Hunting with Dogs in Nicaragua: An Optimal Foraging Approach

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CA+ Online-Only Material: Supplements A–E

Although dogs are used by subsistence hunters in many locations throughout the world, hunters with dogs have not been studied from an optimal foraging perspective. A study of indigenous Mayangna and Miskito hunters in Nicaragua indicates that the use of dogs affects both the encounter rates and the pursuit times of several prey types. Before hunters can identify the prey type and initiate a pursuit, they must first catch up to the dogs, and their dogs sometimes chase unprofitable prey types. These costs are incorporated as an additional constraint in the optimal prey choice model. The results of the optimal foraging analysis indicate that hunters generally focus on prey types that are in the optimal diet set. However, hunters do not consume two rarely encountered species that are in the optimal diet set, giant anteaters and northern tamanduas. Although hunting with both rifles and dogs increases the likelihood of harvesting tapirs, the return rates of hunting with dogs, hunting with rifles, and hunting with both guns and dogs are otherwise comparable. This study therefore demonstrates that dogs can be valuable hunting accessories.

Soon after the first optimal foraging theory research started to appear in the ecological literature, anthropologists began to consider possible ethnographic applications of the basic optimal foraging models (Smith 1983). Anthropologists have used the optimal prey choice model to analyze foraging decisions in a wide variety of environmental and social contexts (O'Connell and Hawkes 1981; Winterhalder 1981; Hill et al. 1987; Kuchikura 1988; Smith 1991; Alvard 1993; Thomas 2007). On the basis of the premise that foragers attempt to maximize the rate at which they acquire food resources, the prey choice model has exhibited generally robust predictive power in these studies (Kaplan and Hill 1992). Although optimal foraging researchers recognize that human foragers sometimes harvest unprofitable prey types for ritualistic purposes, for reasons other than consumption, or to boost prestige (Smith 1991; Hill and Padwe 2000), the consensus among human ecologists is that the prey choice model provides a valuable approximation of actual prey choice decisions.

Hunting dogs are used in a broad range of geographic and ecological settings (Jones 1970; Ikeya 1994; Ruusila and Pesonen 2004; Nobayashi 2006; Lupo, forthcoming; J. M. Koster, unpublished manuscript). However, hunters with dogs have not been studied from an optimal foraging perspective. The value of dogs as hunting companions has long been hypothesized to be a motivating factor in their domestication (e.g., Olsen 1985), but there is little quantitative evidence on the ways in which the use of dogs affects the parameters of the prey choice model.

Through comparisons with hunting with guns, this study shows that hunting with dogs entails a trade-off between encounter rates and time costs. That is, the use of dogs results in increased encounter rates with several prey species, but pursuits are lengthier. There are also some unique dog-related costs that must be addressed in optimal foraging analyses of hunters with dogs.

Study Site

This study was based among the indigenous Mayangna and Miskito of Nicaragua's Bosawas Biosphere Reserve, part of the largest tract of lowland tropical rain forest north of Amazonia (Stocks 2003). From August 2004 to September 2005, research occurred in two communities: Arang Dak (14°30′57″N, 84°59′58″W) and Suma Pipi (14°31′24″N, 85°0′8″W; see fig. A1 in CA+ online supplement A). There is considerable intermarriage between the Mayangna and the Miskito, and families of mixed ethnicity are common in both communities. Both groups practice similar subsistence strategies, relying on swidden horticulture for the majority of the calories in their diet (Stocks 1996). Residents keep livestock, including cattle, pigs, and fowl, but hunting and fishing are the primary sources of dietary protein (Koster 2007).

Hunting is almost exclusively a male activity, and dogs and .22-caliber rifles are the primary hunting accessories. Many hunters rely only on dogs and hand technologies, including machetes, axes, and lances (see fig. A2 in supplement A). On hunting trips into the forest, dogs spread out in search of game, and their barking alerts the hunters that they have detected a prey item. When hunters infer that a prey item will imminently be corralled or brought to bay, they move quickly to catch up to the chase. Pursuits by dogs often end with the prey animal seeking refuge in a hollow trunk or an earthen burrow (figs. A3, A4 in supplement A). Hunters arrive at the site, first inserting sticks to prevent the animal from escaping and then cutting or digging their way into the hole until they can stab with machetes or lances (fig. A5 in supplement A). Alternatively, some species attempt to flee into a waterway, either swimming away or submerging. Hunters catch up to the pursuit, identify the location of the animal, and attack with a variety of weapons, including machetes, makeshift harpoons, and sharpened sticks.

This study benefits from the work of the Saint Louis Zoo's

0011-3204/2008/4905-0010$10.00. DOI: 10.1086/592021

Table 1. List of Large Mammals (1+ kg) in the Lakus River Watershed

Taxonomic Group, Scientific Name	Common Name	Weight (kg)	Consumed
Didelphimorphs:			
Didelphis marsupialis	Common opossum	.6–2.4	−
Didelphis virginiana	Virginia opossum	1.1–2.5	−
Philander opossum	Gray four-eyed opossum	.26–1.4	−
Xenarthrans:			
Bradypus variegatus	Brown-throated three-toed sloth	2.3–5.5	−
Cabassous centralis	Northern naked-tailed armadillo	2.5–3.5	−
Choloepus hoffmanni	Hoffman's two-toed sloth	4–8	−
Dasypus novemcinctus	Nine-banded armadillo	3–7	O
Myrmecophaga tridactyla	Giant anteater	22–39	−
Tamandua mexicana	Northern tamandua	3.8–8.5	−
Primates:			
Alouatta palliata	Howler monkey	3.6–7.6	~
Ateles geoffroyi	Spider monkey	5–9	O
Cebus capucinus	White-faced capuchin	1.8–4.3	~
Rodents:			
Agouti paca	Paca	5–12	O
Dasyprocta punctata	Agouti	3–4	O
Sciurus variegatoides	Variegated squirrel	.45–.91	O
Lagomorphs:			
Sylvilagus brasiliensis	Forest rabbit	.68–1.25	~
Carnivores:			
Conepatus semistriatus	Striped hog-nosed skunk	1.4–3.5	−
Eira barbara	Tayra	3–6	−
Galictis vittata	Greater grison	1.5–3.2	−
Leopardus pardalis	Ocelot	7–14.5	−
Leopardus wiedii	Margay	2.6–5	−
Nasua narica	White-nosed coati	2.7–6.5	~
Panthera onca	Jaguar	30–100	−
Potos flavus	Kinkajou	2–4.6	−
Procyon lotor	Northern raccoon	3.3–7.8	−
Puma concolor	Puma	24–65	~
Ungulates:			
Mazama americana	Red brocket deer	12–32	O
Odocoileus virginianus	White-tailed deer	25–43	O
Tapirus bairdii	Baird's tapir	180–300	O
Tayassu pecari	White-lipped peccary	27–40	O
Tayassu tajacu	Collared peccary	12–26	O

Note: Weight ranges are from Reid (1997). On the basis of interviews with informants, the consumption of species is classified as follows: O = eaten regularly by virtually all residents; ~ = eaten by only a fraction of residents, usually less than half and sometimes much less; − = considered inedible and never eaten.

Proyecto Biodiversidad, which recently inventoried the wildlife in the reserve (Williams-Guillén et al. 2006). Table 1 lists the large (1+ kg) mammalian species in the forest. Many species are considered inedible and are never eaten, including opossums, most carnivores, and all xenarthrans except the nine-banded armadillo. Other aversions are not universal, and the willingness to consume species such as howler monkeys, white-faced capuchin monkeys, coatis, and pumas seems to vary across households and individuals. These latter species are consumed by some members of the communities but are refused by most.[1]

An Optimal Foraging Model of Hunting with Dogs

The decision-making model of hunters with dogs (fig. 1) includes some unique costs. Unlike hunters with projectile weapons, who typically identify their prey visually, hunters with dogs often cannot immediately ascertain the prey types that their dogs are pursuing. Dogs announce their pursuit of prey by barking intensely, but only after catching up to the dogs can hunters successfully identify the prey type. Even when hunters suspect that their dogs are pursuing a paca, for example, they cannot be sure where (or whether) the paca will be corralled and, by extension, the expected profitability of initiating a pursuit. Catching up to the dogs often involves several minutes of arduous bushwhacking through the forest,

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[1] Puma meat was eaten only by two adolescent brothers.

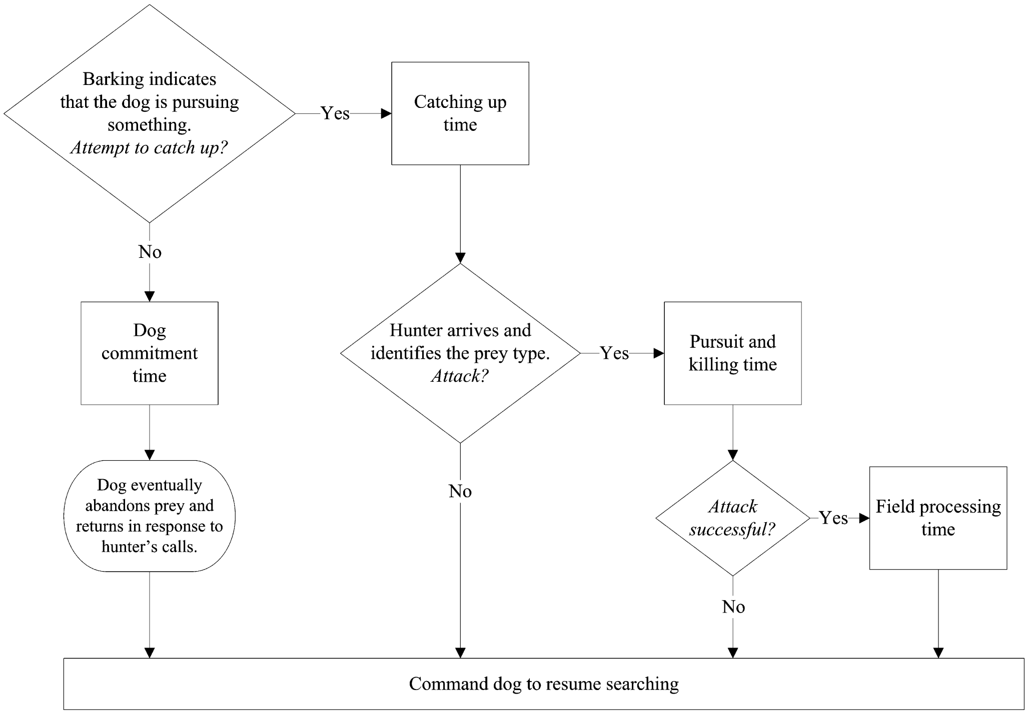

Figure 1. The hierarchical decision-making model of hunting with dogs.

but only by paying this cost can hunters discover whether the prey animal has taken refuge in an easy-to-access trunk or an unfavorably deep burrow.

Perhaps more important, hunters are effectively powerless to stop their dogs from chasing unwanted prey items. While hunters issue commands to dogs in close proximity (e.g., "Get in the boat" or "Sniff this hole"), the Miskito and Mayangna apparently have no effective command for ordering their dogs to abandon a "hot" pursuit. Hunters generally resort to calling the dogs' names when they want them to return, but dogs sometimes ignore these commands if they are intently pursuing an animal. In many cases, the best way to have the dogs resume a general search for prey is to catch up to them and then lead them away from the site where they have corralled an animal. Hunters sometimes choose not to pursue animals corralled in deep burrows, and once the dogs seem to detect the hunters' disinterest in the animals, they likewise abandon the site without much coaxing on the part of the hunters. Until the hunter arrives, however, the dogs usually remain at the site, sniffing and pawing at the opening of the burrow, sometimes for lengthy periods of time.

Also, some hunters do not attempt to give chase once their dogs have begun pursuing certain species, most notably red brocket deer and tayras. Both species can lead dogs on long and futile pursuits, and hunters seem resigned to a long wait once their dogs begin chasing these animals. Unable to match the pace of these pursuits, hunters typically amble impatiently from hilltop to hilltop, repeatedly calling for their dogs to return. This time that the dogs spend in pursuit of virtually unkillable prey represents an additional cost of hunting with dogs, which is called "dog commitment time" in figure 1.

For analytical purposes, dog commitment time and catching up time are similar costs because in both cases the dogs are focused on a particular prey item to the exclusion of a general search for prey. Whether or not the hunter realizes what animal the dog is chasing, the important point is that he cannot begin pursuing the animal or resume a general search until he either catches up to the dog or waits for the dog to abandon the chase. Therefore, whereas in the basic prey choice model foragers incur no costs for prey types that are not included in the optimal diet set, hunters with dogs may pay costs for all prey types encountered by their dogs. While hunters are effectively powerless to stop the dogs from chasing unwanted prey items, they regain a measure of control after catching up to the dogs and identifying the prey type. At that time, they weigh the expected benefits of initiating a pursuit against the opportunities available from resuming a general search for prey, as in the basic prey choice model.

From a modeling perspective, these dog-related costs resemble the recognition costs incurred by shore crabs when they feed on mussels. Shore crabs can distinguish between profitable and unprofitable mussels by lifting them, but manipulating the mussels takes time regardless of the subsequent attack decision (Elner and Hughes 1978). These costs can be incorporated into the basic prey choice model as an additional constraint. The derivation here is an extension of the two-prey case examined by Houston, Krebs, and Erichsen (1980).

As in the original prey choice model, prey types are ranked according to their profitability, which is measured in kilocalories per hour and calculated as the average postencounter energetic benefit divided by the average handling time (i.e., pursuit time and field processing time) for that prey type. After accounting for dog-related costs, 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, in a hunting environment with m prey types, of which n are included in the optimal diet set of hunters with dogs, prey types are added to the diet until

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

where λ_i is the encounter rate with prey type i; e_i is the average expected net energy gain after encounter with prey type i; h_i is the pursuit, killing, and field processing time after encounter with a prey item of type i; and d_i is the catching up time or dog commitment time after encounter with a prey item of type i.

Known as the one-zero rule, a key prediction of prey choice models is that hunters should always pursue prey items in the optimal diet set and never pursue prey outside the optimal diet set (Stephens and Krebs 1986). Prey choice decisions that violate this prediction suggest that the forager is not achieving the maximum possible return rate in that environment (see CA+ online supplement B).

Methods

Like previous optimal foraging researchers, I employed focal observational methods (Altmann 1974). I used a handheld computer and customized observational software to collect continuous data of a focal subject, recording all activities for the duration of the observation (Koster 2006). For each observation, hunters received 15 Nicaraguan córdobas.[2] This sum was designed to compensate hunters for the extra work of an observation (particularly the extended posthunt interview) without motivating them to hunt when they would not otherwise do so. In total, I observed 54 intentional hunting trips on which dogs were the principal hunting technology. All were day trips originating in the community or a nearby residence. The first three hunts were used to finalize the coding scheme and are not included in subsequent analysis. On 21 of the 54 observations, hunters also brought rifles, which they used only rarely. For this reason and because hunters with both dogs and rifles tend to follow strategies used by hunters with only dogs, I include all observations of hunters with dogs in the optimal foraging analysis.

The coding scheme included many behaviors and events that have been used in other optimal foraging analyses, including general travel and search, encounters with prey, pursuits, and postkill processing time (see Alvard 1993). Also germane to this analysis are two activities that are unique to hunting with dogs: catching up time and dog commitment time.

A clarification is needed in the definition of prey types. Anthropologists have traditionally equated prey types with biological species, but this is not a requirement of the model. If subsets of a species consistently differ in the expected profitability of a pursuit, they should be considered distinct prey types (Stephens and Krebs 1986). For example, Hill et al. (1987) report that pursuits of nine-banded armadillos encountered on the surface are 418% more profitable than those that are dug out of earthen burrows, which suggests that they should be treated as different prey types.

For two caviomorph rodents, agoutis and pacas, I make a distinction between pursuits in earthen burrows and pursuits in trunks. Burrows and trunks are similar in that hunters follow a common pattern of assessing the scene, plugging possible exits, digging or cutting to gain access to the animal, and probing to determine the animal's exact location in order to deliver a potentially fatal machete strike. However, trunks and burrows appear to vary in several ways, including the usefulness of the dogs during pursuits, the technologies used during the pursuits (steel blades vs. hands and digging sticks), and the probability that the animal inside will escape. By contrast, when these animals are chased into the water, hunters must determine the exact location of the animal and then maneuver close enough to attack. When swimming, agoutis are easy to kill, but pacas can remain submerged for long periods. Hunters use their boats to look for pacas in the river whereas pursuits in streams occur on foot, and strategies vary accordingly. Combined, these factors seem to merit at least a preliminary examination of the respective differences between the types of pursuit (see CA+ online supplement C).

However, it is important to note that attempts to separate unique encounters into discrete prey types necessarily overlook much of the possible variation in encounter contexts. Hunters consider many factors when deciding whether to initiate or continue a pursuit. For example, while they have certain expectations about the profitability of pursuing agoutis in trunks, they are also attentive to the hardness of the wood and whether the trunk has already been accessed in a previous pursuit. Earthen burrows are likewise variable, as those that wind their way through the root systems of large, buttressed trees appear to be more challenging than burrows without this added obstacle. Similarly, once a paca is flushed into the river, the clarity and depth of the water have obvious effects on the outcome of the pursuit.

I also accompanied hunters on excursions without dogs,

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[2] The exchange rate varied slightly throughout the year, but it was typically about 16.25 córdobas for each American dollar. By comparison, the standard wage received by men for a day of agricultural labor was approximately 55 córdobas.

but these are comparatively rare and I collected data on only six trips. To expand the sample size for a comparison of return rates, I include data from unobserved hunts. With the help of local research assistants, I documented the outcome of all hunting trips during the yearlong study period. Among other questions, we collected data on participants, technologies, time of departure and return, time devoted to activities other than hunting, encounters with potential prey items, and kills. Assistants also weighed the captured prey items.

I define three categories of hunts based on the technologies brought by hunters: hunts with dogs, hunts with rifles, and hunts with a combination of the two. Estimates of hunting productivity are based on hours spent hunting, not the total time spent away from the community, which also included activities such as fishing, cutting and weeding bananas, eating breakfast at an upstream residence, and clearing fields. (See Koster 2007 for additional details on the methods used to record data on unobserved hunts.)

Results

Optimal Foraging Analysis

Table 2 includes the results of the optimal foraging calculations. The prey types are listed in order of profitability, with giant anteaters representing the top-ranked resource. The importance of not treating a biological species as a single prey type is evident in the rankings. Because pursuits of agoutis in the river require little time, they are more profitable than the much larger collared peccary. By contrast, agoutis in earthen burrows are the lowest-ranking prey type in the optimal diet set, largely because of the long pursuit times. Also, pursuits in earthen burrows are more frequently unsuccessful, which reduces the average energetic benefit of this prey type (see also CA+ online supplement D).

Red brocket deer, tayras, and coatis are included in the table despite being virtually impossible to kill by hunters with dogs and hand technologies. Because there were no observed pursuits of these species, it is not possible to estimate handling times for these prey types. However, because the profitability of these prey types is effectively zero, any time devoted to pursuing these species would lower the return rate, and they are therefore not in the optimal diet set. The table also includes the dog-related costs associated with “missing” prey types. These represent situations in which dogs pursue a prey item but the animal escapes before the hunter can arrive to identify the prey type (see CA+ online supplement E).

Figure 2 depicts the actual prey choice decisions by hunters with dogs in the combined sample of observed and unobserved hunting excursions. As predicted by the model, hunters almost invariably pursue many of the prey types in the optimal diet set, including collared peccaries, agoutis, pacas, nine-banded armadillos, and iguanas. One paca was ignored because of an injury to the dog, and an iguana was not pursued because it fled into a tree.

However, the model fails to predict decisions related to two highly ranked resources, giant anteaters and tamanduas. These two species, particularly giant anteaters, are capable of injuring dogs. On finding their dogs engaged with these animals, hunters therefore kill them to protect the dogs and also because the dogs do not resume a general search for prey while the animals are still alive (Koster 2008; see also Hames 1979). However, the meat of these species is not brought back to the community for consumption, which violates predictions of the one-zero rule.

Technological Efficiency

In addition to the dog-related costs (i.e., dog commitment time and catching up time), hunting with dogs entails additional costs for hunters. Specifically, whereas pursuit times for hunters with firearms are generally short, pursuits of prey items chased by dogs into burrows or trunks are considerably longer. Although there are not enough observations of pursuits by rifle hunters in this study to permit statistical testing, comparisons with data from other Neotropical sites are noteworthy. For example, the average handling time for agoutis (*Dasyprocta variegata*) pursued by Bolivian Tsimane hunters with firearms is 5.8 minutes (Allen Gillespie, unpublished data). By contrast, the corresponding average for Mayangna and Miskito hunters with dogs is 28.5 minutes, reflecting the methodical process of plugging all exits to the trunk or burrow before stabbing the agouti and extracting the body. There is a significant difference between these means (Welch’s $t = 6.17$, $\mathrm{df} = 57$, $p < 0.0001$). Similar differences characterize pursuits of collared peccaries, which likewise seek refuge in trunks and burrows when pursued by dogs. Alvard and Kaplan (1991) report that the average handling time for collared peccaries pursued by Piro shotgun hunters in Peru is 7.7 minutes, compared with 40.8 minutes for hunters with dogs in this study. A Mann-Whitney test indicates that this difference is significant ($U = 0.00$; $p = 0.02$). Overall, Mayangna and Miskito hunters with dogs spend 30% of their time actively committed to specific prey items (i.e., catching up time, pursuit, field processing) whereas rifle hunters devote only 7% of their hunting time to pursuits and field processing.

As a trade-off for these costs, the primary advantage of hunting with dogs is an increased encounter rate with several profitable prey types (table 3). For example, hunters with dogs encounter more than nine times as many agoutis as do hunters without dogs. Although nocturnal species such as nine-banded armadillos and pacas are rarely encountered by unassisted rifle hunters, the dogs frequently follow scents to the animals’ burrows, alerting hunters to the presence of these prey. Not all prey types are characterized by increased encounter rates, however, as the rates of brocket deer and collared peccaries are largely indistinguishable with and without dogs. As an additional comparison, table 3 includes the encounter rates of Peruvian Piro and Paraguayan Aché hunters without dogs. Because wildlife population densities vary across sites (Robinson and Redford 1986), it is not possible

Table 2. Calculation of the Optimal Diet Set for Hunters with Dogs

Species, Type	λ	d (h)	h (h)	e (kcal)	Profitability of Prey Type (kcal/h)	Return Rate If Added to Diet Set (kcal/h)	In Optimal Diet Set?
Giant anteater (all)	.005	.146	.200	38,025.0	190,125.0	158	Yes
Agouti (river)	.005	.000	.059	5,830.5	99,289.5	182	Yes
Tamandua (all)	.005	.070	.133	6,971.3	52,284.4	211	Yes
Collared peccary (all)	.021	.073	.680	24,927.5	33,111.4	673	Yes
Iguana (all)	.021	.000	.041	910.0	22,038.3	690	Yes
Armadillo (all)	.049	.073	.444	4,832.3	10,871.5	883	Yes
Paca (earth)	.091	.077	.491	4,085.3	8,312.6	1,162	Yes
Paca (trunk)	.028	.135	.391	3,137.1	8,020.5	1,224	Yes
Agouti (trunk)	.265	.129	.441	2,865.2	6,503.2	1,693	Yes
Paca (river)	.021	.145	.734	4,140.5	5,640.9	1,738	Yes
Paca (stream)	.042	.168	.941	3,675.8	3,907.9	1,800	Yes
Agouti (earth)	.077	.094	.583	2,074.1	3,560.1	1,856	Yes
Red brocket deer (all)	.014	.633	.000	.0	.0	. . .	No
Tayra (all)	.014	.696	.000	.0	.0	. . .	No
Coati (all)	.014	.160	.000	.0	.0	. . .	No
Missing (all)	.133	.118	.000	.0	.0	. . .	No

Note: Caloric estimates were generated using the methods of Hill and Hawkes (1983), who assume that 65% of the carcass is edible meat. The symbols λ, d, h, and e represent the respective encounter rates, dog-related costs, handling time, and energetic benefit of each prey type.

to conclude that the use of dogs is solely responsible for the differences in encounter rates. Nevertheless, it is noteworthy that the encounter rates of agoutis, pacas, and armadillos are again higher for hunters with dogs.[3]

The respective pros and cons of rifles and dogs are evident in a comparison of return rates. As in previous studies (Hames 1979; Yost and Kelley 1983; Alvard 1995), the comparison initially seems to demonstrate the superiority of firearms over alternative hunting technologies. More interesting, however, is the observation that the combination of dogs and rifles yields a higher return rate than either technology by itself. Hunting with both dogs and guns is 80% more productive than hunting with rifles alone and 130% more productive than hunting with just dogs, as measured in kilograms per hunter hour (table 4). All three rates are within the range of variation in Beckerman's (1994) cross-cultural sample of return rates in indigenous Neotropical societies.

The apparent advantage of hunting with both rifles and dogs is somewhat deceptive, however, especially given that rifles were not fired at all on 61% of the hunting trips in this category. Although hunters can occasionally benefit from opportunities to target prey species (e.g., game birds) while their dogs are elsewhere, the combination of dogs and guns dominates for one primary reason: tapirs. Of the eight tapirs killed on daylong hunting trips from the communities, six were first detected by dogs and then killed by hunters with rifles (often in combination with other technologies when bullets failed to down the animal immediately). Tapirs make up almost 60% of the biomass harvested on hunting trips with dogs and guns. The combination of dogs and guns is effective because dogs appear to boost the encounter rate while the rifles provide the means with which to kill the tapirs.

Interestingly, when the hunting trips on which hunters killed tapirs are excluded from the sample, the return rates of hunting with rifles and hunting with both rifles and dogs are essentially identical and only 14% better than hunting with dogs.[4] The disproportionate effect of tapir kills on return

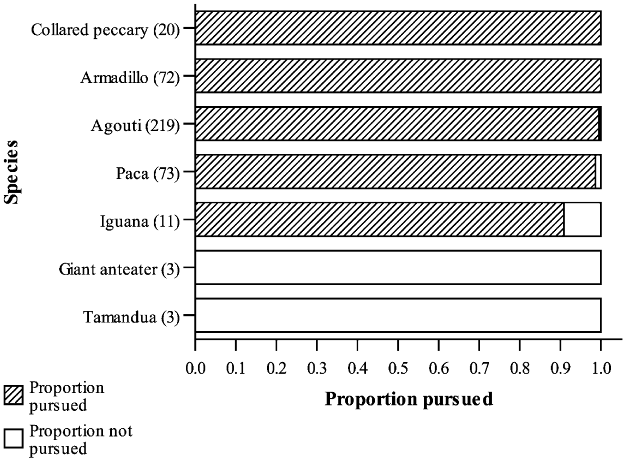

Figure 2. Proportion of encounters that led to pursuits by hunters with dogs. The number of encounters with each prey type is indicated in parentheses.

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[3] Most of the agoutis encountered by the Piro were already fleeing when they were first spotted by the hunters, effectively eliminating the possibility of a successful pursuit (Alvard 1993). The encounter rate of agoutis that were vulnerable to attack appears to be 0.02 per hour.

[4] The revised sample excludes one trip on which a tapir was killed by a rifle hunter, one trip on which a tapir was killed by a hunter with dogs, and six trips on which tapirs were killed by hunters with both dogs and guns (including one excursion on which a hunter with dogs and a rifle killed both a tapir and a collared peccary).

Table 3. Encounter Rates (encounter/hr) by Hunters with Dogs and Hunters without Dogs

Species	With Dogs (This Study)	Without Dogs (This Study)	Piro (Alvard 1993)	Aché (Hill and Hawkes 1983)
Agouti	.346	.038	.138	0
Armadillo	.049	.008	.002	.025
Collared peccary	.021	.017	.066	.020
Paca	.181	0	.004	.010
Red brocket deer	.014	.013	.030	.011

rates is similarly evident in a statistical test of the return rate data from the full sample. By reducing return rate data from each hunting trip in the sample into ranks, a nonparametric Kruskal-Wallis test minimizes the skew introduced by tapir kills. The test is not significant ($K = 3.201$; $p = 0.202$), which suggests that no technology or combination of technologies consistently outperforms the others. Although hunting with dogs and rifles seems to increase the frequency of tapir kills, most trips result in far more modest returns. Because hunters with only rifles or dogs can also harvest large prey, including the occasional tapir and especially peccaries, the daily returns of hunters with these technologies often surpass those of hunters with both rifles and dogs.

Discussion

A weakness of purely observational optimal foraging studies is the difficulty of generating profitability estimates for prey types that are not pursued by hunters (Kaplan and Hill 1992). These data can be acquired experimentally (O'Connell and Hawkes 1981), but researchers who lack such experimental data are unable to assess the profitability of unpursued resources. For example, Alvard (1993) cannot effectively evaluate the possibility that several rarely pursued prey species, including pumas, two-toed sloths, tayras, and collared anteaters, are in the optimal diet set of Piro shotgun hunters. By contrast, because hunters in this study killed giant anteaters and northern tamanduas to protect their dogs, it was possible to generate accurate profitability estimates. These estimates suggest that by not consuming the meat, Mayangna and Miskito hunters violate predictions of the prey choice model.

Informants typically cite two reasons for their reluctance to bring tamanduas and giant anteaters back to the community after a kill. First, because these species can harm or kill the dogs, hunters claim that leaving the bodies in the forest discourages the dogs from pursuing them again in the future. However, hunters do not apply the same logic to similarly hazardous species, most notably the collared peccary. Second, informants claim that the meat of these species is distasteful and not fit for consumption. Although anteater species are known for their acidic taste in places where they are consumed (Smole 1976), this reason may lack explanatory power in the Bosawas Reserve because few informants have actually sampled the meat. Regardless of the underlying motive, it is reasonably clear that hunters sometimes consider factors other than optimal foraging parameters when making prey choice decisions.

Similar taboos and aversions are relatively common throughout the Neotropics (Redford and Robinson 1987). In many cases, these bypassed species are probably in the optimal diet set, and it remains difficult to explain these aversions from an optimal foraging perspective. For example, despite being large animals that are relatively easy to kill, giant armadillos and giant anteaters are tabooed by the Ye'kwana (Hames and Vickers 1982). In light of such evidence, perhaps a modification of the consensus on foraging theory is needed. Specifically, although hunters generally focus on prey types that are in the optimal diet set, they do not necessarily pursue all prey types predicted by the model. In the Neotropics, this latter generalization seems to be particularly true of rarely encountered prey types.

In general, this study demonstrates that dogs can be valuable hunting accessories, providing return rates that compare favorably with those provided by modern firearms. These data therefore provide support for the hypothesis that their usefulness in hunting motivated the domestication of dogs. However, the relative value of dogs in other settings likely depends on a number of variables. First, largely because of differences in their antipredator behavior, prey species vary in their vulnerability to hunters with dogs. For dogs to be a worthwhile alternative in the Neotropics, for example, the hunting environment typically requires prey species that flee from dogs by seeking locations where hunters can subsequently attack them (Redford and Robinson 1987). Furthermore, this study demonstrates that hunting with dogs affects both the encounter rates and the profitability of prey types. In this case, the increase in encounter rates was sufficient to offset the additional costs of hunting with dogs, but that is unlikely to be true in all settings.

Given the similarities in return rates, an interesting question is how hunters decide to hunt with guns, dogs, or both. It should first be noted that all hunters in Arang Dak and Suma Pipi claim to want a rifle and hunters who own rifles invariably bring them when hunting with dogs. As noted, an advantage of hunting with both dogs and guns is the greater likelihood of killing tapirs, the largest prey species in the reserve (cf. Kaplan and Kopischke 1992, 99). The meat from

Table 4. Average Return Rates by Technology Based on a Combined Sample of Observed and Unobserved Hunts

Sample	*n*	Hunter Hours	Return Rate (kg/hunter hour)	Return Rate minus Tapir Kills (kg/hunter hour)
Dog	142	1,150.9	1.04	.90
Rifle	49	496.8	1.33	1.03
Dog and rifle	97	786.1	2.39	1.03

hunted tapirs is gifted and sold to many other households, providing substantial benefits to the hunter. If all of the meat were sold, for example, the hunter could earn the equivalent of a month's wages from a single kill.[5] Gifted meat may be repaid with reciprocal assistance, enhanced prestige, or inclusive fitness benefits (Gurven 2004).

Rifles also allow hunters to protect their dogs from jaguars, which are renowned for ambushing dogs in the forest. Of the four jaguars killed during the study period, three were killed while they were attacking dogs.

Hunters who own both dogs and rifles sometimes hunt with only rifles if the dogs are injured or pregnant. Alternatively, hunters may elect to hunt without dogs when targeting prey species for which dogs offer little assistance, such as game birds or white-lipped peccaries.

Primarily because they are prohibitively expensive, only 26% of the households own a rifle. Even a secondhand rifle can cost more than US$150. By contrast, the highest price paid for any of the dogs in the study was approximately US$24, and prices above US$30 are unprecedented. Puppies can be purchased for much less, usually US$3–$5, depending on ancestry and age at the time of purchase.

Dogs generally eat whatever has been prepared for household consumption, but families sometimes buy cow milk for their puppies. Nevertheless, approximately half of all puppies die as neonates. The annual mortality rate of adult dogs is also high, 49%, and most deaths are caused by snakebites or jaguar attacks. As a result, households are sometimes left without a capable hunting dog, which necessitates the use of rifles or a temporary cessation of hunting. The decision to hunt with either dogs or rifles may therefore be dictated in large part by economics and extrinsic circumstances.

By Western standards, the Mayangna and Miskito are not especially affectionate with their older dogs, but puppies are a source of considerable entertainment. Dogs also serve as watchdogs, and their presence likely discourages burglars. These variables are difficult to quantify, but they merit attention when comparing the costs and benefits of dogs and alternative hunting accessories.

Conclusion

Although they are admittedly reductionist, a benefit of optimal foraging models is their widespread applicability (Smith and Winterhalder 1992). That is, by reducing the predicted outcome of foraging to a small set of measurable variables, optimal foraging models can be employed in a broad range of hunting environments. When the assumptions of the basic models are unfulfilled, additional constraints can be introduced to make them more realistic (Stephens and Krebs 1986). This study illustrates that, contra the basic prey choice model, hunters with dogs typically cannot make pursuit decisions before paying a time cost. The dog-related costs, dog commitment time and catching up time, are an additional constraint, and these variables should be measured in any optimal foraging study of hunters with dogs.

The data presented here indicate that the primary advantage of dogs is an increased encounter rate with several profitable prey types. Similarly, on the basis of Nobayashi's (2006) ethnographic description, it appears that the main advantage of dogs to aboriginal Taiwanese hunters is an increased encounter rate with wild boars (*Sus scrofa taivanus*). By contrast, the primary benefit of dogs on diurnal hunts in the central Kalahari seems to be a reduction in the handling time of prey species such as gemsboks and duikers (Ikeya 1994). Among the Bofi and Aka of the Central African Republic, dogs seem to improve the profitability of giant pouched rats (*Cricetomys emini*) and brush-tailed porcupines (*Atherurus africanus*) but apparently do not increase encounter rates with these species (Lupo, forthcoming).

These observations suggest that the usefulness and benefits of dogs vary considerably at different sites. An optimal foraging approach can elucidate the trade-offs associated with the use of dogs, particularly in comparison with alternative hunting accessories. Additional optimal foraging research on hunters with dogs could therefore inform ethnological studies of the distribution and relative importance of dogs in contemporary and prehistoric settings.

Acknowledgments

This research was supported by a Fulbright student grant, the National Science Foundation (Dissertation Improvement

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[5] Game meat typically sells for 5 córdobas per pound, but tapir meat is highly esteemed and usually sells for 6 córdobas per pound.

Award 0413037), the Hill Foundation, a William Sanders dissertation grant, and a Noldus publication grant. Stephen Beckerman, Katriona Shea, Wesley Allen-Arave, Karen Lupo, and several anonymous reviewers provided many useful suggestions on an earlier draft of this manuscript. I thank Allen Gillespie for sharing unpublished data. Special thanks to David Stephens for his advice and assistance during data analysis. Finally, my gratitude goes to the residents of Arang Dak and Suma Pipi for their friendship and their enthusiastic participation in this project.

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Supplement A from Koster, "Hunting with Dogs in Nicaragua: An Optimal Foraging Approach"

(Current Anthropology, vol. 49, no. 5, p. 935)

Figures

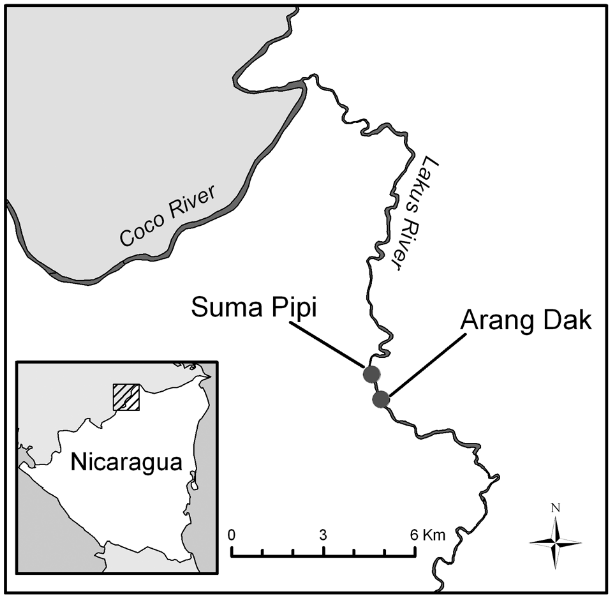

Figure A1. Location of the study site.

Figure A2. A Mayangna hunter and his dog. Photo credit: Menuka Scetbon-Didi.

Figure A3. A Mayangna hunter pursues an agouti in a hollow trunk. Photo credit: Menuka Scetbon-Didi.

Figure A4. Hunters pursue an animal in an earthen burrow. Photo credit: Menuka Scetbon-Didi.

Figure A5. A hunter rewards his dog with a slice of meat after killing a paca. Photo credit: Menuka Scetbon-Didi.

DOI: 10.1086/592021

Supplement B from Koster, "Hunting with Dogs in Nicaragua: An Optimal Foraging Approach"

(Current Anthropology, vol. 49, no. 5, p. 935)

Further Implications of the Expanded Model

An interesting consequence of dog-related costs is the relevance of encounter rates with suboptimal prey types. In the basic prey choice model, the encounter rates of prey types outside the optimal diet set are unimportant because, as predicted by the one-zero rule, they are never pursued on encounter. Therefore, suboptimal prey types impose no costs on the forager. Because dog commitment time and catching up time are unavoidable, however, the encounter rates of all prey types become relevant.

As an example, tayras are associated with high dog-related costs, specifically dog commitment time. As the encounter rate of tayras increases, dog commitment time likewise increases. During this time, the dogs are not searching for more profitable prey, and the overall return rate therefore decreases.

Prey choice models hinge on opportunity costs. That is, time spent pursuing a prey item is a lost opportunity to locate a higher-ranked item. When hunting with dogs, time not spent pursuing a prey item is divided between search time on the one hand and dog commitment time or catching up time on the other. Thus, as progressively more time is lost to dog commitment time and catching up time, the opportunity costs of a pursuit are reduced.

As a result, dog-related costs can promote the inclusion of otherwise suboptimal prey types in the optimal diet set. For instance, in the absence of dog-related costs, a prey type might be outside the optimal diet set. However, by reducing the time available to find a more profitable prey type, dog-related costs may make it worthwhile to pursue relatively unprofitable prey types on encounter. If prey types such as tayras are encountered frequently, for example, hunters will be more willing to pursue low-ranking resources than they would be if the tayras were not there to distract the dogs from locating something better. In short, as a greater percentage of search time is lost to dog-related costs, the breadth of the optimal diet set widens. Stephens and Krebs (1986, 66) provide a useful graphic that illustrates this concept.

By lowering the return rate, dog-related costs also increase the time that hunters should continue to pursue an individual prey item before abandoning the pursuit, a threshold known as the optimal pursuit time (Anholt, Ludwig, and Rasmussen 1987). This may partly explain why hunters are sometimes willing to engage in lengthy pursuits of relatively low-ranking prey, such as agoutis in earthen burrows.

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DOI: 10.1086/592021

Supplement C from Koster, “Hunting with Dogs in Nicaragua: An Optimal Foraging Approach”

(Current Anthropology, vol. 49, no. 5, p. 935)

Variation in Prey Types

Digging into an earthen burrow is perhaps a chancier affair, as there is the possibility that hunters will actually remove dirt in such a way that the animal inside can escape. With trunks, as long as the size of the hole being cut does not exceed the size of the animal, hunters are reasonably assured that the only exit is via the holes that should have already been well plugged. Another difference is that hunters can more easily see the full extent of a trunk, whereas it is more difficult to ascertain the depth and extent of an earthen burrow. Finally, it seems that dogs are more able to detect the sounds and smells of animals in trunks than in burrows, which then helps the hunter to pinpoint the location of the animal and (he hopes) dispatch it more quickly.

Able to remain underwater, the paca can swim from one side of a river to the other without being noticed by the hunter. If hunters lose track of the animal once it takes to the water, the prospects of a successful kill are rather bleak. By contrast, hunters seem to fare somewhat better when the paca attempts to escape in a stream. The animal is effectively limited to swimming in one dimension (i.e., upstream or downstream), and a quick and conscientious hunter can lay branches across the stream in shallow sections above and below the point of submersion, preventing the paca from escaping the pool undetected. At that point, the hunter probes the banks of the stream, looking for the paca’s hiding place. The success of the pursuit seems to depend largely on the depth of the water and whether the hunter saw exactly where the paca entered the water.

DOI: 10.1086/592021

Supplement D from Koster, "Hunting with Dogs in Nicaragua: An Optimal Foraging Approach"

(Current Anthropology, vol. 49, no. 5, p. 935)

Tapirs and the Optimal Diet Set

When pursued by dogs, tapirs may run long distances, but they often seek waterways. In the river, tapirs attempt to swim away from the dogs. Alternatively, tapirs may stop in a streambed and turn to face the dogs. Because I did not observe pursuits of tapirs, it is difficult to estimate the profitability of pursuits in these two situations. For hunters with only hand technologies, it can be difficult to get close enough to injure tapirs in streambeds. However, tapirs are very large animals, and even if few pursuits are successful (perhaps 10%), this prey type would almost certainly be in the optimal diet set if unsuccessful pursuits last no more than a few minutes. Pursuits of tapirs in the river by hunters in boats are more often successful, and pursuits reportedly last no more than 10–15 minutes. Therefore, provided that the hunters have access to a boat, tapirs encountered in the river would also be included in the optimal diet set. Despite their size, however, it is not clear that they would be the top-ranking resource.

DOI: 10.1086/592021

Supplement E from Koster, "Hunting with Dogs in Nicaragua: An Optimal Foraging Approach"

(Current Anthropology, vol. 49, no. 5, p. 935)

Red Brocket Deer and the Optimal Diet Set

There is contextual variability in encounters with red brocket deer. Like white-tailed deer, red brocket deer can be killed when dogs chase them into the river. On observed hunts, two of the four encounters with brocket deer actually led to kills by other individuals in boats, once by a hunter's wife and once by an unrelated party. Some hunters instruct their family members to wait in the boat and watch for deer and other animals while they roam inland with the dogs. Hunters who are sufficiently close to their boats when deer are chased into the river may be able to kill the animals themselves. In such contexts, deer could be considered a different prey type, and they would likely merit inclusion in the optimal diet set.