvard, 1993; Hames & Vickers, 1982; Ojasti, 1984). Our results also suggest that future fluctuations in market prices could alter these preferences and further endanger these species or continue to further reduce their preference by hunters.

Declarations

Ethical Approval This study was approved by the Institutional Review Board of George Mason University (project #1288488–1). Prior informed consent (PIC) was obtained from the community as well as from individual research participants before beginning this study.

Conflict of Interest The authors have no conflicts of interest to declare.

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