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Is Meat Flavor a Factor in Hunters' Prey Choice Decisions?

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Abstract By focusing on the caloric composition of hunted prey species, optimal foraging research has shown that hunters usually make economically rational prey choice decisions. However, research by meat scientists suggests that the gustatory appeal of wildlife meats may vary dramatically. In this study, behavioral research indicates that Mayangna and Miskito hunters in Nicaragua inconsistently pursue multiple prey types in the optimal diet set. We use cognitive methods, including unconstrained pile sorts and cultural consensus analysis, to investigate the hypothesis that these partial preferences are influenced by considerations of meat flavor. Native informants exhibit high agreement on the relative appeal of different meats. Given the absence of other noteworthy differences between spider monkeys (*Ateles geoffroyi*) and howler monkeys (*Alouatta palliata*), the unappealing flavor of howler monkeys seems to be a factor in the partial preference for this species.

Keywords Optimal foraging theory · Taboos · Ethnoecology · Meat science · Signaling theory

Optimal foraging models were designed to test the prediction that the decisions made by individual foragers allow them to maximize the rate at which they acquire food resources (Stephens and Krebs 1986). For anthropological applications, the most

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frequently used optimal foraging model has been the prey choice model, which can illuminate the prey types that rate-maximizing foragers should and should not pursue. Ethnographic tests in a broad variety of environmental and social contexts have provided general support for the predictive power of the prey choice model (O'Connell and Hawkes 1981; Winterhalder 1981; Hill et al. 1987; Kuchikura 1988; Smith 1991; Alvard 1993; Thomas 2007). That is, human hunters appear to focus on prey types that, on average, increase their overall return rate.

Given their focus on the ecological costs and benefits of alternative hunting strategies, optimal foraging scholars and other materialist anthropologists have generally downplayed or disregarded the importance of meat flavor and aroma in hunters' prey choice decisions. For instance, Hill et al. (1987:19) write, "Flavor preferences (i.e., which resource an informant would most like to eat) are a function of the food value of the resource and ignore costs of acquisition and processing. Thus, while most Americans, for example, may prefer the flavor of lobster to that of rice, it is not necessarily the resource that they would most often choose to buy given the cost." From an optimal foraging perspective, therefore, the claim that certain prey types are avoided because they taste bad may be regarded as a convenient emic explanation for an underlying and perhaps unrecognized ecological or economic variable.

Nevertheless, there is abundant evidence that meat flavor is a central consideration in purchasing decisions for Western consumers (Schweigert 1963; Booth 1990; Chambers and Chambers 1999; Sitz et al. 2005, 2006). Similarly, informants in preindustrial societies frequently cite taste as a reason for not consuming some wildlife species. Yet, perhaps because of the assumption that relatively impoverished preindustrial peoples in marginal environments cannot afford to bypass potentially valuable sources of protein and fat, the importance of taste in hunting strategies has so far received little systematic attention. In this paper, we therefore employ conventional optimal foraging analysis and methods from cognitive anthropology to investigate two hypotheses: (1) informants in hunting economies consistently distinguish between the hedonic appeal of different kinds of meat, and (2) hunters consider meat flavor when deciding which prey species to pursue.

Meat Science

Meat palatability and acceptability is associated with the tenderness, juiciness, and flavor of the meat product. Juiciness is easily controlled with degree of doneness and cooking method (dry versus wet), whereas tenderness and flavor, which ultimately influence the acceptability more than juiciness, are affected by numerous factors. Flavor, price, and healthfulness were identified as the primary motivators influencing meat purchases and consumption in the United States, but if an appealing flavor was lacking, the other components were irrelevant (National Research Council 1988).

Meat flavor is derived from both water- and fat-soluble compounds, and both the muscle and the fat in meat therefore contribute to the overall flavor. The water-soluble compounds in muscle give rise to more of the savory flavors associated with meat. For several reasons, humans tend to prefer foods that are high in fat (Drewnowski and Greenwood 1983). First, lipids are energetically dense and therefore ideal for meeting daily caloric needs. Second, fat has long been known as a carrier of many flavor components that help impart desirable texture and organoleptic traits. Numerous studies with beef, pork, goat, and processed meats have generally shown consumer acceptance to be directly associated with higher fat content (Smith et al. 1983; Miller et al. 1997; Miller 2001; cf. Francis et al. 1977).

Subtle differences in the composition of the water-soluble and fat-soluble flavor components lead to very different flavor profiles and thus acceptability of the meat product. For instance, low levels of sulfur-containing compounds contribute to the "meaty" flavor, but excessive levels are objectionable (Drumm and Spanier 1991; Shahidi 1998). A more pronounced meaty flavor is found in fattier meats because of the ATP (Adenosine triphosphate) by-products, inosine monophosphate and hypoxanthine (Shahidi 1998). However, meats with high levels of compounds that impart bitter flavors, such as carnosine and hypoxanthine, usually are rated less desirable. Bitterness can indicate toxicity or spoilage in some foods (Glendinning 1994), and a highly diverse array of bitter receptors has evolved to minimize the risk of ingesting potentially harmful substances (Behrens and Meyerhof 2006).

Diets of both monogastric and ruminant animals play a large role in the flavor acceptability of the meat. Beef studies comparing grass-fed and concentrate-fed finishing diets and pork studies comparing different grains have shown that the meat exhibits different flavor profiles (Melton 1983; Sitz et al. 2005). Differences in the fatty acid profile of the animals' food as well as metallic and sulfur compounds that are broken down during digestion have been shown in some domesticated animals to lead to varying levels of flavor acceptability (Lee et al. 2004; Dannenberger et al. 2005). Domestic animal studies also indicate that animal diets with sour (organic acids), bitter (tannins), and metallic components tend to yield meat that is perceived as less desirable (Vasta and Priolo 2006). Monogastric animals, such as swine, can see greater shifts in flavor profiles owing to dietary differences because the single-stomach digestion system does not break down the flavor compounds, such as polyunsaturated fatty acids, in the same manner as in ruminant animals, although the degree of change depends on the difference in feed (Shackelford et al. 1990).

Thousands of compounds are associated with variation in meat flavor (Shahidi 1989). Because slight changes in these compounds lead to changes in flavor within species, the relatively dramatic differences in digestive systems and diets across species are likely associated with variation in consumer preferences for meat flavor (Matsuishi et al. 2006). Research in meat science has also revealed additional factors that cause meat to be more or less desirable, such as age of the animal, species, muscle cut, post-fabrication handling, and cooking method (Smith et al. 1974; Paterson et al. 1987; Spanier et al. 1997; Miller 2001; Calkins and Hodgen 2007). In addition, sensory research on American consumers indicates that consumers become accustomed to certain meat flavor profiles, and they rate those familiar samples higher for overall acceptability and value (Killinger et al. 2004; Sitz et al. 2005, 2006).

Ethnographic References to Taste Preferences in the Lowland Neotropics

No systematic reviews of ethnographic references to taste preferences exist for wildlife in the lowland Neotropics. Nevertheless, there are some discernible patterns in the literature. For example, the strong preference for paca meat has been described as "almost universal" (Collett 1981:493; see also Smole 1976:182; Henfrey 2002:216; Naughton-Treves 2002:498; León and Montiel 2008:255). By contrast, in locations where capybaras (*Hydrochaeris hydrochaeris*) are consumed, the taste of these large rodents is seldom preferred (Farabee 1967:40; Yde 1965:125; Kracke 1981:105; Bianchi 1988:132; Vickers 1991:69; Alexiades 1999:75; Shepard 2002:107; see also Heath 1896:18; cf. Smole 1976:182). Ojasti (1991:239) notes that capybara meat has a lower fat content than meat of domestic animals and that the taste of capybara meat varies with the age of the animal and its diet, which may explain why the taste seems to vary from "regular" to "foul-smelling" in different locations (Armentia 1905:60). In general, Robinson and Redford (1994:304) note that the meat of frugivorous species is typically preferred over the meat of folivores.

Two primates, spider monkeys (*Ateles* spp.) and howler monkeys (*Alouatta* spp.), provide a particularly interesting comparison. Milton (1981) has shown that these similarly-sized, frequently sympatric primates can be distinguished by their feeding strategies. Spider monkeys are predominantly frugivorous whereas howler monkeys are primarily folivorous. Shepard (2002) suggests that this dietary difference could explain why the meat of howler monkeys might be relatively less appealing. That is, although howler monkeys may attempt to minimize the amount of secondary compounds in the leaves that they consume (Glander 1981), the comparatively high volume of bitter-tasting compounds in their diet could have a negative effect on the perceived taste of their meat. Because they are monogastric animals, the meat of howler monkeys (and other Neotropical primates) is particularly likely to be affected by the consumption of these compounds. Meanwhile, Hershkovitz (1972:11) writes of howler monkeys, "The flesh is more or less tainted by sweet smelling secretions of the cutaneous scent glands but otherwise howler meat, like that of most monkeys, tastes like beef."

In settings where both species are found, the ethnographic record convincingly suggests that spider monkey meat is preferred over the meat of howler monkeys (Rusby 1933:233; Carneiro 1974:124; Smole 1976:183; Estrada and Coates-Estrada 1984; Bianchi 1988; Mittermeier 1991:100; Gonzalez-Kirchner and Sainz de la Maza 1998:16; Lizzaralde 2002:91; Daily et al. 2003:1821; Johnson 2003:57). By contrast, a review of the literature reveals no settings in which the taste of howler monkeys is preferred to the taste of spider monkeys (see also Cormier and Urbani 2008). Westerners who have consumed spider monkeys also express high regard for the meat (Crevaux 1883:54–55; Heath 1896:14; Bates 1962:152, 266).

The percentage of body fat among Neotropical primate species typically varies seasonally, with individual primates becoming fatter during the rainy season (Hershkovitz 1972:11). Numerous reports indicate that this fattier monkey meat is particularly relished (Armentia 1905:60; Grenand 1980:114; Bianchi 1988:102; Shepard 2002:110). During the dry season, by contrast, the Piro and Machiguenga of Peru report that leaner primates are not worth pursuing (Alvard and Kaplan

1991:83). However, there is apparently no evidence that this seasonal variation causes Neotropical hunters to bypass opportunities to pursue the largest primate species (wooly monkeys, spider monkeys, and howler monkeys) upon encountering them during the dry season (Alvard 1993).

Finally, informants sometimes cite the poor taste of meat as a reason not to pursue species that are tabooed or otherwise never consumed. As noted by Kensinger (1995:197), this reason lacks some explanatory power given that few informants have ever sampled the meat. Taboos and aversions to game species are common in Neotropical societies (Redford and Robinson 1987), even though optimal foraging theory predicts that hunters should exploit some of these species. For example, the Mayangna and Miskito hunters kill giant anteaters and northern tamanduas to protect their dogs, but they do not consume the meat although both species are in the optimal diet set (Koster 2008a). It is noteworthy that, in societies where anteater species are consumed, the meat does not appear to be highly regarded (Tastevin 1925:19; Smole 1976:182; Grenand 1980:117; cf. Bates 1962:109). Similarly, howler monkeys are the most frequently tabooed primate genus in the Neotropics (Cormier 2006).

Yet, we hesitate to suggest a causal relationship between meat flavor and taboos because there have been widespread taboos on species that are highly regarded elsewhere. For example, although the meat of brocket deer (*Mazama* spp.) is generally viewed favorably (e.g., Grenand 1980:116), this prey type was traditionally tabooed throughout much of lowland Amazonia (Redford and Robinson 1987). There has been considerable discussion of the adaptive significance of wildlife taboos in the lowland Neotropics (McDonald 1977; Ross 1978). However, in part because we suspect that taboos exhibit both ecological and cognitive dimensions, we emphasize that our subsequent discussion of meat flavor focuses only on prey species that hunters recognize as edible.

Study Site

This research was based in the Bosawas Biosphere Reserve, Nicaragua, which is centrally located in the lowland region of Nicaragua and Honduras known as the Mosquitia. The reserve is part of the largest unbroken tract of lowland tropical rain forest north of Amazonia (Stocks 1996), and remote sensing data suggest that much of the reserve retains mature forest cover (Stocks et al. 2007). Although there is evidence that some wildlife population densities are depressed near the communities, hunting pressure has apparently not resulted in the localized extirpation of any native fauna (Williams-Guillén et al. 2006).

From August 2004 to September 2005, the lead author documented the harvest of wildlife and prey choice decisions in two indigenous Mayangna and Miskito communities, Arang Dak (14°30′57″N, 84°59′58″W) and Suma Pipi (14°31′24″N, 85°0′8″W). In June 2008, two of us (JK and MV) returned to Arang Dak for approximately 3 weeks of interviews with members of the 30 households in the community. Residents describe Arang Dak as a Mayangna community, and at least one adult in each household self-identifies as Mayangna. There is considerable intermarriage between the two ethnicities, however, and there are few discernible differences between the subsistence strategies of the two groups in this part of the reserve.

Like many indigenous societies in the lowland Neotropics, the Mayangna and Miskito are sedentary swidden horticulturalists. Bananas and manioc are their staple crops, and they also cultivate beans, rice, and corn. The residents of Arang Dak and Suma Pipi keep livestock, including cattle, pigs, and chickens, but hunting and fishing are the primary sources of dietary protein (Koster 2007). Compared with some indigenous Neotropical societies, the Mayangna and Miskito rely more heavily on hunting dogs, and Koster (2008b) reports that approximately 85% of the harvested mammals are captured with the assistance of dogs.

Hunting with dogs and hunting with rifles provide comparable return rates, as measured in kilograms of meat per hour (Koster 2008a). Although virtually all men would like to own a rifle, the cost of purchasing even a secondhand rifle is prohibitive for many households. During the 2004–2005 field season, only 26% of the households owned a rifle, all of which were .22 caliber models. Ammunition is not particularly expensive, and the cost of a single bullet is approximately equivalent to the price of 0.3 kg of hunted meat. Acquiring bullets through the mercantile networks in the reserve can be problematic, however, and hunters frequently maintain only a limited supply of bullets.

Hunting with rifles is almost invariably a male activity in the Bosawas Reserve. Although multi-day expeditions occur intermittently, hunters more commonly embark on daylong hunting trips. Usually leaving the community after breakfast, rifle hunters generally follow established hunting trails through the forest. These day trips seldom last longer than about 7 h, often because the hunters perform other subsistence activities (e.g., gathering firewood) afterward. Hunters may travel alone, or they might be accompanied by one or two companions, typically adolescent male relatives. Although hunters may deliberately pass by known resting spots for tapirs, these hunting trips are otherwise characterized by a general search for the full suite of acceptable prey types. Upon discovering white-lipped peccary tracks, hunters usually attempt to locate the herd, but if they are unsuccessful before nightfall, they typically return to the community and organize a party of multiple hunters to track the herd the following day.

Methods

Optimal Foraging Data

The methods used to obtain data on the prey choice decisions of rifle hunters are similar to those of previous optimal foraging studies (e.g., Alvard 1993). Using a handheld computer and customized observational software (Koster 2006), the lead author kept a continuous record of a focal hunter's activities on hunting trips. Behaviors that are relevant for this analysis include those that are germane to most optimal foraging research: general search for prey, encounters with prey items, pursuit, and field processing following successful pursuits.

Because most hunting at this field site includes the use of dogs, however, the lead author observed only six outings by rifle hunters. As with Alvard's (1993) research, structured interviews were therefore used to expand the sample of daylong hunting trips. After all unobserved hunting outings by rifle hunters during the yearlong study period (n=43), indigenous research assistants recorded information on times of departure and return, participants and their technologies, encounters with prey items, pursuit decisions, and outcomes of pursuits. All harvested animals were weighed with Pesola spring scales. See Koster (2008b) for additional details on these methods.

Cognitive Data Collection

In 2008, adult male and female informants were recruited from all households in Arang Dak; one household declined to participate. We first randomly selected a participant from each of the remaining households, then completed the schedule of interviews by drawing a random sample of informants from the remaining pool of eligible adult informants. The same group of informants participated in the second stage of the research, but the same sampling strategy was used to draw a new sample of informants for the last stage of the research.[1] Fifty-six informants participated in the first and second stages of the research, and forty-seven informants participated in the third stage (Table 1).

The first stage of the research consisted of a free-listing task, which is used to define the boundaries and specific elements of a cultural domain (Weller and Romney 1988). Informants were asked to name all of the hunted prey species they know. For subsequent stages of the research, we included only those species that were mentioned by at least 15% of the informants. We also excluded species that weigh less than approximately 1 kg, and we eliminated the forest rabbit (*Sylvilagus brasiliensis*) because this species is rarely encountered or harvested (Koster 2008b).

Using these criteria, 17 prey species were identified as elements in the domain. In the next stage, the names of the species were typed onto index cards and placed at random on a table in front of informants, who were then asked to sort the species according to their similarity (Weller and Romney 1988). With this unconstrained pile sort method, informants were free to divide the species into as many piles as they wished. After they finished sorting the species, informants were asked to explain each pile and why species were grouped together. Their responses were used to ensure that they understood the task and to gain insight into the criteria they used to distinguish between species.

Also, we asked informants to evaluate the potential harmfulness of meat for individuals who are suffering from illnesses. The wildlife species were presented randomly, and respondents were asked whether the meat would have negative effects on a sick individual. That is, informants were required to answer either “yes” or “no” for each species.

In the third stage of the research, informants were asked if they had ever eaten each of the 17 prey species, which were again presented in random order. If they answered affirmatively, they were asked to estimate how many times per year they consume the meat of the species and the last time they had eaten it. Whether or not

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[1] A funeral interrupted data collection, necessitating the change.

Table 1 Demographic characteristics of informants who participated in the cognitive data collection

	Stages 1 and 2 (n=56)		Stage 3 (n=47)	
Ethnic self-identification	86% Mayangna	14% Miskito	81% Mayangna	19% Miskito
Sex	45% Male	55% Female	40% Male	60% Female
Age	Mean=33 (±13)	Range: 17–65	Mean=32 (±13)	Range: 17–65

they had eaten it, informants were asked to rate the flavor of the species, using a five-point Likert scale.

Index cards with images of the species were then placed on the table in front of the informants, who were asked to arrange the cards according to flavor preferences, from the most desirable meat to the least desirable meat. To emphasize the exclusive focus on meat flavor, informants were instructed to imagine the rankings exercise as a series of choices between 1-pound portions of the meats. After completing these rankings, informants were given three additional cards with images of a cow, a pig, and a chicken, respectively. We asked informants to insert these cards into the flavor rankings at the appropriate position. Informants were then asked to re-rank the wildlife species according to the difficulty of preparing and cooking the meat for consumption, again inserting the three domesticated species after the initial ranking of the wildlife species.

Data Analysis

Stephens and Krebs (1986) detail the procedure for determining the prey types in the optimal diet set. Prey types are ranked according to their profitability, which is measured in kilocalories per hour and calculated as the average post-encounter energetic benefit divided by the average handling time (i.e., pursuit time and field processing time) for that prey type.[2] The optimal diet set is reached by including prey types in rank order until the next most profitable prey type provides a lower return rate than could be obtained by continuing to search for the more profitable prey types. That is, for a hunting environment in which n prey types are included in the optimal diet set, prey types are added to the diet until:

$$\frac{\sum_{i=1}^{n} \lambda_i e_i}{1 + \sum_{i=1}^{n} \lambda_i h_i} > \frac{e_{n+1}}{h_{n+1}}$$

where λ_i=encounter rate with prey type i, e_i=average expected net energy gain after encounter with prey type i, and h_i=pursuit, killing, and field processing time after encounter with prey item of type i.

A central prediction of prey choice models is the one-zero rule, which stipulates that hunters should *always* pursue prey items in the optimal diet set and *never* pursue

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[2] We use Alvard's (1993) method for calculating the caloric benefit of prey species.

prey outside the optimal diet set (Stephens and Krebs 1986). Violations of this prediction suggest that the forager is not achieving the maximum possible return rate in that environment. When prey types are pursued inconsistently, foragers are said to have a *partial preference* for the resource (Krebs and McCleery 1984).[3]

Given the limited observations of rifle hunters, the data were insufficient to estimate the handling times of several prey types. We therefore rely on published estimates from other optimal foraging studies in the Neotropics. Estimates of handling times for collared peccaries, howler monkeys, capuchin monkeys, spider monkeys, and the bare-throated tiger heron (*Tigrisoma mexicanum*) come from Alvard (1993:371). Estimates for coatis, white-lipped peccaries, and armadillos come from Hill and Hawkes (1983:167). Regarding the primates, it should be noted that the species in Peru differ from those in Nicaragua, and our method assumes that the handling times are consistent throughout the genus. Also, the handling times in these other studies were based on observations of shotgun hunters whereas the Mayangna and Miskito exclusively use .22 caliber rifles. Despite these differences, we believe that the estimates are adequate for the questions addressed in this paper.

In the analysis of the free-listing data, we use Smith's (1993) method to calculate the salience of each species. This measure is based on both the frequency with which the species were mentioned and the position of the species in the individual lists. That is, the species that are mentioned often and early in the lists are considered particularly salient items in the domain.

From the pile-sort data, we generated an aggregate proximity matrix, which was then used to create a hierarchical clustering dendrogram using the nearest neighbor method. López et al. (1997) note that informants tend to make distinctions based on morphology and behavior, which helps to explain the frequent similarities between folk taxonomies and scientific taxonomies.

We use the informal cultural consensus model of Romney et al. (1987) to analyze the rankings data and the dichotomous illness evaluation. Developed as a way to assess patterns of agreement among a group of respondents, the informal consensus model is a factor analysis of informants' responses. To determine whether there is a single pattern of shared responses or rankings, one compares the ratio of the first and second eigenvalues. In general, consensus may be inferred when the ratio is greater than 3 to 1, indicating a single factor structure. In addition, the first factor loadings for each informant should be positive, not negative. Typically called the informant's "competence," the first factor loadings provide information about the level of agreement because the square of the average competence is approximately equal to the average Pearson correlation coefficient between all dyads of informants (Weller 1987).

Data from the free listing and the pile sorts were analyzed in ANTHROPAC 4.98 (Borgatti 1996), and UCINET 6.252 (Borgatti et al. 2002) was used for consensus analysis. We used SPSS 16.0 for all other statistical analysis. All correlations are two-tailed.

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[3] Pulliam (1980) notes that, when individual prey items vary in their profitability, partial preferences might occur because a prey type is sometimes in and sometimes out of the optimal diet set.

Results

Optimal Foraging Calculations

The optimal diet set for Mayangna and Miskito rifle hunters is depicted in Table 2. In terms of profitability, white-lipped peccaries represent the top-ranked prey type. Because the return rate does not decline with the inclusion of the lowest-ranked resources, all prey types included in Table 2 are part of the optimal diet set. However, we note that pursuits of the lowest-ranked prey types are not dramatically superior to the expected return rate if hunters were to forgo pursuits and continue a general search for prey. Accordingly, if hunters were to exhibit partial preferences for some prey types, the lowest-ranked resources are the most probable candidates.

Although an ocelot (*Leopardus pardalis*) and a puma (*Puma concolor*) were killed on unobserved hunts, we lack the data needed to estimate the profitability of these feline predators. However, if we include highly conservative estimates that half of the pursuits of these prey types are successful with an expected handling time of 1 h, then

Table 2 Calculation of the optimal diet set for rifle hunters. The symbols λ, *h*, and *e* represent the respective encounter rates, handling time, and energetic benefit of each prey type

Species	λ	*h* (hr)	*e* (kcal)	Profitability (kcal/h)	Return rate if added to diet set (kcal/h)	In optimal diet set?
White-lipped peccary	0.008	0.51	233708	458250	1960	Yes
Agouti	0.038	0.04	4914	122850	2142	Yes
Baird’s tapir	0.004	3.00	312000	104000	3405	Yes
Collared peccary	0.017	0.37	33248	89858	3931	Yes
Red brocket deer	0.013	0.39	13047	33453	4072	Yes
Coati	0.004	0.22	7020	31909	4097	Yes
Nine-banded armadillo	0.008	0.27	7800	28889	4152	Yes
Howler monkey	0.038	0.42	8580	20429	4399	Yes
Bare-throated tiger heron	0.004	0.08	1612	20150	4404	Yes
Great tinamou	0.198	0.05	905	18104	4532	Yes
Keel-billed toucan	0.008	0.05	744	14880	4536	Yes
Chestnut-mandibled toucan	0.013	0.05	744	14880	4542	Yes
Spider monkey	0.004	0.59	8320	14102	4565	Yes
Parrots	0.021	0.05	682	13640	4573	Yes
Great currasow	0.025	0.26	3249	12495	4622	Yes
Crested guan	0.093	0.21	2368	11278	4741	Yes
White-faced capuchin	0.025	0.38	3900	10263	4789	Yes
Plain chachalaca	0.021	0.05	459	9176	4793	Yes
Lineated woodpecker	0.017	0.05	248	4960	4794	Yes
Doves	0.017	0.05	248	4960	4794	Yes
Little tinamou	0.025	0.05	248	4960	4794	Yes

both of these species would be in the optimal diet set. The respective profitability estimates would be 9,750 kcal/h for the ocelot and 48,750 kcal/h for the puma.

Actual Prey Choice

As predicted by the prey choice model, rifle hunters invariably pursue many of the prey types in the optimal diet set (Fig. 1). Exceptions to this generalization include pumas and ocelots, which may be killed to eliminate a threat to domesticated animals but which are rarely brought back to the community for consumption. The failure to consume these species therefore represents a violation of optimal foraging predictions.

Rifle hunters exhibit partial preferences for several prey types, including agoutis and several avian species. In most cases, the explanations for these partial preferences parallel Alvard's (1993) conclusions about patterns among Piro hunters. That is, hunters express reluctance to use their limited supply of bullets on relatively small prey types, especially early in the hunting trip when they hope to encounter larger prey. In addition, there is variability in the context of encounters. Hunters sometimes catch prey unawares, but the animals have occasionally started their escape before the hunters notice them. In the latter case, the expected profitability of a pursuit is minimal, and these fleeing animals could therefore be considered a separate, suboptimal prey type.

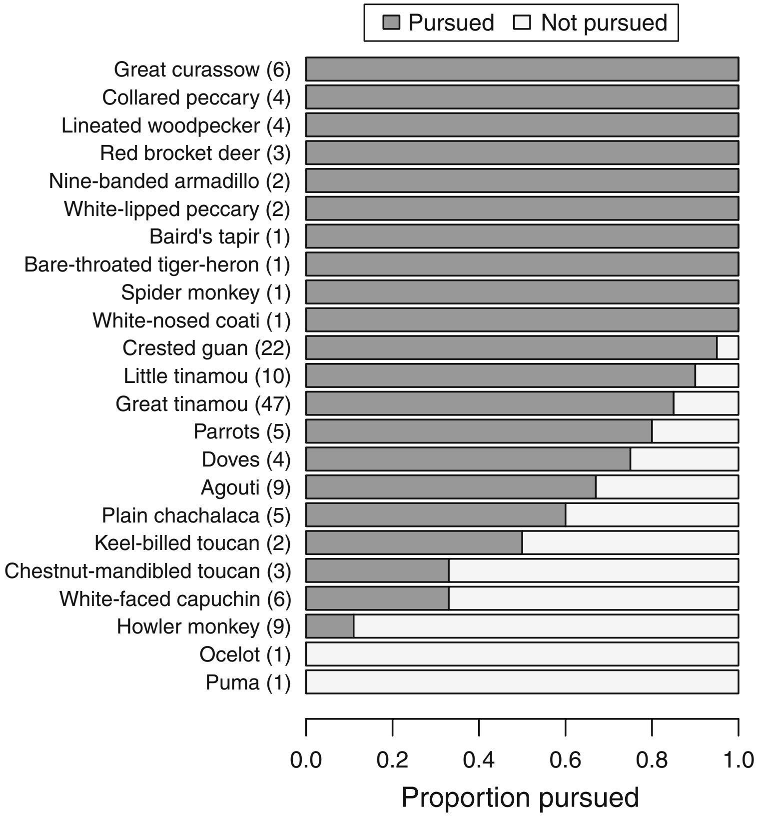

Fig. 1 Proportion of encounters that led to pursuits by hunters with rifles. The number of encounters with each prey type is indicated in parentheses

These considerations do not explain the partial preferences for white-faced capuchins and howler monkeys, however. In other settings, pursuits of these primates are not contingent on catching them unawares (Hill and Hawkes 1983; Alvard 1993), and evidence suggests that these monkeys provide more meat per bullet than most of the game birds. We hesitate to suggest that capuchins are unambiguously in the optimal diet set because this species is among the lower-ranked prey types at other sites. By contrast, howler monkeys clearly belong in the optimal diet set, and the hunters' partial preference for this species cannot easily be explained with optimal foraging logic.

Figure 1 includes only animals encountered on daylong hunting trips originating in the community, but it is important to note that hunters with rifles encountered many other animals, either opportunistically or during multi-day hunting expeditions. For example, there were six additional encounters with spider monkeys, all of which led to pursuits and a total of 13 kills. By contrast, although four howler monkeys were harvested following opportunistic encounters, other encounters did not lead to pursuits, including situations in which howler monkeys were spotted in the trees surrounding the community.

Free Listing and Pile Sorts

In the free-listing exercise, informants named approximately 48 species, 18 of which were mentioned by three or fewer interviewees. The average number of species listed per informant was 14.8 (±4.8). In Table 3, we include the species that were mentioned by at least 15% of the informants.

We compared the salience of the species in Table 3 to the number and biomass of each species harvested by hunters in Arang Dak during the 2004–2005 study period (Koster 2008b). There is a significant positive correlation between salience and the number of individual specimens harvested (Pearson's $r=0.565$; $p=0.002$; $n=27$). There is also a significant positive correlation between salience and the harvested biomass of each species (Pearson's $r=0.758$; $p<0.001$; $n=27$). Both number ($\beta=0.306$; $p=0.03$) and biomass ($\beta=0.632$; $p<0.001$) retain significance as predictors in a multivariate regression model that explains much of the variance in salience ($R^2=0.652$; $p<0.001$; $n=27$). These results suggest that both the frequency and the volume of consumption have noteworthy effects on the cognitive salience of prey species.

In the indigenous folk taxonomy, a primary distinction exists between arboreal and terrestrial animals.[4] Another fundamental distinction is between four-footed animals and two-footed animals, primarily birds. These dimensions are clearly evident in a hierarchical clustering analysis of the aggregate proximity matrix (Fig. 2), which reveals a cluster of terrestrial mammals (nine-banded armadillo, agouti, paca, collared peccary, white-lipped peccary, Baird's tapir, red brocket deer, and white-tailed deer), a cluster of arboreal animals (spider monkey, howler monkey, capuchin monkey, variegated squirrel, coati, and iguana), and a cluster of birds (crested guan, great curassow, and great tinamou).

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[4] Arboreal and terrestrial animals are likewise distinguished from riverine animals, which explains in large part why informants did not include turtles in the cultural domain.

Table 3 Percentage of informants who listed wildlife species in free-listing exercise and salience of species. Harvest data for each species are from a yearlong study of wildlife consumption (Koster 2008b)

Scientific name	Common name	Percentage	Salience	Number harvested	Biomass harvested (kg)
Cuniculus paca	Paca	98	0.750	115	848.8
Dasyprocta punctata	Agouti	93	0.689	350	1031.1
Dasypus novemcinctus	Nine-banded armadillo	89	0.654	155	645.6
Tapirus bairdii	Baird's tapir	87	0.680	13	2338
Penelope purpurescens	Crested guan	85	0.454	38	72.3
Tayassu pecari	White-lipped peccary	85	0.721	20	744.9
Tayassu tajacu	Collared peccary	84	0.611	39	768.2
Crax rubra	Great curassow	82	0.431	16	45.6
Tinamus major	Great tinamou	73	0.283	48	45.1
Mazama americana	Red brocket deer	69	0.487	15	215.8
Ateles geoffroyi	Spider monkey	58	0.270	11	76.2
Amazona spp.	Parrots	49	0.181	7	3.8
Cebus capucinus	Capuchin monkey	49	0.163	3	7.8
Ramphastos swainsonii	Chestnut-mandibled toucan	49	0.181	6	3
Geotrygon spp.	Doves	45	0.110	7	1.7
Ara spp.	Macaws	44	0.156	1	1
Alouatta palliata	Howler monkey	33	0.086	5	35
Nasua narica	Coati	31	0.104	8	24.4
Rhynchortyx cinctus	Tawny-faced quail	27	0.071	7	2.5
Ortalis vetula	Plain chachalaca	27	0.075	7	2
Pteroglossus torquatus	Collared aracari	22	0.065	6	3.4
Sciurus variegatoides	Variegated squirrel	22	0.069	5	1.4
Odocoileus virginianus	White-tailed deer	18	0.106	1	49
Dryocopus lineatus	Lineated woodpecker	16	0.033	3	0.8
Crypturellus soui	Little tinamou	16	0.038	7	2.2
Iguana iguana	Iguana	15	0.068	54	123.6
Sylvilagus brasiliensis	Forest rabbit	15	0.055	0	0

Because the two types of deer were placed in the same pile by 98% of the informants, the analysis suggests that red brocket deer and white-tailed deer are considered the most similar pair of species in the domain. Among other pairs of species, crested guans and great curassows (96%) and spider monkeys and howler monkeys (95%) also exhibit considerable similarity.

Flavor Rankings

There was a high level of agreement on the flavor rankings of the twenty different kinds of meat. The ratio of eigenvalues is 29.58/3.05, or 9.70/1, which exceeds the recommended 3/1 ratio. The average competence is high (0.79±0.10) with a range of 0.50 to 0.93. These data therefore suggest a single, shared cultural model with

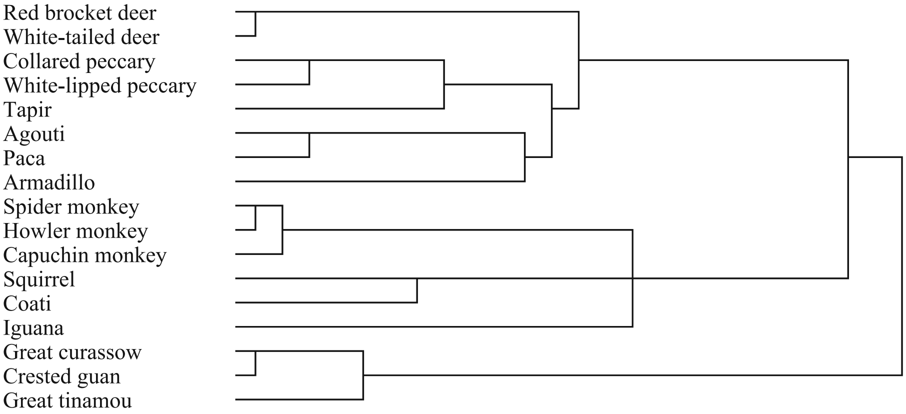

Fig. 2 Dendrogram based on hierarchical clustering analysis of the aggregate proximity matrix

consensus on the desirability of meats. The weighted averages for each species are included in Table 4.

In order to assess whether the consensus is an artifact of low rankings given to species that have not been sampled by most of the informants, we removed from the dataset the four species that had been eaten by less than 90% of the respondents: howler monkey, white-faced capuchin, coati, and variegated squirrel. After re-ranking the remaining 16 species accordingly, the results still exhibit a consensus pattern (eigenvalue ratio=20.15/5.47, or 3.68/1). The average competence declines but is still relatively high (0.64±0.15). The range of competence scores is 0.23 to 0.90, and most (83%) are greater than 0.50.

Similarly, if we remove domesticated animals from the dataset, the rankings still exhibit consensus (eigenvalue ratio=21.57/5.82, or 3.71/1). The average competence remains high (0.65±0.18). The range is 0.14 to 0.94, and most (81%) are greater than 0.50. These results indicate considerable shared agreement about the desirability of the 13 most commonly sampled wildlife species.

Using an alternative approach, if we consider only the rankings of the 17 informants who have sampled the meat of at least 16 of the 17 wildlife species, the rankings continue to exhibit consensus (eigenvalue ratio=11.30/.92, or 12.33/1). The average competence is high (0.81±0.12), and the range is 0.49 to 0.93. Given this high level of agreement, no more than 10 informants are needed to provide aggregated responses with high validity (0.95). In other words, the reduced sample of 17 informants was more than adequate to accurately infer the consensus rankings. Furthermore, the rankings generated from these 17 informants are highly correlated (Pearson's $r=0.96$) with the rankings of the remaining informants, and few species moved more than one position in the relative rank order.

For the 17 wildlife species in the flavor rankings, a significant correlation was found between the average flavor ranking and the salience of the species (Pearson's $r=-0.773$; $p<0.001$). That is, during the free-listing exercise, the most salient species tended to be highly rated in terms of flavor.[5]

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[5] Note that several of the correlations involving the flavor rankings are negative because low numbers in the rankings indicate preferred species.

Table 4 Weighted averages of flavor and cooking difficulty, the proportion of informants who consider the meat of the species to be safe for ill individuals, and the proportion of informants who have sampled the meat of the species. Based on the flavor rankings, species are listed from most appealing to least appealing

Species	Flavor rankings	Cooking difficulty rankings	Safe for ill individuals	Sampled by informants
White-lipped peccary	3.42	5.27	0.70	0.98
Paca	3.75	12.76	0.93	1.00
Beef	4.65	6.58	–	1.00
Collared peccary	6.31	5.80	0.30	0.98
Pork	6.48	7.50	–	1.00
Chicken	7.06	17.83	–	1.00
White-tailed deer	8.71	9.95	0.61	0.94
Red brocket deer	8.91	9.60	0.52	0.98
Great tinamou	9.35	18.02	0.87	0.94
Nine-banded armadillo	9.43	14.27	0.30	0.96
Great curassow	9.48	16.61	0.61	0.96
Crested guan	9.77	17.38	0.61	1.00
Baird’s tapir	11.15	6.33	0.02	0.90
Agouti	11.74	11.00	0.80	0.98
Spider monkey	13.72	6.24	0.11	0.90
Iguana	15.17	13.79	0.43	1.00
Capuchin monkey	16.80	5.60	0.13	0.63
Variegated squirrel	17.59	11.34	0.57	0.56
Coati	18.26	7.70	0.04	0.35
Howler monkey	18.29	6.42	0.07	0.44

The flavor rankings are also correlated with the total biomass of each species consumed during the 2004–2005 study period (Spearman’s $\rho=-0.571$; $p=0.02$; $n=17$).[6] This result may therefore provide support for a causal relationship between familiarity and flavor preferences.

The amount of harvested biomass for each species is in large part a function of the technologies used by hunters. In a reflection of the heavy reliance on dogs in Arang Dak, the harvested biomass of all prey species except white-tailed deer in the cluster of terrestrial mammals exceeds the harvest of all species in the arboreal cluster (Koster 2008b).

A Kruskall-Wallis test reveals significant differences in the flavor rankings of species in the three primary clusters ($H=11.449$; $p<0.001$). A post-hoc Dunn’s comparison indicates that the rankings of species in the arboreal cluster differ significantly from the cluster of terrestrial mammals ($p<0.01$). The cluster of birds does not differ significantly from either the arboreal cluster or terrestrial mammals,

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[6] We use a nonparametric test because the biomass of harvested tapir meat is more than twice the value for any other wildlife species, and this moderately ranked species therefore has a disproportionate effect on the correlation coefficient. When we exclude this outlier from the dataset, the Pearson’s correlation is likewise significant (Pearson’s $r=-0.613$; $p=0.012$; $n=16$).

but the small sample size of birds precludes definitive conclusions. In general, because of the aforementioned association between the clusters and hunting technologies, the difference in flavor rankings among the clusters may be an artifact of the relationship between harvested biomass and hunting technology.

Cooking Difficulty

As with the flavor rankings, consensus is apparent in the rankings of preparation and cooking difficulty for the twenty kinds of meat (eigenvalue ratio=25.82/6.84, or 3.77/1). The average competence is high (0.71±0.18), and the range is 0.16 to 0.93, with most (92%) scores greater than 0.50.

Although we anticipated that these rankings would be based in large part on variation in cooking methods, most informants cited variation in the butchering of the animals as the primary consideration. For example, primates received low rankings because informants complained about the hassle of peeling their multiple layers of hair.

The weighted averages of the cooking and preparation rankings are included in Table 4. There appears to be no significant relationship between these rankings and the flavor rankings (Pearson's $r=-0.120$; $p=0.61$).

Effects on Ill Individuals

The informants' evaluations of the potential negative effects of meats on ill individuals also exhibit consensus (ratio of eigenvalues=17.83/4.99, or 3.57/1). The average competence was relatively high (0.59±9.20), and all values were positive (range=0.09 to 0.93). In Table 4, we include for each wildlife species the proportion of informants who evaluated the meat as harmless for sick individuals. For example, only 2% of the respondents indicated that tapir meat was harmless for ill people whereas 93% rated paca meat as safe for sick individuals.[7] There appear to be no significant differences in the extent to which the three primate species are associated with deleterious effects for sick consumers ($\chi^2=1.113$; $p=0.57$; df=2).

For the 17 wildlife species, there was a significant correlation between the flavor rankings and the percentage of informants who ranked the species as safe for sick people (Pearson's $r=-0.602$; $p=0.01$). In other words, the meats that are considered desirable are generally rated as safer for ill individuals.

Discussion

Before addressing the relationship between flavor preferences and prey choice decisions, we note that Mayangna and Miskito hunters violate predictions of foraging theory by not pursuing and consuming several species, including ocelots and pumas. These results parallel Koster's (2008a) observation that, although hunters kill giant anteaters and northern tamanduas to protect their dogs, these

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[7] For the Kagwahiv, by contrast, pacas are considered the most dangerous meat for sick individuals (Kracke 1981:99).

wildlife species are not subsequently consumed despite being in the optimal diet set. Given that similar aversions and taboos are common in the Neotropics (Hames and Vickers 1982), it appears that human hunters generally focus on prey types in the optimal diet set, but they do not necessarily pursue the full suite of predicted resources.

When asked why they do not consume the meat of carnivores, including jaguars (*Panthera onca*) and tayras (*Eira barbara*), informants usually emphasize that these species eat raw meat. Because of an association between raw meat and potentially harmful pathogens, the thought of consuming carnivorous species that eat raw meat may elicit reactions of disgust, which make these species unpalatable according to the "you are what you eat" principle (Nemeroff and Rozin 1989). Given that carnivores appear to be disproportionately represented among proscribed wildlife species (Koster 2007:14), it would be worthwhile to devote additional consideration to the psychological dimensions of these aversions and taboos (Fessler and Navarrete 2003).

Among the prey species that the Mayangna and Miskito recognize as edible, the apparent ambivalence toward howler monkeys is the most noteworthy partial preference. That rifle hunters invariably pursue spider monkeys upon encounter accentuates the conspicuousness of the aversion to howler monkeys because the two species are similar in many respects. These large-bodied primates are similarly profitable in the context of foraging theory, for example, and essentially identical strategies are used to hunt them. Because of their prehensile tails, howlers can remain suspended even after being shot, and hunters occasionally expend multiple bullets in an attempt to dislodge them. Yet, this trait likewise characterizes spider monkeys (see Yost and Kelley 1983:204). Additionally, Crockett (1998) notes that howler monkeys seem particularly susceptible to bot fly parasitism and yellow fever. The bot fly parasitism may lack a clear parallel in spider monkeys, but informants in the Bosawas Reserve recall that spider monkeys were similarly affected by yellow fever during the last major epidemic in the 1950s (K. Williams-Guillén, personal communication, March 2006). Also, Alvard (1993) notes that partial preferences for slow-breeding and easily overhunted species like howler monkeys could reflect a conservation ethic, but it is not clear why hunters would choose to conserve howler monkeys and not spider monkeys. Finally, in other parts of the Mosquitia, some Miskito informants report that they do not consume primates because of their resemblance to humans (Dunn 2004:72; see also Kracke 1981:105), but this anthropomorphization would presumably apply equally to both spider monkeys and howler monkeys.[8]

Indeed, the pile sorts suggest that local informants view howler monkeys and spider monkeys as very similar species, and the emic view that they are similarly dangerous for ill people further reinforces the comparison. From the hunters' perspective, the only salient differences might therefore be related to bot fly parasitism and meat flavor. Yet, while we recognize that the discovery of parasite-ridden meat could dramatically reduce the gustatory appeal of howler monkeys (da Silva et al. 2005), informants in the Bosawas Reserve do not mention this factor, instead emphasizing that the meat itself is

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[8] In other societies, informants suggest that the similarity of monkeys to humans makes primates less disgusting than other prey (Cormier and Urbani 2008).

not appetizing. Given the lack of noteworthy ecological or economic differences between the two species and the apparently widespread preference for spider monkeys over howler monkeys, we conclude that meat flavor is an important factor in the inconsistency of pursuit decisions upon encountering howler monkeys.

Nonetheless, it is important to acknowledge that ambivalence toward howler monkeys in the Mosquitia dates to at least the nineteenth century, when Bell (1989:183, 201) observed that howler monkeys were never pursued by indigenous hunters. By contrast, spider monkeys were a preferred prey species (Bell 1989:201), and this preference persisted in the early twentieth century (Conzemius 1932:88). The timing of these observations is important because the disregard for howler monkeys apparently predates the widespread influx of firearms into the Mosquitia, and hunters were instead relying on bows and arrows. Because there are no published data on the respective profitability of spider monkeys and howler monkeys to bow hunters in the Neotropics, it is not possible to conclude definitively that the two species would have been similarly profitable and that howlers would have unambiguously belonged in the optimal diet set for hunters with bows.[9] In the absence of such data, it could be argued that the current partial preference for howler monkeys represents a persistent (but gradually dissipating) holdover from a once-adaptive aversion (see Yost and Kelley 1983 for a similar discussion applied to the Waorani taboo of several large ungulates before the incorporation of dogs and shotguns).

More generally, the observed consensus on the flavor rankings (including the rankings of the 13 most commonly sampled wildlife species) has potentially interesting implications for ongoing research in human behavioral ecology. For instance, proponents of costly signaling theory have recently suggested that some apparently suboptimal foraging decisions may be explained by the foragers' motivation to broadcast honest information about their abilities. Spearfishers on Mer violate predictions of foraging theory when they bypass opportunities to harvest shellfish, for example, and these decisions could be explained by the social status associated with being known as a successful spearfisher (Bliege Bird et al. 2001). Thus far, costly signaling research has generally focused on pursuits of unprofitable resources in order to gain social benefits, but we suggest that foragers could also bypass profitable prey types to avoid social costs. In terms of reputations, it might be preferable to return home empty-handed than to be known as a hunter who must pursue widely disliked game species in order to secure an adequate amount of meat.[10] In this study, our evidence is only anecdotal, but it is worth noting that local research assistants indicated to the lead author in 2005 that households were reluctant to notify the assistants after killing howler monkeys because they were "embarrassed." Although we suspect that variation in the prestige and desirability of meats is often associated with differences in flavor, we note that this explanation could also apply to situations in which desirability is associated with other characteristics of prey species.

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[9] Based on Shepard's (2002) general description of spider monkey pursuits by Matsigenka bow hunters, it seems unlikely that spider monkeys are dramatically more profitable than howler monkeys.

[10] This explanation is consistent with the argument of Fessler and Navarrete (2003:17–18) that the prestige-biased cultural transmission of food habits might explain the origin of food taboos.

Finally, we note that these results have potentially important implications for wildlife conversation efforts. Because primates are characterized by relatively slow life history strategies (Bodmer et al. 1997), primate populations are particularly vulnerable to over-hunting. Yet, even though they are considered “easy game” because of their inactivity and large size, the black colobus monkeys (*Colobus satanas*) in Gabon are reportedly pursued by hunters primarily when other preferred species have been depleted (Brugière 1998; cf. Kümpel et al. 2008). By contrast, as with spider monkeys, the generally frugivorous guenons are considered tasty, which may contribute to unsustainable harvests of these species (Butynski 2002; see also Fa et al. 2002). The willingness of hunters to voluntarily limit harvests of flavorful species merits further investigation.

Conclusion

The high levels of agreement among informants on the gustatory appeal of prey species in the Bosawas Reserve compellingly suggests that meat flavor is a worthwhile topic for additional research. Meats may be imbued with symbolic significance (Fiddes 1991), however, and with data from only one cultural setting, it remains possible that factors other than meat flavor have influenced the rankings. If this study were replicated in a broad variety of cultural and ecological settings, it would be possible to further test the hypothesis that people respond to the chemical properties of meat in similar ways. Based on our reading of the ethnographic literature, we anticipate that cross-cultural replications will produce rankings that correlate with the results of this study. Among other results, we specifically anticipate that pacas and peccaries will consistently be rated favorably, agoutis will receive moderate rankings, nine-banded armadillos will receive moderate to low rankings, coatis will be rated unfavorably, and spider monkeys will be ranked higher than howler monkeys and capuchin monkeys.

Given the relationship between the flavor rankings and the harvested biomass of prey species, it would be particularly worthwhile to replicate this study in settings where dogs are a relatively unimportant hunting accessory. Hunters who rely primarily on firearms and other projectile technologies tend to harvest relatively more arboreal prey, especially primates (Yost and Kelley 1983). If these differences are associated with variation in flavor rankings, then it could be inferred that the chemical properties of meat interact with hunting technologies and wildlife population densities to condition flavor preferences for game species.

Consensus analysis is a powerful tool for assessing patterns of agreement regarding taste preferences, but it would be preferable to incorporate the experimental methods used by meat scientists, systematically controlling for muscle types across species, cooking techniques, and serving methods while testing consumer preferences for tenderness, juiciness, and flavor (AMSA 1995). The logistics of such experiments in remote preindustrial settings can be formidable, but researchers in Africa have conducted preliminary taste tests of bushmeat versus meat from domesticated animals (Schenck et al. 2006). Expanded variations of this research are needed in the Neotropics, first to determine if subjects can correctly identify different kinds of meat based on flavor and second to test the relationship between their stated preferences and the results from blind taste tests.

In summary, the observation that hunters regularly bypass profitable prey types does not negate the heuristic value of the prey choice model. To the contrary, this study supports previous optimal foraging research by showing that hunters generally pursue prey types in the optimal diet set, which suggests that hunters are keenly attentive to the ecological costs and benefits that undergird foraging theory. However, it is becoming increasingly clear that hunters do not pursue the full suite of prey types predicted by foraging models. Depending on the context, the reasons for these suboptimal deviations from the predicted set of resources are likely to be many and diverse. This research suggests that the flavor of meat is one of those factors, and this topic merits additional attention from anthropologists and researchers in related disciplines.

Taking a broad evolutionary perspective, consistent human preferences for certain meat flavors do not necessarily reflect an adaptation to the consumption of meat. Instead, these preferences are more likely a by-product of generalized predispositions. The human appetite for energetically dense foods and the dislike of bitter foods are apparently phylogenetically conserved preferences that predate the advent of habitual meat-eating in the genus *Homo* (Dominy et al. 2001; see also Cashdan 1998). As noted, meats that are high in fat provide relatively more calories, and preferences for fattier animals serve as a proximate mechanism for foragers to help identify the most profitable prey types. As for the dislike of bitterness, this predisposition has clear adaptive value when consuming plants, which frequently contain bitter-tasting secondary compounds that compromise digestion and metabolic functions (Glander 1982). Yet, the post-ingestive consequences (e.g., the costs of detoxification) of eating meat infused with secondary compounds are not clear, especially given that many bitter-tasting compounds are benign (Glendinning 1994). In other words, additional research may be needed to determine whether meats that are less palatable solely because of these compounds are also less nutritious. Meanwhile, given the evidence that cooking can dramatically affect meat flavor as well as tenderness, insights from meat scientists are needed to elucidate the ways in which variation in cooking techniques intersect with prey choice and the palatability of different wildlife species. Recent research has focused on the energetic significance of cooking, and increased intake associated with the enhancement of meat flavor might be an important factor in inethe evolutionary history of cooking (Carmody and Wrangham 2009).

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