Journal of Archaeological Science 32 (2005) 1147–1158

Journal of Archaeological SCIENCE

http://www.elsevier.com/locate/jas

The prey as patch model: optimal handling of resources with diminishing returns

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Received 20 November 2004; received in revised form 15 February 2005

Abstract

Foraging theory provides archaeology with a valuable set of tools for investigating the constraints that influenced procurement decisions of the past. The prey-choice model has been used extensively by archaeologists, but has significant limitations given the nature of archaeological data. This paper suggests that the seldom-used Marginal Value Theorem (MVT) is a valuable tool for examining the ecological constraints on foraging decisions and merits further archaeological application. Ethnoarchaeological and experimental cases are presented demonstrating how patch–gains curves can be generated from quantitative data on butchering return rates and handling times. Results indicate that such curves are diminishing return functions. This provides a basis for examining the linkage between processing intensity and resource fluctuation. This model allows archaeologists to address the relationship between attribute-states of faunal remains and predicted optimal post-acquisition decisions. The MVT is valuable to ethnoarchaeology because it identifies how mean foraging return rate influences the handling of acquired prey and makes quantified predictions of return rate based on processing intensity. The MVT can also be applied to archaeological studies of foraging behavior and processing intensity as it can be used to estimate the set of environmental constraints in which a given kill was made (e.g., "good" vs. "bad" times). This approach may also identify the degree to which certain currencies, such as fat, are optimized at the expense of others, such as total caloric intake.

Keywords: Marginal value theorem; Optimal foraging theory; Zooarchaeology; Resource depression

1. Introduction

Archaeological studies of butchery practices are a central focus of research into prehistoric hunter–gatherer subsistence strategies due to the evolutionary importance of meat in the hunter–gatherer diet [21] and the preservation of bone in a variety of archaeological contexts. Attempts at quantifying subsistence practices commonly incorporate insights from foraging theory by considering the economic basis of human decision-making [3,4,35,56,57,61]. Such decisions involve time allocation trade-offs and energetic currency maximization strategies in the face of alternative foraging behaviors available to a hunter–gatherer. Archaeological applications of foraging theory have focused on the prey-choice (or diet-breadth) model with a focus on understanding the range of items that enter the diet and/or how they are transported [24,26,37,42,44,45] but, with few exceptions (e.g., [43]), the Marginal Value Theorem (MVT) [15] has been underutilized. The MVT predicts the optimal amount of time to spend acquiring resources from a patch based on the relationship between an energetic gain function for a patch of a given type and the overall foraging return rate, which is conditioned by the frequency with which patches are encountered [15,55]. The MVT is an optimization

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doi:10.1016/j.jas.2005.02.012

model, like the diet-breadth model, but the decision variable is resource processing time or effort (optimal patch residence time) rather than the specific array of resources that are acquired (e.g., optimal diet-breadth).

Working from the assumption that the archaeological record preserves the consequences of foraging decisions, and that those foraging decisions were non-random but constrained by simple economic trade-offs, we suggest that the MVT is a valuable tool for the archaeological analysis of resource processing as it identifies how mean foraging return rate R conditions the optimal effort exerted extracting energy from prey after they are acquired. As such, the MVT is a useful tool for investigating behavioral responses to resource fluctuation, providing a conceptual link between ecological constraints and their economic consequences. Additionally, the perspective presented here provides a needed means for investigating post-acquisition foraging decisions, which have received relatively little attention, as archaeologists have tended to (over-) emphasize transport decision analysis and prey choice. We demonstrate the utility of this approach by constructing patch–gains curves for ungulate prey using experimental data, but the approach is broadly applicable to any prey or patch where the rate of gain decelerates with time (or effort). The predicted relationship between carcass-processing intensity and overall return rate R is supported by ethnoarchaeological case studies.

We see two primary avenues for applications specifically dealing with ungulate prey resources. First, the perspective builds on O'Connell's [47] call to utilize behavioral ecology as the primary theory for ethnoarchaeology. Ethnoarchaeological applications of the MVT to post-acquisition carcass handling can aid in establishing the important constraints and currencies being optimized by human hunters and quantitatively link this handling, as a behavioral response, to changes in R. Second, the model has theoretical implications for the archaeological analysis of faunal materials by extending foraging theory to attribute-based analyses [52] of the characteristics of the prey (patch) itself.

2. The prey as patch model: rationale and assumptions

The MVT was developed by Charnov and Orians [16][1] to investigate optimal foraging behavior in relation to resources that cluster in space. While the prey-choice model predicts which items from a set of potential resources should be included in the diet, the patch residence model (a derivation of the MVT) is concerned with how much effort, usually measured in time, is used in extracting energy from a given resource patch. The MVT predicts the optimal time to leave a patch as a function of the return rate in the present patch and travel time λ to the next patch [15]. A forager enters a patch of aggregated food items and consumes them sequentially. The rate of gain decelerates with time t and the forager is expected to leave when the marginal gain drops to the average gain across all patches, thus maximizing the overall return rate R (Fig. 1).

If a forager, human or otherwise, alters the amount of time invested in extracting energy from a given prey item, the prey itself can be thought of as a "patch" [16,20]. For carcass butchery, anatomical elements vary in profitability in terms of gain per unit of time and can be ranked in terms of their economic utility [5,32,44]. The MVT suggests that economic decisions should reflect this ranking such that the "best parts" of the prey should be consumed before parts of lesser quality [16]. Archaeologically, we wish to investigate behavioral responses to resource fluctuation via patch residence time. For vertebrate prey, fluctuation in R is linked to changes in time between successful animal kills (individual patches) and patch residence time is equivalent to processing intensity. Processing intensity is directly inferred from archaeologically recognizable signatures of carcass processing, including impact fractures, green bone breaks, and the relative degree of long bone fragmentation tempered by appropriate concern for taphonomic agents [26,38,58,59,62]. Processing effort is used as a proxy for patch residence time and the travel time between patches (time between kills) reflects the mean foraging return rate. In this sense, information regarding the average foraging return rate is preserved in the handling of all resource patches or prey items. As the time between kills increases, the forager maximizes the long-term rate of resource gain by lengthening the amount of time spent processing each carcass (Fig. 2). Archaeologically, this is evidenced by the use of lower ranked skeletal elements, by the increased intensity of

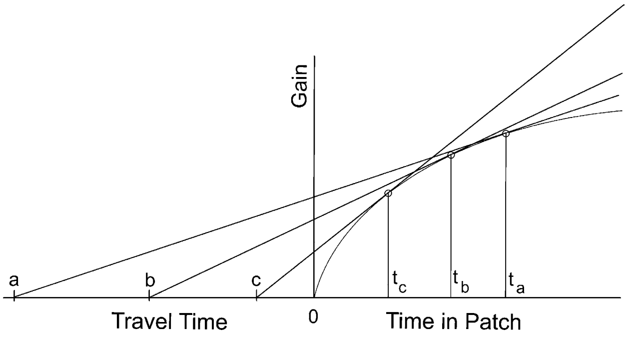

Fig. 1. The marginal value theorem. The y axis labeled "gain" is generally measured in calories but any appropriate currency could be substituted. Modified from Charnov and Orians [16].

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[1] This often cited unpublished manuscript was recently made available as a .pdf for download from Dr. Charnov's homepage (http://biology.unm.edu/Charnov/Charnov.htm).

carcass processing, or both. Processing time may also increase if fats become especially limiting while other resources remain constant. Such nuances can potentially be identified using this perspective in concert with existing foraging models [13,14,45].

Fitting a gains curve for time spent butchering a prey item (patch) to real data on per element return rate allows the researcher to take the derivative (slope of the tangent line) at any point on the curve in order to calculate the instantaneous return rate during carcass processing. The x-intercept of this line is an estimate of time between patches in the traditional MVT and equates to time between kills in the prey as patch model. When the gain function for a patch is known, estimating the processing intensity as time of abandonment from the patch also estimates R or some relative measure of foraging success. The shape of the gain function can be determined through the use of experimental butchery data and/or ethnoarchaeological data [32,43,47]. In order to infer the density of patches, the only required variables are amount of time spent in the patch and the benefit function for time, which is usually based on energetic gain. Inferring foraging return rate with the diet-breadth model requires knowledge of all the prey items acquired, their handling costs, and their encounter rates. In this sense, the decision variables for the MVT have direct archaeological correlates whereas the decision variables of the diet-breadth model do not.

As with other standard foraging models, the forager is assumed to have "perfect knowledge" of the travel time between patches, which is equivalent to knowing the relative densities and abundances of particular prey items [55]. The forager also knows the relationship between processing time and total gain for the average patch encountered of a given type. Such assumptions are not over-drawn given the extensive knowledge that hunter–gatherers have been shown to have of their prey [8] and the degree to which hunters make decisions reflecting such knowledge [5,29].

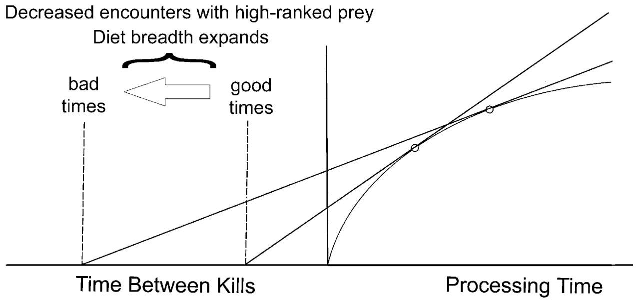

Fig. 2. The prey as patch model. "Good" and "bad" times are defined qualitatively based on encounter rates, which are assumed to reflect the mean foraging return rate. As time between kills increases more lower ranked patches enter the diet and the amount of energy extracted from each patch increases.

As with all applications of foraging theory, we assume that human foragers were designed by natural selection to favor behavioral variants that maximize the rate of resource acquisition as long as one of the following three conditions applies (from [33]): (1) increase of food acquisition increases fertility and/or survivorship; (2) time spent foraging could be spent on other tasks that would increase fitness or survivorship; and (3) foraging is in some ways dangerous. In this respect, foragers will attempt to maximize the rate of food acquisition while seeking and processing food items. Predictions made by researchers using the logical structure of either the diet-breadth model or the MVT that are not supported by a given case study do not reject the validity of the models for understanding human behavior (contra [1]) because any such predictions make certain assumptions regarding currencies and other variables that are more immediately subject to evaluation than the central principle of optimization. Optimal foraging theory provides a quantitative framework from which null hypotheses of optimal behavior can be drawn. Falsified predictions of foraging models simply identify inaccuracies in the specific assumptions regarding currencies and constraints framing the particular hypotheses and in doing so identify the learning opportunities that foraging models are well designed to provide.

Ethnoarchaeological tests demonstrating the relevance of the MVT to human foragers are presented. The prey as patch model assumes that a non-random rationality underlies decisions regarding the post-acquisition handling of prey. The archaeological "test" of this relationship lies in establishing its observable material consequences and in refining the constraints and currencies that affect optimal behaviors at large temporal scales. As archaeology deals with past decisions, the decisions themselves cannot be predicted. Rather, the model offers a theoretically grounded method for retrodicting the conditions under which foraging decisions were made. In doing so, we shift the emphasis toward using foraging models to identify the important constraints and currencies that conditioned past decisions. Archaeologists can test the accuracy of assumptions regarding past environmental and social contexts, but we suggest caution in asserting that archaeological applications of foraging models are actual tests of the basic tenets of optimality or the general aspects of the models themselves, they are simply predictions of the archaeological consequences of the economic decision-making process.

The marginal value theorem differs from the prey-choice model in that the decision variable is *time* spent in a patch (measured as processing intensity), rather than the decision of whether or not to attack a prey item upon encounter: note that this also differs fundamentally from the decision variables in the patch-*choice* model, which applies the logic of the diet-breadth model to aggregated resources (e.g., [34]). The MVT has certain advantages over the prey-choice model in terms of archaeological visibility in that the decision variable and its key constraints can be measured directly, whereas encounter rates and diet-breadth are at best inferred from samples that are generally lacking in adequate temporal and spatial resolutions [26,39]. For the prey as patch model, the time invested per carcass is a function of the foraging return rate or the perceived density of food resources in the forager's environment. Decisions regarding which prey items enter the diet are exogenous to the MVT model, which is equivalent to assuming that prey-choice decisions have already been made [36]. Likewise, handling or processing time is exogenous to the prey-choice model, which is the same as assuming either that the forager has no control over the time spent processing a resource or that the energy gained per patch is a constant [55:32]. In this sense, the two models compliment one another and can be used in tandem, given appropriate (and rigorous) attention to their respective assumptions [36,55]. However, the diet-breadth model can only be applied to assemblage level patterning and assumes a certain formational equivalence across localities, whereas the MVT shifts the emphasis towards the characteristics of the prey. Acknowledging the utility of the MVT is important for exploring the degree of variance in human processing intensity (handling time).

In sum, the patch residence time model predicts that an optimal relationship exists between the time spent extracting energy from a patch and the time between alternative patches of equivalent value. In order to adapt this model to the analysis of prehistoric human foraging decisions, processing intensity is equated with patch residence time. Here, we focus on ungulate prey because of the data that are available for developing gains curves, but the exploitation of many types of resource patches could be modeled in an analogous manner [14,43]. Time between patches is a measure of the average time between successful kills, likely a primary determinant of mean foraging return rate, especially in pre-agricultural contexts. For the model to be effective it must be shown that: (1) the butchery of animal prey by humans can be described by a negatively accelerating gain function derived from actual data; (2) ethnoarchaeologically observed human butchers exhibit non-random variability along this gain function and make decisions reflecting its shape; and (3) time spent processing varies as a function of prey encounter rate. The following three sections offer support for these three characteristics of the model.

2.1. Building a gains curve

The construction of a patch residence gain function requires data on energy return per unit time spent processing a prey item. While such data are rare, much can be learned from the few data sets that are available. Binford's [5] Nunamiut study and a recent analysis by Madrigal and Holt [40] can be used to build patch gain functions for vertebrate prey. These studies are useful in demonstrating the utility of applying the marginal value theorem to the analysis of carcass butchery and suggest further that macronutrients, especially fat, are essential variables in investigations of human butchery practices.

In spite of Binford's skepticism regarding the use of optimal foraging theory in archaeology ([6:219–220], see also [3,25]), he gathered one of the most useful data sets for applying optimality approaches to human hunting decisions while working among the Nunamiut of northern Alaska [5]. Nunamiut decision-making was analyzed in reference to a series of indices placing the skeletal elements of the caribou carcass in rank order based on the nutritional values of meat weight, bone marrow, and grease quality. Binford established that the economic utility of caribou anatomy could account for Nunamiut foraging and transport decisions better than factors such as cultural variability and human preference, such as taste.

Nunamiut butchery meets the fundamental optimality prediction mentioned above that the "best parts" of a carcass are typically consumed before parts of lesser quality. Binford's [5] data on marrow extraction form a negatively accelerating gain function demonstrating that more intensive processing leads to lower marginal gains per carcass (Fig. 3). Jones and Metcalf [32] estimate that during the "normal conditions" of Binford's study the Nunamiut were processing a carcass until the return rate was about 500 kcal/h, which occurs at a point between the metacarpal and the mandible. This value should reflect the optimal processing time as a function of the average caribou density for the study period. In Fig. 3, this value is the slope of the tangent line intersecting the curve at the point when Nunamiut hunters leave a depleting caribou patch. Hypothetically, if foraging returns were to decline, the first additional element to be processed for marrow would be the mandible, followed by the pelvis (Fig. 3).

The decelerating gain in marrow processing is an important observation since marrow extraction from long bones is a behavior with a relatively good chance of archaeological detection [7,11,49]. The implication is that the profitability of the "stop element", or lowest-utility portion of the carcass butchered, can be inferred from archaeological fauna. The stop element should represent the optimal time to abandon the prey patch. However, the patch residence relationship may also be represented as an overall increase in processing intensity, which may not be measured with a stop element per se, but in the degree of fragmentation and the thoroughness of marrow extraction noted across all elements and especially long bones.

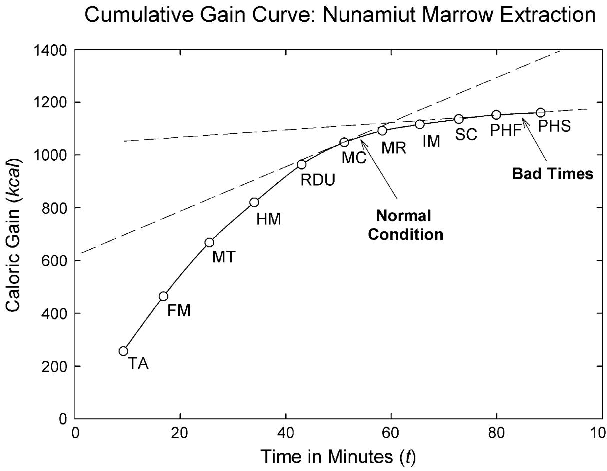

Fig. 3. Caloric gains from Nunamiut marrow extraction. Data are from Binford [5:26]. Nunamiut "old timers" recall extracting marrow from phalanges, scapulae, and other elements that are not used today. The curve is a connection of the data points. The dotted line is an approximated instantaneous gain line, or the tangent to the curve. It would be calculated by taking the derivative of the curve. Abbreviations: TA, tibia; FM, femur; MT, metatarsal; HM, humerus; RDU, radius–ulna; MC, metacarpal; MR, mandible; IM, innominate; SC, scapula; PHF, first phalanx; PHS, second phalanx [58].

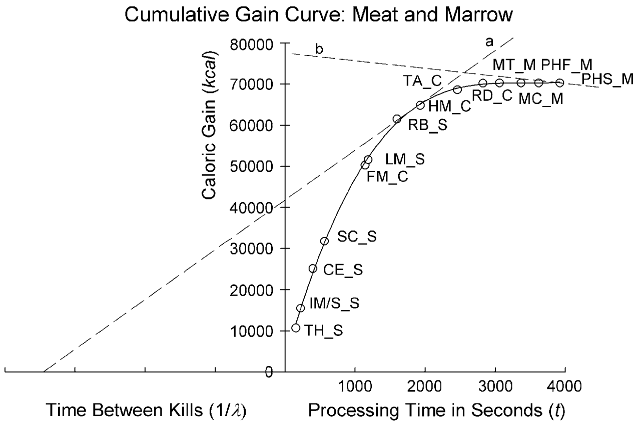

Fig. 4. Caloric gains from deer processing. For elements marked with a "C" processing time and caloric gain for meat and marrow are combined. Elements that have only meat values are marked with an "S". Elements with only marrow data available are marked with an "M". Line a depicts "good" times, with relatively high encounter rates. Line b depicts a situation of extreme processing intensity. Data are from Madrigal and Holt [40:748]. Abbreviations: TH, thoracic; IM/S, innominate/sacrum; CE, cervical; SC, scapula; FM, femur; LM, lumbar; RB, rib; HM, humerus; TA, tibia; RD, radius–ulna; MT, metatarsal; MC, metacarpal; PHF, first phalanx; PHS, second phalanx [58].

Madrigal and Holt [40] present experimental butchery data for white-tailed deer (*Odocoileus virginianus*) including separate processing times for meat and marrow removal for each anatomical element. From their observations, gross caloric values and processing times are combined for elements containing both meat and marrow (Fig. 4). For instance, the femur's meat processing time of 318 s was added to its marrow processing time of 262.5 s to obtain a combined processing time [40, Tables 1 and 3]. The same procedure was performed in obtaining the net yield in caloric gains for each element. The top three elements (thoracic vertebrae, innominate/sacrum, and cervical vertebrae) do not contain marrow. The profitability of these elements predicts them to be the first butchered and first transported. Ethnoarchaeological observations among Hadza foragers indicate that these elements are in fact the most consistently transported from kills to camps, regardless of season [44].

Two hypothetical lines are drawn as tangents to the curve representing possible optimal patch residence times as inferred for archaeological assemblages (Fig. 4). Line a represents a group with a relatively high patch encounter (kill) rate. Archaeological sites indicative of this strategy would not show signs of processing intensity beyond the caloric rate of gain occurring between the humerus and the tibia. Line b has a slightly negative slope and represents cases, such as the Australian Aborigines of arid northern Australia discussed below, of foragers accustomed to encounter rates so low that negative caloric return rates will be accrued in order to obtain fat [23].

While calories are often the default currency for optimization models, numerous studies have shown that within-bone fat stores are an important consideration for human butchery and foraging decisions [5,29,30,45]. In this case, both meat and marrow have decelerating gain functions with respect to calories but meat has higher per element yields and consistently higher return rates suggesting that foragers not limited by fat should not exert energy to extract marrow unless necessary. However, given the prevalence of animal products in most hunter–gatherer diets, fat is always likely to be in high demand [21,54]. While fat is actually more calorically dense than meat, it is distributed in smaller parcels in an animal carcass and requires more effort to extract (Fig. 5). Moreover, humans are limited in the amount of protein they can consume, whereas fat is more efficiently metabolized and contains important vitamins and fatty acids [53]. Consequently, some amount of energy will always be exerted for fat extraction but the variability exhibited in such expenditure may be informative regarding its limitation in the diet.

Intensive marrow processing may be an archaeologically visible sign of a macronutrient trade-off in the sense that caloric gain alone would be maximized by abandoning the patch before processing low-yield marrow-bearing elements. This relationship is seen more clearly when meat and marrow are placed on the same gains curve as separate values (Fig. 5). However, such ranking will change seasonally with the nutritional states of the animals [5] and marrow may need to be seen as a separate currency in many cases. Analyzing the situation from this perspective could allow us to identify

Table 1
Cumulative return rate data to calculate the gain function and intercept values

Rank	Skeletal element	Cumulative time (s)	Cumulative gain (kcal)	Slope	x-Intercept (h)
1	TH_S	152	10 694	–	–
2	IM/S_S	222	15 505	69.42	−0.001
3	CE_S	394	25 164	55.99	−0.015
4	SC_S	561	31 808	39.71	−0.067
5	FM_C	1142	50 304	31.86	−0.121
6	LM_S	1185	51 611	30.26	−0.145
7	RB_S	1597	61 479	23.97	−0.269
8	HM_C	1930	64 838	10.08	−1.251
9	TA_C	2460	68 608	7.11	−1.996
10	RD_C	2823	70 214	4.42	−3.625
11	MT_M	3060	70 267	0.22	−86.909
12	MC_M	3369	70 297	0.10	−199.523
13	PHF_M	3621	70 302	0.02	−927.514
14	PHS_M	3922	70 307	0.02	−1276.830

Return rate data by element are from Madrigal and Holt [40]. For skeletal element codes, see Fig. 4.

a processing strategy that invested very little time in meat processing (high encounter rates) while simultaneously investing a larger relative proportion of time in marrow extraction, for example if animal prey were exceptionally lean [46]. Future considerations of this issue may benefit from combining our approach with the use of indifference curves that model trade-offs in investment between alternative resource combinations [28]. Fig. 5 would help identify the relative utility of meat and marrow in different archaeological contexts. Further ethnoarchaeological work along these lines could help identify situations in which groups butcher as calorie maximizers, fat maximizers, or along an indifference curve incorporating both strategies. Moreover, ethnoarchaeological observation might indicate the conditions favoring one strategy over another.

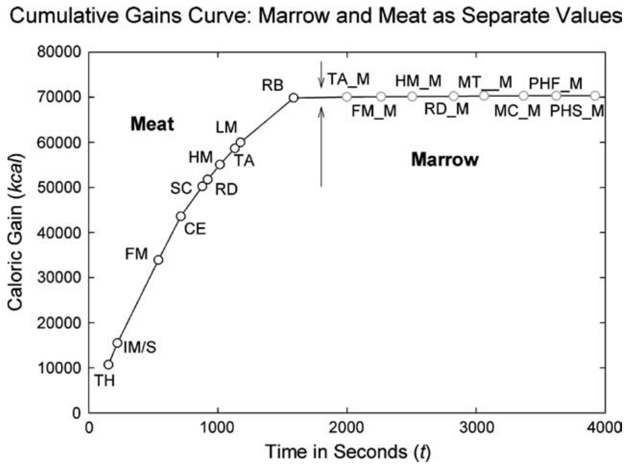

Fig. 5. Caloric gains from deer processing, holding marrow and steak values separate. The arrow marks the point at which further carcass processing will incur a loss in caloric return rate. This occurs between the lowest ranked steak element and the highest ranked marrow element. Data are from Madrigal and Holt [40:748].

2.2. Encounter rates and x-intercepts

The Madrigal and Holt data set can also be used to calculate x-intercepts for different butchering intensities. The x-intercept can be thought of as the anticipated travel time between patches, which are equivalent to kill events in an ungulate prey as patch model, such that $1/\lambda$ is the anticipated kill rate per unit time. Since the kill rate is a function of the conditional probability of kill upon encounter and the encounter rate, the value of the x-intercept provides a feel for predicted kill rates reflected by butchery intensity. The x-intercepts are calculated by taking the rate of gain between any two neighboring points on the curve as the slope of the tangent line connecting them, which approximates the derivative:

$$\frac{\mathrm{d}g}{\mathrm{d}t} \approx \frac{(g_x - g_{x-1})}{(t_x - t_{x-1})} = \frac{\Delta g}{\Delta t}$$

where g_x is the gain in calories of the xth ranked element and t_x is the cumulative time associated with the xth ranked element. This treats the elements of the carcass as if they were simultaneously encountered items and predicts that processing effort should work its way up the curve until the return of the next item is below the average return rate. Using the average of two adjacent points in this manner is equivalent to calculating the return rate (e.g., kcal/s), which is also a measure of the instantaneous rate of gain. We present the calculation in this way to emphasize that the rate of gain approximates the slope of the tangent line to the curve [15]. The slope of the tangent line can be used to calculate the x-intercept for each point on the curve and the values at these intercepts should indicate something about the anticipated kill rates with vertebrate prey (Table 1). Importantly, the x-intercept is a quantitative estimate of R, representing the link to estimating kill rate based on patch residence time.

The calculated time between patches may deviate from actual kill rates for a number of reasons. For example, the calculated kill rate for the processing of a white-tailed deer to the point of extracting marrow from the first phalanx is a calculated kill rate of about 928 h which equates to 38 days without controlling for the number of hours actually spent foraging (Table 1). If several foragers each acquired carcasses at this rate and all shared with a group, this might not be unreasonable as an approximate average. A lone hunter with no other food income could obviously not sustain themselves with a kill rate so low. The caloric return rate shaping the optimal patch residence time decision is influenced by inputs from gathered foods and a variety of game sources so we might expect the calculated *x*-intercept to overestimate the actual kill rates. However, the dietary importance of fat should prevent the processing of animal carcasses in a low-intensity manner when time between acquisition increases because other foods (such as plants) are not likely to fulfill the nutritional role of fat and possibly of protein depending on the foods available. We might expect that the estimated kill rate is the closest approximation of actual kill rates among groups specialized in the hunting of a narrow range of game animals. The butchery of extremely large animals (such as mammoths or whales) might take on very different functions because butchery itself would likely require several persons and extremely large transport units may introduce a number of unique constraints.

The model derives an exact (quantified) kill rate that for archaeological purposes is probably best used for relativistic comparisons between strata and/or assemblages, as required by the low-resolution nature of most archaeological assemblages. Additionally, we acknowledge that the calculated *x*-intercepts may be influenced by a number of confounding variables, some of which may not be recognizable archaeologically. However, challenges of equifinality are in many respects inherent to the discipline and not unique limitations of this model per se. At the least, the *x*-intercepts provide a baseline for assessing relative change in archaeological assemblages and could be used for fairly exact quantitative applications in an ethnoarchaeological context.

While the experimental data and calculations are useful, they are not applicable to archaeological analysis of human decision-making without demonstrating that foragers recognize the relationship between the gains function and mean foraging return rate. Ethnoarchaeological research provides some support.

2.3. "Good times and bad times": ethnoarchaeological evidence for marginal butchery

Ethnoarchaeological studies demonstrate that carcass-processing time is a function of mean foraging return rate. Observations from these studies suggest that the fracturing of long bones and low-yield marrow-bearing elements are the primary indicators of lengthy patch residence times. Stories from Nunamiut elders [5] and ethnoarchaeological observations among the Ngatatjara [23] provide anecdotal support for the model and a case study with the Aka [22] provides quantitative support.

Nunamiut marrow extraction can be used to characterize behavioral responses to two general subsistence states, "good times" and "bad times". Both conditions are qualitatively defined as functions of overall return rate. In good times, encounter rates with high-ranked resources are high and patch-residency times are low. In "bad times", decreases in the rate of successful kills upon encounter cause declines in mean foraging returns, which in turn cause an increase in processing time per carcass (Fig. 2). Shifts between "good" and "bad" times occur seasonally but longer-term trends may occur as well. When conditions shift from "good" to "bad", the MVT predicts that foragers should intensify their per carcass-processing intensity given the increase in between-patch travel time due to the decreasing slope of the mean foraging return rate [17].

Interviews with Nunamiut informants demonstrate that foraging conditions shift from "bad" to "good" times within the lifetime of an individual hunter such that low-yield elements that were processed in the past are completely ignored by the younger generation [5]. For instance, younger hunters have no recollection of processing phalanges for marrow and many of them do not even recognize the phalanx as a marrow-bearing element [5]. The "old timers", on the other hand, recall processing phalanges at times when encounters with caribou were especially low. It may be the case that the younger generations of Nunamiut have not known "bad times" of this sort. An overall shift to "good times" was likely due to decreases in search and handling time resulting from the adoption of metal tools, shotguns, and snow mobiles in addition to novel food sources [5]. As noted by Binford [5:32], "suggestions from informants that phalanges were processed in the past during times of food scarcity are provocative, in that the degree to which phalanges are processed for marrow may be used as a measure of the subsistence security enjoyed by a group at the time of observation". This implies that the processing of low-ranked carcass elements is indeed a recognizable archaeological signature of a response to resource depression measured as periods of lower return rates.

Gould [23] observed that the Ngatatjara of arid northern Australia are accustomed to encounter rates so low that negative caloric return rates will be accrued in order to obtain fat. In Gould's study, only 26 of 200 hunts resulted in the capture of large game. Unlike the Nunamiut, who will often ignore caribou in poor nutritional condition, the Ngatatjara seemed not to practice any prey selectivity, taking every large animal encountered [23]. As expected, the Aborigines invested large amounts of time in each patch (carcass), processing bones so thoroughly that very few fragments could be identified to skeletal element [23]. Every scrap of marrow was consumed including small morsels in crevices of the interior of long bone shafts. Even teeth were broken open for small quantities of nutrient [23]. Soft bones were eaten and small fragments of cortical bone were sometimes ingested with the meat [23]. A hypothetical average gains line for this situation is depicted as line b in Fig. 4. As the Ngatatjara process elements that lie on the asymptote of the diminishing returns function, the *x*-intercept of the average gains line is essentially infinite.

In this sense, the Ngatatjara seem to process every animal carcass as if they might never encounter another. Gould employs these observations in the interpretation of bone fragmentation patterns at two early Holocene caves in the area exhibiting similar levels of processing. The archaeological record of these practices would not be very informative in regard to diet-breadth because so few of the remaining bones can be identified to species. However, if viewed from a patch-residency perspective, the extremely long per carcass-processing times would indicate limited prey availability as well as an extremely fat-limited diet. Furthermore, such extreme processing efforts cannot be explained by calorie maximization alone since the marginal returns on a gains curve accounting for such processing intensity would eventually become negative (Fig. 4, line b).

A recent study conducted among the Aka foragers of the African Congo provides an ideal situation in which to investigate the relationship between variance in mean foraging return rate and processing intensity between two foraging groups in similar ecological and cultural contexts [22]. Fancher and colleagues' results offer quantitative support for modeling butchery intensity as a behavioral response to variation in encounter rates with high-ranked prey [22]. In their study, two Aka villages (Grima and Ndele) occupied non-overlapping hunting ranges with similar prey species compositions. During the study time, 22 days for Grima and 20 for Ndele, each group experienced different encounter rates with their highest ranked prey items. Grima foragers obtained 5 blue duiker (*Cephalophus* spp.) and 1 medium duiker while the Ndele foragers obtained 131 blue duiker and 10 medium duiker [22]. Results of faunal analysis indicate that neither cut mark frequency nor number of impacts on bone differed between the two groups ($x^2 = 0.024$, $p > 0.05$), however, the relative percentage of elements fractured was much higher among the group from Grima who successfully acquired high-ranked resources less often, though not statistically significant at the $\alpha = 0.05$ level ($x^2 = 3.427$, $p > 0.05$). This difference increased further, becoming statistically significant rather than just nearly so, for limb bones only (75% fractured for Grima, 48% for Ndele, $x^2 = 5.297, p < 0.05$). The increased frequency of limb bone fracturing due to decreases in encounter rate with major prey items represents an archaeologically visible response to lower return rates. It also demonstrates that this relationship can apply to relatively small game such as duiker (typical adult live weigh less than 14 kg). While the differences in butchery process between the two groups do not indicate a stop element, they do demonstrate that response in patch residence time is variable with respect to encounter rate and visible in the differential processing of long bones. This example with the Aka cannot be used to quantify kill rates because duiker are too different from white-tailed deer to use the same data set on returns per element, but more importantly, data are not available to directly link the percentage of long bones fractured to different patch residence times.

3. Discussion

The three ethnoarchaeological cases presented above demonstrate that in contemporary human foraging groups a consistent relationship exists between the mean foraging return rate and the degree of carcass-processing intensity, as predicted by the prey as patch model. Moreover, such behavior has archaeologically recognizable correlates. The MVT can be applied to any such scenario when the criteria for optimization are met and the prey are not wholly consumed at every encounter (kill). These observations also support the notion that within-bone nutrients are more limiting to foragers than calories gained from meat. Because this relationship is evident among three very different faunas and habitat types (Arctic circle, African Congo, and arid Australia), the prey as patch model has the potential to be broadly applicable. This model offers a direct contribution to existing applications of foraging theory in archaeology in the sense that it provides a means of investigating post-acquisition behaviors reflecting the mean foraging return rate, R, a largely untapped source of information from the perspective of optimal foraging theory. The prey as patch model can also be easily integrated with prey-choice analyses for a more inclusive examination of foraging behaviors, and extends foraging theory *within* assemblages to the specific characteristics of the constituent prey.

Quantitative ethnoarchaeological studies of carcass use and butchery practices that can be used to establish marginal gains curves are rare in the literature, although the data that are available demonstrate that gain functions describe decelerating, marginal returns. These functions demonstrate that butchery decisions affect patch residence time and suggest implications for kill rates of similar-sized prey. The Aka and Nunamiut examples demonstrate that variation in carcass-processing intensity can be linked to changes in kill rate, suggesting that this variation reflects behavioral responses to resource fluctuation [14,45]. Furthermore, the proposed generality of this approach is supported by the fact that these groups are culturally and environmentally independent, yet meet the predictions of the prey as patch model with respect to a single prey species. Most importantly, archaeologically visible butchery practices including the intensive extraction of within-bone macronutrients suggest extremely low encounter rates with high-ranked resources and possible periods of nutrient stress for local hunter–gatherer groups.

In general, the prey as patch relationship may be recognized in two ways. As with the Nunamiut, carcass-processing tends to follow a stepwise function from "best" to "worst" element (in terms of net gain) with the lowest quality element processed reflecting the degree to which times were "bad". In archaeological assemblages, this stop element approach should be especially useful in circumstances where the perspective is large in scale (e.g., macroecological) and seeks general directional trends, spatial and/or temporal, in terms of the location of the stop element on the gains curve. For example, a monotonic pattern through time toward stop elements of lesser value may be indicative of a selective gradient toward extractive technologies such as boiling for grease or the construction of weirs and nets to improve foraging efficiency [41]. Second, the overall degree of butchery induced long bone fragmentation may also reflect responses to resource depression or stochastic variation in prey availability as shown with the Aka processing of Duiker bone [22]. The specific contexts of either response to resource fluctuation are worth further exploration, as there may be an economic basis to situations where changes in the stop element are more or less likely to occur than more intense bone fracturing across the carcass. The stop element approach may be more applicable to larger bodied prey where inter-element variance in marrow gain is larger and the cost of extraction is more pronounced. The patch–gains curves constructed above reflect only stop element butchery explicitly, although functions could be developed for a range of processing strategies, once the data become available. In general, the latter approach of increasing overall processing intensity (as seen with the Aka) is likely the more common of the two processing responses. In the absence of a specific gain function the model can still be applied heuristically to such cases but the paucity of data currently prevent the quantification of kill rates based on processing intensity in cases like the Aka. The Aka study quantifies patch residence time through the percentage of long bones fractured. Archaeologists have also made inferences akin to patch residence time based on breakage frequencies and fragment length [45,50]. Notably, experimental work on bone grease extraction from boiled fragments suggests that smaller fragments do not necessarily increase grease yields from boiled bone [19]. In terms of a patch–gains function, this implies an asymptote in minimum fragment size, probably associated with maximizing bone-breakage surface area, beyond which more intensive fracturing for smaller pieces fails to yield additional gain.

Archaeological samples are often spatially restricted relative to the actual episodes of behavior contributing to the materials represented [48]. If the excavated materials were from a camp site, several species of prey could remain in the sediments outside the excavation unit, causing an under representation of the diet-breadth. Species-level identification is often difficult when analyzing highly fragmented faunal remains, and for this reason skeletal portions are often sorted according to body size class [9]. Within a range of body sizes the post-acquisition handling of prey items does not require a spatially complete sample since the relative processing effort can be observed from the skeletal elements of just a few prey patches. Thus, an additional value of the prey as patch model is that inferring change in the processing of assemblages reflecting R are not contingent on being able to achieve species-level identification in the assemblage.

4. Limitations to the model

Statements regarding the utility of this model need to be tempered with an appropriate consideration for its limitations. The prey as patch model is most informative in cases where there is recognizable variation along the gains curve in different patches of equivalent prey types through time and/or space. If processing intensity is constant across all sampled patches, the prey as patch model would suggest no effective difference in the set of constraints behind the decision of how long to remain in a patch. In such cases it would not be possible to discern "good times" from "bad times", simply "stable times". Of course, identifying stability in foraging behavior over any length of time or space would be very interesting as the consistency (and intensity) of the patch residence time would suggest important features of prey density, encounter rates, and the possible stability of predator–prey population dynamics. However, long periods of stability in foraging behavior are probably rare in the archaeological record, at least at a fine-grained level, due to the constant stochastic fluctuations of most naturally occurring biological populations.

As such, the applicability of the prey as patch model is limited in cases where all possible energy is extracted from all acquired carcasses through intensive processing and boiling. However, we suggest that such cases, where the intensity remains constant, are not common. Furthermore, if such a case were found, it would still be informative of a perpetual limitation or exceptionally high demand for the resource. For example, because central-place foraging inevitably leads to resource depression of some sort [17], low-mobility or sedentary groups might be more likely to adopt an always-intensive strategy of butchery. However, Potter's [50] analysis of the fauna from the Pueblo IV site of Pueblo Colorado in central New Mexico found an increase in the fragmentation of ungulate long bones and the processing of phalanges and calcanei through time. The relative proportions of lagomorphs also increased. Thus, Potter found a widening of diet-breadth and an increase in patch residence time that both seemed to occur as responses to resource depression. Moreover, Potter was able to link the lack of such trends in a nearby site to trading for bison meat with Plains societies. Thus, cases where intensive processing prevents the recognition of movement on the patch gain function may be fairly rare, as even sedentary groups that boil bone exhibit variability in processing intensity. It should also be noted that qualitative predictions consistent with the prey as patch model have been formed to identify differences between elite and commoner households in middle range societies [31,51], where residents essentially have higher *R* values or feasting lowers optimal residence times.

Also, the MVT assumes that processing time is exclusive of travel time [29,55]. If the two activities do not compete with one another, the costs of carcass transport and for increased processing intensity may be underestimated. For instance, processing may be carried out in the evening or at times when hunting is not an option, potentially resulting in exaggerated estimates of patch residence time (Kim Hill, personal communication, 2003). This is a problem for fine-grained assemblages where a group of individuals not foraging because of a rainstorm might crack phalanges for snacks or out of boredom potentially leaving an assemblage that was heavily processed. Although this scenario is still linked to a decrease in *R* because no one was foraging during the rainstorm, causing a necessary decline in *R*, the increased processing could be misinterpreted as a decline in herbivore density (or resource availability). One way to avoid this dilemma archaeologically is to seek a large scale perspective rather than relying on ethnographic or fine-scale reconstructions of behavior. Examining macroecological patterns can average out fine-scale problems of variation [10]. Linking models designed for instantaneous decision-making to diachronic change at archaeological time scales is always a challenge but one that can be overcome as demonstrated by several recent studies [2,12,26,27,45,56,57,60].

An additional limitation of our approach is the implicit assumption that two cases of experimental butchery (one caribou and one white-tailed deer) can be generalized across most vertebrate prey patches. In one respect the consistency of the vertebrate bauplan allows for such generalization, however, more data on handling effort, especially if linked to actual kill rates and dietary contributions of non-vertebrate resources, would be highly valuable. In the absence of additional data for patch gain functions addressing other prey types, the current model has heuristic value and augments numerous previous approaches that have qualitatively or implicitly suggested that processing intensity may be linked to declines in prey density [5,45,50]. However, since the MVT assumes that either patches are homogenous or a unique function exists for each type, it follows that a number of factors could influence the nature of the gain function.

Archaeological analysis of butchery or foraging is always challenging. This is especially evident given the complexity of variables conditioning the patterns that become the basis for our inferences. All residues of such patterns are the result of numerous processes, only some of which may be cultural [26,62]. We do not wish to make light of such challenges but feel that taphonomy, equifinality, and complexity do not preclude the extraction of meaningful behavioral information if questions are formed at scales appropriate to the data. This model does not solve the zooarchaeological challenge of inferring behavior from fractured assemblages but provides a way to utilize the elegance of optimality modeling for the attribute-based investigation of the prey themselves. Many zooarchaeological issues are confronted when attempting to infer processing intensity in archaeological contexts, but we suggest that the MVT is less sensitive to certain issues of time and space averaging than the diet-breadth model. Additionally, this paper presents a specific application of the MVT applied to data gathered on one ungulate game species but the implications of the approach are intended to be read in general terms and are applicable to any resource that diminishes with use or consumption (see [14,32,43]). Many of the issues of quantification confronted in deriving the kill rate based on patch occupancy time could be refined through ethnoarchaeological observation. However, the application of optimal foraging theory to archaeological cases, in general, may also require more complicated models, perhaps analogous to the approach used by Charnov and Parker [18], that preserve the generality of optimality but gradually add case-specific variables of increasing detail.

5. Conclusion

Ethnoarchaeological case studies demonstrate that foragers alter patch residence time as a function of encounter rate as predicted by the prey as patch model and that these foraging decisions are consistent across widely varying environmental conditions. In many settings it may be appropriate to combine the prey-choice and the patch-residence time models to investigate how background changes in return rate influence both the range of patches (prey) acquired and the manner in which they are handled. In spite of the limitations acknowledged above, a few initial conclusions can be hazarded: (1) the structure of vertebrate resources conform to a diminishing marginal returns curve (as suggested by [14,43]). Human foragers exhibit variability in processing intensity along this gain function and this variation is at least in part a function of the mean foraging return rate; (2) fat limitation is an important variable in human forager optimization studies and appears especially relevant for variation in processing intensity; and (3) the prey as patch model can be a tool for understanding long-term behavioral responses to mean foraging return rate. More ethnoarchaeological data sets, such as that generated by Madrigal and Holt, would be extremely useful to archaeological analyses of butchering decisions, by generating data from additional types of prey. Further studies might include times and returns for grease extraction and explore other variations in the butchery process.

Hill et al. [29] and Stephens and Krebs [55] discuss the importance of developing general models in a piecemeal fashion, making modifications to improve explanatory power for specific cases while preserving the advantages of the model's generality. The complexity of inferring past foraging decisions from archaeological samples will require such piecemeal modifications. While these modifications may limit the model to particular contexts based on our ability to recognize change in complex data sets or in poorly preserved samples, these same modifications may highlight contingencies specific to similar foraging conditions. By accommodating different sets of confounding variables in the modeling process we can improve our understanding of the most salient features of foraging decisions and the conditions that shaped them. The prey as patch model described here can play a valuable role in the building of a piecemeal approach, by providing an additional perspective for seeking relevant currencies, constraints, and behavioral trends in the archaeological record.

Acknowledgments

The ideas presented in this paper originated during a course in evolutionary ecology taught by Eric Charnov at the University of New Mexico, which all three authors attended. We are grateful to Dr. Charnov's help and encouragement. Many improvements were made due to thoughtful commentary from James Boone, Bruce Huckell, David J. Rapson, Robert Leonard, Sheridan Potter, and C. Mark Nicholson. Charles Egeland offered especially useful critiques. Kim Hill provided valuable insight from his experience with the Ache. We are grateful for the use of unpublished material from Washington State University's Aka research in the Central African Republic. We acknowledge the following funding sources: OB – Binford Fellowship (UNM) and an NSF Fellowship in Ecological Complexity; MJH – Binford Fellowship and a Hibben Foundation Senior Fellowship (UNM); RSW – Binford Fellowship and an NSF Graduate Fellowship.

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