

The behaviour and diet breadth of central-place foragers: an application to human hunters and Neotropical game management

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ABSTRACT

Questions: When incorporating space, time, and attack limitation, how do predicted hunting strategies of Neotropical hunters differ from predictions based on classical diet-breadth models?

Mathematical methods: Dynamic state-variable models of central-place foragers implemented by stochastic dynamic programming.

Key assumptions: Neotropical hunters are central-place foragers who maximize their energetic return over the course of a single hunt with finite available ammunition. Encounters with game are sequential and hunters decide whether to attack each of nine Neotropical game species depending on (1) their own state variables including distance from home, time, number of attacks used, and meat already acquired, and (2) game-specific parameters such as encounter rate, kill rate, handling time, and body mass.

Predictions: Hunters expand their diet late in the hunt because there are few remaining encounter opportunities. Attack limitation restricts the diet breadth to large-bodied species with a high probability of being killed because ammunition can be used to hunt larger-bodied prey later in the hunt. Very late in the hunt, hunters will accept low-value game even if there are few attacks remaining. High-value prey with long handling times may be ignored late in the hunt if there is not time to pursue. When vulnerable game species are depleted, hunter return rates are lower but remain consistent (i.e. most hunts still result in moderate harvest levels that meet subsistence needs). Our results question the efficacy of using longitudinal records of the composition and proportion of prey items (the prey profile) to assess levels of wildlife depletion. When space is included in foraging models, prey profiles do not change substantially even when several high-value game species are locally extirpated.

Keywords: behavioural ecology, central-place forager, diet breadth, marginal value theorem, optimal foraging theory, state-variable models, stochastic dynamic programming.

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INTRODUCTION

In this paper, we advance human forager–prey models so as to inform the ongoing debate among ecologists and anthropologists about the sustainability of Neotropical hunting (Redford, 1992; Redford and Stearman, 1993; Terborgh, 1999; Schwartzman *et al.*, 2000; Schwartzman and Zimmerman, 2005). The creation of a tropical game management framework is impeded because hunter actions and off-take are exceedingly difficult to monitor and because terrestrial game species populations are spatially structured. New, spatially explicit models that combine human demography and settlement geography with game species biology allow for projections of the impact of hunting over space under different management regimes (Levi *et al.*, 2009, in press). However, existing models are limited to estimating the impact of hunting on one species at a time, and one must exogenously assume a given amount of hunting effort for a given focal species (Levi *et al.*, 2009). Thus, existing models cannot be applied directly to assemblages of species. The difficulty arises due to the uncertainty in the behavioural strategy employed by human hunters as abundant prey species are locally depleted. Previous work in this direction has combined behaviour and game species population dynamics by using diet-breadth models (Lu and Winterhalder, 1997; Rowcliffe *et al.*, 2003; Mangel and Wolf, 2006). However, both the diet-breadth models and the game species population dynamics models employed have the major limitation of being non-spatial. Projecting the spatial impact of hunting allows for the assessment and management of hunting in tropical forests by managing the spatial distribution of human settlements (Levi *et al.*, 2009).

A desirable multi-species model must predict spatially important behavioural information, such as the distribution of distances walked by hunters and of energy and/or protein obtained while hunting, the combination of which would reveal how access to high-quality protein changes as game species become depleted. An additional complication is the involvement of subsistence hunters into markets. Lu (2007) notes that integration into the market economy has increased for many Neotropical indigenous populations due to government-led and extractive industry-facilitated infrastructural development. Road networks, rainforest urbanization, and wage labour opportunities increase access to markets and monetary income that can be used to purchase firearms and ammunition for hunters.

As game species become locally depleted, and if hunters exhibit low demand elasticity (are unwilling to switch to substitute prey species), hunters will walk greater distances in search of the same prey. In contrast, if hunters exhibit high demand elasticity, hunters will begin to accept a wider variety of prey, some of which may be of lower value to the hunter. With further depletion of game, the level of demand elasticity and how it is affected by the strength of opportunity costs and by the availability of ammunition will determine whether hunters hunt less frequently or not at all. An example of such behavioural dynamics is given by Brashares *et al.* (2004), who showed that depletion of pelagic fish stocks by industrial fisheries increased hunting effort and impact among local resource users in West Africa. A reduction in the local supply of fish, which is a substitute for game, reduced the opportunity cost of hunting and caused an increase in time allocated to hunting.

In this paper, we develop a dynamic state-variable model to explore the range of human hunting strategies for central-place foragers as prey become locally depleted and as ammunition becomes more affordable. Our model sits squarely within a large body of work in behavioural ecology that is collectively called optimal foraging theory (Schoener, 1971; Stephens and Krebs, 1986). Foraging theory has focused on predictions about which species are included in the diet (MacArthur and Pianka, 1966; Schoener, 1971; Pulliam, 1974), in which patch to forage (Orians and

Pearson, 1979), and how long to stay in a patch (Charnov, 1976). The theory was not originally developed with humans in mind, but it has since been applied in the human behavioural ecology literature, particularly to hunting strategies (Winterhalder and Smith, 1981; Hames and Vickers, 1982; Hawkes *et al.*, 1982; Hill *et al.*, 1987; Alvard, 1995). The basic diet-breadth model used to describe hunting strategies assumes that foragers behave so as to maximize their long-term rate of energy acquisition in a fine-grained environment (*sensu* MacArthur and Pianka, 1966), where ‘fine-grained’ implies no spatial structure, and sequential, rather than simultaneous, encounter.

In its simplest form, the rate maximization framework is formulated as follows. The first assumption is that over a very long period, the only things that the forager does is encounter and handle prey. We let the energy content, encounter rate, and handling time of species i be given by E_i , λ_i , and h_i respectively. The profitability of a species upon encounter is given by the rate of energy gain after encountering and capturing species i , E_i/h_i . The first step of the model is to rank each of n available species according to their profitability, such that $E_1/h_1 > E_2/h_2 > \dots > E_n/h_n$. The basic diet-breadth model predicts that when the forager considers two species, the more profitable will be pursued and the less profitable will be ignored, as long as the encounter rate λ_1 of the more profitable species is sufficiently high. In other words, an optimal forager ignores low-profit prey when the time spent on its capture and consumption, h_2 , is time that could be more profitably spent searching for high-profit prey, which is more likely as the abundance of high-profit prey increases. Comparing the long-term rate of energy acquisition, the forager specializes if

$$\frac{E_1\lambda_1}{1+h_1\lambda_1} > \frac{E_1\lambda_1+E_2\lambda_2}{1+h_1\lambda_1+h_2\lambda_2}, \quad (1)$$

which yields a condition for specialization that depends only on the encounter rate of the more profitable species:

$$\lambda_1 > \frac{E_2}{E_1h_2 - E_2h_1}. \quad (2)$$

As a result, optimal foragers are predicted to exhibit a knife-edge behaviour, such that prey items are either fully included or excluded from the diet. Equations (1) and (2) are easily generalized for more prey species.

Despite many applications of optimal foraging theory to human hunters, human hunting does not meet the assumptions of this simple optimal foraging theory model (see Table 1 for a comparison of foraging models). For instance, hunters typically leave home in the morning with a finite amount of ammunition, hunt for a finite amount of time, and return home before dark, making them central-place foragers who are limited in the number of attacks they can undertake per hunt (Alvard, 1993). Because of this, rather than maximize the *long-term rate* of energy acquisition, which is the assumption of the basic diet-breadth model, an optimally foraging human is constrained to maximize the *energy acquired per hunting day*, given the ammunition available, the time available to hunt, and the maximum energy that can be carried back home. Tropical game species are sequentially encountered, in a manner more akin to the original fine-grained framework (MacArthur and Pianka, 1966) than to a system of foraging patches that are depleted during single foraging bouts (Charnov, 1976; Orians and Pearson, 1979). Furthermore, prey encounter rates are not constant in space, since more vulnerable game species are depleted near settlements (Peres and Palacios, 2007; Levi *et al.*, 2009;

Table 1. A comparison of the assumptions made by four optimal foraging models, including the state-variable model introduced here

Rate maximization	Encounters at a distance (Schoener, 1979)	Patch choice (Charnov, 1976; Orians and Pearson, 1979)	State-variable model
Sequential encounters	Prey detected from central place	Rate of energy acquisition in patch decreases with time	Sequential encounters
Infinite time horizon	Infinite time horizon	Infinite time horizon	Finite time horizon
No opportunity costs	No opportunity costs	No opportunity costs	Includes opportunity costs
No attack limitation	No attack limitation	No attack limitation	Includes attack limitation
No spatial structure	Considers travel cost when attacking distant prey	Considers patches arranged at different distances	Considers encounters made at different distances
Deterministic results	Deterministic results	Deterministic results	Hunter behaviour is stochastically simulated

Endo *et al.*, 2010). Finally, market involvement decreases attack limitation by making ammunition and firearms more affordable. What is needed is a unified central-place foraging model that incorporates the trade-offs unique to human behavioural ecology, thereby accounting for changes in behaviour as distance, encounter rate, time, hunting success, and the accessibility of shotgun shells vary. Our purpose is to introduce the method of dynamic state-variable modelling to human foraging ecology to move the field beyond the rate maximization framework.

METHODS

The behavioural ecology of central-place foragers

We present our foraging model for Neotropical hunters with access to an assemblage of game species. Our assemblage of nine species contains major prey groups including white-lipped and collared peccaries (*Tayassu pecari* and *Pecari tajacu*), tapirs (*Tapirus* sp.), brocket deer (*Mazama* sp.), large primates including spider monkeys and howler monkeys (*Ateles* sp. and *Alouatta* sp.), the agouti (*Dasyprocta* sp.), the medium-sized capuchin monkey (*Cebus* sp.), and a prey grouping of large game birds. We use field data collected from Piro shotgun hunters in Peru (Alvard, 1993) (Table 2) and compiled by Rowcliffe *et al.* (2003) to derive handling times, kill rates, and body mass to parameterize our models. To estimate encounter rates, we use group encounter rates from a series of line transects outside of an indigenous community in Manu National Park, Peru (Endo *et al.*, 2010).

Consider a hunter leaving a central place such as a village. The states are $X(t)$, the distance the hunter has travelled, $A(t)$, the number of attacks (i.e. shotgun shells) that the hunter has used, and $E(t)$, the energy acquired by the hunter at time t . As the hunt

Table 2. The assemblage of nine Neotropical prey types we consider and their encounter rates ($\text{groups} \cdot \text{km}^{-1}$), λ_i , energy contents (kg), E_i , handling times (h), h_i , and kill rates ($\text{kills} \cdot \text{group}^{-1}$), k_i

Species	λ_i	E_i	h_i	k_i
White-lipped peccary	0.032	45	0.70	1.00
Collared peccary	0.024	21	0.37	0.81
Tapir	0.008	149	1.00	0.20
Deer	0.032	30	0.13	0.08
Spider monkey	0.215	8	0.59	1.25
Howler monkey	0.143	7	0.42	1.11
Agouti	0.04	3	0.04	0.22
Game birds	0.072	2	0.08	0.47
Capuchin monkey	0.095	4	0.38	0.40

progresses, a hunter may (1) have already acquired e units of energy, $E(t) = e$, (2) have used up a of a_{\max} ammunition, $A(t) = a$, and (3) be at distance x from home, $X(t) = x$. A hunter's behaviour depends on the potential combinations of the above state variables. To determine the optimal behavioural strategy for every possible combination of the state variables (the state-space), we use state-dependent behavioural theory implemented by stochastic dynamic programming (Mangel and Clark, 1988; Clark and Mangel, 2000). Let the maximum expected energy (meat) acquired by the end of the hunt, given that $E(t) = e$, $A(t) = a$, and $X(t) = x$, be given by the utility function

$$U(e, a, x, t) = \max\{\text{expected accumulated energy given that } E(t) = e, A(t) = a, X(t) = x\}. \quad (3)$$

We begin by recognizing the following constraint relating distance and time for a central-place forager. Given a total hunting time, T , at time t there is $T - t$ time left in the day. If the distance from home, x , divided by the walking speed, w , equals $T - t$, then there is no time left to hunt because the time that it will take to return home equals the time left in the day. The distance–time constraint, plus the constraint that the hunt ends if all the ammunition (a_{\max}) is used, defines the boundary condition on the utility function

$$U(e, a, x, t) = e \quad \text{if} \quad \frac{x}{w} = T - t \text{ or } a = a_{\max}. \quad (4)$$

Hunters receive no utility by travelling distances beyond which they cannot return by time T (i.e. we assume no overnight forays),

$$U(e, a, x, t) = 0 \quad \text{if} \quad \frac{x}{w} > T - t. \quad (5)$$

The value of not attacking game species i at location $X(t) = x$, given that $E(t) = e$ and $A(t) = a$ is the utility of being at the next point in space and time without acquiring additional energy or using any additional attacks,

$$V_{N_i}(e, a, x, t) = U(e, a, x + 1, t + 1). \quad (6)$$

For simplicity (and consistency with the rate-maximization model), we assume an equal handling time whether or not an attack is successful, which occurs when game are pursued for long periods, but distinct handling times are easily incorporated. Since species i has an associated handling time h_i , and the value of attacking depends on whether there is enough time to handle it, we let $I_{\frac{x}{ws} < T-t-h_i}$ be an indicator variable that equals 1 if the condition in the subscript (there is enough time left to hunt) is met, and 0 otherwise. If there is time, the value of attacking species i depends on the expected utility if it is killed, which occurs with probability, p_i , and the expected utility if it is not killed, which occurs with probability, $1 - p_i$. The probability of kill, p_i , is derived by assuming a Poisson process with rate parameter, k_i , the kill rate per group encounter. Thus $p_i = 1 - e^{-\frac{k_i}{T}}$. An attack unit is used whether or not a kill is made, $A(t + h_i) = a + 1$. The value of attacking game species i is thus

$$V_{A_i}(e, a, x, t) = I_{\frac{x}{ws} < T-t-h_i} [(1 - p_i)U(e, a + 1, x + 1, t + h_i) + p_i \cdot U(e + E_i, a + 1, x + 1, t + h_i)]. \quad (7)$$

In addition to deciding whether to attack a species upon encounter, a hunter can also choose whether to hunt or not. This decision depends on the probability that game is encountered and whether there is time to pursue. The probability that species i is encountered is given by l_i , which can be derived from λ_i by noting that (1) hunters can only encounter one individual per time step, (2) that the probability that a prey species is encountered in the next time step is $1 - e^{-\sum_i \lambda_i}$, and (3) that the probability that species i is encountered given that something is encountered is $\lambda_i / \sum_i \lambda_i$. Combining probabilities, we obtain

$$l_i = (1 - e^{-\sum_i \lambda_i}) \frac{\lambda_i}{\sum_i \lambda_i}. \quad (8)$$

The value of continuing to hunt depends on the expected utility if no prey are encountered, which occurs with probability $1 - \sum_i l_i$, and the expected utility if something is encountered and is either attacked or not depending on whether the value of attacking is greater than the value of not attacking. Thus, the decision to attack a game species upon encounter is a nested decision within the broader decision of whether to continue hunting at all. There is no value to hunting if there is not enough time left in the day:

$$V_H(e, a, x, t) = 0 \quad \text{if} \quad \frac{x}{w} \geq T - t. \quad (9)$$

Otherwise, the value of hunting is

$$V_H(e, a, x, t) = \left(1 - \sum_{i=1}^n l_i\right) U(e, a, x + 1, e, t + 1) + \sum_{i=1}^n l_i \max[V_{A_i}(e, a, x, t), V_{N_i}(e, a, x, t)], \quad (10)$$

where, as above, $V_{A_i}(e, a, x, t)$ and $V_{N_i}(e, a, x, t)$ is the value of attacking and not attacking species i respectively.

From the definition in equation (3), we thus have

$$U(e, a, x, t) = \max[V_R(e, a, x, t), V_H(e, a, x, t)], \tag{11}$$

where the value of returning home is given by the current level of acquired energy $V_R(e, a, x, t) = e$. The decision process used in the stochastic dynamic programming algorithm is summarized with a flowchart (Fig. 1).

Many game species are gregarious and any number $k \leq g$ (where g is the group size) can be killed upon group encounter. Incorporating this feature is straightforward by noticing that this can be framed as the probability of killing k individuals in g trials. The probability that k of g individuals are killed is

$$\binom{g}{k} p^k (1-p)^{g-k},$$

which yields $k \cdot E_i$ units of energy. For simplicity, here we assume that one individual is killed per group encounter, but we note that multiple kills per group encounter can be easily incorporated.

Prey depletion scenario

Because central-place foragers can deplete resources locally, we account for the depletion of game species by making the probability of encounter a function of distance, so that the encounter probability is now a function $l_i(x)$ of spatial location. This allows us to predict how hunter behaviour changes as preferred prey become depleted. Of the game species that we consider, tapirs, spider monkeys, and white-lipped peccaries are often especially locally depleted by hunting. We analyse forager behaviour in a ‘depletion’ scenario with these three species locally extirpated to $x \leq 10$ distance units (km) to assess how local extirpation of some high-value prey affects hunter behaviour and the availability of protein availability.

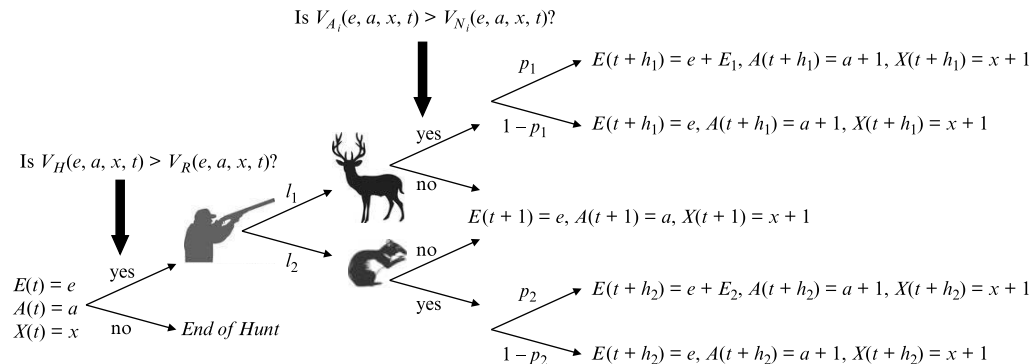


Fig. 1. The decision tree that is used to find the optimal hunting strategy and simulate hunts. Hunter state and behaviour are stochastically simulated using the optimal strategy for all combinations of $x, e, a,$ and t .

Forward simulation

Once the optimal strategies have been developed for the entire state-space, it is straightforward to simulate hunters behaving according to these strategies, producing predictions for the behaviour that hunters follow (Mangel and Clark, 1988; Clark and Mangel, 2000). Since the method is stochastic, each variable of interest has a distribution, which provides a general framework for understanding the distribution of diverse field observations. For game management, we are especially interested in the distribution of trip lengths (maximum walking distance), hunter prey profiles, and the spatial distributions of kills of each species as prey are depleted and increased market involvement allows for affordable ammunition, reducing the degree of attack limitation.

The simulation is not only useful for prediction, but it also serves as a null hypothesis against which to compare behavioural observations. For example, an anthropologist may conclude that hunters are not behaving optimally because certain prey items are only occasionally pursued (in apparent violation of the basic diet-breadth model), or because they choose to hunt infrequently or only in the immediate vicinity of the household. The simulation results can produce qualitatively distinct distributions of optimal behaviour, so that instead of using an overly simplistic model of foraging to ask, ‘Are these hunters behaving optimally?’, the question becomes, ‘What levels of attack limitation and prey depletion (among other constraints) can explain the observed behaviour?’

RESULTS

The species included in the diet depends on the full assemblage of state variables. While diet-breadth models predict that a prey item should either always or never be included in the diet, the optimal strategy in the state-variable model depends on space, time, ammunition availability, and what has already been killed.

Based on the state-variable model, we predict that low-value game species will be included late in the hunt, because as the time left to hunt approaches zero, the expected number of future encounters with the high-value game species also approaches zero. In addition, high-value game species that require long handling times cannot be pursued late in the hunt if there is no time for successful pursuit. This is in accordance with observed hunts by Matsigenka bow-hunters in the Peruvian Amazon (Ohl-Schacherer *et al.*, 2007) in which spider monkeys, *Ateles chamek*, were ignored or abandoned after a long pursuit near the end of the day (T. Levi, personal observation). Our result is distinct from theory that predicts increasing specialization on high-value species as distance from the central place increases (Orians and Pearson, 1979; Schoener, 1979). These classic central-place foraging models assumed that the forager sees prey from a central place and then decides whether it is worth the energetic cost of foraging to a certain distance. In contrast, when central-place foragers encounter prey sequentially, we predict that diet breadth expands with distance.

The point at which it becomes optimal to pursue the low-value game species depends strongly on the availability of ammunition (Fig. 2). If few attack opportunities remain due to attack limitation, the less profitable game species is ignored for a greater fraction of the hunt. Thus, one prediction of the model is that attack limitation increases specialization on high-value game species. Increased ammunition availability increases the frequency of attacks on lower-value game. Large primates appear to be sensitive to attack limitation because they are included in the optimal diet when there is ample ammunition but are excluded in favour of larger-bodied ungulates if ammunition is limiting (Fig. 2). This

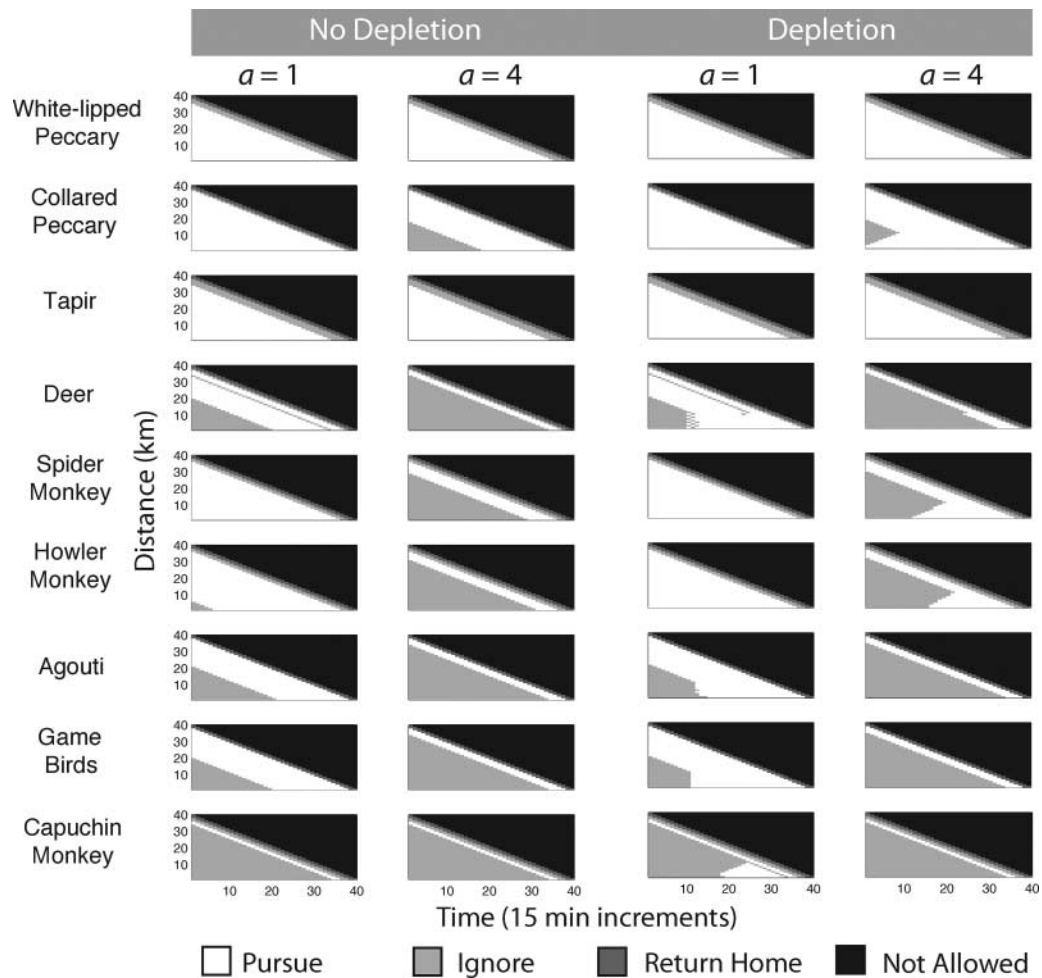


Fig. 2. The optimal hunting strategy for hunters of nine Neotropical species as a function of distance from home and time spent hunting can show partial preferences that appear in the form of lower-value game species entering the diet late in the hunt. With less ammunition remaining ($a = 4$ of 5 possible attacks), it is less profitable to attack a lower-value game species or one with a low kill rate (e.g. deer), causing hunters to focus a greater proportion of the hunt on high-value prey. In our 'depletion' scenario, white-lipped peccaries, tapirs, and spider monkeys are extirpated to 10 km. Howler monkeys become profitable during the entire hunt, but agoutis, game birds, and deer become only slightly more preferred.

presents a conservation problem because large primates are the least fecund game species and highly vulnerable to over-exploitation. In contrast, increasing ammunition availability is not predicted to impact the largest prey, white-lipped peccaries and tapirs, since they are always attacked when encountered. Furthermore, although deer are large bodied, the probability of killing a brocket deer is so low (they hide until the hunter is near and then quickly sprint away into the forest) that they are not always pursued even when ammunition is available and are not pursued when ammunition is rare. This prediction of the model implies that the probability of killing an animal becomes very important when a forager is

ammunition limited because not only is time wasted (an aspect that rate maximization models also include) that could otherwise be spent searching, but one of few available attacks is wasted.

The spatial distribution of harvest across species (Fig. 3) is derived from forward simulation of hunters performing the optimal behaviours (i.e. those in Fig. 2). Owing to their abundance and high kill rate, spider monkeys are the most frequently killed species in an unexploited system. We predict that howler monkeys are not killed early in the hunt in the ‘no depletion’ scenario because time spent hunting them is better spent walking to more distant hunting grounds where spider monkeys, white-lipped peccaries, and tapirs are still abundant.

As long as the three depleted species (white-lipped peccaries, tapirs, and spider monkeys) are eventually abundant (i.e. after hunters walk past the area in which they are locally extirpated), hunter demand is largely inelastic, meaning that rather than substitute agoutis, game birds, and capuchin monkeys, hunters mostly ignore these prey species en route to high-value prey available past 10 km.

Whether there is depletion of some high-value game species or not, we predict that hunters walk similar distances in pursuit of prey (Fig. 4). In the depletion scenario, more

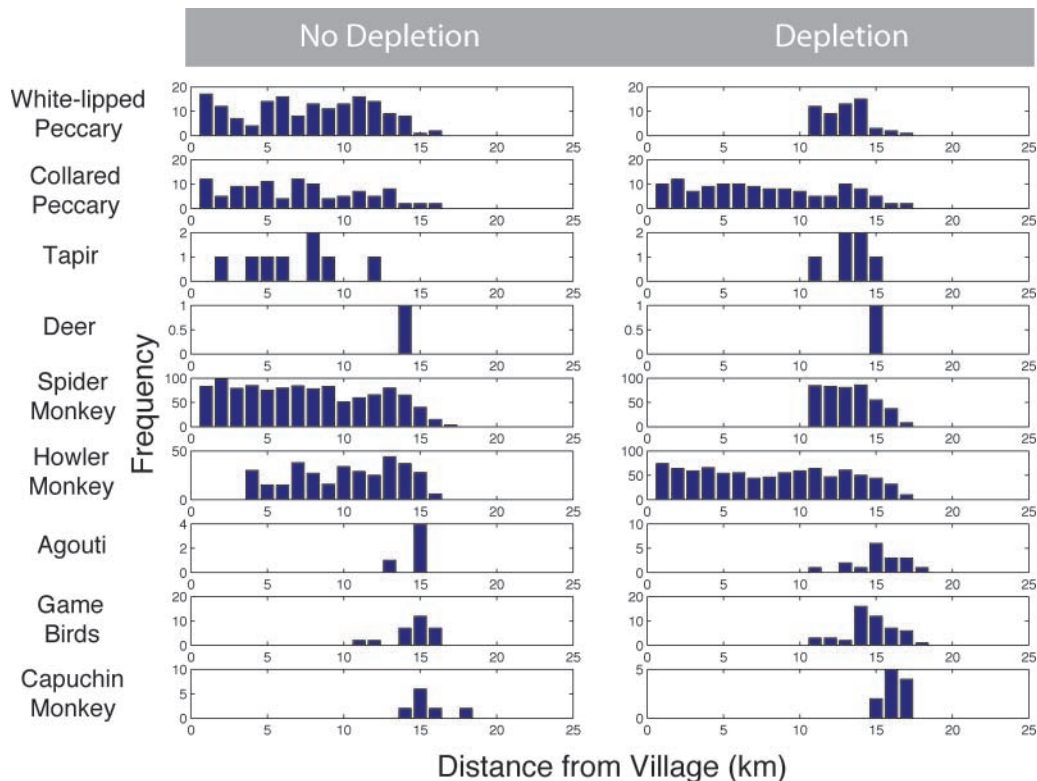


Fig. 3. The spatial distribution of kills of each species. Spider monkeys are the most important prey when there is no depletion, but howler monkeys become the most important prey with spider monkeys second most important in our depletion scenario. Lower-value game do not significantly expand into the diet even in the ‘depletion’ scenario.

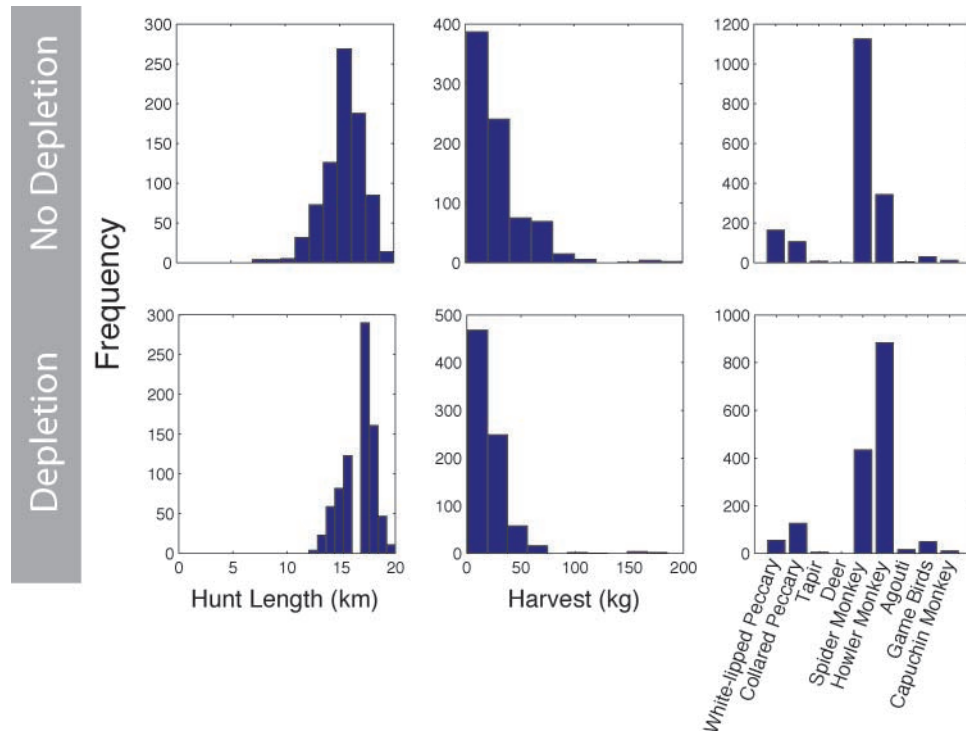


Fig. 4. The summary of the forward simulation based on optimal hunting. Hunting distances increase only slightly when prey are depleted. In our depletion scenario, more hunters return empty-handed and fewer return with very large harvests. Depleted prey are only slightly less represented in prey profiles, casting doubt on using prey profiles as a measure of hunting sustainability.

hunts result in no kills and fewer hunts result in large harvests (Fig. 4). However, despite local extirpation of three primary game species, hunters still obtain consistent (although smaller on average) yields. More surprising is the relatively constant prey profile despite depletion. Although spider monkeys, tapirs, and white-lipped peccaries are less represented in prey profiles when extirpated to 10 km, the difference is not great (Fig. 4).

DISCUSSION

The application of optimal foraging theory to understand human behaviour was an innovative advance in behavioural ecology (Smith and Winterhalder, 1992). In a Neotropical context, applications of foraging theory have helped to explain variability in hunting patterns and human adaptation to changes in environmental conditions (Hames and Vickers, 1982). In addition, predictions from optimal foraging theory have been used as a null hypothesis to identify conservationist behaviour for intra- and inter-specific prey choice (Alvard, 1993, 1995). What has lagged in human evolutionary ecology is the consideration of state-dependent behaviour and the revision and application of models to more accurately reflect contemporary changes among resource-dependent populations such as native Amazonians. Infra-structural development has led to increasingly sedentary populations with wholesale shifts in hunting technology from traditional weapons (e.g. bows, blowguns) to firearms. The

model that we have presented here reflects these challenges of technological change, integration into the market economy, increased sedentarism, and declining availability of highly desired game.

We revisited the central-place foraging model (Orians and Pearson, 1979), which predicts that foragers will increasingly specialize on higher quality exhaustible food patches as distance from the central place increases, because the total rate of energy acquisition must incorporate the travel and transport costs associated with foraging in a more distant patch. Schoener (1979) considered the diet breadth of a forager that scans for food items from a central place and found increasing specialization on high-value resources as distance from the central place increases. In contrast, we consider central-place foragers who sequentially, and probabilistically, encounter prey as they walk away from the central place.

Our work has extended the ideas of optimal foraging theory to account for the state dependence of foraging behaviour. By considering state dependence, we predict that when there is a finite time horizon (which there always is), foragers exhibit increased diet breadth as distance from the central place increases. This is because the finite distance and time horizon of a hunt means that, as time progresses, there are fewer potential encounters with prey, which makes it optimal to expand the diet breadth to include prey that a rate maximization approach would predict to be absent from the diet breadth. In practice, this state dependence is observed through the partial preferences of hunters who sometimes ignore and sometime pursue prey species of marginal quality. In support of the results, Alvard (1993) found that game birds are significantly more likely to be pursued later in the hunt. It is important to note that while our results robustly predict that diet breadth expands late in a hunt, they do not accurately predict the distance where this occurs. We have considered only outgoing hunts, but game species that enter the diet breadth 'late' in the hunt may be killed either far from home, or near to home if encountered during the return trip.

Market participation can increase the affordability and accessibility of ammunition, which expands the diet breadth. Notably, spider monkeys appear to be in the optimal diet if there is plenty of ammunition but fall out of the optimal diet (for part of state-space) when ammunition is highly limiting because hunters would do better to save that ammunition for an encounter with a larger-bodied animal. This result suggests that a slowly reproducing large primate has the most to lose by hunter access to markets both because shotguns have high kill rates and because if ammunition is plentiful, large primates are more profitable.

Development and increased market participation will increasingly localize subsistence hunting effort on prey species of lower value. This prediction breaks down when market hunting is considered. Commercial hunting behaviour is more inelastic because the high market value of certain species causes hunters to travel ever greater distances in search of high-profit prey. It is straightforward to include the economic value of game species in these models to account for commercially exploited species. The energetic value of a commercially exploited species can be set to the equivalent energy (although cash actually has more value because it is fungible) that can be purchased with the profit made from the sale of the game species. If the profitability of a species is high enough, it is worthwhile for hunters to specialize on it. Bodmer and Lozano (2001) suggested that increasing the market participation of subsistence hunters could make hunting more sustainable by enticing subsistence hunters to allocate more effort to more resilient game with a high market value, rather than to slowly reproducing large primates, which have poor market value. However,

the behavioural dynamics are more complicated because income obtained by commercial hunting decreases attack limitation, which can unintentionally increase rather than decrease hunting of vulnerable large primates.

Our results suggest that prey profiles do not necessarily change dramatically when high-value prey are depleted (Fig. 4). Longitudinal comparisons of prey profiles are commonly used to assess whether hunting has caused depletion (e.g. Ohl-Schacherer *et al.*, 2007). The theoretical basis for prey-profile comparison to detect depletion comes from non-spatial diet-breadth models. The assumption is that a relatively constant diet breadth indicates that there is little depletion. However, when accounting for spatial structure hunters can simply walk to distant areas where high-value prey are still abundant instead of substituting low-value game. In general, this creates a tendency to stabilize the diet breadth of central-place foragers.

The energy histogram produced by forward simulation under different levels of depletion quantifies the human cost of the over-exploitation of wildlife. Qualitatively, we have shown that when there is depletion, the energetic returns are lower but not necessarily less reliable. It is desirable to quantify this cost for hunters when evaluating management options. For example, one management option to prevent over-exploitation is to ban hunting of particularly vulnerable species. The efficacy of a management option depends on the cost to human livelihoods, with an ideal management plan conferring a low livelihood cost and receiving a large conservation payoff. This can be assessed using a state-variable model approach.

A promising future for applied behavioural ecology concerns understanding coupled human–natural systems, since environmental and social problem solving depends heavily on human behavioural decisions. This idea has been proposed in fisheries for a long time. For example, most fisheries problems arise from a failure to understand and manage fishers, and the study of fishers should be a major part of fisheries research (Hilborn, 1985). Here we have developed the requisite theory to begin to couple hunter behaviour with game species biology to model subsistence hunting spatially and with many game species. A promising use of this approach is to create the behavioural rules for individual-based models of hunters to assess the impact of hunting in space.

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