

Heterogeneity of hunting ability and nutritional status among domestic dogs in lowland Nicaragua

Jeremy M. Koster¹ and Kenneth B. Tankersley

Department of Anthropology, University of Cincinnati, Cincinnati, OH 45221

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In past and modern human societies, dogs have played an important role as hunting companions. Given considerable ethnographic evidence that dogs vary in their hunting abilities, this paper addresses the effects of key demographic variables, namely age and sex, on the amount of harvested game that dogs contribute in an indigenous Nicaraguan community. Controlling for variation in the time spent potentially hunting, male dogs and older dogs are significantly associated with greater harvests. These results may account for documented preferences for males in both archaeological and ethnographic contexts. Among societies in which dogs are used both as hunting companions and sources of food, the age-related delay in peak hunting ability also suggests a tradeoff that might explain the consumption of dogs shortly after they have reached adult size. Informant rankings of two cohorts of dogs indicate that residents of the community exhibit high agreement about the relative abilities of the dogs, and the rankings indicate that dogs from the same household exhibit comparable skill. There is little evidence that talented, highly-ranked dogs are provided a more nutritious diet, as measured by nitrogen-based and carbon-based isotopic analysis of hair samples. Overall, although dogs can be quite advantageous as hunting companions, this research suggests that the heterogeneity of hunting ability combines with the high mortality of dogs to impose risks on households that depend on dogs as a source of harvested meat.

Canis lupus familiaris | life history theory | Mayangna | Miskito | stable isotopes

Dogs are currently used for hunting in preindustrial societies across the globe (1), and there is also considerable archaeological evidence for the important role of hunting dogs in past societies (2). In a variety of settings, ethnographers have frequently commented on two related aspects of heterogeneity among the dogs, specifically that individual dogs vary considerably in their skill as hunting companions and that better hunting dogs receive better care from their owners (refs. 3–9 and additional references in ref. 1).

Despite the ubiquity of such ethnographic observations, apparently there have been no previous quantitative attempts to account for the heterogeneity of hunting skill as a function of basic demographic variables, namely the age and sex of the dogs. Among other implications, such analysis could provide valuable context for archaeological research on dogs in past societies. Based on evidence from burials, for example, Warren (10) reported a cultural preference for male dogs among native populations in eastern North America. If male dogs exhibit greater hunting prowess, this preference may have a straightforward ecological explanation. Similarly, archaeological evidence suggests that dogs were often eaten in the past (11), and such exploitation may be reflected by the butchery of year-old dogs that have recently reached adult size (12, 13). Among societies in which dogs serve as both hunting companions and potential sources of food, if dogs are several years old before they become valuable hunting companions, their owners could face a tradeoff between current consumption of a full-sized dog and the prospect of hunted meat acquired by the dog in the future.

Given that the nutritional needs of dogs resemble those of children, owning dogs can represent a significant cost. Consumed foods vary in their costliness, however. On a per-calorie basis, crops like banana and manioc require less effort to produce than grains and meat, but they lack the protein and fat provided by the latter resources (14). In settings in which dogs are important as hunting companions, owners could therefore choose to reserve high-quality grains and meat for talented hunting dogs while forcing unskilled dogs to consume less nutritious options or to scavenge for scraps in the community.

The present paper is based on fieldwork in lowland Nicaragua over a period of 13 mo in 2004 and 2005 and 1 mo of follow-up research in 2008. The structure of this paper reflects the different samples and methodologies used during these studies. In the first study, we use harvest data to examine the effects of demographic characteristics on the hunting success of dogs. We also use informant rankings and consensus analysis to gauge the relationship between documented contributions to harvests and the perceived variation of hunting skill among dogs. In the second study, we again use informant rankings to examine the relationships between perceived hunting skill and the consumption of meat and maize, as reflected in isotopic data from hair samples.

Study Site

This study was conducted in Nicaragua's Bosawas Biosphere Reserve, which is part of the largest unbroken tract of Neotropical rain forest north of Amazonia (15). Specifically, the research was based in two indigenous Mayangna/Miskito communities along a tributary of the Coco River (Fig. S1). As of 2008, the largest community, Arang Dak, was home to approximately 245 residents in 30 households. Suma Pipi, which is located 1 km downstream of Arang Dak, was home to 76 residents in 10 households in 2005. The Mayangna and Miskito are sedentary swidden horticulturalists, and staple crops include bananas and plantains, manioc, beans, rice, and maize. Hunting and fishing are the leading sources of dietary protein, but the residents also keep livestock, most notably cattle, pigs, and fowl (16). Whereas women sometimes hunt with dogs in other small-scale societies (1, 9, 17, 18), hunting is almost exclusively a male-oriented activity in Arang Dak and Suma Pipi. As an exception to this generalization, women in dugout canoes opportunistically pursue deer and other animals that have been chased by dogs into the river.

Compared with most indigenous Neotropical societies, the Mayangna and Miskito exhibit a greater reliance on hunting dogs, and Koster (19) reported that approximately 85% of the harvested mammals are captured with the aid of dogs. Households acquire dogs in multiple ways, sometimes as the puppies of

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¹To whom correspondence should be addressed. E-mail: jeremy.koster@uc.edu.

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their current dogs. Puppies are also exchanged as gifts between closely related households. Dogs are also purchased or traded, either as puppies or as adult dogs, and the most renowned hunting dogs can command a high price, approximately equivalent to 45 kg of purchased meat.

There is little formal training of hunting dogs. As they approach adulthood, dogs are frequently brought along with older hunting dogs with the hope that they will learn via imitation. The perceived skill of a dog is closely related to the size of the animal that it can successfully corral or bring to bay. Therefore, dogs that contribute to harvests of ungulates like tapirs (*Tapirus bairdii*) and collared peccaries (*Tayassu tajacu*) are considered superior to dogs that contribute only smaller prey, such as agoutis (*Dasyprocta punctata*), pacas (*Cuniculus paca*), and nine-banded armadillos (*Dasyopus novemcinctus*).

Although dogs commonly seek scavenging opportunities around the community, they generally are given portions of the same foods that have been prepared for household consumption. Milk is sometimes purchased for puppies that have been separated from their mothers. Some dogs seem malnourished, which may contribute to the high mortality rate of dogs, particularly puppies. The leading sources of mortality for adult dogs, however, are attacks by jaguars and snakebites (20). There is no evidence that the Mayangna and Miskito consume dogs or view them as edible.

Study One: 2004–2005 Data

Methods. Data on dogs during the 2004–2005 study period come from multiple sources (Dataset S1). First, basic demographic data, namely age and sex, stem from an initial census that was updated periodically throughout the study period. Ages were estimated based on interviews with the owners, which included attempts to identify the month (and year) in which the dogs were born. For dogs older than 2 y, ages were rounded to the nearest integer. Second, for approximately 1 wk per month over a period of 12 mo, the lead author collected time allocation data in Arang Dak by using spot-check observational methods (21). Observations occurred every 30 min between 5:30 AM and 6:00 PM. Households were the sampling unit and randomly sampled without replacement on each day of data collection such that households were observed only once per day. During an observation, the location and activities of household members and their dogs were recorded. When a dog was beyond the boundaries of the community (e.g., accompanying its owner on an excursion to get firewood), it was coded as “outside of the community.”

Third, the lead author and local research assistants documented the harvest of all hunted game that was acquired by residents of Arang Dak and Suma Pipi during the study period (19). Following the acquisition of game, a questionnaire was used to record the identity of the hunters, the technologies that they brought (e.g., rifles), the dogs that accompanied the hunters (if applicable), and the weights of harvested animals. In addition, for each harvested animal, the hunters were asked if dogs contributed to the kill, either by detecting the animal or pursuing it to a location where the hunters could successfully dispatch it (e.g., a hollow trunk). If multiple dogs accompanied the hunters, the format of the questionnaire allowed the hunters to distinguish the dogs that contributed to the kill from those that did not. Note that hunters are typically able to discern from the barking which dog first detected the animal (see also refs. 22, 23).

Finally, at the end of the study period, a random sample of 38 adult informants from Arang Dak and Suma Pipi was recruited for a rankings exercise. The sample of informants included 21 men and 17 women. Photographs of the 34 dogs that were already full-grown at the beginning of the study period were placed on a table and presented to the informants, who were asked to rank the dogs in order of hunting skill.

Analysis. Modeling contribution of dogs to harvests of hunted game. In the first analysis, the response variable is based on the harvest data, specifically the weights of the animals that the dogs helped to acquire. When a single dog contributed to a kill, it was credited with the full weight of the animal. When hunters reported contributions from multiple dogs, however, the credited weight for each dog was the total weight of the animal divided by the number of contributing dogs. For example, if two dogs helped to harvest a 6-kg paca, each dog would receive credit for 3 kg of harvested meat. In reality, of course, the contributions of some dogs are likely to be more important than others. If two dogs are simultaneously pursuing an animal, for example, one of the dogs might play a greater role in forcing the animal to seek refuge in a hiding place. Without detailed observations of the dogs throughout the pursuits, however, it is difficult for hunters and researchers to assign differential credit for the harvest. Under the circumstances, an equal apportionment among all contributing dogs is preferable to ad hoc alternatives.

Primarily to account for the deaths of dogs throughout the study period, we divide the credited weight by the number of months that each dog was alive and present in the community. Mainly because dogs vary in their ability to pursue and corral large game, the distribution of the monthly harvest rates exhibits positive skew, which we address via a base-10 logarithmic transformation of the monthly rate. Dogs that contributed to no harvests during the study period were assigned an arbitrary value of 0.5 kg per month.

Explanatory variables in this analysis include sex, age, and the proportion of time that dogs are outside of the community, which we consider first as bivariate predictors and then as covariates in a multivariate model. There are few well established predictions for sex-related variability in harvest rates among domestic dogs, but we predict that males will make greater contributions than females, if only because they are marginally larger in size* (see also 2008 data). This prediction is consistent with evidence that male wolves (*Canis lupus lupus*) outperform relatively smaller females when hunting elk (ref. 24; see also ref. 25).

We expect that age will positively covary with harvest rates as dogs become more proficient throughout their lifetimes. As dogs senesce, we would anticipate that they would gradually become less proficient, thus producing a convex age-related pattern of hunting proficiency that characterizes both wolves (ref. 26; cf. ref. 25) and humans (27, 28). For two reasons, we choose not to include a quadratic term for age. First, the sample size discourages the consideration of a fourth covariate. Second, because many dogs succumb to jaguar attacks or snakebites at young ages relative to maximum lifespans, few dogs exhibit extended senescence. In this sample of full-sized dogs, for example, only 11% eventually reached 8 y of age, and the average age at death was 3.7 y (± 2.2 y).

Finally, we anticipate a positive relationship between harvest rates and time spent outside the community. Dogs that are more frequently away from the community have more opportunities to encounter and pursue game, and owners might be more inclined to bring talented hunting dogs on excursions. Although it may seem preferable to use a variable for the time that hunters and their dogs are actively hunting, the distinction between “hunting” and “not hunting” is often unclear. While men are poling their boats upstream to work in their fields, for example, they may allow their dogs to roam the riverbank in case game animals can be

*The dogs in the 2004–2005 sample were not weighed, but the lead author presented photographs of 33 of the dogs to 30 students and personnel at his university. When asked to rank the dogs according to perceived body size, the informants exhibited consensus (eigenvalue ratio, 17.6:1.9). Among the aggregated rankings, the average for male dogs was 19.7, and the average for females was 13.7. A two-tailed *t* test revealed a significant difference in these means ($P = 0.02$). However, when the rankings and analysis were limited to the 27 dogs from Arang Dak, the effect was more modest and not significant ($P = 0.13$).

encountered and pursued opportunistically (16). In many cases, bringing a dog is therefore an indication that someone is willing to interrupt planned activities to initiate a pursuit, and 36% of the harvested biomass is acquired opportunistically (16). Accordingly, the variable for time allocation outside the community is a comparatively inclusive measure of potential hunting activity.

Given the assignment of partial credit, as noted earlier, and because the contributions of hunting dogs partly depend on the activities and skills of their owners, we anticipate a positive intraclass correlation among dogs from the same household, which we address by specifying a household-level random effect (29). Partly because this analysis is limited to the 27 dogs in Arang Dak for which we have time allocation data, the estimates of the household-level variance are imprecise and not reported. For illustrative purposes, however, we use symbols to denote dogs from the same household in the scatterplots that accompany the analysis.

The analysis was conducted in MLwiN software, version 2.23, by using restricted iterative generalized least-squares (IGLS) estimation. The reported Akaike information criterion (AIC) values are based on iterative generalized least-squares estimation. Relatively low AIC values indicate models that best fit the data without being overly complex. The values for each dog were weighted by the number of months that it was present in the community during the study period.

Sources of variation in time spent outside of the community by dogs. Given the results of the first analysis, we use the unaggregated observational data ($N = 1,524$ observations) to investigate variation in time allocation by the 27 dogs from Arang Dak in the sample. The binary response variable is coded as 1 if the dog was outside of the community when the observation was conducted and 0 if not. We first consider demographic characteristics of the dogs, namely sex and linear and quadratic terms for age. To test the prediction that time outside of the community is contingent on hunting ability, we divide each dog's credited harvest by the proportion of time that it was observed outside of the community to generate a "harvest rate" that is analogous to return rates used in other studies (30). In separate models that control for age and sex, we consider the effect of a dog's own harvest rate and the best harvest rate among dogs in a particular household on the day of the observation. This latter variable allows us to evaluate the possibility that dogs are brought on excursions largely because their more talented household peers are being brought.[†] To account for the repeated observations of individual dogs and household-level clustering, we use logistic regression models with random effects for the identities of dogs and their respective households. We used MLwiN 2.23 software to estimate these models by using Markov chain Monte Carlo sampling.

Informant rankings of dogs and association with observational harvest data. We use the informal cultural consensus model (31), as implemented in UCINET 6.238 (32), to assess the agreement of informants on the rankings of the hunting dogs. Consensus analysis is essentially a factor analysis of informants' responses, and consensus (i.e., unidimensionality) is generally inferred when the ratio of the first to the second eigenvalue is greater than 3:1. Conventionally called the informant's "competence," the first factor loadings provide perspective on the level of agreement because the square of the average competence is approximately equal to the Pearson correlation coefficient between all pairs of informants (33). Because hunting is primarily a male-oriented activity, we predict that the average competence of male informants will be higher than the competence of women. Alternatively, as the preparers of meals, women may be relatively more attentive to the variation

in the hunting ability of dogs and their owners. We use a two-tailed t test to test these alternative predictions.

The first set of factor scores, conventionally called the answer key or simply the aggregated rankings, provides an average of the rankings for each dog, weighted by the competence scores. The rankings were scaled such that higher numbers represent the better hunting dogs.

To test for a relationship with the harvest data, we specify the aggregated rankings as the response variable. The log-transformed harvest data (i.e., the response variable from the first analysis) represent the sole covariate, but we again include a household-level random effect to account for the nonindependence of dogs from the same household. We present an "empty model" that includes only an intercept and the estimated random effect. Compared with the "full model" that includes the harvest data, this empty model allows us to investigate the extent to which the dogs' contributions to harvests account for the household-level variation in the rankings.

Results. Predicting harvests among dogs in Arang Dak. With the dogs' log-transformed monthly harvests as the outcome variable, Table 1 includes estimates for models that include the three explanatory variables: age, sex, and the proportion of time outside of the community. There is a clear bivariate relationship between the proportion of time that dogs spend outside of the community and the amount of wild meat they help to harvest (Fig. 1). The AIC comparisons suggest that this is the best bivariate predictor, and the effect of this variable remains strong in the multivariate model. For example, predictions based on the parameter estimates in model 4 suggest that a 3-y-old female dog that spends 10% of its time outside of the community will contribute to harvests of 1.5 kg/mo [95% confidence interval (CI), 0.9–2.6 kg/mo], and an increase to 20% of time outside the community will result in a harvest of 5.7 kg/mo (95% CI, 3.4–9.4 kg/mo).

Both age and sex are also significant as bivariate predictors. Although the logged harvest data exhibit some nonlinearity when regressed on age,[‡] there is a general tendency for older dogs to contribute more to harvests than younger dogs (Fig. 2). This effect remains consistent in all multivariate models. Sex likewise exhibits a significant effect, with males harvesting significantly more than females. Based on the parameter estimates from that model, for example, 3-y-old male dogs that are outside of the community 20% of the time are predicted to contribute to harvests of 15.3 kg/mo (95% CI, 9.4–24.2 kg/mo) compared with the aforementioned estimate of 5.7 kg/mo for female dogs.

The AIC comparisons indicate that model 4, which contains all three explanatory variables, is clearly distinguishable and preferable to the other models. In summary, the dogs' contributions to harvests are largely contingent on the time spent outside of the community, and older dogs and male dogs are associated with greater harvests even after controlling for the effect of this variation in time allocation.

Predictors of time outside of the community. Our models of time allocation (Table 2) suggest that demographic characteristics of the dogs have little effect on their likelihood of being away from the community. There is a tendency for dogs to be away from the community more often as their harvest rate increases, but this effect is not significant at conventional levels. By contrast, the positive effect of the best harvest rate in the household significantly predicts time outside of the community. Overall, the evidence therefore suggests that owners' decisions to bring dogs on excursions are motivated primarily by the skill of their most

[†]This variable is based solely on within-household comparisons and therefore underestimates the effect of the harvest rate of superior dogs because, for six of the 228 observations in which dogs were observed to be out of the community, they were brought along with a dog from another household that had a dramatically superior harvest rate.

[‡]In a model that includes no other covariates, both age and age-squared exhibit significant positive and negative effects, respectively. When proportion of time outside the community is added as a covariate, however, the quadratic term is no longer significant at conventional levels.

Table 1. Regression models in which the response variable is the log-transformed monthly harvest for 27 dogs in Arang Dak

Model	Model 1	Model 2	Model 3	Model 4
Intercept	-0.32 (0.16)*	0.21 (0.29)	0.31 (0.21)	-0.85 (0.17)*
Proportion of time out of community	6.88 (0.75)*	—	—	5.68 (0.59)*
Age	—	0.17 (0.07)*	—	0.16 (0.03)*
Male sex	—	—	0.66 (0.26)*	0.43 (0.16)*
Akaike information criterion	43.6	62.5	60.2	34.2

Coefficients (and standard errors in parentheses) are based on IGLS estimation.

* $P < 0.05$.

talented dogs. When they have committed to bringing dogs, owners frequently bring all their dogs, including comparatively unskilled dogs.

Notably, as time away from the community increases, usually the relative proportion of time spent on planned hunting excursions also increases (Fig. S2). That is, much of the variation in time allocation is explained by the dogs' participation on hunting trips. Hunters with skilled dogs apparently aim to facilitate encounters with prey, not only opportunistically but also by bringing them on hunting excursions relatively often. This evidence is consistent with a previously reported positive correlation between the time that men in Arang Dak allocate to hunting and the return rates that they exhibit while hunting (30).

Consensus analysis. There was consensus agreement on the relative skill of the 34 hunting dogs in the sample from both communities. The ratio of eigenvalues is 19.04:3.24, which exceeds the recommended 3:1 ratio. The average competence is high (0.69 ± 0.15), with a range of 0.35 to 0.91. These results suggest that there is considerable agreement on the abilities of the hunting dogs.

The average competence of male informants was $0.74 (\pm 0.15)$, whereas the average for female informants was $0.64 (\pm 0.14)$. There is a significant difference between these means (two-tailed t test statistic, 2.19; $P = 0.02$; $df = 36$). This result may indicate that female informants exhibit comparatively more randomness in their rankings, which would imply that men are more attentive to variation in the performance of hunting dogs.

An important caveat is that two of the three highest competence scores were registered by long-term assistants of the lead author. For much of the yearlong study period, these two assistants recorded the harvest data that were used in the afore-

mentioned analysis, and this experience apparently provided them a unique ability to rank the dogs in ways that match the aggregated rankings. When the rankings by these two men are excluded from the analysis, a two-tailed t test no longer reveals significant differences between male and female informants ($t = 1.81$; $P = 0.08$; $df = 34$). Furthermore, although the second factor loadings reveal no residual sex-related agreement ($t = 0.69$; $df = 36$; $P = 0.49$), if there were any systematic differences in the rankings of male and female informants, note that the greater number of male informants in the sample increases the likelihood that their competence scores would appear higher than those of female informants.

Modeling the relationship between informant rankings and observational harvest data. Before addressing the relationship between the aggregated informant rankings and the harvest data, it is important to note that there is substantial variance associated with the household-level random effect in the empty model (Table 3). A likelihood ratio test that compares the empty model to an intercept-only model (i.e., without a random effect) indicates that there are significant between-household differences in the rankings ($\chi^2 = 14.9$; $df = 1$; $P = 0.0001$). Following Rasbash et al. (29), the variance partition coefficient is 0.756, which indicates that 76% of the total variance in the aggregated rankings can be attributed to household-level differences.

In the full model, the log-transformed harvest data significantly predict variation in the rankings (Table 2). That is, the higher-ranked dogs are generally those that contribute the most to harvests of wild game (Fig. 3). The coefficient for the log-transformed harvest predicts that, for each incremental increase in the order of magnitude, there is an increase of 7.42 spots in

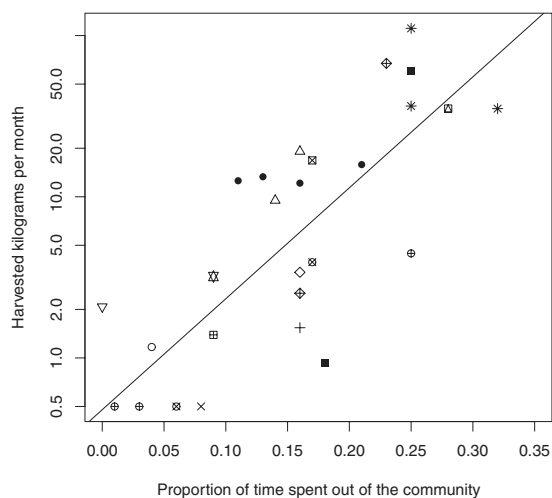


Fig. 1. Scatterplot of the proportion of time that dogs spend outside of the community and the monthly amount of hunted meat that they help to harvest. Note the logarithmic scale on the y axis.

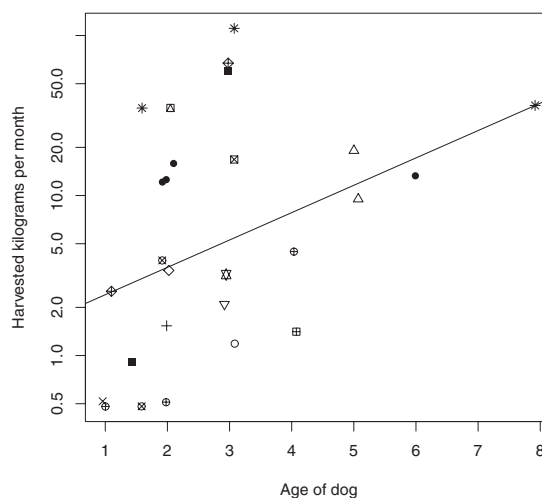


Fig. 2. Scatterplot of the proportion of the ages of the dogs in the 2005 study and the monthly amount of hunted meat that they help to harvest. Note the logarithmic scale on the y axis.

Table 2. Logistic regression models of time spent outside of the community by dogs in Arang Dak, based on time allocation observations ($N = 1,524$)

Model	Demographics	Own harvest	Best harvest
Fixed effects			
Intercept	-2.90 (0.61)*	-2.30 (0.60)*	-2.89 (0.49)*
Sex (male)	0.30 (0.32)	0.06 (0.34)	0.03 (0.27)
Age	0.40 (0.34)	-0.02 (0.36)	0.37 (0.26)
Age squared	-0.03 (0.04)	0.01 (0.04)	-0.04 (0.03)
Dog's own harvest rate	—	0.0035 (0.0018)	—
Best harvest rate in household	—	—	0.0032 (0.0010)*
Random effects			
Household-level	0.31	0.07	0.08
Individual-level	0.21	0.34	0.13

These models were estimated via MCMC sampling, using the default Metropolis Hastings algorithm that accompanies the logit link for binomial responses in MLwiN 2.23. We specified a chain of 100,000 iterations, discarding the first 5,000 (i.e., the burn-in). We included random effects for the individual dogs and their respective households, and we used orthogonal parameterization for the fixed effects, which have been reconvered to their original units. The parameter estimates are the sample mean (and standard deviation in parentheses) from the posterior distribution. Asterisks denote the parameters for which the 95% credibility intervals do not encompass zero.

the aggregated rankings. These results therefore suggest that the informants are well aware of the variation in the hunting prowess of the dogs in the sample.[§]

Meanwhile, the household-level variance estimate in the full model is greatly reduced in comparison with the estimate from the empty model, which is evidence that the between-household variation in the rankings is explained by differences in the hunting ability of the dogs. That is, some households have multiple skilled dogs whereas other households have dogs that are comparably less proficient. It is apparently rare for households to own multiple adult dogs that differ greatly in their hunting ability. Notably, the most prominent outlier in Fig. 3 belongs to the same household as the third-most proficient dog, as measured by its monthly harvest. Informants may have assumed that the less proficient of those two dogs would be comparable to its counterpart, but this is a rare case in which dogs in the same household exhibit substantial differences in their hunting ability. Note, however, that the logarithmic transformation partially obscures some relatively substantial within-household variation in harvests, particularly in the higher ranges.

Discussion. This study confirms that there is considerable heterogeneity in the productivity of hunting dogs. Several dogs contribute more than 50 kg of harvested meat per month whereas several others contribute nothing. The activity patterns of the dogs account for much of this variation. That is, dogs that frequently accompany their owners on excursions away from the community contribute more hunted meat than dogs that remain home most of the time. Owners seem particularly motivated to bring the most capable dogs on excursions, which helps to account for the exponential increase in harvests as dogs spend more time away from the community.

Controlling for the variation in time allocation, older dogs and male dogs are associated with greater harvests of game. This analysis suggests that dogs are typically at least 2 y old before they contribute more than 5 kg of meat per month. The increase in proficiency is presumably related to both physical maturation and experiential learning, and additional research will be needed to address the relative importance of these effects (e.g., ref. 28). The comparatively high proficiency among the oldest dogs in the

sample may reflect selective mortality, such that better hunting dogs are more likely to survive to older ages.

The most unexpected result from this analysis is the significantly greater productivity of male dogs. As in wolves, this difference might stem from the generally larger size of male dogs in the sample, as there is evidently a relationship between harvests and body size (Fig. S3). Alternatively, experimental evidence on mice and rats suggests a link between testosterone and foraging persistence (34, 35), which would presumably be advantageous when higher-testosterone male dogs are pursuing prey. Aside from these possible explanations, if this sex-related difference characterized dogs in other settings, it might account for observable preferences for males in both ethnographic (3) and archaeological contexts (10). However, informants in other settings report that male and female dogs are comparable in their abilities (9), so replications of this study are needed to assess the generality of sex-related variation in hunting proficiency.

The household-level heterogeneity in the rankings data suggests topics for future research. It may be that dogs in the same household exhibit comparable ability because they have learned primarily from older peers and each other, which is a common belief in small-scale societies (1, 9). Alternatively, given that dogs in the same household are often related as siblings or as mothers and offspring, the similarity in their rankings may reflect heritable phenotypic differences (36). Also, if hunting with multiple dogs of comparable skill increases return rates, then owners might be motivated to acquire additional dogs as complements to their current dogs, which could result in an intrahousehold correlation of hunting ability. Residents are aware of differences in the hunting ability of the dogs in the community, and such knowledge would be valuable when considering opportunities to purchase or trade for renowned dogs (see also ref. 1).

Table 3. Regression models in which the response variable is the aggregated ranking (from consensus analysis) for 34 dogs in Arang Dak and Suma Pipi

Model	Empty model	Full model
Household random effect	37.83 (14.66)	4.91 (4.84)
Intercept	16.26 (1.49)*	12.48 (1.01)*
Log-transformed monthly harvest, kg	—	7.42 (1.04)*
Akaike information criterion	221.65	198.47

Coefficients (and standard errors in parentheses) are based on IGLS estimation.

* $P < 0.05$.

[§]A conventional nonparametric test does not account for the household-level nonindependence, but it likewise suggests that the aggregated informant rankings are highly correlated with the monthly harvests associated with the dogs (Spearman $\rho = 0.84$, $P < 0.0001$).

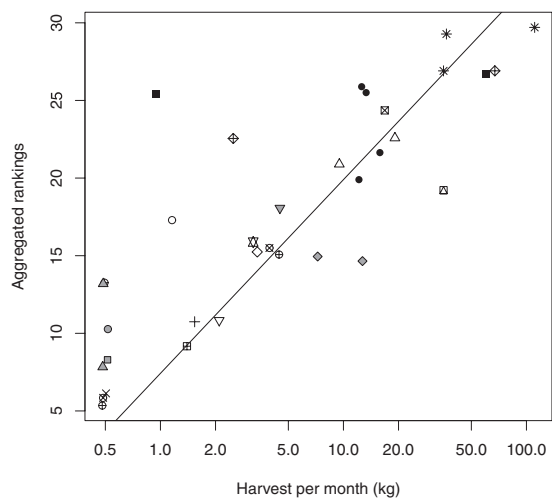


Fig. 3. Scatterplot of the monthly amount of hunted meat that dogs help to harvest and the aggregated rankings from the consensus analysis of the 2005 sample. Note the logarithmic scale on the x axis.

Because dogs generally locate the prey, which is often the hardest skill to learn for human hunters (28), one might imagine that the use of dogs would reduce age-related differences in hunting efficiency while enhancing hunting opportunities for comparatively unpracticed hunters, such as women. On the contrary, a preliminary analysis of the outcomes of 288 planned hunting trips in 2004 and 2005 indicates that ungulates are harvested primarily by men between the ages of 30 and 45 y. Mayangna and Miskito hunters therefore exhibit a convex pattern of age-related hunting success (Fig. S4), which resembles the results from other settings in which dogs are relatively less important or absent (27, 28). It is possible that only middle-aged men have the resources to acquire and support talented dogs, the experience to interpret the dogs' barking and the likely trajectory of pursuits, and the stamina and strength to sprint through the forest and dispatch large animals when they have been corralled or cornered by the dogs. Furthermore, on 16 occasions when teenage boys ($n = 8$) borrowed dogs from their male relatives for hunting excursions, their harvests exceeded the median harvests of the dogs' owners only 31% of the time.^{||} Given this preliminary evidence for age-related effects among hunters, disentangling the independent effects of hunters and their dogs on harvests is a clear priority for future research.

Similarly, it would also be worthwhile to investigate the extent to which informants consider the hunting performance of dogs to be a byproduct of their owners' abilities, or vice versa. That is, related research by the lead author (30) shows that there is also a clear consensus about the relative skill of human hunters. Given perspectives and evidence that hunting success may be a signal of general phenotypic quality (37, 38), and because highly ranked hunters tend to have highly ranked dogs, the value of such signals would presumably be dampened if hunting success were primarily attributable to the quality of the hunters' dogs.

Study Two: 2008 Data

Methods. When the lead author returned to Arang Dak in 2008, a census of the community revealed 38 dogs living in the community. Samples of hair were taken from 34 of these dogs for an isotopic analysis. Ages were again estimated based on interviews

^{||}On four of these trips, all of which resulted in harvests below the median, the teenage hunter did not (or could not) use the full complement of dogs that normally accompanied the dogs' owner.

with the owners, and ages greater than 2 y were rounded to the nearest integer. With a standard bathroom scale, 31 of the dogs were successfully weighed while in the arms of their owners, whose weights were subtracted to estimate the weights of the dogs.

Eighteen dogs were identified by their owners as full-sized dogs (Dataset S2). Among these dogs, the weight of the nine male dogs (12 ± 6 kg) was slightly higher than the weight of the nine female dogs (11.1 ± 2.3 kg).

Photographs of these 18 dogs were taken and subsequently presented to a random sample of 39 adult informants, which included 17 men and 22 women. As in the 2005 study, the informants ranked the dogs in order of hunting skill. Largely because of the short life expectancy of dogs in this setting, only one of the dogs was represented in both the 2005 and 2008 rankings.

Analysis. Unidimensionality in the rankings data were again assessed by using consensus analysis. Using conventional statistics, we subsequently tested for correlations between the answer key (i.e., the factor scores for the 18 dogs) and the age, sex, and weight of the dogs. We predicted that older dogs, males, and heavier dogs would be associated with higher rankings.

We then used the answer key as an explanatory variable to test for linear relationships between the rankings and the isotopic data. The methods for estimating the isotopic content of the hair samples were described by Tankersley and Koster (39). In short, nitrogen isotope ratios (i.e., $\delta^{15}\text{N}$) are positively associated with the consumption of meat whereas carbon isotope values (i.e., $\delta^{13}\text{C}$) are positively associated with the consumption of C_4 photosynthetic plant foods such as maize (40, 41). As noted, because meat and maize are relatively nutritious foods compared with many local alternatives (e.g., bananas), we hypothesized that the rankings data would be positively associated with the nitrogen isotope ratio and the carbon isotope value. The use of hair samples is advantageous in this context because, whereas bone samples integrate several years of dietary input, hair samples largely reflect consumption over the preceding weeks to months (41). Accordingly, hunted meat that was contributed by older peers and given to puppies does not obscure the relationships between hunting ability and diet when the puppies have reached adulthood.

Results. Consensus analysis. A consensus analysis of the rankings indicates that there is high agreement about the relative hunting skill of the 18 dogs in the sample. The ratio of the first to the second eigenvalues is 17.46:2.95. The average competence is high (0.65 ± 0.16), with a range of 0.35 to 0.91.

The mean competence of male informants (0.69) is again moderately higher than the female informants' mean competence (0.61), but a t test does not indicate that the difference is significant ($t = 1.42$; $df = 37$; $P = 0.16$).

Modeling variation in rankings and isotopic data. Except for one prominent outlier, there appears to be little relationship between a dog's age and its aggregated rank (Fig. S5). Sex is likewise an uninformative predictor of variation in the rankings, as the average rank of the nine female dogs (9 ± 2.9) differs little from the mean for the nine male dogs (10 ± 4.5). By contrast, there is a significant positive correlation (Pearson $r = 0.57$, $P = 0.01$) between the rankings and the weights of the dogs (Fig. S6). That is, although the effect is primarily evident among the three heaviest dogs, larger dogs received significantly higher rankings.

Contrary to our hypothesis, there is little relationship between the isotopic data and the aggregated rankings (Fig. 4). There is seemingly no correlation between the rankings and the nitrogen ratios (Pearson $r = -0.01$; $P = 0.97$; $n = 18$). Surprisingly, the correlation between the rankings and the carbon isotope data are negative, but the effect is weak and not significant (Pearson $r = -0.21$; $P = 0.40$; $n = 18$).

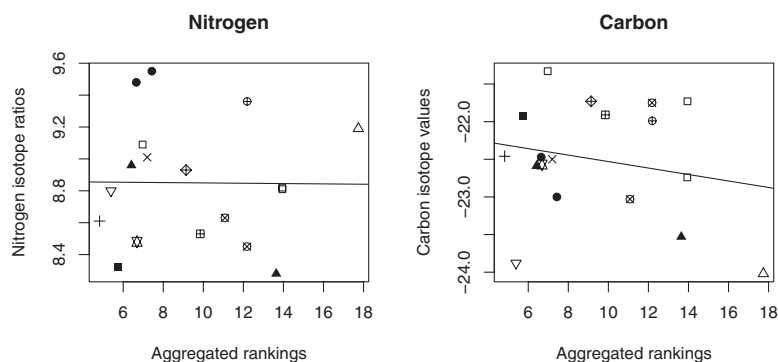


Fig. 4. Scatterplots of the aggregated rankings from the 2008 consensus analysis and the $\delta^{15}\text{N}$ ratios and $\delta^{13}\text{C}$ isotope, respectively.

Discussion. Assuming that the aggregated informant rankings reflect observable differences in the harvests of dogs, as in the 2004–2005 data, the apparent lack of a relationship between the aggregated rankings and the nitrogen ratios is surprising. When dogs regularly contribute to wildlife harvests, we would typically anticipate greater consumption of meat, if only because there is relatively more meat in their households. A possible explanation for the lack of a correlation is suggested by the ethnographic literature from lowland South America, which indicates that owners reportedly refrain from feeding their dogs to ensure their motivation for hunting (1). Such perspectives are rarely evident among the Mayangna and Miskito, however. Many hunters present a slice of meat to the dogs immediately after an animal has been killed, and others claim that their dogs are given cooked meat from the household's pot as a reward for their contribution and an incentive for future hunting (16).

As context, several informants in Arang Dak informally observed that there was notably less hunting in 2008 than during the 2004–2005 study period. Among other contributing factors, several informants observed that the dogs in 2008 were less skilled as hunting companions than their counterparts in the 2004–2005 sample. Quantitative data are lacking, but it is noteworthy that the 8-y-old male dog that topped the rankings in 2008 was only the 10th-ranked dog in the 2004–2005 informant rankings. Whereas several dogs in the 2004–2005 sample had contributed to harvests of ungulates, interviews with the owners suggest that only the top-ranked dog in the 2008 sample had ever assisted in the harvest of an animal larger than a paca, and hunting with dogs in 2008 was likely limited to occasional harvests of agoutis and armadillos.

In other words, the rankings from the two study periods are not necessarily comparable because of the apparently greater variation in harvests in the 2004–2005 study. The positive correlation between the aggregated rankings and the weight of the dogs is suggestive, but the lack of harvest data precludes definitive conclusions about the importance of body size to hunting success by dogs. Because the dogs in the 2008 sample apparently exhibited less variation in their abilities, informants may have relied on general assumptions about body size and hunting ability when ranking the dogs. For similar reasons, the absence of significant correlations between the aggregated rankings and the age or sex of the dogs in the 2008 sample detracts only slightly from the significant results of the 2004–2005 study.

The apparent lack of a correlation between the hunting ability of dogs and their consumption of maize likewise suggests that skilled dogs do not receive comparatively nutritious foods from their owners. It is important to note, however, that better care from owners can be reflected in multiple ways. Owners of skilled dogs may be more likely to seek remedies when the dogs have been wounded or infected by pathogens and parasites, which are common in lowland populations of dogs (42) (Fig. S7). Owners

of skilled dogs could also be more likely to abort a hunting excursion if they detect (via fresh tracks) the presence of a nearby jaguar. There is considerable potential for anthropologists to investigate such questions in subsistence-based societies.

Conclusion

The use of dogs for hunting has advantages. With talented hunting dogs as companions, hunters exhibit return rates that compare favorably to those of hunting with projectile weapons, including modern firearms (ref. 1, 20; see also ref. 5). Also, whereas a veteran dog with a reputation for hunting can be quite costly, puppies can be acquired at relatively little cost. Yet, multiple years may pass before a young dog approaches its peak hunting ability, and the heterogeneity that is evident in this study suggests that owners of puppies cannot be certain about the long-term usefulness of their dogs as hunting companions. Although the Mayangna and Miskito do not consume dogs, comparable age-related patterns of hunting proficiency in other settings could effect the aforementioned tradeoff between certain short-term benefits and possible long-term benefits, specifically the consumption of a full-sized 1-y-old dog versus the possibility of hunted meat acquired by the dog as it ages.

Although hunting proficiency increases with age, dogs frequently die unexpectedly, often while hunting, and dogs in small-scale societies seldom live longer than 3 to 4 y (9, 20, 42, 43). Accordingly, hunters frequently lose skilled hunting dogs in their prime. Ethnographic data indicate that the short-term productivity of individual hunters can fluctuate greatly as they acquire and lose capable hunting dogs (4, 16). We therefore expect households that rely on dogs for hunting to exhibit greater year-to-year variance in their acquisition of hunted game than households that rely on hunting weaponry and accessories other than dogs.

In Arang Dak and Suma Pipi, there are enough alternative sources of dietary protein and fat that a steady supply of hunted meat is not a necessity for households (44). In settings in which hunted game is relatively more important, risk-reducing strategies would likely be needed to accommodate these household-level fluctuations in hunting productivity. Whereas the archaeological data generally suggest that the importance of hunting dogs in small-scale societies declined with the transition to agriculture (ref. 2, p. 176), it is noteworthy that ethnographically documented hunting and gathering societies frequently display minimal reliance on hunting dogs, at least until they are increasingly integrated into larger state societies (refs. 4, 45–47; see also ref. 48). The extent to which this apparent unimportance of dogs in foraging societies is attributable to the absence of mechanisms to minimize the aforementioned risk, the lack of low-quality agricultural foods to sustain dogs, the high mortality of dogs in isolated settings (1), the ability of mobile hunters and gatherers to exploit different, more profitable wildlife resources than sedentary groups (48), or broader political and cultural influences (e.g., ref. 49) remains an open question.

The present study contributes to the discussion by demonstrating that, in a preindustrial setting, there is considerable variation in hunting ability among dogs, which is related to both the age and sex of the dog. Residents of the community are seemingly aware of this variation and can rank dogs accordingly. The variability might not be visible to archaeologists, however, given that hunting ability is seemingly unrelated to variation in diet, as measured by isotopic data. In addition, dogs that are brought on hunting excursions are more likely to be lost in the forest as victims of attacks by jaguars and other predators, perhaps skewing burials in the community

toward dogs with limited hunting abilities (see also ref. 9). It would therefore be worthwhile to have additional ethnographic data on the hunting ability and nutritional status of dogs in preindustrial societies to evaluate the generality of the results of this study.

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