

Evolutionary Foraging Models in Zooarchaeological Analysis: Recent Applications and Future Challenges

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Abstract The last few decades have witnessed a rapid rise in the use of foraging models derived from behavioral ecology to explain and predict temporal and spatial differences in faunal assemblages. Although these models build on conventional ideas about utility firmly embedded in zooarchaeological analyses, when cast in an evolutionary framework these ideas produce some of the most sophisticated and elegant interpretations of archaeofaunas to date. In this article I review the methodological and practical strengths and weaknesses of current zooarchaeological applications of foraging models. Recent applications of foraging models to the zooarchaeological record reveal important variability in human-prey interactions across time and space. Case-specific applications generate theoretical and methodological advances that augment and are complementary to model building in allied fields. Recent applications also identify shortcomings in the underlying assumptions and rationale of some foraging models that mirror past and on-going discussions in anthropology and biology. I discuss how these shortcomings can fruitfully direct future applications and research in foraging economics.

Keywords Zooarchaeology · Foraging models · Behavioral ecology

Introduction

The last three decades have witnessed a rapid increase in the use of foraging models and rationale grounded in Neodarwinian theory to interpret zooarchaeological assemblages (e.g., Bayham 1979, 1982; Broughton 1994a; Butler 2000; Cannon 2000; Byers and Broughton 2004; Lupo 1998, 2006; McGuire and Hildebrandt 2005; Munro 2004; Nagaoka 2002a; Stiner et al. 2000; Szuter and Bayham 1989;

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Ugan 2005a). The use of foraging economics in zooarchaeology has generated a number of very sophisticated models to explain and predict patterning in archaeofaunal assemblages on several different analytical scales from specimen to regional levels. The results of some analyses identify important changes in foraging efficiency and have wide-ranging implications for a number of prehistoric and contemporary issues. Overexploitation of prey accompanied by declining foraging efficiency and resource intensification, for example, is often identified as one of a constellation of conditions associated with the rise of social, political, and technological complexity among hunter-gatherers (e.g., Cohen 1979; Hildebrandt and Jones 1992; Sassaman 2004) and experimentation with domesticatable resources (Munro 2004). Resource stress, marked by overexploitation, is widely viewed as a catalyst for declining health and fertility, increased interpersonal violence, and major changes in life history (e.g., Broughton and O'Connell 1999; Yesner 1994). Although quite controversial, the identification of prey overexploitation by prehistoric hunters has implications for human and prey interactions (Barnosky et al. 2004; Fiedel and Haynes 2004; Grayson and Meltzer 2003, 2004), contemporary wildlife conservation efforts, and the retention of indigenous hunting rights among contemporary foraging populations (e.g., Stearman 1994).

The use of foraging models derived from human behavioral ecology to interpret zooarchaeological assemblages is not surprising. Animal bones are often recovered in archaeological contexts and can provide one tangible, though not unambiguous, reflection of human dietary choice. The use of foraging theory is, in many ways, an outgrowth of preexisting rationales embedded in zooarchaeological analysis. The focus on quantitative measurements in optimality models such as costs and benefits builds on long-standing principles of food value and utility that guide traditional zooarchaeological analyses (e.g., Binford 1978; White 1952, 1953, 1954). Nearly two decades ago, Grayson (1988, 1989; Grayson and Cannon 1999, pp. 142–143) noted the close parallels between the rationale underlying Binford's (1978) utility analysis and foraging economics. In discussing the popularity and value of utility curves, for example, Grayson (1988, p. 123) noted: "These curves assume that people optimally forage across the body of an animal, as some believe people optimally foraged across larger landscapes."

While a variety of models explain prehistoric changes in subsistence and behavior using logic derived from foraging theory (e.g., Beck et al. 2002; Surovell 2000; Zeanah 2004), my focus is on recent applications that directly address the interpretation of zooarchaeological assemblages.

My purposes in this review are threefold. First, to explain and understand why human behavior varies, we need to know something about the full range of behavioral variation. The zooarchaeological record is eminently designed to provide information about variability in human foraging behavior across time and space, and it potentially records behavior not recapitulated in contemporary or historic populations.

Second, case-specific examples in zooarchaeology are complementary to developments in foraging theory led by biologists and anthropologists and can enhance current methods in human behavior ecology (also see Grayson and Delpech 1998, p. 1128). Foraging models were originally developed in biology and

anthropology and applied to the archaeological record. However, a number of recent zooarchaeological analyses have already identified and implemented important theoretical modifications that can direct future model building in allied disciplines (e.g., Burger et al. 2005; Metcalfe and Barlow 1992). A number of analyses use rigorous methodologies for testing among causal agents and particular hypotheses that can be more widely applied to other aspects of the archaeological record.

Finally, despite the overall success of these applications, a growing number of analyses highlight shortcomings in some of the assumptions underlying classic foraging models. Several analyses point to the lack of agreement between predictions derived from specific models and the archaeological evidence, while others question the standards used to evaluate resource profitability (e.g., Egeland and Byerly 2005; Lupo and Schmitt 2005; Stiner et al. 2000). The recognition of these shortcomings should come as no surprise to analysts; classic foraging models were designed to be simple and have few assumptions for widespread applicability to nonhuman foragers. Many of the current controversies involving applications of foraging models in zooarchaeology mirror past and on-going discussions in biology and anthropology (e.g., Kacelnik and Krebs 1997; Ydenberg 1998; Ydenberg and Hurd 1998; Ydenberg et al. 1992). My intention is to draw attention to concepts and processes that are still poorly or incompletely understood. Recognition of these shortcomings does not diminish the value of foraging models but provides important avenues of future research.

Because most zooarchaeological applications of foraging theory use extended rationales or predictions derived from the specific models, I begin this review by briefly discussing the use of human behavioral ecology and the underlying rationale of the classic foraging models most often used in zooarchaeological analysis. Recent developments in risk theory and social foraging have applications to the archaeological record (e.g., Caraco et al. 1980; Kacelnick and Bateson 1996; Winterhalder 1986; especially Winterhalder et al. 1999) but thus far have not been applied directly to archaeofaunal analysis (but see Pinson 1990). I then discuss current difficulties linking foraging theory to the common units of analysis used in zooarchaeology. This is followed by a discussion of current applications of foraging models used to explain and predict patterning of different characteristics of archaeofaunal assemblages. Although these two uses are not necessarily mutually exclusive, I partition current applications into one of these two frameworks solely as an organizing device. I conclude by summarizing potential future areas of analyses that can strengthen the use of foraging economics in zooarchaeological analysis.

Human behavioral ecology and foraging models

Human behavioral ecology is a style of evolutionary thought that examines how environmental and ecological factors influence variability in human behavior (e.g., Cronk 1991; Kelly 1995, 2000; Smith and Winterhalder 1992; Smith et al. 2001; Winterhalder and Smith 2000). This line of reasoning builds on concepts from evolutionary ecology, which examines the interaction between evolutionary forces and ecological variables by focusing on behavior (Broughton and O'Connell 1999;

Winterhalder and Smith 2000). Application of human behavioral ecology to contemporary and prehistoric human populations began some three decades ago (Chagnon and Irons 1979; Cronk et al. 2000; Winterhalder and Smith 1981). One of the most prominent and active research themes has been and continues to be the analysis of foraging behavior (e.g., Bliege Bird and Bird 1997; Hawkes and O'Connell 1981, 1985; Hawkes et al. 1982; Hames and Vickers 1982; Hill and Hawkes 1983; Smith 1991; Winterhalder 1981; Yesner 1981), but a number of recent applications of human behavioral ecology focus on a wide range of questions about life histories, parental investment, cooperation, and reproduction patterns (e.g., Alvard and Gillespie 2004; Bock 2005; Borgerhoff Mulder 2000; Hill and Hurtado 1996; Mace and Eardley 2004; Marlowe 2004, 2005; Smith 2004; Voland 1998; Walker et al. 2002).

The basic premise of behavioral ecology is that organisms are designed by natural selection to optimize lifetime reproductive success and are capable of rapid adaptive shifts in behavior to contemporary environmental conditions, which can be broadly defined to include ecological, social, and political dimensions (e.g., Bliege Bird and Smith 2005; Giraldeau and Caraco 2000). Within behavioral ecology, foraging models or foraging economics consist of a set of models that purport to explain different aspects of an organism's foraging behavior such as what to eat and where to forage (prey and patch choice models), when to leave a patch (patch choice and marginal value theorem), how far to transport resources and when and where to process a resource (central-place foraging models) (see Stephens and Krebs 1986). Under certain circumstances, some of these questions, such as what to eat and where to forage, are interrelated and analysts often make use of several models to explore different dimensions of a foraging strategy.

An important feature of behavioral ecology is the use of quantitative tools such as optimization models to evaluate different strategies available to an organism (Emlen 1966; MacArthur 1972; MacArthur and Pianka 1966; also see Stephens and Krebs 1986). An optimization model is a quantitative tool used to assess the costs and benefits of different foraging strategies that defines (1) the range of available choices, (2) the currency used to evaluate those choices, (3) the presumed goal(s) of the organism, and (4) the constraints that limit the payoffs of different choices (Krebs and Davies 1997; Smith 1983; Stephens and Krebs 1986). Two important and interrelated concepts underlie optimization analysis: the idea of trade-offs and the principle of lost opportunities. Trade-offs are the consequences to reproductive fitness resulting from pursuing one strategy over another (Smith 1991, p. 35). The basic premise is that organisms unconsciously make trade-offs between strategies by comparing potential gains from exploiting a particular resource against the lost opportunity to do better by pursuing an alternate resource (Stephens and Krebs 1986, p. 11).

Currency refers to the units used to measure the costs and benefits of different decisions aimed at fulfilling the forager's goal. The general assumption is that foragers maximize a goal function that is indirectly linked to reproductive fitness (Stephens and Krebs 1986). Thus, the currency used to assess the proficiency of different strategies depends on the foragers proximate goal and is assumed to be a good proxy measure of reproductive fitness (but see Salant et al. 1995; Ydenberg

1998). Many simple and complex currencies can be used to assess the productivity of different resources, but rate maximization (as reflected by gross or net acquisition rates) and efficiency are the most common general currencies used in analyses (Table 1). Constraints include intrinsic and extrinsic factors that may limit the payoff derived from a strategy. Intrinsic constraints are those particular to the organism such as physiological limitations (i.e., gullet size, rate of digestion), nutritional requirements, and cognitive abilities (Dukas 1998). Extrinsic constraints are those placed on the organism by the environment such as encounter rates with prey, daily or seasonal variation in resource availability and distributions, predator defense mechanisms of prey, and other ecological circumstances. Importantly, deviations between the predictions derived from any model and the observed patterns invite a reconsideration of currency, goal, and constraints.

Prey choice or diet breadth model

Probably the most widely used of all the foraging models is the prey choice or diet breadth model. The prey choice model assumes that a forager searches for all prey simultaneously and encounters them randomly and sequentially within the environment (the fine-grained environment assumption). Foraging time is partitioned into two mutually exclusive categories: search and handling (Fig. 1). Because search is assumed to be randomized, the time devoted to searching for a resource is generalized across all of the resources. Handling time includes the time spent pursuing, processing, and consuming the prey after it has been encountered. Foragers rank resources on a single scale of profitability, usually kcals (kilocalories) obtained per unit of handling time (i.e., postencounter return rate). The basic assumption is that foragers attempt to maximize the long-term net rate of energy acquisition by adding resources into their diet in rank order from highest to lowest until the return rate per unit of time is maximized (e.g., MacArthur and Pianka 1966; Pullam 1974; Smith 1983). Three predictions follow from the prey choice model: (1) Foragers should always pursue high-ranked resources whenever they are encountered. (2) The inclusion of lower-ranked resources in the diet depends on the chance of encountering higher-ranked resources; lower-ranked resources are added into the diet as a function of the abundance of high-ranked resources and not as a function of their own abundances. (3) Resources are added to and deleted from the

Table 1 Examples of different common currencies used in optimality models (after Smith 1979)

Currency	Description
Efficiency (F) ^a	Ratio of energy (measured in kcal) acquired (E_a) to energy expended (E_c), such that $F = (E_a/E_c)$
Gross acquisition rate (R_g)	Ratio of energy captured (E_a) per unit of handling time (T_a), such that $R_g = (E_a/T_a)$
Net acquisition rate (R_n)	Ratio of net energy, energy acquired less energy expended ($E_a - E_c$) per unit of handling time (T_a), such that $R_n = (E_a - E_c)/T_a$

^a Smith (1979, p. 61) calls this specific currency output/input efficiency. Here I follow Ydenberg's (1998) definition and designate this currency as efficiency

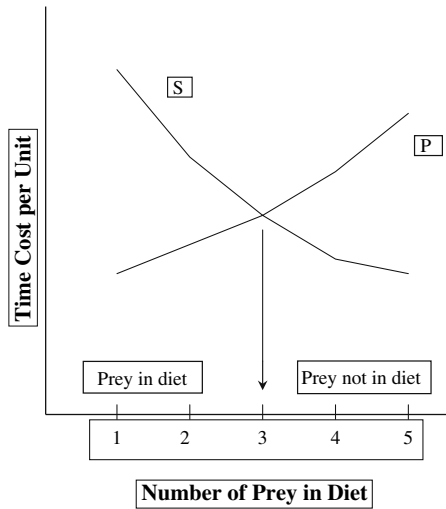


Fig. 1 The diet breadth model after MacArthur and Pianka (1966) showing the two costs curves: search (S) and handling (P). The point at which the two cost curves intersect (here shown with an arrow) defines the optimal diet. Resources right of the arrow are out of the diet and those to the left are in the diet. Changes in where the two costs curves intersect changes the diet breadth. If, for example, search costs increase, the S curve will shift upward and increase the breadth of the diet

diet in rank order. A number of recent modifications to the classic prey choice model continue to expand and improve applications to accommodate circumstances that violate the assumptions of the original model, such as simultaneous prey encounters (e.g., Berc 2000; Kacelnik and Krebs 1997; Pyke 1984; Schmidt 1998; also see Stephens and Krebs 1986).

The prey choice model generally predicts overall resource selection for combined samples of adult foragers in several well-known ethnographic contexts (e.g., Hames and Vickers 1982; Hawkes and O'Connell 1981, 1985; Hawkes et al. 1982; Hill and Hawkes 1983; Hill et al. 1987; Smith 1991). Some of the earliest anthropological applications of the prey choice model present data supporting some of the model's predictions. Hill and Hawkes (1983) present data showing that some low-ranking prey (monkeys and small birds) drop out of the diet when Ache hunters use shotguns, which raise overall foraging returns, rather than the bow and arrow. Winterhalder's (1981) analysis of hunting as practiced by the Cree in Ontario shows how the advent of high-velocity motorized search technology in recent times (snowmobiles and motorized boats) lowers the search costs of high-ranking prey and narrows the diet.

Yet some of the most rigorous studies suggest significant modifications to the prey choice model. Hill et al. (1987), for example, present data showing that resource selection among contemporary foragers does not always appear to maximize energetic gain (also see Bird and Bliege Bird 1997; Hames 1989). Hill et al. (1987, pp. 11-12) found that Ache men could reap larger energetic rewards from exploiting palm (2,630 kcal/h) than by hunting (1,340 kcal/h). They attribute Ache men's preference for hunting to differences between meat and carbohydrates

in the macronutritional content (also see Hill 1988). Meat, and especially animal fat, may be highly valued because those products contain important amino acids, vitamins, and lipids not found in carbohydrates. They also suggest that possible nonconsumptive benefits such as access to more mates or better treatment of children associated with meat sharing might also shape resource choice. Hawkes (1990, 1991; Hawkes et al. 1991) identifies potential nonconsumptive goals such as social, political, or reproductive advantages gained by sharing meat a highly valued resource among Hadza big-game hunters. In a recent review, Smith (2004) outlines qualitative and quantitative evidence from five different ethnographic cases suggesting that hunting prey that are high risk, costly, or inefficient relative to other resources can signal specific qualities and confer a variety of nonconsumptive benefits such as enhanced reproductive success, social or political status, and increased economic advantages (e.g., Bliege Bird and Smith 2005; Smith 2004; Smith and Bliege Bird 2000; Sosis 2000; Weissner 2002).

A second modification, suggested by Hill et al. (1987), closely parallels the findings in biology that state and context influence human foraging strategies (e.g., Bateson et al. 2003; Houston 1997; Houston and McNamara 1999). Resource choice often varies as a function of the sex, age, composition of the task group, and other factors (e.g., Bird and Bliege Bird 1997; Hurtado et al. 1985; Jochim 1988; Lupo and Schmitt 2002, 2005; Sosis 2000; Weissner 2002). Women foraging with their offspring, for example, target resources that are easily handled by children or that can be efficiently taken in tandem (Hawkes et al. 1995). Children foraging by themselves focus on low-ranking but easily handled resources because physical constraints limit their ability to efficiently collect and process some foods (Bird and Bliege Bird 2000). These modifications, and others, do not invalidate the use of predictive value of the prey choice model but clearly show a higher degree of complexity underlies human resource choice than once imagined.

Patch choice model

The assumption of a fine-grained environment is not universally applicable to all types of prey taken by human hunters. Some resources occur in patches, clumps, or cluster in specific microhabitats. Ethnographic studies show that human hunters often choose to exploit specific microhabitats for particular prey and arm themselves with the most appropriate hunting technology in anticipation of encountering those resources. Whenever resources are distributed in patches, foragers face the problem of deciding which set of patches to include in their foraging regime. The patch choice model was developed to predict which patches a forager will exploit (MacArthur and Pianka 1966). As discussed by Smith (1991, p. 249), resource patches can be defined as “spatially bounded entities characterized by the set of prey (of one or more types) contained within it and by the predictable (expected) return rate curve or gain function.” However, patches do not need to be so strictly defined and can refer to any entity with a predictable gain function. Thus, a patch can be an individual prey item, a foraging strategy (i.e., hunting or gathering), or a specific habitat type or a type of hunt, which can be defined by habitat, technology,

and/or prey type. Smith (1991), for example, made use of the patch choice model by dividing Inujjuamiut resources into hunt and habitat types and evaluating their productivity at different temporal scales (seasonal vs. monthly).

Some of the same assumptions underlying the prey choice model apply to the patch choice model. Travel (called search in the prey choice model) and handling time are partitioned into two cost curves; resource patches are encountered randomly and sequentially in the environment and are ranked on single scale of profitability (the expected return rate). The model assumes that foragers evaluate the average return rate from different patches (including the travel time) and add patches into the diet in rank order until the average foraging returns per unit (including travel time) declines.

When used in concert with the marginal-value theorem (MVT), the patch choice model can be used to predict when a forager should leave a patch for another in circumstances where the foraging process gradually depletes the patch (Charnov 1976; Charnov et al. 1976). This depletion scenario is probably very common for a variety of resources, but not all (Fig. 2; for alternate depletion scenarios see Smith 1991, p. 252; Stephens and Krebs 1986, p. 26). The MVT makes the following assumptions: Resource patches have a gain function that negatively accelerates as a function of patch time (Stephens and Krebs 1986, p. 26), foraging time in the patch is limited, and resource regeneration time is high. The optimal time to leave the patch is when the marginal capture rate (defined as the instantaneous capture rate at the end of a foraging period within the patch) is equal to the overall mean capture rate (including travel times between patches) for all resource patches in the habitat.

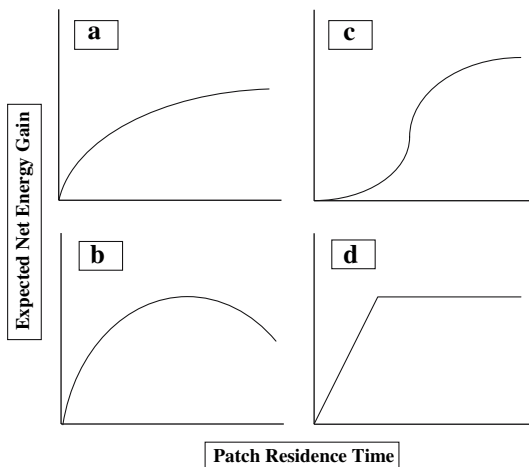


Fig. 2 Examples of different hypothetical gain functions (after Stephens and Krebs 1986, pp. 25–26). (a) An exponential gain function that increases asymptotically to some maximum value and generally describes within-patch gains. (b) A humped gain function that shows net gains as the patch becomes depleted. In this case eventually as more time is spent in the patch, more energy is spent searching for prey than can be gained from the patch. (c) A sigmoid gain function that defines circumstances where mobile resources are able to avoid a predator but are eventually discovered in clusters. (d) An example of a gain function that depletes but does not show patch depression

Several predictions follow from the model: (1) A forager should leave the patch when it is depleted to the point where foraging in another patch will yield higher returns per unit of time (including travel costs). (2) Because the optimal time allocation in any patch is a function of the average yields for all patches in the habitat, as the overall productivity of the habitat increases, less time should be spent in any one patch and conversely. (3) With changes in travel costs, the lower the travel costs between patches the less time should be spent in any one patch and conversely. (4) Any patch not in the utilized set will not be added unless it can yield a marginal rate of return equal to or greater than the average rate for all utilized sets.

As pointed out by Smith (1991), the use of the patch choice model and MVT is most appropriate for answering questions about time allocation. The use of this model requires that the analyst know something about the gain functions and availability of other resource patches in the habitat (also see Sosis 2002). It is possible, for example, that the return rate from some other patch(es) may increase and alter the utilization of a patch originally exploited by a forager, even though the profitability of that patch remains unchanged. This important requirement makes the patch choice model difficult to test in anthropological and archaeological contexts because the researcher may not know all patches or their gain functions. Furthermore, not all patches deplete in exactly the same manner, and some may be nondepleting (Fig. 2; see Smith 1991).

Ethnographic applications of the patch choice model show that hunters often allocate more time to the most profitable patches but do not necessarily forage exclusively in the most highly profitable patches because of variability in returns as a function of seasonal and daily fluctuations, as well as individuals goals (e.g., Hames 1989; O'Connell and Hawkes 1984; Smith 1991; Sosis 2002). The patch choice model has been especially useful for explaining apparent cases of conservation among aboriginal hunter-gatherers, such as patch switching, when game becomes depleted in localized areas (e.g., Dwyer 1982). Studies show that when return rates from patches close to a permanent settlement become depleted, hunters venture to more productive patches that are further away (Alvard 1993, 1994; Hames 1987, 1991; Vickers 1988), resulting in epiphenomenal conservation. Alvard (1993, 1994), for example, found that Piro hunters in Peru focused on hunting areas more distant from residential bases where returns were higher but still opportunistically exploited prey encountered as they passed through depleted zones in close proximity to their village. In this particular case, patch switching cannot be viewed as intentional conservation and is more consistent with behavior anticipated by the patch choice model (Smith and Wishnie 2000).

Central place foraging models

Central place foraging (CPF) is an umbrella term that refers to several different models that examine the behavior of nonhuman foragers who transport resources to a central place to consume and/or provision offspring (Orians and Pearson 1979; Schoener 1979; Stephens and Krebs 1986), store (Elliott 1988) or engage in other activities (Guerra and Ades 2002). CPF models were originally developed by Schoener (1979) and Orians and Pearson (1979) to model resource choice for

predators transporting prey to consume or provision. CPF models consider how the costs of transporting a resource influences resource choice, load size, distances between foraging patches, the placement of central places, and the degree to which prey are processed (Kaspari 1991). Cumulatively, applications of CPF models show that at greater distances from central places, organisms become more selective by transporting loads/prey that are larger sized (Cuthill and Kacelnik 1990; Elliott 1988; Fryxell et al. 1991; Jackson 2001; Stephens and Krebs 1986, pp. 187-194) and/or have a higher nutritional value (Sodhi 1992).

In an anthropological context, CPF rationale has been applied to the selective transport of different large-prey skeletal parts (e.g., O'Connell et al. 1988, 1990). Based on observations of contemporary East African Hadza big-game hunters, O'Connell et al. (1988, 1990) found that (1) the number of transported bones decreased with increasing distances between kill to residential sites; (2) carcasses were often field processed by filleting meat from high-value parts such as upper limbs, and the stripped bone was discarded in the field; and (3) there was a high degree of taxonomic variation in transport decisions even among prey that were similar in body size. They argue that skeletal transport decisions are based on the trade-offs between the costs and benefits of field processing and transporting different parts with the overall goal of maximizing the amount of nutrients returned to camp within a limited time frame (e.g., Metcalfe and Barlow 1992). They suggest that parts with high processing costs and a large amount of edible nutrients relative to part weight have a higher probability of being field processed and discarded than parts with low field processing costs and low ratios of edible to tissue to part weight (O'Connell et al. 1990).

A formal model proposed by Metcalfe and Barlow (1992) builds on the classic CPF theory developed by Orians and Pearson (1979). This model assesses how human foragers trade off the time spent field processing a resource against the costs of transporting an unprocessed load of that resource with the goal of maximizing the rate at which nutrients are returned to a central location. Key elements in their model include the time it takes to process a load and increases in load utility and decreases in transport costs resulting from field processing. They propose an inverse relationship between improvements in load utility and the minimum distance at which it becomes efficient to process a load. Processing that realizes a large gain in load utility will decrease the maximum distances from central locations at which field processing becomes efficient and conversely. The model further assumes that processing resources at central places has no costs or that the costs are incurred by someone other than the person who transported the load. This assumption may be warranted because some (but not all) food processing at residential camps can often be conducted in tandem with other activities such as child care or can take place at night when foraging is not possible. In these cases, food processing at base camps may have few, if any, opportunity costs. Metcalfe and Barlow (1992) demonstrate the usefulness of this model for understanding the field processing and transport decisions of simple, sessile resources that consist of high- and low-value components such as nuts and shellfish (see also Bird and Bliege Bird 1997). For some simple resources, field processing can increase load utility because low-value parts with no consumptive value are discarded and more useful products can be transported in fewer trips.

The model requires modification when applied to more complex resources, such as animal carcasses, that are composed of several different products with different caloric and nutritional values and that require sequenced processing to exploit (i.e., meat must be removed before bone marrow can be extracted). Unlike some renewable resources found in patches, carcasses are nonrenewable and time-limited and must be consumed and/or transported or stored within a relatively short time frame. For most (but not all) carcasses, forager processing and transport decisions are made within the context of each discrete event and are usually not linked to anticipated future repeated visits to the resource. Further modification to the model is required if field processing can result in the discard of edible product (see Lupo 2006). Even if the meat and marrow are removed from a body part, stripped bone may still retain grease, remnant marrow, and bits of adhering meat that will be unrealized if the bone is discarded at field locations without further processing. Under these circumstances, any potential increase in load utility resulting from culling low-value inedible bone can be greatly devalued if large amounts high-value remnant edible product are discarded (for a solution see Lupo 2006).

Using ethnographic transport data derived from contemporary Meriam Islanders on the Torres Strait, Bird and Bliege Bird (1997) demonstrate the value of this model for predicting the maximum terminal foraging distance (MTFD) for processing shellfish loads. The Meriam processed shellfish in such a way as to maximize the rate that edible flesh is delivered to a central place. Shellfish species that are difficult to field process and that will not significantly increase the proportion of edible flesh transported if they are processed are transported whole and generally collected from areas in close proximity to camps. Those that are easily field processed and increase the proportions of transported edible flesh when processed are taken at greater distances from camps and are processed at field acquisition locations. Thomas (2002) uses a similar approach to evaluate shellfish processing among the Western Kiribati in Micronesia.

Jones and Madsen (1989) propose another model that assumes a resource load will not be transported beyond the maximum transport distance (MTD) or the point where the energetic expenditure for carrying the load exceeds its caloric value (but see Hitchcock and Houston 1993; Ydenberg 1998, pp. 348–349, 355). This approach is best used to rank the relative transport distances of resources from their place of procurement, rather than to calculate absolute MTD (Madsen et al. 2000), because transport costs are difficult to measure accurately and can vary as a function of terrain, grade, body mass, mass of burden, shape of package, ambient temperature, and ontogenic factors (see Brannan 1992; Burstein et al. 1996; Heglund et al. 1995; Knapik et al. 1996; Kramer 2004; Legg and Mahanty 1984; Maloiy et al. 1986; Mudambo et al. 1997; Rhode 1990; Spinney 1995).

Zooarchaeological quantification units and foraging theory

One central difficulty of applying foraging theory to archaeofaunal analysis concerns how zooarchaeological quantification units are linked to the currencies used in the models. As discussed by Grayson and Delpéch (1998), the units used to

quantify zooarchaeological remains are not the same as those used to test optimality models in biological or ethnographic contexts. Furthermore, the questions about behavior addressed by some of the models are not the same as those often asked of the archaeological record (i.e., patch time allocation). Archaeological and ethnoarchaeological research identify several significant issues surrounding the application of foraging models to zooarchaeological analysis concerning (1) how prey is ranked, (2) how standard zooarchaeological quantification units correlate with proxy measures of rank, and (3) what dimensions of diet breadth zooarchaeological units actually reflect.

Resource rank in zooarchaeological analysis

Few zooarchaeological analyses rely on actual return rates derived from experimental, historical, or ethnographic sources (e.g., Egeland and Byerly 2005; Lupo 1998; Madrigal and Holt 2002; Raab 1992). The problems with ethnographically and experimentally generated return rates are discussed elsewhere (see Bettinger 1991, 1993; Bettinger and Baumhoff 1982, 1983; Broughton and Grayson 1993; Grayson and Cannon 1999; Simms 1987; Zeanah and Simms 1999) and are only summarized here. One of the main problems is that the current range of published return rates are derived from a limited number of sources (e.g., Hawkes et al. 1982; Hill and Hawkes 1983; Kelly 1995; Lindström 1996; Lupo 1998, 2006; Lupo and Schmitt 1997b, 2002, 2005; Raymond and Sobel 1990; Simms 1987; Smith 1991; Winterhalder 1981). Even as these sources grow, the range of variation reflected in these data may not sufficiently represent the past.

Replicative experiments with aboriginal technologies can fill the gaps left by ethnographic and historical sources (e.g., Egeland and Byerly 2005; Madrigal and Holt 2002; Madsen and Kirkman 1988; Madsen and Schmitt 1998; Simms 1987), but modern experiments generated by novices can significantly misrepresent the potential gains from specific resources (Bettinger 1991, 1993; Bettinger and Baumhoff 1983; Grayson and Cannon 1999). Because return rates vary as a function of acquisition technology and context (see Bettinger and Baumhoff 1983), analysts may be unaware of all potential acquisition contexts and technologies available to prehistoric populations (Bettinger 1991) and are limited to those circumstances described in the ethnographic and historic records.

Recent archaeological investigations further question the ordering of resources based on energetic returns (e.g., Perry 2004; Wohlgemuth 2004). Wohlgemuth (2004), for example, found incongruencies between the frequencies of low- and high-ranked plant resources at Pie Creek Shelter, Nevada, given the assumption that resources are added into the diet in rank order based on postencounter return rates. Deviations between resource rank and the order in which it is incorporated into the diet were originally discussed by Simms (1987) in his seminal application of the diet breadth model. Using ethnographic, historic, and experimental data, Simms (1987) calculated return rates for common plant and animal resources exploited by ethnographic populations in the Great Basin to evaluate questions about when certain resources should enter the diet. He found that some small prey and plant seeds exploited in the ethnographic record are not predicted by the optimal diet. He

accounted for this discrepancy by the failure of the model to adequately account for the storage value of seeds. The storage value of many resources may make them more valuable than might be anticipated solely by their energetic return rate (see Hitchcock and Houston 1993), including some specific prey or body parts (e.g., Speth 1983). Animals that seasonally store large quantities of body fat for hibernation could be preferentially ranked higher than other similarly sized prey that do not store large quantities of body fat (e.g., Speth 1983; Speth and Spielmann 1983). Foraging human populations may selectively process fat-rich bones even though the caloric returns from bone grease are quite low when compared to other resources. Bone grease, albeit time intensive to exploit and with low yield, is composed largely of fat, which is nutritionally important to human populations (e.g., Lupo 2006; Lupo and Schmitt 1997b; Saint-Germain 1997; Speth 1983). More importantly, some types of animal fats are highly storable and, when combined with other resources, can provide a crucial food source in times of scarcity.

Proxy measures of rank and prey body size

One solution to the problems generated by the use of return rates is to rely on proxy measures of resource rank. Zooarchaeologists often make use of the strong generalization from the existing data, which show a positive relationship between prey body size and return rate (see Hawkes et al. 1982; Simms 1987). A corollary idea is that prey of similar body size and overall anatomical proportions have similar relative ranks and may be considered as a group (e.g., Grayson and Cannon 1999; Simms 1987; but see Jones 2004; Smith 1983). Groups of larger-sized prey such as artiodactyls are ranked higher than those of smaller size such as rabbits and hares. This assumption allows zooarchaeologists to make use of fragmentary remains that can be identified only to genera or size class and quantify aggregate specimen counts with indices of prey abundance based on body size or prey type (i.e., large mammals, small mammals, aquatic animals, etc.). Empirical ethnographic and experimental studies show that when animals are acquired individually, larger prey are usually ranked higher than smaller animals (e.g., Hawkes et al. 1982; Kelly 1995; Simms 1987; Winterhalder 1981). There are, however, important exceptions to this generalization. Extremely large-bodied prey such as whales or some pinnipeds often have excessive handling costs that depress their rank relative to overall body size (e.g., Byers and Ugan 2005; Jones 2004; Smith 1991). Mass collecting dense patches of some small and low-ranked prey can be more profitable than might be predicted based solely on body size (Madsen and Kirkman 1988; Madsen and Schmitt 1998; Schmitt et al. 2004).

Recognition that prey profitability varies as a function of circumstances of capture and hunting technology has led some to suggest modifications to current prey ranking systems (Grayson and Cannon 1999, p. 150; Jones 2004, 2006). Grayson and Cannon (1999) suggest that prey that can be acquired by mass-collecting technology should be considered separately from animals that are individually acquired. Using collated data from a variety of sources, Ugan (2005a) argues that the increase in return rates from mass collecting are significant only for smaller fish and insects. He argues that there is no substantial increase in return rate

from mass collecting smaller terrestrial prey such as small mammals and birds over the individual acquisition of these same resources. In fact, for some (but probably not all) smaller mammals, encounter hunting of single animals provides a higher return rate than mass collecting (also see Lupo and Schmitt 2005).

Ugan suggests that low returns from mass collecting small mammals and birds result primarily from the higher processing costs of these prey in comparison to insects and small fish, which have low processing costs. These results challenge the problem of ranking prey by body size raised by mass-collecting technology; they do not completely vindicate the technique. Although Ugan admirably assembles all available data, the current database is small and does not cover a wide range of ecological and cultural contexts. Ethnographic and ethnoarchaeological studies of hunters using mass collecting show that while individual returns from mass collecting can be lower than those that can be achieved by encounter hunting, other foraging benefits not solely measurable in energy often accrue to the participants (Lupo and Schmitt 2002, 2004). These additional benefits can take the form of increased encounters with other types of resources and potential social benefits associated with mass collecting (see Lupo and Schmitt 2002, 2004, 2005; Noss, 1995). Furthermore, the lack of correlation between prey rank and body size remains a problem for some larger prey with excessive handling costs (see Jones 2004; Smith 1991).

As discussed by Lyman (2003), ranking prey by body size is also problematic for highly sexually dimorphic species such as some pinniped species, in which males can be more than twice as large as females. Ranking these prey by body size can create dubious distinctions in prey value and obscure important differences in predatory defense mechanisms that may change the costs of pursuing different animals. This potential problem is not necessarily fatal, however, and can be easily controlled by the analyst's awareness of the range of species, including the degree of sexual dimorphism and predator avoidance behavior, within a specific assemblage.

Stiner (2001; Stiner and Munro 2002; Stiner et al. 1999, 2000; see also Munro 2004) found that measures of faunal diversity based on Linnean divisions or body size are not sensitive enough to show subsistence changes that were known to have occurred in the Paleolithic record of Europe and Eurasia. Standard taxonomic measures and abundance indices do not show an expansion of the diet supported by other classes of material evidence such as botanical remains, the frequency of milling stones, storage facilities, and human skeletal evidence (Richards et al. 2001). Stiner argues that the differences in the costs of capture may be more significant in the ranking of smaller prey and that these differences will not be reflected in rankings based on body size. By focusing on locomotor habits, predator defense mechanisms, and resilience to predation of the smaller-sized faunal component, she demonstrates a shift from slow-moving and sessile resources such as tortoises and shellfish during the Middle Paleolithic to a greater reliance on fast-moving but small prey (i.e., rabbits and birds) in the Upper Paleolithic. She argues that prey ranking schemes should consider physiologic and behavioral characteristics that limit a hunter's access to prey (also see Lyman 2003). A consideration of these characteristics is likely to be most useful and potentially provide a greater degree of resolution for ranking prey that are similar in body size.

Units of measurement and diet

A variety of complex and simple measurements are used to monitor changes in zooarchaeological assemblages, such as abundance indices (AIs) and measures of taxonomic diversity (Table 2). Abundance indices combine groups of taxa into a single measurement usually based on body size. Diversity measurements have a long history of use in archaeological analyses (see Grayson 1984, 1991) and are often measured in zooarchaeological assemblages by Σ TAXA and evenness. Σ TAXA (the number of different taxa in an assemblage) is often used to characterize assemblage richness. Evenness reflects the distribution of bone specimens among different taxonomic categories and can be measured by several different indices (see Jones 2004). Regardless of which measurement is used, most zooarchaeological applications assume a positive relationship between archaeological abundances and the encounter rate with high-ranking prey on the landscape (but see Simms 1987, p. 24; Waguespack and Surovell 2003, p. 337). Higher encounter rates with high-ranked prey result in increased abundances of those animal remains in zooarchaeological assemblages (but see Waguespack and Surovell 2003, p. 337).

Obviously, any assumption about the meaning of archaeological abundances must be very carefully evaluated. Well-known issues arising from the use of zooarchaeological data in general, such as preservational bias, taphonomic history, sample size, excavation techniques, analyst methodology, and space and time compression, can significantly and selectively impact faunal abundances and the resulting interpretation (e.g., Cannon 1999, 2001; Cruz-Uribe 1988; Grayson 1984; Grayson et al. 2001; Schmitt and Lupu 1995, 2005). Analysts need to carefully evaluate the differential impact of these potential biases before making inferences, but even in the face of careful analysis, zooarchaeologists are beginning to explore what dimensions of the diet these units actually measure (e.g., Broughton and Grayson 1993; Jones 2004; Lupu and Schmitt 2005; Ugan and Bright 2001).

Σ TAXA is believed to be a gross measure of expansion of the faunal component of diet breadth (i.e., broader diet = more taxa). The assumption is that decreases in the encounter rate with high-ranking prey can result in a broader or more diverse diet, but as several analysts have shown, this is not always true (see Grayson and Cannon 1999, p. 149; Stiner 2001; Stiner et al. 2000). Given the aggregated nature of the archaeological record and possible effects of time compression and variability in human foraging strategies, Σ TAXA likely reflects the maximum range rather than

Table 2 Examples of some common simple and complex indexes used to monitor dietary changes in zooarchaeological assemblages

Index	Derivation
Abundance Index (AI)	$\Sigma i / (\Sigma I + \Sigma j \dots)$, where i and j are the taxonomic categories of comparison
Richness	Σ TAXA or the number of taxa in the assemblage
Evenness ^a	$1 / \Sigma p_i^2$ where p_i represents the proportion of individuals in the total site aggregate that fall in species I

^a Evenness is represented here by the reciprocal of Simpson's index; other indices are possible

an average diet breadth for a prehistoric population (also see Broughton and Grayson 1993; Grayson and Delpech 1998).

Evenness is often assumed to reflect decreased encounter rates with high-ranked prey as the diet expands. As discussed by Jones (2004, p. 308), because low-ranked resources are added into the diet as a function of the encounter rate with high-ranking prey, the total numbers of low-ranking resources will not reflect the encounter rate of those resources. She found that evenness values vary as a function of the encounter rate with high-ranking prey, the total number of prey items in the diet, and the degree to which high-ranking prey are similar in return rate. The latter two factors can be controlled by complementing the use of evenness with other analyses (such as richness) and examining the kinds of prey in the diet. Using ethnographic data on Inujuamiut hunting collected by Smith (1991), she found that evenness values tracked encounter rates with high-ranking prey but noted the potential problems with using evenness in archaeological assemblages arising from mass collection and the presence of multiple high-ranking prey. When two (or more) high-ranking resources with similar return and encounter rates are exploited, evenness values will increase if archaeologists treat them as different prey types even if the encounter rates with the highest-ranked prey do not change (also see Kimball 2004, for the effects of multiple high-ranking prey on evenness).

Explanatory frameworks in zooarchaeology

A large number of analysts view different characteristics of archaeofaunal assemblages as reflecting changes in foraging efficiency resulting from anthropogenic or natural processes (e.g., Broughton 1994a, b, 1997, 1999, 2002; Butler 2000, 2001; Byers and Broughton 2004; Byers et al. 2005; Grayson 1991, 2001; Grayson et al. 2001; Munro 2004; Wolverson 2005). Increases or decreases in foraging efficiency can be linked to many different anthropogenic and natural phenomena. Anthropogenic phenomenon can include changes in technology that alter the costs of searching for and/or handling prey (e.g., Hawkes and O’Connell 1992; Hill and Hawkes 1983; Winterhalder 1981), changes in how populations organize themselves on the landscape (e.g., Binford 1980), and changes in the value of nonconsumptive benefits derived from pursuing high-ranked prey (e.g., Hildebrandt and McGuire 2003). Modifications to local habitats such as environmental degradation due to agricultural activities can attract some types of small mammals (e.g., Quirt-Booth and Cruz-Urube 1997) and depress the abundances of others (e.g., Peacock et al. 2004; Redford and Robinson 1987; also see Stahl 1996). Intentional burning of vegetation serves many different functions, including possibly increasing the encounter rates with some types of prey. Recent ethnographic research among the Martu aborigines in western Australia shows that intentional burning of vegetation has the short-term benefit of increasing the efficiency of women’s hunting of small prey in some habitats (Bird et al. 2005). The long-term benefits to the hunting efficiency of large prey are not clear, but anecdotal evidence suggests that larger game might be attracted to new growth (e.g., Bird et al. 2005; Bowman 1998). As detailed by Stahl (1996, pp. 114–115), the systematic effects of habitat

degradation from agricultural practices, deforestation, and intentional fire setting can create new habitats and destroy old ones. They are not always detrimental to wildlife and can actually improve habitats for some herbivores.

Probably the most widely recognized anthropogenic influence on prey encounter rates is exploitation depression resulting from overhunting (e.g., Broughton 1994a, b, 1997, 1999; Butler 2000; Kay 1994; Smith and Wishnie 2000). Overhunting has particularly strong and predictable implications for changes in human foraging efficiency because the prey choice model predicts that foragers will target high-ranking prey and pursue them whenever these animals are encountered (Grayson 2001; Penn 2003; Winterhalder and Lu 1997). Consequently, overhunting should preferentially influence encounter rates with high-ranking prey. Prey overhunting is documented by a number of contemporary ethnographic, historical, and wildlife conservation sources, and there is good reason to believe this process also operated in some places and times in the past (e.g., Alvard 1993, 1994, 1995; Aswani 1998; Hames 1987; Jerzolimski and Peres 2003; Kay 1994; Laliberte and Ripple 2003; Penn 2003; Simenstad et al. 1978; Steadman 1995; Vickers 1994).

In contemporary contexts, the degree to which harvesting pressure is manifested by declining abundances of particular species depends on a number of factors related to human populations; most significant among these are the population density and the age of the settlement (Redford and Robinson 1987; Vickers 1988). Physiologic aspects of the prey and threat type also influence susceptibility to harvesting pressure (Cowlshaw et al. 2005; Isaac and Cowlshaw 2004). Larger-bodied prey generally reproduce more slowly and are found in lower densities on the landscape than smaller prey and thus are less likely to rebound from hunting pressure (Mittermeier 1987; Vickers 1991; Winterhalder and Lu 1997). Citing several different studies, Mannino and Thomas (2002, p. 456) note that the resilience of different shellfish species to overexploitation depends, in part, on species habitat, geographic distribution, and life history characteristics (also see Pimm 1991). Although the role of human hunters in animal extinctions on a continental scale is controversial (e.g., Barnosky et al. 2004; Grayson and Meltzer 2002, 2003, 2004; Haynes 2002; Haynes and Eisele 1999; Martin 1967, 1984, 1990), there are recent and historical examples from island habitats where overhunting likely played an important contributory role in the extinction of a species (e.g., Anderson 2002; Burney et al. 2003; Duncan et al. 2002; Kirch 1996; Steadman 1995; see especially Grayson 2001).

Even so, studies also show that hunting does not always lead to exploitation depression and can be sustained under a variety of conditions, especially when population densities are low, settlements dispersed, and traditional hunting technologies prevail (see Hill et al. 1997, 2003; Leach and Davidson 2001; Mannino and Thomas 2002; Penn 2003, p. 278; Vickers 1988, 1991). Winterhalder and Lu (1997) model how adding a species to the diet or prey switching could temporarily allow high-ranking prey to rebound after being depleted. Importantly, they demonstrate that “a resource species’ vulnerability to a predator sometimes will depend on the suite of resources that are harvested along with it” (Winterhalder and Lu 1997, p. 1363). Butler and Campbell (2004) recently found no evidence of resource depression in their analysis of 63 archaeological sites spanning

10,000 years from the Northwest Pacific Coast and the northern Columbia Plateau despite evidence of sustained hunting, increasing population densities, and the development of complex hunter-gatherer social organization in coastal areas (also see Etnier 2002; Lyman 2003).

Natural phenomena can include processes that temporarily influence prey encounter rates and those that can change the absolute abundances of different prey. Behavioral depression can result when prey seasonally change their spatial location or avoid areas in response to predation (Charnov et al. 1976). Microhabitat depression occurs when prey relocate to another area to avoid predation. These changes do not result in an absolute decline in prey abundances and may only temporarily change the encounter rates with prey. Changes in the absolute abundances of prey or exploitation depression from overhunting also can be associated with nonhuman predators, especially the introduction of new predatory species by humans or via migration and colonization (e.g., Grayson 2001; Johnson and Wroe 2003). Less well recognized are changes in the density of nonhuman predators, which also can have a systematic effect of ecological communities (Mannino and Thomas 2002; Simenstad et al. 1978). Geological phenomena such as earthquakes, tsunamis, and volcanic activity can change prey (and human) population densities and distributions (e.g., Losey 2005; also see Stahl 1996), as can disease (e.g., Gifford-Gonzalez 1998; Macphee and Marx 1997). Probably the most widely recognized natural influences on prey encounter rates are climatic changes that can diminish or expand favorable habitats or conditions (Byers and Broughton 2004; Byers et al. 2005; Grayson 2006; Grayson and Delpech 1998, 2005; Grayson et al. 2001; Lupo and Schmitt 1997a; Schmitt and Lupo 2005; Schmitt et al. 2004; Ugan 2005b; Wolverton 2005).

Clearly, both anthropogenic and natural phenomena can simultaneously influence prey abundances and distributions and assessing the relative importance of either of these factors can be difficult (see Butler and Campbell 2004; Leach and Davidson 2001; Ugan 2005b). The dynamic link between dietary change and resources availability is quite complex. Resource depression, for example, can result from complex interactions among a variety of anthropogenic and natural phenomena (see Stahl 1996). The reduction in one species, regardless of the cause, can have a cascading effect on larger ecological communities and the availability of many other resources (e.g., Simenstad et al. 1978).

Anthropogenic exploitation depression models

Probably the most widely used and elaborately developed zooarchaeological applications of foraging theory identify declining foraging efficiency resulting in resource intensification associated with anthropogenic exploitation. Resource intensification refers to the process whereby total productivity per unit of land is increased, but at increasing costs to the individual resulting in a decline in foraging efficiency. The definition of resource intensification has multiple meanings in current anthropological literature. As noted by Butler and Campbell (2004, p. 336), intensification as used in models of resource depression refers to decreases in

foraging efficiency “wherein the total productivity of a unit of land is increased but individuals work harder (spend more energy, per unit time) in the process.”

In most archaeological analyses, resource depression refers to decreases in the absolute abundance of prey from aboriginal overhunting resulting from increases in local human population densities (in situ growth or packing) (e.g., Broughton 1994a, b, 1997, 1999; Butler 2000, 2001; Grayson 1991, 2001; Nagaoka 2002a, b; Stiner et al. 2000). In general, foragers are predicted to pursue high-ranking prey within a patch whenever it is encountered. As the local abundance of high-ranking prey becomes depleted, foragers may respond to declining foraging efficiency in several different ways depending on their circumstances. Central place foragers can travel to distant resource patches (or buffer zones) to acquire high-ranking prey but will incur additional costs by traveling to and transporting prey from distant patches to residential camps. Mobile foragers may move their residential camp closer to distant patches but will incur relocation costs (see Grayson and Cannon 1999; Kelly 1995) or may meet resistance and/or competition from entrenched neighboring groups (see Hickerson 1965; Martin and Szuter 1999; but see Lyman and Wolverton 2002). As high-ranking resources decrease in abundance, foragers may respond by incorporating lower-ranking but locally available prey (or patches) into the diet, increasing the number of patches used and/or intensifying how prey (or patches) are exploited (Broughton 1994a, b, 1997, 1999; Cannon 2000; Nagaoka 2001, 2002a, b).

However, and as pointed out by Grayson and Cannon (1999, p. 148; see also Butler and Campbell 2004, p. 338), declining abundances of high-ranking prey in concert with increasing abundances of low-ranking prey is not unequivocal evidence of exploitation depression. A similar pattern might be expected if smaller and lower-ranking prey use increases and the encounter rate and use of larger prey remains the same or increases at a slower pace than the use of smaller animals (Grayson and Cannon 1999). The advent of mass-collecting technology can increase the abundance of certain small prey relative to larger prey without changes in the encounter rate with high-ranking prey. Larger human population sizes also could result in a per capita decline in large prey but not change the absolute abundance of high-ranking prey (Broughton 1994a, b; Butler and Campbell 2004).

Models of resource depression have strong appeal because they often combine rationale from several different foraging models and rely on multiple (albeit intersecting) classes of faunal evidence and levels of analysis. The use of multiple threads of foraging rationale to link different lines of archaeofaunal evidence is nowhere more well developed than in the analysis of the Emeryville Shellmound in California (Broughton 1994a, b, 1997, 1999, 2002). This single case study of a site spanning from 2620 to 720 B.P. stands as the model for subsequent studies in exploitation depression and comprises a large piece of evidence used to infer localized resource depression in the Sacramento Valley, California. This study and a number of subsequent analyses rely on abundance indices that combine similarly sized or types of prey. Where appropriate, analysts partition and analyze prey resources by habitat, hunt type, or patch (i.e., coastal vs. inland, upland vs. valley). This allows analysts to control for the patchy distribution of prey within different habitats and maintain the fine-grained search assumption that underlies the prey

choice model (Broughton 1997). Independent evidence of resource intensification and harvesting pressure is crucial to support the inference of overhunting (see Grayson and Cannon 1999, p. 146). As outlined by Broughton (1999, 2002), several different lines of zooarchaeological evidence can be used to further support an inference of resource depression, including mortality profiles, taphonomic damage, and skeletal part profiles.

Changes in prey mortality profiles are one line of evidence often used to infer harvesting pressure. Differences in animal physiology, behavior, and spatial characteristics influence how harvest pressure is manifested, thus the evidence for overexploitation tends to be prey-specific. For example, Broughton (2002) summarizes evidence for terrestrial and aquatic resources that can be used to support inferences of resource depression, and Mannino and Thomas (2002) review evidence that might indicate the overexploitation of shellfish. Harvesting pressure can be manifested in animals not susceptible to behavioral depression and characterized by discrete breeding areas by a decrease in the mean and maximum ages of exploited specimens (Broughton 2002). Harvesting pressure can decrease the mean and maximum ages of exploited specimens because (1) larger and older individuals that have a higher return than smaller and younger individuals will be preferentially targeted by hunters; (2) as mortality increases, even if it is unbiased, intraspecific competition will decrease and increase the recruitment of juvenile specimens; and (3) increased mortality leads to a decreased probability of surviving into adulthood as the average lifespan decreases (Broughton 2002). For species that grow throughout their lifetime, such as shellfish, reptiles, and fish, size is correlated with age, so evidence of harvesting pressure can be manifested by a decrease in overall prey size. As the frequency of preferred larger individuals declines, smaller individuals are targeted. Archaeological evidence of harvesting pressure has been documented in fish through decreasing sizes of dentary width (Broughton 1997, 2002; Butler 2001), the humeral shaft diameter of tortoises (Stiner et al. 2000), and size of molluscan shell (e.g., Anderson 1981; Botkin 1980; Stiner et al. 2000; also see Thomas 2002).

Decreasing mean age at capture also can reflect harvesting pressure on some gregarious herd animals with restricted growth, such as gazelles. As discussed by Munro (2004), hunters should target adult gazelles with the greatest body weight and highest percentage of body fat to lean meat compared with younger animals. Mortality profiles dominated by prime age adult animals indicate low harvesting pressure, but as adult mortality increases, the population falls below carrying capacity, reducing intraspecific competition and the population undergoes growth. High proportions of juvenile animals are expected in a population undergoing growth because of the high turnover. Munro (2004) documents an increase in juvenile gazelle remains based on tooth wear and eruption sequences and the abundance of unfused elements during the Natufian period from several sites in the Levant, in concert with other evidence of resource depression and intensification.

In other species, hunting pressure may be manifested by an increase in the mean age of exploited specimens. This is particularly true of species that are sensitive to predation and form discrete breeding areas, such as some pinnipeds, or animals that seasonally form spatially and sexually segregated herds, such as deer (Broughton

2002; but see Lyman 2003). Localized breeding areas or rookeries containing females and vulnerable offspring can represent a huge bounty for human hunters, but they can very quickly lead to behavioral/microhabitat depression as these species respond to predation. Hildebrandt and Jones (1992; Jones and Hildebrandt 1995; Jones et al. 2004; Porcasi et al. 2000; but see Colten and Arnold 1998; Lyman 1995, 2003) argue that predation on mainland rookeries of migrating populations of seal and sea lion along the Oregon and California coasts resulted in these species shifting to offshore rocks and islands and a decline in the abundance of these populations. Evidence from Middle Holocene archaeological sites containing females and pups indicate the existence of and predation on mainland rookeries for some migratory species such as the northern fur seal (*Callorhinus ursinus*) in central and northern California (Burton et al. 2001, 2002; Burton and Koch 1999; Porcasi et al. 2000; also see Etnier 2002). Isotope composition of these skeletal remains shows that the pups were not weaned when they were dispatched and the adults and subadults were consuming local fish, further indicating that these were resident and not migrating populations. However, Lyman (2003) argues that the predatory defense behavior of some otariids such as California (*Zalophus californianus*) and Steller (*Eumetopias jubatus*) sea lions could lead to higher levels of predation on adult males at rookery locations. California and Stellar sea lions practice resource defense polygyny, whereby the males establish and protect a breeding territory and often fail to abandon the territory even when threatened by predators. Data from Seal Rock in Oregon, a near offshore rookery, shows evidence of 600 years of human predation, and the assemblages are dominated by adult males. Lyman (2003) asserts that selective hunting of adult males would not depress local populations and would result in epiphenomenal conservation (*sensu* Hunn 1982).

Several analyses of exploitation depression and intensification draw on additional evidence representing resource intensification in the form of cutmark frequencies and bone fragmentation patterns (e.g., Broughton 1999; Munro and Bar-Oz 2005; Potter 1995). The underlying assumption is based on logic derived from the patch choice model, which suggests that as overall foraging efficiency declines, foragers should spend more time in a patch and/or processing a prey item, and cutmark and bone fragmentation frequencies (and patterns) are assumed to be proxy measures of increased processing effort (also see Burger et al. 2005). This assumption parallels an argument originally advanced by Binford (1978, 1984, 1988), who also asserted that cutmark frequencies should reflect butchering intensity and that marrow removal from specific low-yielding skeletal parts such as the mandible, metapodials, and phalanges represents an index of resource stress. Another purported index of animal resource intensification is specific bone fragmentation patterns that are believed to reflect evidence of processing bones for grease, a time-intensive yet low-yielding activity (Binford 1978; Lupo and Schmitt 1997b; Saint-Germain 1997).

Finally, a number of analyses of exploitation depression use rationale derived from central place foraging theory to explain changes in the patterning of skeletal part representation. As foragers use resource patches farther from their residential base, they are expected to show greater selectivity in transport decisions (see Speth 1991; Speth and Scott 1989). Greater selectivity should be manifested in spending more time field processing prey at kill sites and transporting fewer but more highly

valued skeletal parts of larger prey to residential locations (see Broughton 1999; Cannon 2003; Nagaoka 2005).

Some of the best applications of models of resource depression make use of some or all of the different lines of evidence discussed above. Demonstration of multiple supporting lines of evidence is crucial for supporting exploitation depression as the causal agent of change in foraging efficiency, because, taken individually, some evidentiary sources can be ambiguous. For example, harvesting pressure in ever-growing species can be potentially confounded by the effects of climatic change, which has a well-known influence on the body size of different animals (e.g., Ashton et al. 2000; Lyman 2004). Size diminution in some ever-growing prey can be attributable to small-scale environmental shifts that might be difficult to detect in the archaeological record. As discussed by Mannino and Thomas (2002), the size of some molluscan species can reflect a short-term natural phenomenon such as poor recruitment and high mortality of older individuals, which can change the age structure available to predators. Leach and Davidson (2001) note that age structure in fish also can be influenced by environmental short-term phenomena such as changes in juvenile recruitment rates as a function of surface seawater temperature. Similarly, changes in age profiles can be potentially misleading and be produced by the use of certain hunting technology. For example, in an ethnoarchaeological study among Bofi and Aka, central African foragers, Lupo and Schmitt (2002; also see Noss 1995) found that mortality profiles of small duikers obtained by mass collecting with nets contained higher proportions of juvenile and immature individuals than those generated by hunting with snares. Net-generated assemblages contained a higher proportion of immature and juvenile specimens because these animals are likely to follow their mothers into nets, and they lack the body size and weight to spring snares. Consequently, depending on the prey, changes in age composition could reflect shifts from individual hunting techniques to the use of mass capture technology (see also Jones 2006).

Perhaps the least strongly developed line of evidence in these models concerns the link between resource intensification and taphonomic damage. At present, the data supporting a link between intensification and specific taphonomic damage are limited (see Fancher et al. 2003; Gould 1996; Potter, 1995). Fancher et al. (2003), for example, found higher frequencies of bone fragmentation in central African ethnoarchaeological assemblages created in prey-impooverished regions compared with those produced in prey-rich regions. But their analysis did not show a similar difference in the frequencies of cutmarks between these two areas. Although resource intensification is supported by theoretical rationale, it is not yet clear if (1) variability in different types of bone damage (e.g., cutmarks and fragmentation) actually reflects intensification, and (2) the different evidence of intensification vary concurrently in response to one process such as overhunting. Do increases in cutmark frequencies and bone fragmentation reflect the same intensification process? It is possible that bone fragmentation resulting from grease rendering may mark the exploitation of a storable, over-wintering resource in circumstances unrelated to the declining abundances of high-ranking prey. Similarly, increases in the number of cutmarks on bones may be intercorrelated with the types of skeletal parts that are transported. For example, increases in the transport of high-value body

parts might be associated with increases in cutmark frequencies because high-value parts with large amounts of attached meat generally require more butchering effort and may display more cutmarks (see Lyman 2005). In this case, the two lines of evidence may well be intercorrelated but not necessarily reflect intensification. Given the current ambiguity surrounding the factors that shape cutmark frequency and distribution (see Lupo and O'Connell 2002; Lyman 2005), these lines of evidence need to be clarified and strengthened with future research.

Environmental models

An alternate set of models proposes changes in foraging efficiency in response to environmental change (e.g., Byers and Broughton 2004; Byers et al. 2005; Grayson et al. 2001; Lupo and Schmitt 1997a; Ugan 2005b; Wolverton 2005). These models often rely on patterned changes in zooarchaeological assemblages in concert with paleoclimatic indicators of climate change. The change in taxonomic composition resulting from climatic change can be quite different from those arising from exploitation depression. Continent-scale changes in climate may result in decreases in the abundances of large prey (i.e., megafauna), and changes in the distribution of smaller prey on the landscape (Cardillo et al. 2005; Guilday 1967, 1984). Climatic changes also can have a far more selective effect by increasing or decreasing the abundances of particular prey in response to habitat expansion or decline (Byers and Broughton 2004; Byers et al. 2005; Grayson 2000, 2006; Grayson and Delpech 1998, 2005; Grayson et al. 2001; Lupo and Schmitt 1997a; Schmitt et al. 2004).

For example, Grayson et al. (2001; also see Grayson and Delpech 2005) document declining evenness values in the Upper Paleolithic faunas of Grotte XVI in the Dordogne France culminating in the Magdalenian. Using several different techniques, they show how Upper Paleolithic evenness is unrelated to differential fragmentation, differential bone transport, or sample size. Paleotemperature data from southwestern France show that decreasing evenness values for reindeer are associated with decreasing July temperatures and increasing June precipitation, creating a favorable environment for reindeer and resulting in increased encounter rates with these prey.

On a regional scale, Byers and Broughton (2004; Byers et al. 2005; see also Broughton and Bayham 2003) use a suite of data from Homestead Cave in Utah, in concert with paleoclimatic indicators from California and other parts of the Great Basin, to track environmental changes that led to changes in artiodactyl abundances during the Holocene. In Homestead Cave, abundances of Utah chub remains track changing lake levels and monitor moisture levels in the Bonneville Basin throughout the Holocene. Frequencies of artiodactyls feces in the cave serve as a proxy measure for artiodactyl abundances. Overall these data are in good agreement with more conventional paleoclimatic records for the region that show a well-established pattern of droughtlike and arid conditions during the middle Holocene (8000-4000 B.P.), which depressed artiodactyl populations. More favorable mesic conditions in the Late Holocene increased the abundances and encounter rates with artiodactyls, resulting in higher proportions of artiodactyl relative to small-mammal

remains in archaeological assemblages (e.g., Byers et al. 2005; see also Wolverton 2005, for another interesting example).

Hockett (2005), however, presents evidence showing that in some parts of the Great Basin the remains of artiodactyls outnumber leporids in mid- to high-elevation sites during the Middle Holocene. These data imply no real change in the hunting intensity of artiodactyls from the Middle to Late Holocene but indicate a shift of artiodactyl and human populations to higher elevations and, perhaps, a change from ambush and encounter hunting to communal hunting at the Middle to late Holocene transition. The advent of communal mass hunting could account for an increase in artiodactyl remains, but Hockett's evidence for a change in hunting technology at that time is limited. Furthermore, Hockett's evidence does not disprove Byers and Broughton's argument; it only demonstrates that artiodactyl hunting shows continuity in some elevational zones from the Middle to Late Holocene. Hildebrandt and McGuire (2003) argue that while climate influenced human subsistence and settlement in that region, simplistic cause-and-effect models cannot explain increasing abundances of artiodactyl remains in the Late Holocene. They point out that the early Holocene (11500–7500 B.P.) witnessed favorable climatic conditions for artiodactyls, yet archaeological sites occupied during that time interval show a broad-based diet and are not rich in artiodactyl remains. As discussed further below, they point to social and cultural changes that may influence the value of different foraging choices (see also Bettinger 1999).

On a finer spatial and temporal scale, Ugan (2005b) found that the zooarchaeological evidence from two Fremont age residential sites in central Utah did not entirely match the patterns expected from exploitation depression and that climatic change may have served as a catalyst for a change in foraging efficiency. Increased frequencies of ^{14}C dates from around the region suggests that human populations were at their peak during this approximately 250-year interval, and tree-ring widths indicate variable climatic conditions. Age profiles and abundance indices show that artiodactyl populations were not steadily declining in response to exploitation depression but were variable and appear to have responded to climate changes (also see Lupo and Schmitt 1997a). Ugan (2005b) further identifies a potential confounding factor in density-mediated carnivore attrition, which could vary as a function of climate and the intensity of bone processing. During periods of increased xericity, when returns are low, human populations may intensify resource extraction by processing bones for grease. The discarded bones contain miniscule amounts of edible product and may not be extensively ravaged by carnivores with other food choices (after Lupo 1995). Consequently, when returns are poor and resource intensification is expected, artiodactyl skeletal part profiles will appear to be more even. He asserts that when returns are high, resources are less intensively processed by human foragers, and animal bones may be discarded when they still contain a substantial amount of bone grease. These discarded bones may be ravaged more extensively by scavengers than skeletal parts more intensively processed by foragers. As result, when returns are high the skeletal representation of artiodactyls may be very uneven and abundance indices depressed.

A central difficulty in applying these models is demonstrating a close cause-and-effect relationship between environmental and the proposed faunal changes (e.g.,

Barnosky et al. 2004). This often requires establishing close temporal association in evidence of environmental change as reflected by several classes of paleoclimatic-sensitive indices such as plant communities (e.g., Grayson 2000; Madsen et al. 2000) or cultural adaptations (e.g., storage facilities, different hunting technology, changes in settlement patterns). Optimally, climate changes should be demonstrated by evidence displayed in the physical remains of the animals in the assemblage (Grayson, personal communication, 2005). For example, changes in dental annuli or isotope values of high-ranking prey in a stratified sequence can be marshaled to strengthen causal inferences about climate change.

Other factors influencing resource choice

Building on recent studies in costly signaling theory in human behavioral ecology (e.g., Bliege Bird and Smith 2005; Hawkes and Bliege Bird 2002; Hawkes et al. 1991; Smith 2004), Hildebrandt and McGuire (2002; McGuire and Hildebrandt 2005) point to social and political payoffs that guide resource choice to explain increasing emphasis on large and high-risk prey during the Middle Archaic (4000–1000 B.P.) in California. They argue that an increased focus on large and high-risk prey during that time interval runs counter to arguments based on exploitation depression resulting from increased population densities (*sensu* Broughton 1994a, b, 1999), but it makes sense if other social and political benefits greatly enhanced the value of procuring large prey. Material evidence that purportedly reflects the rise of prestige hunting includes increased abundances of large prey, a rise in biface production, and increases in the production of symbolic manifestations of hunting such as in split-twig figurines, trophy caches, and rock art. The procurement of large high-value and high-risk fish such as swordfish, marlin, tuna, and dolphin with ocean-going plank canoes also is viewed as manifestations of prestige hunting (e.g., Porcasi and Fujita 2000).

An interesting aspect of this argument is Hildebrandt and McGuire's attempt to understand the rise of prestige hunting within a long-term temporal and cultural framework beginning in the Middle Holocene, when work groups were more heterogeneous in composition and tasks were less strictly divided along the lines of gender (McGuire and Hildebrandt 1994). In this scenario, the Middle to Late Holocene transition gave way to a greater degree of sedentism and increased reliance on stored foods and women's labor, thus producing the conditions for greater elaboration and segregation by gender in work groups, including increased logistical hunting of high-prestige prey by men. In their model, prestige hunting persists even though it lowers overall foraging returns; once it emerges it continues to develop within its own trajectory and organizing principles (McGuire and Hildebrandt 2005; but see Broughton and Bayham 2003; Colten 1995). While acknowledging that social and political benefits shape human choice, Broughton and Bayham (2003, p. 785) assert that prestige hunting would be focused on larger prey and is an "unknown constant" in the record. Because it is not possible to predict variability in prestige hunting, they argue that increases in large prey are still best explained by appeal to the diet breadth model. Broughton and Bayham (2003) argue that the patterns documented by Hildebrandt and McGuire (2003) can be explained

more simply by climatic evidence for increasing mesic conditions that favored an increase in artiodactyl populations throughout most, but apparently not all, of the region (as discussed above).

Costly signaling theory is an important emerging area of research in human behavioral ecology. Although the anthropological literature is still quite limited on this subject, one way hunters signal good qualities and build social capital is by acquiring large, high-risk, and/or dangerous prey and by generously sharing the meat in a highly visible context (Hawkes et al. 1991; Smith 2004; Wiessner 2002). According to costly signaling theory, signals are usually quality dependent for specific traits (i.e., accurate and honest signals of the trait) and, therefore, are not used by every member of the community. The high cost of the signal mitigates against potential cheaters. Signaling benefits both the signaler and receiver; signalers convey information about specific qualities they possess, and receivers garner accurate information about the signaler. However, the arena for signaling is fluid and culturally variable (e.g., Bliege Bird and Smith 2005; Hawkes and Bliege Bird 2002; also see Zahavi 1975, 1977).

The obvious challenge in an archaeological context is for analysts to demonstrate that specific patterns in the material record are manifestations of costly signals. Zooarchaeologists, for example, cannot routinely assume that changes in the abundance of high-ranking prey are necessarily manifestations of prestige hunting as a costly signal. Not all high-ranking resources are necessarily high cost or risky or wasteful to acquire. Furthermore, it is not clear how the emergence and persistence of a signal keyed to prey acquisition will influence zooarchaeological assemblages. One might not expect the rise of costly prestige hunting to result in an increase in the archaeological abundance of high-ranking resources within a single site or in multiple but temporally synchronous sites over a large geographic area. Signals that garner the most prestige should be those that can be conducted only by a limited pool of people who possess the right qualities and abilities. If many possess the ability to procure costly or high-risk prey, then the signal no longer conveys information about a unique ability or quality and should lose its value as a prestige builder.

Analysts who identify changes in foraging efficiency in zooarchaeological assemblages face two central difficulties. First, they must demonstrate that the changes they identify actually reflect a change in the diet and are not attributable to some other process(es) such as site taphonomic history, assemblage sample size, recovery and identification techniques, or changes in how the prehistoric occupants used the site. As demonstrated by the cases discussed here, a second and far more difficult challenge faced by analysts using foraging rationale is to demonstrate that the changes in foraging efficiency they identify really are attributable to one cause and not another (see Grayson and Cannon 1999). Most analyses proceed by identifying the different possible causes for changes in foraging efficiency (e.g., climate change, overhunting), eliminating some of these possibilities (or minimally narrowing the list down) and using theoretical rationale to identify patterned responses and lines of evidence that support one causal agent over another. Eliminating the influence of all other possible causes can be difficult because (1) analysts may not be aware of all the potential processes influencing foraging

efficiency, (2) some processes, such as social or cultural factors, may be archaeologically obscure, and (3) other processes presumed to influence foraging efficiency (such as technology) may not correlate with observable changes in zooarchaeological assemblages.

Grayson and Cannon (1999) discuss several different ways in which analysts can control for different processes but acknowledge that some may be very difficult to accommodate in analysis. For example, while most acknowledge that changes in technology can influence foraging efficiency, in practical application analyses often have difficulty controlling for the effects of technology (see Grayson and Cannon 1999; Stiner et al. 2000). Unless there is an identifiable change in the material record of technology that coincides with changes in the faunal assemblage, analysts must conclude that technology did not influence foraging efficiency. Obviously some types of technological change such as food preparation activities or fiber-based hunting technology might not leave tangible evidence (but see Jones 2006; Lupo and Schmitt 2002). Perhaps these factors may best be addressed by the construction of predictive theoretical models (e.g., Ugan et al. 2003).

Predictive frameworks in zooarchaeology

Another series of models uses foraging theory as a predictive tool to evaluate the likelihood of certain subsistence strategies in specific environments or anticipate the composition of assemblages given a set of certain assumptions (e.g., Byers and Ugan 2005; Grayson 1991; Haynes 2002; Haynes and Eiselet 1999; Lupo 1998; Waguespack and Surovell 2003). Foraging models are particularly useful predictive devices in cases where the archaeological record is limited, ambiguous, or poorly understood. The application of predictive models allows for greater precision in defining the circumstances under which specific strategies or decisions might have prevailed in the past, but such models have not decreased the controversy surrounding many of these issues.

Dietary specialization or generalization?

The predictive use of foraging theory has recently been used to both bolster and challenge the feasibility of big-game specialization among Clovis-age hunters in the Americas (e.g., Byers and Ugan 2005; Haynes 2002; Haynes and Eiselet 1999; Surovell et al. 2005; Waguespack and Surovell 2003). Most of these arguments turn on reconstructions of the return and encounter rates for proboscideans (mammoth and mastodonts), which are found in association with Clovis-age materials more frequently than other Pleistocene megafauna (see Haynes 2002, p. 398; also see Grayson and Meltzer 2002, 2003, 2004). Haynes, (2002; Haynes and Eiselet 1999) argues that Clovis hunters specialized in hunting mammoths and mastodonts because proboscideans were the highest-ranking prey resource based on body size and were easy to locate by highly visible elephant footpaths. Pleistocene hunters spent more time hunting proboscideans (and other large Pleistocene fauna) in highly productive refugia patches, where prey congregated and biotic diversity was high.

He estimates mammoth and mastodont densities in refugia as high as 2 or 4 individuals per 2 km, which is higher than the densities attained by most modern large herbivores.

Waguespack and Surovell (2003) use data from 33 archaeological sites to evaluate whether Clovis populations were big-game specialists or generalists. Generalists take prey in proportion to their relative abundance on the landscape; this strategy prevails when high-ranking prey are infrequently encountered and/or rarely successfully captured, or when there is little variability in the return rates among prey. Specialist hunters focus on specific prey and ignore those that are less productive. This strategy prevails when high-ranking prey are frequently encountered and the return rates derived from those prey exceed the expected rates from other prey. The negative relationship between animal body mass and densities among contemporary wildlife populations serves as a relative estimate of the potential densities of Pleistocene fauna and, by extension, encounter rates of different size prey available to Clovis-age hunters. They calculate the expected number of archaeological sites that should contain different prey size classes given a generalist strategy and compare this to the observed number of sites containing those prey classes. In their analysis, proboscideans are represented far more than might be expected based on body size in comparison to smaller fauna. They argue that a Clovis big-game focus would be possible at low human population densities and when large game were encountered regularly, but they acknowledge that other types of prey likely would have been exploited.

Byers and Ugan (2005) use anatomical, ethnographic, and actualistic data derived from modern experiments with elephant carcasses to calculate potential return rates for mammoth and mastodont. These data are used to model thresholds of on-encounter return rates that would have been necessary to exclude medium and small prey from the diet. Despite excessive processing costs, the return rates for mammoths and mastodonts are higher than those for most other small and medium-sized mammals. Using the allometric relationship between body size and prey density, they model encounter rates to determine how often mammoth and mastodont would have to be taken to exclude small and medium mammals from the diet. According to their estimates, the only way Paleoindian populations could specialize in proboscideans was if they encountered one every hour.

More realistic encounter rates, based on body mass, suggest that proboscideans would never have been encountered frequently enough to exclude some other prey species from the diet (also see Simms 1987, p. 96). Megafaunal specialization is not supported by their data and would require “mammoth encounter rates 15 time higher than those predicted by the body mass allometry data, encounters with 30 different taxa similar in size and post-encounter returns to *Bison antiquus*, or overall encounter rates with bison 30 time higher than suggested here.” (Byers and Ugan 2005, p. 1634). The novelty with this approach is that it allows researchers to estimate more accurately the circumstances under which specific strategies might persist, given the encounter rate with high-ranking prey. While return rates determine the order in which prey will be incorporated into the diet, encounter rates determine the proportions of different prey in the diet. In this case, high search costs resulting from low encounter rates depress the overall return rates so that other prey

cannot be excluded from the diet. Modeling the prey return and encounter rates, with quantitative data, allows researchers to calculate how changes in the encounter rates with high-ranking prey influence the proportions of different prey in the diet and lead to more specialized or generalized strategies.

Anatomical part representation

Predictive applications also are fruitfully applied to questions about selective skeletal part processing and transport by prehistoric populations. A central point in these analyses concerns what economic scale or measure (if any) adequately predicts selective skeletal part processing and/or transport of medium and large prey by prehistoric hunters. These analyses build on Binford's (1978) pioneering work that developed economic utility indices to explain the differential treatment of skeletal parts by modern Nunamiut Eskimos. Binford's utility indices were based on the amount of meat, marrow, and grease associated with different skeletal parts but largely ignored the processing cost associated with extracting different edible products. A natural extension of this approach, and one entirely compatible with foraging theory, is the incorporation of processing and pursuit times into economic values to derive return rates for different skeletal parts. Metcalfe and Jones (1988) not only provided a simplified method for deriving utility measures but were among the first to suggest incorporating pursuit and processing costs into measures of utility. Binford's observations about differential marrow bone processing by Nunamiut Eskimos provided the backdrop for one of the first applications of return rates to skeletal part selectivity by Jones and Metcalfe (1988, pp. 420–422). Binford (1978, p. 31) notes that "old-timers" reported processing phalanges during times of stress, but contemporary Nunamiut ignored low-yielding marrow-bearing bones such as the scapula, phalanges, and mandible. Using return rates derived from Binford's data on caribou coupled with observations of which marrow bones were currently exploited by the Nunamiut, they calculated a mean return rate threshold of 500 kcal/h below which marrow bones should not be exploited. In the past, during times of stress mean return rates must have been below this threshold to make processing low-ranking phalanges profitable.

Building on this methodology, several researchers have constructed gross return rates (i.e., kcal of product/handling time or weight of product/handling time) for different skeletal parts of different types of prey using data derived from butchering experiments (Egeland and Byerl 2005; Lupo 1998, 2006; Lupo and Schmitt 1997b; Madrigal and Holt 2002). Several analyses have attempted to use return rates as a predictive tool to analyze skeletal part representation in archaeological and ethnoarchaeological settings (Lupo 1998; Madrigal and Holt 2002). Thus far, these analyses show that the composition of transported assemblages are generally not predicted by experimental return rates (but see Madrigal and Holt 2002). The current set of available gross return rates might predict the order in which skeletal parts are processed, but they should not be expected to predict the composition of transported assemblages unless transport costs are accounted for, a point returned to below (also see Lupo 1998). This point is demonstrated by Egeland and Byerly (2005), who argue that return rates predict the order in which parts are processed if

the goal is to maximize the caloric gain per unit of time but not necessarily the order in which they are transported. They analyze cutmark and bone percussion marks at the ST Site Complex at Peninj and find that the low-return metapodials of small and large prey do not display cutmark or percussion marks, suggesting high encounter rates with carcasses.

Burger et al. (2005) suggest that the patch choice model as applied at single-carcass levels can predict selective part processing. Using experimental data to build gain functions for meat and marrow, they show that carcass products exhibit a negatively accelerating gain curve. In their model, time in patch is equivalent to processing intensity, which is reflected by the frequencies of cut and percussion marks on bones and by the processing of specific low-yield parts. The travel time between patches is measured as time between kills, which reflects the mean foraging return rate. Long time intervals between kills depresses the mean foraging return rates and results in longer in-patch residency and more intensive processing of carcasses. Short intervals between kills increase the mean foraging return and result in shorter in-patch time and processing effort. The advantage of this model is that it can be used to calculate the time between patches (or between kills) and yield information about overall environmental productivity. As they suggest, however, in practice this model may be more useful as a relative device to compare assemblages rather than compute the actual time intervals between kills.

One potential difficulty associated with the use of foraging models as predictive tools for selective skeletal part exploitation is that all of the available published return rates are gross acquisition rates (see Table 1). While handling time, by definition, should include all of the costs associated with pursuing, processing, and consuming a resource after it is encountered, most calculations do not include the costs of resource transport. Classic applications of the prey choice model do not include transport costs because the model was originally designed to predict the behavior of nonhuman predators who consume their prey on encounter. But transport costs can significantly influence part choice, field processing decisions, and selective skeletal part transport for human (and nonhuman) foragers (see Lupu 1998, 2006). Because human foragers field process and transport resources to central locations, more appropriate methodology for assessing transported assemblages might entail the use of central place foraging models, which not only include transport costs but may also identify a different goal (such as maximizing the rate that nutrients are returned to a central place). Thus far, central place models that incorporate transport costs have been applied in several different archaeological contexts (e.g., Beck et al. 2002; Cannon 2003; Jones and Madsen 1989; Madsen et al. 2000; Zeanah 2004), and their application to problems of skeletal part transport are still in a nascent state (but see Lupu 2006).

Future directions and conclusions

Applications of foraging theory in zooarchaeological analyses have thus far produced a number of compelling interpretations and hold the potential for generating some of the most sophisticated analyses yet applied to archaeofaunas.

Nevertheless, challenges to foraging theory and human behavior ecology, in general, have emerged on several fronts (e.g., Dwyer 1986; Martin 1983; Pyke 1984; summarized by Krebs and Davies 1997, pp. 10–11). Even within the community of scholars who use evolutionary theory as an explanatory paradigm there is widespread disagreement about the assumptions underlying human behavioral ecology, the forces that guide decision-making, and assumptions underlying foraging economics (e.g., Boone and Smith 1998; Cosmides and Tooby 1987; Kelly 2000; Lyman and O'Brien 1998; O'Brien et al. 1998; Schiffer 1996; Symons 1987, 1989, 1990; Tooby and Cosmides 1990). The nature and extent of these criticisms are beyond the scope of this article and are addressed in several prominent recent reviews (e.g., Broughton and O'Connell 1999; Laland and Brown 2002; Smith 1991, 2000). There are, however, several conceptual and practical issues in applying foraging theory to the zooarchaeological record, foreshadowed by recent biological and anthropological research, that can guide future research and strengthen the use of foraging models in the analysis of archaeological faunas.

One well-known limitation is that most explanations tend to focus solely on the circumstances influencing the acquisition and processing of prey and other potential influences on dietary choice tend to be underemphasized. Because analyses focus only on the faunal component of prehistoric diets, it does not address all of the dietary options available to prehistoric foragers (Broughton and Grayson 1993; Grayson and Cannon 1999). Consequently, most, but not all, applications assume that changes in the faunal component of the diet can be explained by circumstances influencing the acquisition of prey animals (i.e., factors influencing search and handling costs) and are unrelated to circumstances influencing different components of the diet such as plants (Grayson and Cannon 1999, p. 149) or other cultural phenomenon (e.g., Bettinger 1999; Hildebrant and McGuire 2002, 2003; McGuire and Hildebrant 2005). However, changes in the use of plant resources, such as an increased reliance on storable seeds or nuts, can potentially influence the ranking of those resources relative to some smaller prey (see Grayson and Cannon 1999; Simms 1987). These circumstances may influence different characteristics of the faunal record but are not explained solely by reference to the circumstances influencing prey acquisition and handling. Foraging models have the best explanatory and predictive potential value when the full suite of subsistence choices available to the forager is considered. This is because foragers make decisions about what to exploit based on all the options available to them. Future applications can be greatly improved by considering (whenever possible) the full range of resources available to prehistoric foragers rather than simply one component of the diet.

A second important area that begs for reconsideration and clarification concerns currencies and goals. Issues surrounding the use of experimental and ethnographic return rates can be partially resolved by expanding the existing database, but a potentially larger and related issue concerns how currency is measured and defined by a forager's goals. Zooarchaeological analyses often proceed as if currency and proximate goal are well known and invariant. Most analysts assume that foragers always attempt to maximize the long-term net rate of gain. However, it might surprise anthropologists and archaeologists to know that the choice of currency and

identification of goal are not presumed to be static or invariant in current studies of nonhuman foragers (e.g., Bergman et al. 2001; Kacelnik and Krebs 1997; Welham and Beauchamp 1997). Studies of foraging animals show that different currencies yield different predictions about behavior and that different currencies successfully predict foraging strategies in different contexts even within the same species (Bateson and Kacelnik 1996; Rasheed and Harder 1997; Waite and Ydenberg 1994; Weimerskirch et al. 2003; Welham and Beauchamp 1997; Ydenberg 1998, pp. 350–351). A recent study by Weimerskirch et al. (2003), for example, shows that different currencies predicted the behavior of blue petrels (*Halobaena caerulea*) depending on the length and context (provisioning vs. self-feeding) of the foraging trip. Among nonhuman species, efficiency (or input/output analysis, see Table 1) actually predicts foraging behavior more often than rate maximization in a number of circumstances (Waite and Ydenberg 1994).

Given the range of currencies and goals that predict the foraging behavior of nonhuman animals, zooarchaeologists need to revisit the underlying assumptions about currency and goal as applied to human populations. Recently, Kacelnik and Krebs (1997, p. 24) comment on anthropological applications of foraging economics and argue that the correct choice of currency and goal depends on a forager's state and the context. Individuals may choose to maximize different currencies depending on their own immediate circumstance or state (e.g., reproductive state, social status; Houston and McNamara 1999). Different contextual goals for human populations might include provisioning offspring or foraging for stored resources or those that have social and political value (Ydenberg 1998). Kacelnik and Krebs (1997) suggest the use of dynamic techniques or computer simulation to analyze these more complex circumstances (e.g., Houston 1997; Houston and McNamara 1999; Houston et al. 1988).

Even though state- and context-dependent foraging decisions are well demonstrated in biological and anthropological research (e.g., Bird and Bliege Bird 1997; Hill and Hawkes 1983; Hill et al. 1987; Kelly 1995; Smith 1991), zooarchaeological and archaeological researchers have made few attempts to accommodate these behavioral factors. Several analysts, for example, have modeled how the foraging differences between men and women might impact archaeological remains (see, e.g., McGuire and Hildebrandt 2005; Simms 1987; Zeanah 2004). These kinds of analyses are clearly only the beginning. Zooarchaeological analyses can be greatly enhanced by increased recognition of how different states and contexts influence foraging strategies. Some might believe that this variability has no impact on their analyses because the aggregate nature of archaeological assemblages will mask the effects of context- and state-dependent differences in foraging strategies. However, recent ethnoarchaeological analyses show that context- and state-dependent foraging can influence the composition of faunal assemblages. Bird and Bliege Bird (2000), for example, describe how the foraging efforts of Meriam children on the Torres Strait target low-ranking but easily handled resources that satisfy immediate nutritional needs. Because children are more likely to transport and process resources at residential locations than are adults (who may handle larger and higher-ranking prey items), faunal middens may be artificially enriched by low-ranking resources. Similarly, Lupo and Schmitt (2005) found that state-dependent

differences in target prey and goals among Aka and Bofi forest hunters produced significant differences in the composition of ethnoarchaeological bone assemblages. These differences were manifested in assemblages from neighboring camps that were occupied during the same time interval by different people.

In an archaeological context, state and context variability in foraging strategies can potentially be identified in zooarchaeological assemblages in some, but not all, contexts. High-resolution assemblages (single use or occupation) are more likely to reflect this type of variability than low-resolution assemblages (e.g., Lupo 2001). In practical application, zooarchaeologists might explore intrasite spatial differences in standard measures of diversity or abundance indices, or skeletal part present. The central challenges for zooarchaeologists are to determine (1) what types of state and context behavioral variation leave tangible and measurable patterns in the material record, and (2) the circumstances under which this variability in foraging behavior might actually be inferred from the archaeological record. State- and context-dependent foraging strategies represent one of the most fertile avenues for future research, not only in zooarchaeology but in archaeology in general. An obvious important line of research here is ethnoarchaeological analysis. Focused and theoretically grounded ethnoarchaeological research aimed at applying foraging models with an eye toward identifying the material correlates that result from state and context will likely provide the single best source of information (e.g., O'Connell 1995).

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