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PREY BODY SIZE AND RANKING IN ZOOARCHAEOLOGY: THEORY, EMPIRICAL EVIDENCE, AND APPLICATIONS FROM THE NORTHERN GREAT BASIN

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The use of body size as an index of prey rank in zooarchaeology has fostered a widely applied approach to understanding variability in foraging efficiency. This approach has, however, been critiqued—most recently by the suggestion that large prey have high probabilities of failed pursuits. Here, we clarify the logic and history of using body size as a measure of prey rank and summarize empirical data on the body size–return rate relationship. With few exceptions, these data document strong positive relationships between prey size and return rate. We then illustrate, with studies from the Great Basin, the utility of body size-based abundance indices (e.g., the Artiodactyl Index) when used as one component of multidimensional analyses of prehistoric diet breadth. We use foraging theory to derive predictions about Holocene variability in diet breadth and test those predictions using the Artiodactyl Index and over a dozen other archaeological indices. The results indicate close fits between the predictions and the data and thus support the use of body size-based abundance indices as measures of foraging efficiency. These conclusions have implications for reconstructions of Holocene trends in large game hunting in western North America and for zooarchaeological applications of foraging theory in general.

El uso del tamaño del cuerpo como un índice de rango presa en zooarqueológico aplicaciones de la teoría del forrajeo ha fomentado un enfoque ampliamente aplicado a la variabilidad de la comprensión en la eficiencia de forrajeo y amplitud de la dieta. Este enfoque ha sido criticado periódicamente, con una preocupación más recientes derivados de los datos etnográficos que sugieren que la presa de gran tamaño puede estar asociado con altas probabilidades de actividades y por lo tanto no las tasas de retorno bajo. En este documento, clarificar la lógica y la historia de la utilización de tamaño corporal como una medida de rango de presas y resumir los datos empíricos sobre el tamaño de la relación cuerpo-la tasa de retorno, haciendo hincapié en los artiodáctilos y los lagomorfos. Estos documento de datos fuertes relaciones positivas entre el tamaño de las presas y tasa de retorno, con excepciones limitadas a los casos que no incluyen los artiodáctilos, y que se caracterizan por estrechos márgenes de tamaños de las presas. A continuación, ilustran con estudios de caso de la cuenca del norte de la Gran la utilidad del tamaño corporal basado en los índices de abundancia (por ejemplo, el Índice de Artiodáctilo: Σ NISP Artiodáctilos/Σ[NISP Lagomorfos + Artiodáctilos]) cuando se utilizacomo un componente de análisis multidimensionales de amplitud de la dieta prehistórica. En estos estudios de caso, utilizamos modelos de la teoría de forrajeo para obtener predicciones sobre la variabilidad del Holoceno en la amplitud de la dieta de la hipótesis de clima tendencias determinadas en la densidad de artiodáctilos. A continuación, prueba de las predicciones utilizando el Índice de artiodáctilos y más de una docena de otros índices derivados de la fauna arqueológica, floral, y ensamblajes de la herramienta. Los resultados indican una estrecha encaja entre las predicciones y los datos empíricos y con ello proporcionar un fuerte apoyo para la utilización del tamaño corporal basado en los índices de abundancia como medidas de eficiencia de forrajeo. Estas conclusiones tienen implicaciones de largo alcance no sólo para las reconstrucciones de las tendencias recientes del Holoceno en la caza mayor y la variabilidad del comportamiento relacionados en el oeste de América del Norte, pero para las aplicaciones de la teoría del forrajeo zooarqueológico en general.

In the past several decades, models from evolutionary ecology have been applied with increasing sophistication to a wide range of archaeological issues ranging from life-history evolution in early *Homo,* to the origins of agriculture, to Mayan monument construction (see reviews in Bird and O'Connell 2006; Broughton and Cannon 2010). The approach has become es-

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pecially well-developed—reaching almost main-stream status—in zooarchaeology, the context of several of the earliest applications of evolutionary ecology in archaeology (Bayham 1977, 1979, 1982; Beaton 1973). In this context, foraging theory models have been effectively applied as tools for understanding prehistoric behavioral variability and diachronic trends in foraging efficiency and diet breadth. Such variability and trends have, in turn, been linked to many broader developments in human behavior and morphology, including changes involving technology, the division of labor, the emergence of agriculture, population replacements, violence and warfare, social inequalities, settlement systems, material display, and human health (e.g., Bird and O'Connell 2006; Broughton and O'Connell 1999; Broughton et al. 2010; Cannon 2003; Fitzhugh 2003; Jones and Raab 2004; Kennett 2005; Kuhn et al. 2001; Morin 2004, 2010; Ugan et al. 2003).

Central to these applications has been the effective estimation of key parameters of foraging theory models and articulation of these to the imperfectly preserved archaeological residues of past human foraging decisions. Perhaps most important in this context is the estimation of *prey ranks,* which are essential to application of the fine-grained prey model, the most widely applied of all foraging models. Prey-rank estimates are typically defined in standard model formulations as post-encounter return rates, measured as e/h, where e represents the net energy gain provided by a resource and h represents the handling costs associated with acquiring and processing it. Of these variables, only energy gain is more or less directly measurable in archaeological contexts because it is directly proportional to prey body size. Because most of the handling costs are highly variable, context-dependent, and difficult to estimate from archaeofaunal materials, prey body size has been commonly used as a proxy measure of prey rank in the deployment of the prey model in archaeofaunal contexts. This convention was initially advanced in early archaeological applications of the prey model (Bayham 1977, 1979, 1982) and has more recently been bolstered by extensive ethnographic and experimental data sets bearing on the relationship between prey size and post-encounter return rate (e.g., Alvard 1993; Hill et al. 1987; Simms 1985, 1987; Smith 1991; Winterhalder 1981).

While the use of body size as a measure of prey rank has fostered a robust and successful approach to understanding variation in the archaeofaunal record, most often operationalized through the calculation of body-sized-based taxonomic "abundance indices" (e.g., Bayham 1979, 1982; Broughton 1994a, 1994b, 2004; Broughton et al. 2010; Broughton et al. 2007; Butler 2000; Butler and Campbell 2004; Byers and Broughton 2004; Byers et al. 2005; Byers and Smith 2007; Cannon 2003; Faith 2007; Grayson 2001; Grayson and Delpech 1998; Hildebrandt and Jones 2002; Jones et al. 2008; Kennett 2005; Lyman 2003a, 2003b; Morin 2004, 2011; Nagaoka 2002a, 2002b, 2005, 2006; Porcasi et al. 2000; Ugan 2005a, 2005b; Ugan and Bright 2001; Wolverton 2005; Wolverton et al. 2008), the approach has also been critiqued periodically over the past few decades. The critiques have involved concerns about the effects of mass-capture techniques on prey return rates (e.g., Madsen and Schmitt 1998; Rick and Erlandson 2000; see also Lupo 2007), the high travel costs presumed to be associated with large-game exploitation (McGuire et al. 2007; but see Grimstead 2010), and, most recently, the high mobility of large game, which is presumed to result in both high pursuit costs and high probabilities of failed pursuits (Bird et al. 2009). This last issue, emerging from ethnographic data collected from the Martu of western Australia, has led Bird et al. to contend that failure to incorporate pursuit costs into the ranking of a prey item may well compromise "interpretations of variability in prehistoric resource use" (2009:8). Apparently reflecting these concerns, Bird and O'Connell (2006) refer to the use of body size as an index of prey rank in archaeofaunal applications as a "fragile" assumption, a conclusion that is very different from the one we reach here.

In this paper, we discuss the role of prey-rank estimates as one of many assumptions contained in prey model applications. We clarify the original logic of using body size as a hypothetical measure of prey rank in archaeological applications of foraging models, and we summarize available empirical evidence that speaks to the utility and limitations of prey body size when used in this way. We also explore the potential influence of mobility-related costs on the return rates for the North American mammalian prey most commonly used

in body size–based abundance indices—artiodactyls and lagomorphs—and we illustrate with case studies from the northern Great Basin the role that abundance indices can play in broader, multidimensional analyses of prehistoric foraging behavior. The main points that we make here are (1) that the relationship between prey body size and post-encounter return rate is thoroughly supported for a wide range of prey types, especially those most commonly employed in foraging theory-inspired abundance indices; and (2) that conclusions about variability in prehistoric foraging efficiency that are based on patterns observed in abundance indices are frequently well-supported by other, independent archaeological measures. These points have far-reaching implications not only for recent reconstructions of trans-Holocene trends in large game hunting in western North America and the debate about whether those trends are driven by foraging efficiency or by factors related to costly signaling and prestige rivalry (Broughton and Bayham 2003; Broughton et al. 2008; Byers and Broughton 2004; Hildebrandt and McGuire 2002; McGuire and Hildebrandt 2005), but also for zooarchaeological applications of foraging theory in general.

Body Size and Prey Ranking in Zooarchaeology: The Original Rationale

Recognition of the importance of prey body size as a significant variable influencing food choice has a long history in zooarchaeology (e.g., White 1952, 1953), even prior to its use as a proxy for prey rank in early foraging theory applications in the field. As a prey characteristic that is readily derived from archaeological faunas, the use of body size in this context grew out of the limitations of earlier biomass-based efforts to understand the selective utilization of animals, which required data difficult to derive from archaeological settings (e.g., Grayson 1974; Munson et al. 1971; Smith 1974, 1979; Yesner and Aigner 1976; see Bayham 1982 for further discussion). Pioneering the articulation of prey model predictions with archaeological measures of the relative abundance of different-sized prey species, Bayham reasoned:

> It is clear that a variety of factors influence which animals are selected for food, such as size, density, palatability, search time and pro-

cessing time. Among those, abundance of prey in the diet and size of the prey item are the only direct quantifiable variables that the faunal analyst has access to. The attempt is made here to characterize the prehistoric diet using size and abundance, thereby facilitating comparisons from one site to another...In the arid Southwest it is easy to understand the conceptual utility of this scheme, when we consider the most dominant animals in the prehistoric diet, deer and rabbits. It is assumed that deer are the most preferred food item, and therefore, the representation of rabbit species in the diet is an indirect index of how abundant deer were [Bayham 1977:357].

Further work emphasized that ratios of the abundances of such taxa could be extended to provide measures of hunting efficiency, with high proportionate abundances of large-sized taxa (e.g., deer) indicating higher overall return rates (Bayham 1982, 1986; Szuter and Bayham 1989). Using measures such as the Artiodactyl Index (ΣNISP Artiodactyls/ΣNISP [Artiodactyls + Lagomorphs]), Bayham (1977, 1979, 1982, 1986; Szuter and Bayham 1989) explored patterning in Southwestern hunting efficiency related to a variety of factors including resource depression and changes in settlement system organization.

At the same time, analogous approaches were being developed in early applications of the prey model within the field of zoology. Wilson (1976), for instance, argued that the abundance of large, relative to small, insect prey found in the stomach contents of birds could be used to measure the quality of their foraging environments and thus foraging efficiency. Since large, high-ranked prey should always be pursued, Wilson (1976:96) argued, their relative abundances measure both how frequently they were encountered and the amount of energy "available in the environment."

We emphasize that these structurally similar early prey model applications in zooarchaeology and zoology both fully recognized the potential importance of pursuit costs, but, since they dealt only with the residues of past foraging decisions, neither had any secure way to access them. Thus, adopting a standard modeling convention, variables perceived to be intractable—albeit potentially significant—were held constant to allow the analysis to proceed (see also Griffiths 1975).

Both approaches therefore adopted body size as a proxy for prey rank given its intrinsic link with energetic gain.

We also emphasize that the assumptions about prey ranks incorporated in this tradition of prey-model applications in zooarchaeology have always been viewed as hypotheses that enable the generation of testable predictions, rather than as absolute or deterministic characterizations of past human foraging behavior. As with all model components (currency, constraints, etc.), the assumptions made about prey rankings are at risk whenever a model is applied in a particular context. Predictive failures imply that one or more of the assumptions incorporated into a model, including those associated with prey rankings, may be inappropriate. Predictive successes, on the other hand, imply that model assumptions are valid. The wide range of successful tests involving models that assume maximization of foraging efficiency as a goal and currency, and that use body size as a proxy for prey ranks, attest to the generality of these particular assumptions.

Ethnographic and Experimental Evidence Support the Body Size-Return Rate Relationship

The first wave of prey model applications in zooarchaeology reasoned that, though context-dependent, pursuit costs would typically not vary to such a degree that an ordinal scale ranking based on size alone would become reversed, especially for taxa of such disparate size as artiodactyls and lagomorphs. This conclusion began to be empirically supported as soon as ethnographic and experimental analyses of post-encounter return rates started to emerge in the 1980s (e.g., Hawkes et al. 1982; Hill et al. 1987; Simms 1985, 1987; Winterhalder 1981). By the early 1990s, summaries of the empirical data on the relationship between vertebrate prey body size and return rate showed positive correlations in each and every case (e.g., Broughton 1994a). These data supplied estimates for other critical model parameters and enabled a surge in the application of foraging models not only in zooarchaeology but throughout archaeology in general (see Bird and O'Connell 2006; Cannon and Broughton 2010).

To our knowledge, there are now ten data sets in existence that include return-rate estimates for suites of vertebrate prey types consisting of five or more taxa or prey types; these data sets are summarized in Table 1. In all of these cases, the direction of the relationship between post-encounter return rate and body size is positive, and in eight of the ten cases the correlation is significant at an alpha level of .10 (Table 1). Because the effects of prey mobility and failed pursuits on return rates have been recently highlighted (Bird et al. 2009), we point out that all of the ethnographic-observational data sets represented in Table 1 explicitly include the costs of failed pursuits in their return rate estimates. Since significant correlations between prey body size and return rates are indicated in almost of all of these cases, it would appear that prey mobility may be less influential than has been suggested.

Pursuing this further, the two empirical cases that fail to produce significant correlations between prey body size and return rate—those involving the Mayangna-Miskito and Martu—are instructive in that they elucidate an important general factor that appears to affect the body size–return rate relationship. Specifically, compared to data sets derived from other cases that involve terrestrial hunting, these two incorporate very narrow prey size ranges and very small maximum prey sizes: the Martu data, for example, exhibit the lowest range of exploited prey sizes, with hill kangaroo (*Macropus robustus*), the largest prey type, weighing only 22 kg and cossid larva, the smallest type, weighing just 13 g. In contrast, the prey-size range for the Cree is over 415 kg, with moose (*Alces alces*) and grouse (Phasianidae), representing the largest and smallest prey sizes, respectively (Table 1). We also note that the Mayangna-Miskito and Martu cases are the only two involving terrestrial hunting in which artiodactyls are not included in the suite of prey exploited. Thus, we can only conclude that *the lack of truly large-bodied prey and the relatively narrow range of prey sizes in these two cases must accentuate the effect of variation in prey mobility on prey rankings.* This, of course, is not a new point, having previously been articulated most notably by Stiner and colleagues (e.g., Stiner et al. 1999; Stiner et al. 2000; Stiner and Munro 2002; see also Morin 2011), who have

Table 1. Correlation Coefficients for the Body Size (kg) and Post-Encounter Return Rate (Kcal/hr) Relationship for Vertebrates Derived from Experimental and Ethnographic Contexts.

Cultural Affiliation	Location: Environment	Vertebrate Classes (no. of prey species or weight classes)	Size Range (max size) kg	r_s	P	Primary Capture Method	Failed Pursuits Included in Return Rates	Reference
Cree[a]	N. Ontario: Boreal Forest	Mammals (10); Fishes (6); Birds (3)	415 (416)	.52	.03	Single, Mass	yes	Winterhalder 1981: Table 4.4
Cree[b]	N. Ontario: Boreal Forest	Mammals (4); Fishes (1); Birds (2)	258 (259)	.75	.07	Single, Mass	yes	Winterhalder 1981: Table 4.4
Ache[c]	E. Paraguay: Tropical Forest	Mammals (7); Fish (1); Reptile (1); Bird (1)	29 (30)	.56	.09	Single	yes	Hawkes et al. 1982: Table 3
Modern Utah Hunters[d]	Utah: Temperate Forest, Sage Steppe	Mammals (9); Birds (1)	56 (57)	.73	.04	Single	na	Simms 1985, 1987
Ache[e]	E. Paraguay: Tropical Forest	Mammals (7)	27 (30)	.71	.08	Single	yes	Hill et al. 1987: Table 2
Experimental[f]	W. Nevada: Wetland Marshes	Fishes (12 see note)	.042 (.058)	.67	.03	Mass	na	Raymond and Sobel 1990: Table 5
Inujuamiut[g]	NW. Quebec: Low-Arctic Coastal	Mammals (11); Fishes (5); Birds (9)	498 (499)	.81	<.001	Single, Mass	yes	Smith 1991; Table 6.11; Jones 2004: Table 2
Inujjuamiut[h]	NW. Quebec: Low-Arctic Coastal	Mammals (5); Fishes (3); Birds (3)	498 (499)	.63	.05	Single, Mass	yes	Smith 1991: Table 6.11
Piro[i]	S. Peru: Tropical Forest	Mammals (8); Birds (1)	261 (263)	.65	.07	Single	yes	Alvard 1993: Table 2 and p. 372;
Washoe, Historic Euro-American[j]	E. California: Riverine	Fishes (22, see note)	3.17 (3.18)	.54	.01	Single, Mass	na	Lindstrom 1996: Table 9a
Washoe, Historic Euro-American[k]	E. California: Riverine	Fishes (22, see note)	3.17 (3.18)	.81	<.001	Single, Mass	na	Lindstrom 1996: Table 9b
Mayangna and Miskito	Nicaragua: Tropical Forest	Mammals (6); Reptiles (1)	29 (30.5)	.32	.43	Single (w/dogs)	yes	Koster 2008a: Table 2
Martu	W. Australia: Desert	Reptiles (4); Mammals (2); Birds (1); Insect (1)	22 (~22)	.23	.53	Single	yes	Bird et al. 2009: Table 2
Martu[l]	W. Australia: Desert	Reptiles (4); Mammals (2); Birds (1); Insect (1)	22 (~22)	.71	.06	Single	no	Bird et al. 2009: Table 2

a Return rates are separated by season. For reference to costs associated with failed pursuits see Winterhalder (1977:Table 4.3). Weights for moose and caribou are 416 kg and 102.5 kg, respectively.

b Mean return rates (seasons lumped). Moose and caribou weights are averaged and equal 259 kg.

c For reference to costs associated with failed pursuits see Hill and Hawkes 1983.

d Midpoint of return rate ranges. Pursuit costs estimated from interviews with experienced Utah hunters.

e This data set is independent from Hawkes et al. 1982. Return rate for white-lipped peccary excludes tracking time.

f Twelve wt. classes for G. bicolor. Does not include failed pursuits since every net set contained some fish (A. Raymond, pers. comm.)

g Return rates separated by season. For reference on costs associated with failed pursuits see Smith (1991:Table 6.2).

h Mean return rates (seasons lumped).

i Includes return rates for Brazilian tapir (Tapirus terrestris) and Capybara (Hydrochaeris hydrochaeris); handling times estimated.

j Fresh consumption; 22 size/capture method categories used; mean return rates reported here from ranges.

k Dried for storage; 22 size/capture method categories used; mean return rates reported here from ranges.

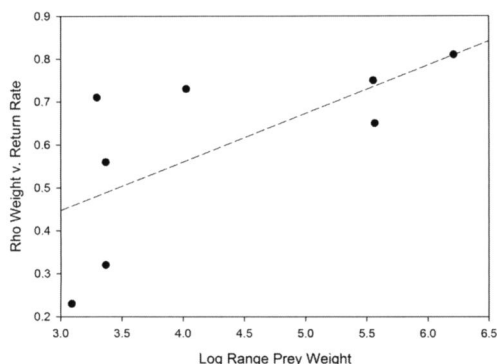l Excludes tracking and pursuit time.

Figure 1. Relationship between log range of prey weight within a data set and the strength of the correlation between body size and return rate (from terrestrial prey data sets in Table 1).

pointed out that post-encounter return rates *for small-bodied prey* might vary considerably due to variation in prey mobility. Indeed, in the entire sample of studies that include terrestrial hunting, the size range of exploited prey is positively correlated with the strength of the correlation observed between body size and post-encounter return rate (r_s = .73, p = .04; Figure 1; see Morin 2011 for further discussion). That is, the studies that incorporate a greater range of prey sizes tend to produce stronger correlations between body size and return rate, suggesting that variability in factors such as prey mobility is likely to confound the general body size–prey rank relationship only when the range of body sizes involved is small to begin with.

In sum, the logic outlined above and the complementary empirical support just summarized provide a secure foundation for using body size as a proxy measure of prey rank in many cases. In turn, this provides a basis for constructing and testing specific hypotheses about variability in overall foraging efficiency, as measured by the relative abundances of different-sized prey, in relation to trends in human demography and/or environmental change. To be sure, the empirical data do suggest that attention should be paid to the magnitude of the range in body size among the prey types that are considered in any analysis. We next illustrate how this might be taken into account by exploring in further detail the relevant characteristics of artiodactyls and lagomorphs, the vertebrate taxa most often considered in North

American archaeological applications of foraging theory. We then show how concerns about the generality of the body size–return rate relationship can be further alleviated by employing body-size-based abundance indices as only one of a battery of archaeological and paleoenvironmental indices in tests of hypotheses about foraging efficiency.

Mobility, Return Rates, and North American Terrestrial Mammals: Artiodactyls and Lagomorphs

Artiodactyls and lagomorphs were primary faunal resources used by prehistoric peoples in North America, and collectively they dominate many, if not most, archaeological faunas from the interior of the continent. These prey types differ considerably in body mass and were the focus of the original foraging theory-based abundance index, the Artiodactyl Index, which has since become the single-most widely applied abundance index used to track foraging efficiency and diet breadth. The Artiodactyl Index has figured prominently in recent reconstructions of trans-Holocene trends in large-game hunting in western North America and the associated debate about whether those trends are driven solely by concerns of foraging efficiency or, alternatively, by factors related to mating effort, costly signaling, and prestige rivalry (Broughton and Bayham 2003; Broughton et al. 2008; Byers and Broughton 2004; Hildebrandt and McGuire 2002; McGuire and Hildebrandt 2005). While much of this debate has centered on the economics associated with harvesting artiodactyls and lagomorphs, the potential influence of differences in mobility between artiodactyls and lagomorphs on their return rates has not been examined in detail.

Mobility, Failed Pursuits, and Return Rates for Artiodactyls and Lagomorphs

To begin such an examination, we first point out that, using the classification of Bird et al. (2009:11), all artiodactyl and lagomorph taxa would be considered "fast" prey—the highest category on their scale of prey mobility. The maximum running speeds for black-tailed jackrabbits (*Lepus californicus*), for example, exceed 64 km/hr, falling within the range of speeds for most artiodactyls, including mule deer (*Odocoileus*
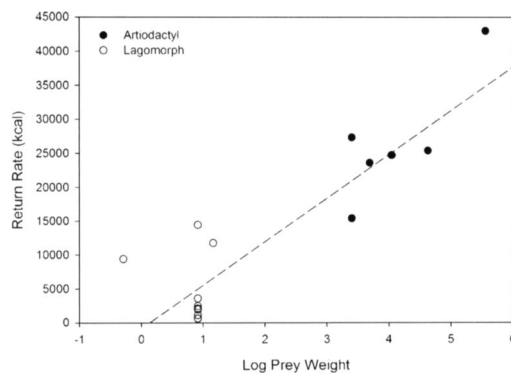
Figure 2. Relationship between log weight and return rate for artiodactyls and lagomorphs. Data from references in Table 1 and Ugan (2005a).

hemionus), elk (*Cervus canadensis*), bison (*Bison bison*), and bighorn sheep (*Ovis canadensis*) (Garland 1983; Garland and Janis 1993; Morin 2011). The great agility and elusiveness of lagomorphs, although difficult to quantify, is also legendary and may be enhanced by their smaller size relative to artiodactyls. These considerations suggest that pursuit costs and the probability of failed pursuits might be broadly comparable for artiodactyls and lagomorphs—or even higher for lagomorphs—all else being equal. If so, then post-encounter return rates for artiodactyls and lagomorphs would, on average, be largely a function of the substantial differences in body size that separate the two orders. This is, in fact, born out by the available empirical data on returns for these taxa.

Figure 2 shows the relationship between log prey-body size and empirically derived post-encounter return rates for the entire sample of North American artiodactyls and lagomorphs. These include all of the relevant data from the studies in Table 1 as well as several return-rate estimates for lagomorphs provided in Ugan (2005a). The relationship is positive and highly significant ($r^2 = .80$, $p < .0001$; $r_s = .84$, $p = .0004$), with dramatically significant differences in mean return rates between the two orders ($t = 6.58$, $df = 17$, $p < .0001$).

Further information on mobility-related pursuit costs are available from studies involving modern lagomorph and artiodactyl hunters in eastern North America (Holsworth 1973; Morgan 2005; Ruth and Simmons 1999; South Carolina Department of Natural Resources 2009). In these

studies, data on the number of animals pursued per hunt—that is, animals either shot at or "jumped"—are presented along with the total number of animals harvested, enabling the probability of successful pursuits to be estimated. The data on lagomorphs include 11- and 3-year survey periods for cottontail (*Sylvilagus* spp.) hunters from South Carolina and Kentucky, respectively. The artiodactyl data are for white-tailed deer (*Odocoileus virginianus*) hunters from single-year surveys in Ontario and South Carolina.

The average pursuit success rate for 14 years of survey data for rabbits is .56, with yearly values that range between .62 and .42. This means that lagomorphs escape from modern shotgun hunters between 60 percent to 40 percent of the time. The two different white-tailed deer studies produced nearly identical pursuit success rates of .82 and .79, with a mean of .80. Failed pursuits thus occur in only about 20 percent of encounters. The substantial differences in target size and the greater visibility of artiodactyls within areas of dense vegetation, we suspect, may lie at the heart of the difference in pursuit success between artiodactyls and lagomorphs. In any case, these data are consistent with the ethnographically derived return-rate estimates in that they indicate no overlap in pursuit success rates between rabbits and deer.

We are under no illusion that these actualistically derived return-rate and pursuit-success data are necessarily representative of the actual absolute values associated with prehistoric foragers in any particular context. They do, however, provide no challenge to using prey size, the most important knowable economic quality of artiodactyls and lagomorphs, as a source to hypothesize an ordinal-scale ranking of them in archaeofaunal studies. If anything, they suggest that lagomorphs are generally more difficult to capture than artiodactyls, which only reinforces the point that lagomorphs should, in general, provide lower post-encounter return rates than artiodactyls.

Modeling the Effect of Pursuit Success on Return Rates

This analysis can be made somewhat more general by deconstructing, on a theoretical level, the effect of prey capture success on post-encounter return rates. As noted above, in standard formulations, post-encounter return rates are calculated

as e/h, or energetic gain per handling time. As a characteristic of a prey type, the quantity e/h is generally recognized to be an expected or average value (e.g., Stephens and Krebs 1986:13–17), in light of the fact that there may be some intra-prey-type variability in return rate, due to, among other factors, success or failure in pursuit. The effect of capture success on prey ranks can be understood more explicitly by substituting into the calculation of the post-encounter return rate the equality $e = p*g$, where p is the probability of successfully capturing a prey type and g is the average energetic gain provided by that prey type *when pursuit is successful*. Thus, for prey type i, the average post-encounter return rate (r) can be calculated as $r_i = (p_i*g_i)/h_i$, with h representing handling time averaged across both successful and unsuccessful pursuits.[1]

To illustrate, a prey type that could be captured without fail (i.e., $p = 1$) with an average energetic value upon capture (g) of 1,000 kcal and an average handling time of 1 hr would provide an average post-encounter return rate of 1,000 kcal/hr. The exact same average post-encounter return rate would also be provided by a larger-bodied but more elusive prey type with an average energetic gain of 10,000 kcal and an average handling time of 1 hr that could only be captured in one out of ten pursuits $(p = .1)$. When the effects of capture success are made explicit in this manner, it can be seen that the average post-encounter return rate of a large-bodied prey type might indeed be lower than that of a smaller-bodied prey type if the probability of capture success is sufficiently lower for the former than for the latter. Specifically, if prey type 1 is the large-bodied type and prey type 2 is the small-bodied type, then for prey type 2 to provide the higher average post-encounter return rate, it must be the case that

$$\frac{p_2}{p_1} \rangle \left(\frac{g_1}{h_1} \div \frac{g_2}{h_2} \right).$$

Applying this to artiodactyls and lagomorphs, the data used to generate Figure 2 suggest average values of g and h, respectively, on the order of 51,000 kcal and 2.35 hours for artiodactyls and 1200 kcal and 6 minutes for lagomorphs. In turn, this would suggest that the probability of successful capture would have to be at least 1.8 times

greater for lagomorphs than for artiodactyls for the average post-encounter return rate of lagomorphs to exceed that of artiodactyls. Given the modern hunting survey data discussed above, which suggest that pursuit success is likely to be *lower* for lagomorphs than for artiodactyls (perhaps by half), it is difficult to see how prehistoric lagomorph capture success could ever have exceeded that for artiodactyls by such a margin.

Multiple Quantitative Indices of Diet Breadth and Foraging Efficiency

The data just discussed strongly suggest that analyses of patterns in foraging efficiency that rely on the body size–return rate relationship, at least as applied to artiodactyls and lagomorphs, are valid. However, as in any archaeological analysis, even stronger cases regarding trends in foraging efficiency can be made when multiple, independent lines of evidence are employed. In other words, a single abundance index is only one of many individually less-than-fool-proof tools that can be and have been used in these kinds of analyses. It is therefore worth noting that the most compelling examples of prehistoric changes in foraging efficiency do not rely solely on the body size–return rate relationship, but instead have been demonstrated through the use of multiple measures that collectively signal comparable trends. Zooarchaeological complements to body size-based abundance indices may include, but are not limited to, measures of evenness and richness as indicators of faunal diet breadth; skeletal part representation reflecting local depression and distant patch use; age, size, and sex structure as they relate to harvest pressure, prey depression, and habitat quality (e.g., Stiner et al. 2000; Wolverton et al. 2008); and bone fragmentation and other variables that may relate to processing intensity (Ugan 2005b). Abundance indices constructed to reflect the harvesting of prey types from proximal and distant patches have also played a key role in documenting declining returns for central-place foragers in a number of studies (Broughton 1999, 2002; Nagaoka 2002b). Indices constructed to represent the relative frequency of high and low ranking small-sized prey have also been effectively deployed, in many cases relying on distinctive dif-

ferences in prey mobility (Stiner et al. 2000; Stutz et al. 2009; Wolverton 2005).

In addition to these variables—now industry standards in zooarchaeological applications of foraging theory—trends in frequencies of tools (tool abundance indices) associated with the harvesting of particular resources can be established to further test hypothesized trends in prey abundances. In more exceptional cases, independent paleontological data can also provide supporting evidence, as in the example we discuss below involving the trans-Holocene artiodactyl fecal pellet record from Homestead Cave, Utah. Quantitative paleoclimatic indices of many kinds have also long been employed in the context of tests involving trends in foraging returns. And finally, trends in human skeletal paleopathologies and stature have also been linked to trends in foraging efficiency derived from faunal indices: insofar as lower foraging efficiency implies greater foraging effort required to meet minimum caloric requirements and an increased risk of malnutrition, higher levels of morbidity and mortality, slower growth rates, and reduced adult body size should accompany declines in the former (Bartelink 2006; Broughton and O'Connell 1999; Broughton et al. 2010).

To these more established measures we can add promising but still experimental use of faunal bone isotopic and ancient mtDNA analyses. Bone isotope analyses have been used to determine the geographic origin of prey animals and identify possible instances of distant patch utilization driven by local patch depression (Grimstead 2005, 2009). Ancient mtDNA analyses of faunal bone can potentially reveal trends in genetic diversity that may reflect changes in prey population sizes, and preliminary work with California tule elk and Northern fur seal shows promising signs for the approach (Beck 2010).

With the exception of these last measures, where work is still in its infancy, good use of indices constructed from all the other variables listed above has been made in analyses of trends in prehistoric foraging behavior the world over, with most also attentive to taphonomic issues that may cloud their meaning. Table 2 presents a noncomprehensive sampling of studies in this tradition that use body-size based abundance indices, along with the numbers and types of additional in-

dices used to independently inform on foraging efficiency and prey abundances in these settings. We next further illustrate the strength of the "multiple lines of evidence approach" with recent research and ongoing analyses involving Holocene climate change and trends in human hunting efficiency in the northern Great Basin.

Holocene Climate Change and Human Diet Breadth and Foraging Efficiency in the Northern Great Basin

In recent work, we tested the hypothesis that the seasonality of temperature and precipitation played a major role in controlling the population densities of artiodactyls (e.g., bighorn sheep [*Ovis canadensis*], mule deer [*Odocoileus hemionus*], and pronghorn [*Antilocapra americana*]) across the terminal Pleistocene and Holocene of western North America (Broughton et al. 2008). For much of this region, general circulation climate models and a range of paleoclimatic data suggest that seasonal extremes in temperature peaked during the terminal Pleistocene and early Holocene and that early and middle Holocene precipitation followed a winter-wet, summer-dry pattern—conditions known to depress artiodactyl densities. These trends are mirrored in a macrophysical climate simulation model (MCM) developed for the northern Bonneville Basin (Figure 3), northwestern Utah, from which we derived terminal Pleistocene and Holocene climatic values and three indices of climatic seasonality: (1) intra-annual temperature range, (2) summer precipitation intensity, and (3) winter precipitation intensity. These indices were then arrayed against detailed late Quaternary artiodactyl abundance records in the Bonneville Basin. These included a unique paleontological record of fecal pellet densities from Homestead Cave and archaeological records of artiodactyl faunal remains (i.e., an Artiodactyl Index) and large-game hunting tools from Hogup Cave. Each of these artiodactyl abundance records showed significant correlations with the model-derived seasonality indices and suggested that artiodactyls occurred in low densities from the terminal Pleistocene through the middle Holocene, while substantial increases occurred during equable, summer-wet periods of the late Holocene. Although geographic, site- and species-specific variability is

Table 2. Types and Numbers of Different Quantitative Indices used in Tests Involving Trends in Foraging Efficiency and Diet Breadth.

| Location; Primary Site(s)	Body Size AI	Distant Patch AI	Fast-Slow AI	Evenness/ Richness	Skeletal Part Rep.	Age/Size /Sex	Processing Intensity	Human Skeletal	Climate	Tools	Total	Reference
S. Arizona; Ventana Cave	2	-	-	-	3	-	-	-	-	3	8	Bayham 1982, 2010
San Francisco Bay; Emeryville Shellmound	9	2	-	-	1	6	3	-	3	-	24	Broughton 1995, 1999, 2004
Utah; multiple Sites	1	-	-	-	3	-	-	-	-	-	4	Janetski 1997
France; Le Flageolet I	1	-	-	2	1	-	1	-	-	-	5	Grayson and Delpech 1998
New Mexico; multiple sites	1	-	-	-	2	2	-	-	2	-	7	Cannon 2000, 2003
Pacific Northwest; multiple sites	7	-	-	2	-	-	-	-	-	-	9	Butler 2000; Butler and Campbell 2004
S. New Zealand; Shag River Mouth	2	1	-	7	9	0	9	-	1	1	29	Nagaoka 2001, 2002a, 2005, 2006
Pacific Northwest; multiple sites	3	-	-	-	-	-	-	-	-	-	3	Lyman 2003a
Wyoming Basin	4	-	-	-	-	1	-	-	1	-	6	Byers and Smith 2007, Byers et al. 2005, Smith et al. 2008
Great Basin; Hogup, Homestead Caves	1	-	-	-	-	1	-	-	6	1	9	Broughton et al. 2008; Byers and Hill 2009
Utah; Evans Mound, Median Village	1	1	-	-	-	2	12	-	1	-	17	Ugan 2005b
Canadian Arctic; multiple sites	6	-	-	-	-	-	-	-	-	-	6	Betts and Friesen 2006
Hawaii; Nu'alolo Kai	2	1	-	6	-	-	-	-	-	-	9	Morrison and Hunt 2007
NW Coast; Ozette, Moss Landing	1	-	-	-	-	2	-	-	-	-	3	Etnier 2007
Mesoamerica; multiple sites	2	-	-	-	-	-	-	-	-	-	2	Emery 2007
France; Grotte XVI	1	-	-	-	3	-	-	-	-	-	4	Faith 2007
Central California; Diablo Canyon	4	-	2	2	1	1	-	-	-	1	11	Jones et al. 2008
Alaska; Sanak Islands sites	4	-	-	-	-	1	-	-	-	-	5	Maschner et al. 2008
Levant; multiple sites	4	-	2	-	-	1	-	-	-	-	7	Stutz et al. 2009
Central California and SW New Mexico	5	-	-	-	-	-	-	4	-	1	10	Broughton et al. 2010
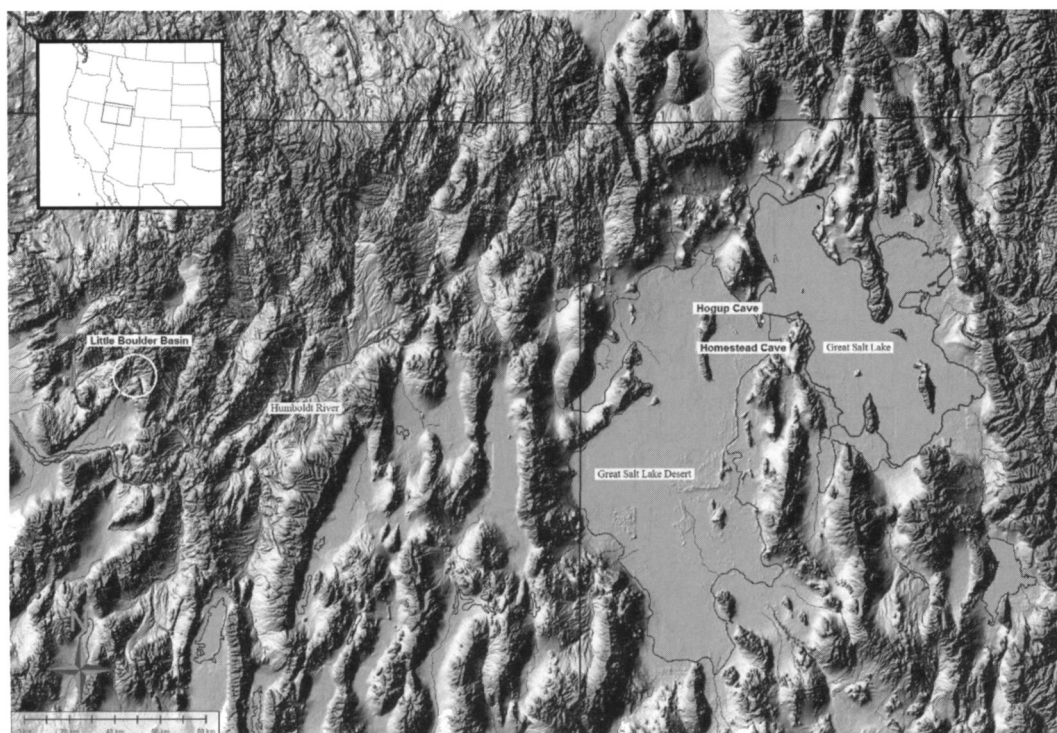
Figure 3. Map of the northeastern Great Basin showing locations of sites discussed in the text.

anticipated and clearly exists (see detailed discussion in Broughton et al. 2008:1931–1932; Byers and Broughton 2004; see also Hockett 2005),[2] archaeological vertebrate records from across western North America showed very similar temporal patterns in artiodactyl abundances, suggesting that the trend and its climate-based correlates may be a very general one.

Insofar as artiodactyls represented high-return prey types to ancient hunters in these settings, these trends should have caused substantial changes in hunting efficiency and diet breadth. More specifically, it can be predicted that the late Holocene spikes in artiodactyl densities should be associated with higher overall hunting efficiencies, and these should be reflected in multiple additional lines of evidence. In this section, we synthesize previous research bearing on Holocene trends in Bonneville Basin foraging efficiency with new tests applied to the Hogup Cave vertebrate fauna and with new data from the Little Boulder Basin, located to the west of the Bonneville Basin in northern Nevada.

Hogup Cave: Previous Research

The deep, well-stratified deposits of Hogup Cave have been the focus of renewed interest in the effect of climate change on trans-Holocene hunting patterns in the Bonneville Basin (Broughton et al. 2008; Byers and Broughton 2004; Byers and Hill 2009; Hockett 2005; Figure 3). Hogup Cave is a limestone cavern located along the southern end of the Hogup Mountains. Sixteen stratigraphic units were encountered during the excavation of the Hogup Cave sediments, which reached over 4 m in depth (Aikens 1970). One-quarter-inch screens were used to collect not only an enormous sample of artiodactyl bones and other faunal remains, but also an extensive record of perishable artifacts, including textiles, nets, and moccasins (Aikens 1970; Durrant 1970; Parmalee 1970). Thirty-two ^{14}C dates place the human occupation of the cave between about 8,800 and 480 years B.P.[3] Although several of these dates are out of stratigraphic order, as others have noted (e.g., Grayson 1993; Madsen and Berry 1975; Mullen 1997), the Hogup Cave dates
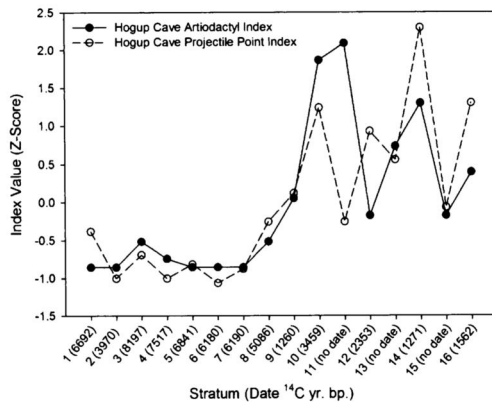
Figure 4. The distribution of the artiodactyl and projectile point indices (standardized) across the Hogup Cave strata.

Figure 5. Comparison between Hogup Cave early/middle and late Holocene aggregate pronghorn age profiles (from Byers and Hill 2009: Table 9).

overall are highly correlated with stratigraphic position ($r_s = .77$, $p < .0001$).

As previously documented, Artiodactyl Index values derived from the Hogup Cave archaeofaunal assemblage are consistently low during the early and middle Holocene but increase, with two marked spikes, during the late Holocene. This pattern is very similar to the trend documented in artiodactyl pellet densities at Homestead Cave (Madsen 2000). Not only are artiodactyl bones proportionately more abundant in the collective set of late Holocene strata compared to those of the early and middle Holocene, their fluctuations within the late Holocene are well aligned with the artiodactyl pellet spikes at Homestead Cave. Both data sets show dramatic peaks in artiodactyl specimens between about 4,000 and 3,000 yrs B.P. and again between 1,200 and 1,000 B.P. Both are also significantly correlated with model-derived indices of climatic seasonality (Broughton et al. 2008).

These patterns are also consistent with temporal trends across the Hogup Cave strata in the relative abundances of artifacts likely used to harvest artiodactyls and lagomorphs. Insofar as nets and snares were commonly used to capture lagomorphs and projectile points were used to kill artiodactyls, then the projectile point index (Σ Projectile Points/[Σ Projectile Points + Σ Cordage]) provides yet another measure of artiodactyl densities and overall hunting efficiency. A theoretical basis for the use of such an index is given by the "tech investment model" (Bright et al. 2002; Ugan
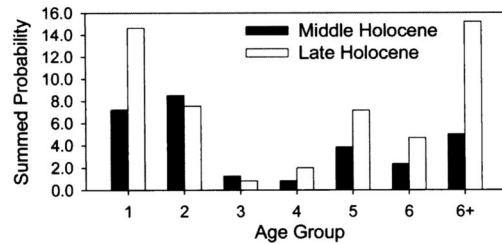
et al. 2003), which provides an innovative framework for linking technological and subsistence change. This model does so by showing that the greater the amount of time spent harvesting a particular resource, the higher the payoff for time invested in technology associated with handling it. The model thus predicts that relative abundances of different kinds of technologies should vary in tandem with the relative abundances of the food resources with which they are associated. Figure 4 shows both the artiodactyl and projectile point indices plotted together across the Hogup Cave strata. The two variables appear well aligned, and a correlation analysis confirms this impression ($r_s = .80$, $p < .01$). Further, this tool-based index of artiodactyl encounter rates and foraging efficiency is also correlated significantly with climatic seasonality indices derived from the local climate model (Broughton et al. 2008).

Recent fine-scale analyses of pronghorn demographic structure at Hogup provide no evidence for any change that might suggest that these patterns in the abundances of faunal remains or tools are related to a shift in the functional use of the cave or a change in the dominant mode of procurement (Byers and Hill 2009; but see Aikens 1970). Dentition-derived mortality profiles are statistically indistinguishable between early/middle and late Holocene assemblages, with both being characterized by an attritional profile suggestive of encounter hunting (Figure 5; Byers and Hill 2009). Planned analyses of skeletal part representation will allow further evaluation of potential changes in site function.

Finally, we note that previous taphonomic analyses of the Hogup lagomorph assemblage provide no suggestion that these trends are related

to changes in the proportionate use of the cave by people and other agents. Most notably, no significant differences are evident in the relative frequencies of raptor/carnivore marks compared to human-induced damage (cut marks, burning) between the early/middle and late Holocene assemblages (Byers and Broughton 2004; Hockett 1993, 1994).

Hogup Cave: New Tests

To further test whether the trends previously documented at Hogup Cave truly reflect changes in hunting efficiency and diet breadth, we apply several additional indices to the vertebrate fauna from this site here. These include a selective efficiency index that incorporates the entire assemblage of identified mammals, rather than only artiodactyls and lagomorphs, and taxonomic richness and diversity indices applied to both the mammal and avian collections from the site (Tables 3 and 4).

Although the trend in the Artiodactyl Index at Hogup Cave is correlated in the expected directions with indices of seasonality, a tool-based measure of foraging efficiency, and the Homestead Cave pellet record, it incorporates only the identified artiodactyl and lagomorph specimens from the collection, and these taxa comprise only 64 percent of the total mammalian MNI from the site. More taxonomically comprehensive tests thus seem warranted, and one such approach is to use a version of Bayham's (1982, 2010; Szuter and Bayham 1989) selective efficiency index (SEI). As adapted here, the SEI may be defined as:

$$SEI = (\Sigma M_i E_i)/\Sigma M_i$$

where M_i is an estimate of the relative abundance of prey type i and E_i is an estimate of the weight in kg per individual of prey type i. In addition to artiodactyls and lagomorphs, values of this index thus include the contributions of the variably abundant rodents and carnivores in the sequence and provide the aggregate mean weight of individual animals recovered from any given stratum. Insofar as body size is an appropriate measure of prey rank in this setting, this index should be low during the early and middle Holocene strata and increase in tandem with other measures during equable climatic periods of the late Holocene. Figure 6 shows that it does just this.

Moreover, the SEI is significantly correlated with the Artiodactyl Index ($r_s = .74, p < .01$), the projectile point index ($r_s = .79, p < .01$), and the three indices of climatic seasonality (winter precipitation: $r_s = -.73, p < .05$; temperature range: $r_s = -.86, p < .01$; summer precipitation: $r_s = .73, p < .05$), which, again, are hypothesized to be driving the trends in artiodactyl densities and overall hunting efficiency. Finally, we note that the SEI is uncorrelated with the underlying strata sample sizes in the Hogup collection ($r_s = -.34, p > .15$), alleviating any concerns that might arise were such a correlation present (e.g., Grayson 1984).

Taxonomic diversity and richness measures can provide additional indices of diet breadth and foraging efficiency in archaeological faunas, especially if used alongside other measures that directly incorporate prey rank estimates. All else being equal, faunas deposited by foragers with wide diet breadths and low foraging efficiencies should be represented by many prey types, with more equal distributions of abundances across them (Grayson 1991; Grayson and Delpech 1998; Jones 2004; Nagaoka 2001; but see also Broughton and Grayson 1993). Conversely, in contexts characterized by high overall returns, hunters should focus disproportionately on only a few of the highest ranked prey. Thus, as has been articulated elsewhere, wide diet breadths should be associated with high numbers of taxa (NTAXA) and high diversity values as measured by measures such as the Shannon-Wiener index ($H' = -\Sigma p_i \log p_i$). We can therefore hypothesize that the early/middle Holocene assemblages at Hogup should be characterized by high NTAXA and Shannon-Wiener diversity values, while those for the late Holocene samples should be characterized by low values of these measures.

Since NTAXA is widely known to be highly dependent on sample size, measured either as total MNI or total NISP (e.g., Grayson 1984, 1991), sample size must be taken into account when assessing variation in richness across the Holocene deposits at Hogup Cave. The approach that we take here to doing this is to compare regressions of NTAXA on sample size for sets of assemblages that are hypothesized to differ in richness (i.e., to test for differences in richness through analysis of covariance). Assemblages that are sampling broader underlying diets should exhibit

Table 3. Hogup Cave ^{14}C Dates and Corresponding Faunal and Climatic Indices.

Stratum	Date[a]	Artiodactyl Index[b]	Projectile Point Index	Shannon-Wiener Index (Mammals)	NTAXA (Mammals)	MNI (Mammals)	Period[c]	Shannon-Wiener (Bird)[d]	NISP (Bird)	NTAXA (Bird)	SEI
1	6692	.04	.20	1.541	15	102	emh	2.146	58	12	2.48
2	3970	.04	.10	1.901	11	111	emh	2.340	24	11	3.29
3	8197	.07	.15	1.811	19	231	emh	1.856	24	6	2.96
4	7515	.05	.10	2.274	16	394	emh	2.289	39	12	4.68
5	6841	.04	.13	1.595	20	428	emh	2.115	28	8	6.01
6	6180	.04	.09	2.356	16	585	emh	2.364	17	10	4.44
7	6190	.04	.12	1.537	20	399	emh	1.714	15	5	5.75
8	5086	.07	.22	2.364	21	441	emh	2.505	26	12	8.73
9	1260	.12	.28	1.710	21	193	emh	1.040	4	2	10.97
10	3459	.28	.46	1.577	9	80	lh	.000	1	1	19.34
11	-	.30	.22	1.693	8	25	lh	.000	0	0	15.88
12	2353	.10	.41	.924	13	137	lh	-	1	1	24.07
13	-	.18	.35	1.512	11	81	lh	.000	1	1	16.62
14	1271	.23	.63	1.764	14	85	lh	.000	1	1	25.99
15	-	.10	.25	2.043	9	25	lh	-	0	0	3.39
16	1562	.15	.47	.548	11	59	lh	.000	1	1	26.73

[a]The dates for strata with multiple radiocarbon determinations are pooled mean dates calculated using Calib 5.1.0 software (Stuiver and Reimer 2005). For strata with more than three assays, dates in excess of one standard deviation from the mean date were omitted prior to calculating the pooled mean.
[b]Raw data for mammalian abundance indices from Durrant (1970).
[c]emh = early/middle Holocene; lh = late Holocene.
[d]Raw data for avian abundance indices from Parmalee (1970).

Table 4. Hogup Cave Strata and Climatic Indices and Artiodactyl and Projectile Point Index Z-scores.

Stratum	Moisture Index[a]	Winter Precip.	Summer Precip.	Temperature Range	Artiodactyl Index (Z-score)	Proj. Pt. Index (Z-score)
1	-40.63	25.80	3.28	31.87	-.856	-.381
2	-	-	-	-	-.856	-1.003
3	-38.08	24.68	3.79	32.46	-.517	-.692
4	-38.27	25.05	3.25	32.20	-.743	-1.003
5	-40.69	25.75	3.11	32.11	-.856	-.817
6	-40.77	25.84	3.40	31.50	-.856	-1.065
7	-40.77	25.84	3.40	31.50	-.856	-.879
8	-40.39	25.69	4.66	30.32	-.517	-.257
9	-	-	-	-	.050	.117
10	-40.11	23.49	8.04	29.88	1.861	1.236
11	-	-	-	-	2.088	-.257
12	-39.51	24.09	9.42	29.32	-.177	.925
13	-	-	-	-	.729	.552
14	-40.00	22.50	9.28	28.90	1.295	2.294
15	-	-	-	-	-.177	-.070
16	-38.95	22.57	8.30	28.73	.389	1.299

[a]The climatic values presented here are from Broughton et al. (2008). As discussed therein, values were not calculated for strata that lacked dates (11, 13, 15) or were represented only by anomalous ones (2, 9).

higher regression slopes and/or intercepts, indicating that they contain more taxa, on average, at any given sample size (e.g., Cannon 2004; Grayson and Delpech 1998). Figures 7 and 8 display the relationships between logarithmically transformed sample size values and NTAXA for the Hogup mammals and birds, respectively, with regression lines plotted separately for the early/middle and late Holocene assemblages (see Grayson 1991 for the protocol we used to count "overlapping" taxa). These data suggest greater richness among the early/middle Holocene assemblages than the late Holocene assemblages— and hence broader diets at times when artiodactyl

densities were low—but the differences are not statistically significant at an alpha level of .05 (Table 5). We do note, however, that the difference in elevation for mammals ($p < .08$) and the difference in slope for birds ($p = .11$) are nearly so.

Turning to diversity, as Figure 9 shows, mammalian and avian Shannon-Wiener diversity indices for the Hogup Cave fauna each decline dramatically in the late Holocene from consistently higher values during the early and middle Holocene. In fact, comparisons between the collective sets of early/middle and late Holocene strata at Hogup show significant differences, in the expected directions, in average diversity index
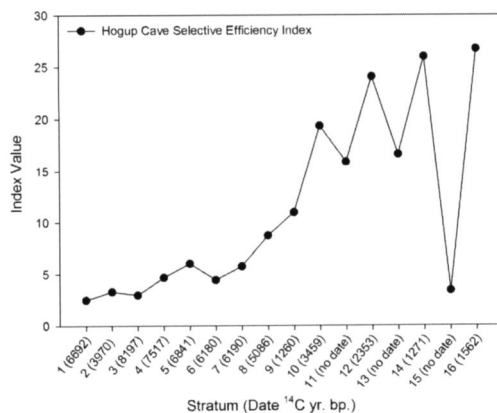

Figure 6. Distribution of the selective efficiency index (SEI) across the Hogup Cave strata.
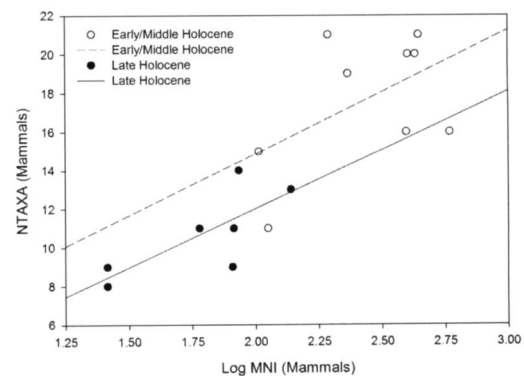

Figure 7. Relationships between NTAXA and sample size for early/middle and late Holocene mammalian assemblages from Hogup Cave.

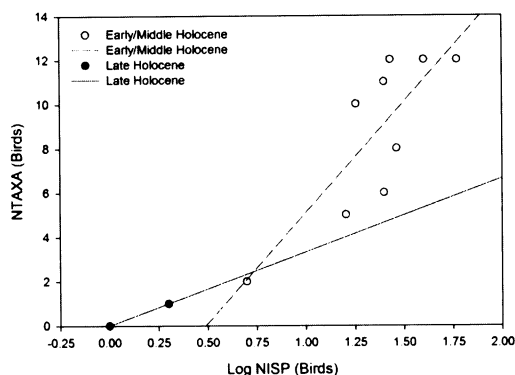**AMERICAN ANTIQUITY** [Vol. 76, No. 3, 2011]

Figure 8. Relationships between NTAXA and sample size for early/middle and late Holocene avian assemblages from Hogup Cave

Table 5. Test Statistics Comparing the log Sample Size-NTAXA Relationships Between the Early/Middle and Late Holocene Assemblages from Hogup Cave.

	Mammals		Birds	
	t	p	t	p
Difference in slope	.06	.47	1.30	.11
Difference in elevation	1.47	.08	.99	.17

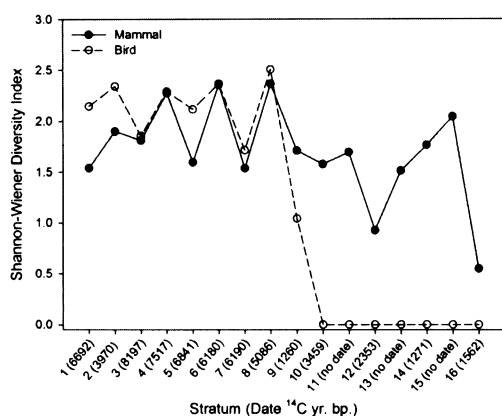Note: All tests are one-tailed.

Figure 9. Distribution of the Shannon-Wiener diversity index for birds and mammals across the Hogup Cave strata.

values (mammals: $t = 2.13$, $p = .05$; birds: $t = 11.87$, $p < .001$). We also observe that there is no significant correlation between the Shannon-Wiener index and sample size for the large collection of mammal materials from the site ($r_s = .40$, $p > .10$).

For the Hogup Cave bird collection, the decline in the diversity index is potentially clouded by a correlation with sample size ($r_s -.87$, $p < .001$). However, we note that the pattern of positive correlations between sample size and both diversity and richness in the avian data set may actually provide further insight into an underlying common cause of the correlations in this instance. It is readily apparent that bird-bone frequencies decline substantially in the late Holocene strata (Table 3), a period when other indicators suggest that foraging efficiency was increasing. Although systematic taphonomic analyses of the Hogup avian assemblage have yet to be conducted, preliminary examination suggests that, while raptors undoubtedly made a contribution, many bird bones exhibit cutmarks or evidence of burning indicative of human involvement in their deposition. Insofar as people played a substantial role in the deposition of the Hogup avian fauna, the intensity of bird harvesting—relative to, say, large mammal hunting—could provide a negative index of foraging efficiency, given both the small size and high mobility of the best represented taxa in the collection (e.g., ducks, eared grebes).

Indeed, the total bird NISP per stratum is negatively correlated with the Artiodactyl Index ($r_s = -.72$, $p < .01$), the mammalian SEI ($r_s = -.57$, $p < .05$), and the projectile point index ($r_s = -.62$, $p < .05$). The precipitous late Holocene drop in bird-bone deposition may thus have its roots in the diet-breadth changes indicated in other aspects of the fauna but at the same time may be generating the depression of both NTAXA and diversity across this period.

Hogup Cave: Summary

Seven distinct indices of foraging efficiency and diet breadth have now been applied to the Hogup Cave vertebrate fauna: two abundance indices based on prey body size (the Artiodactyl Index and the SEI), one abundance index derived from the hunting tool assemblage, and four measures involving taxonomic richness and diversity (two each for mammals and birds). With only a few ambiguities stemming from sample size issues, the indices consistently reflect wide diet breadths and low foraging efficiencies throughout the early and middle Holocene, with dramatic increases in foraging efficiency and reductions in diet breadth

during certain periods of the late Holocene. These trends closely mirror model-derived simulations of variation in climatic seasonality, paleoenvironmental proxy data on seasonality, and paleontological evidence for dramatic Holocene shifts in artiodactyl densities in the region. Although further analyses are planned involving artiodactyl skeletal part representation and bird taphonomy, extant data strongly support the hypothesis that climatic seasonality played a major role in controlling artiodactyl densities across the Holocene in the Bonneville Basin and that human foraging efficiency and diet breadth responded accordingly. Moreover, that such a wide variety of measures vary in a predictable fashion with the body size-based Artiodactyl Index strongly suggests that the body size–return rate relationship is robust in this case and that the Artiodactyl Index is a useful measure of foraging efficiency.

Little Boulder Basin

Insofar as the climatic changes evident in the Bonneville Basin paleoenvironmental record also characterized adjacent regions of the northern Great Basin, we anticipate similar trends in artiodactyl densities and hunting efficiencies in those settings. One such setting is the Little Boulder Basin (LBB), which, though occupied over a shorter span of time limited primarily to the late Holocene, provides a data set comparable to that from Hogup Cave both in the variety of archaeological evidence that can be marshaled and in its consistency with regional paleoenvironmental patterns. The LBB is located approximately 300 km to the west of Hogup Cave in the upper Humboldt River drainage (Figure 3). Research conducted in the context of cultural resource management in this area has resulted in what may be the densest concentration of professionally excavated prehistoric archaeological sites ($n = \sim50$) anywhere in the Great Basin (see Cannon 2010). These sites are predominately open-air artifact scatters, many with numerous hearth features, which appear to have been occupied on a short-term basis by mobile hunter-gatherers who passed through the area during the course of seasonal foraging rounds.

The extensive radiocarbon record from the LBB suggests that sustained human occupation of the area began around 3,000 B.P. and continued without interruption into the protohistoric period. Time-sensitive projectile points indicate sporadic use during earlier portions of the Holocene, but evidence for human occupation from the terminal Pleistocene through the middle Holocene is exceedingly rare. Following convention for the area, our discussion of the LBB archaeological record divides materials into three discrete time periods, necessitated by the fact that many assemblages can be dated only with reference to projectile-point chronologies that are tied to these periods (see Cannon 2010). These include the Middle Archaic period, which in the case of the LBB incorporates materials dating to between about 3,000 and 1,300 B.P. (comprising only approximately the latter half of the Middle Archaic period as this period is recognized throughout the upper Humboldt River region as a whole); the Maggie Creek phase, spanning the period between about 1,300 and 650 B.P.; and the Eagle Rock phase, which ranges from 650 B.P. to the time of Euro-American contact. The Eagle Rock phase is by far the best represented in the LBB excavated site sample, while excavated Maggie Creek and Middle Archaic assemblages are less abundant.

The Maggie Creek phase is closely aligned in time with one of the late Holocene spikes in artiodactyl densities that are evident at the Bonneville Basin sites of Hogup and Homestead caves. Indeed, this period of about 1,300 to 650 B.P. was a time when climatic conditions throughout much of the Great Basin appear to have been quite favorable for both human foragers and their large mammal prey (see overview in Grayson 2006). Winter temperatures were likely elevated during this period, and summer precipitation likely reached its late Holocene maximum due to more frequent incursions of monsoonal storms. Both of these conditions should have resulted in increases in artiodactyl population densities (Broughton et al. 2008). By contrast, the LBB Middle Archaic and Eagle Rock assemblages date to periods (3,000 to 1,300 B.P. and 650 B.P. to contact, respectively) characterized by less-favorable climatic conditions for artiodactyls. We can thus predict that archaeological indices of foraging efficiency in the LBB should be higher during the Maggie Creek phase than either the preceding Middle Archaic period or the subsequent Eagle Rock phase.

Table 6. Little Boulder Basin Vertebrate Faunal Data by Time Period.

Period/Phase	Number of Sites or Site Loci with Faunal Material	Artiodactyl NISP[a]	Lagomorph NISP[b]	Artiodactyl Index	NTAXA	Total Vertebrate NISP[c]
Eagle Rock	14	326	640	.34	9	1013
Maggie Creek	3	423	15	.97	5	446
Middle Archaic	2	2	29	.06	7	83

[a]Includes specimens identified to artiodactyl taxa as well as specimens not taxonomically identifiable but identifiable to the size classes "large mammal" and "very large mammal".
[b]Includes specimens identified to lagomorph taxa as well as specimens not taxonomically identifiable but identifiable to the size classes "small mammal" and "medium mammal".
[c]Includes only specimens identified to taxon; specimens identified only to size classes are excluded.

A summary of faunal data, including Artiodactyl Index values, for the three LBB time periods is presented in Table 6. The Artiodactyl Index is highest for the Maggie Creek phase, and differences in this index among the three periods are highly significant ($X^2 = 503.6$; $df = 2$, $p < .001$; all adjusted standardized residuals fall beyond two standard deviations). This is consistent with the prediction that the favorable climatic conditions of the Maggie Creek phase led to increased foraging efficiency.[4] And, as at Hogup Cave, several additional lines of evidence are available from the LBB to further test this prediction, supplementing the test provided by the body size-based Artiodactyl Index.

One such line of evidence is the taxonomic richness of both faunal and macrobotanical assemblages. As noted above, a basic implication of the prey model is that diet breadth should expand as rates of encounter with high-return resources decline, and such an expansion should be reflected in an increase in taxonomic richness. Vertebrate richness data from the LBB are presented in Table 6. A comparison of regressions of NTAXA on sample size is not useful in the case of the LBB data, as it was above in the case of Hogup Cave, because the very small number of assemblages from the earliest two time periods preclude meaningful regression analyses. Instead, simple aggregate NTAXA values, calculated by pooling the assemblages from each period and counting the total number of taxa present in the aggregate sample from each period, are considered. As expected, aggregate NTAXA is lowest during the Maggie Creek phase and higher during the Middle Archaic period and the Eagle Rock phase, suggesting that artiodactyl encounter rates

and diet breadth changed in tandem in the manner predicted by the prey model. Though we do not evaluate these differences in richness statistically, we do note that they do not appear to be driven solely by sample-size effects: fewer taxa are present in the Maggie Creek phase assemblages than in the Middle Archaic assemblages, even though the Maggie Creek sample is much larger than the Middle Archaic one.

A virtually identical pattern occurs in the taxonomic richness of plant resources. This is shown in Table 7, which presents data derived from counts of charred seeds from radiocarbon-dated hearths. Aggregate plant richness is lowest for the Maggie Creek phase, and this cannot be purely an effect of sample size since aggregate sample size is equal for the Maggie Creek phase and Middle Archaic period; instead, this result is likely reflecting a narrowing of diet breadth during the Maggie Creek phase. At the level of the individual hearth feature, as illustrated in Figure 10, plant richness increases with increasing sample size for the Middle Archaic period and the Eagle Rock phase but does not do so for the Maggie Creek phase, again suggesting that diet breadth was narrowest during this latter period. The differences in regression slope shown in Figure 10 are not statistically significant ($F = .85$; $df = 2$, $p = .434$), but they are consistent with the pattern that is to be expected given the Artiodactyl Index and vertebrate richness data presented above. Collectively, these lines of evidence from the LBB faunal and floral data present a coherent picture of high foraging efficiency and narrow diet breadth during the span between 1,300 and 650 B.P., with lower foraging efficiency and broader diets both before and after this period.

Table 7. Little Boulder Basin Macrobotanical
Data by Time Period.

Period/Phase	Number of Radiocarbon-dated Features with Macrobotanical Material	NTAXA	Total Number of Macrobotanical Specimens
Eagle Rock	38	16	352
Maggie Creek	9	5	56
Middle Archaic	14	8	56

Figure 10. Relationships between macrobotanical richness
and sample size for each LBB time period.

Table 8. Little Boulder Basin Projectile
Point Counts by Time Period.

Period/Phase	Number of Temporally Diagnostic Projectile Points Reported from Excavated Sites	Number of Projectile Points per Calendar Year
Eagle Rock	207	.35
Maggie Creek	618	1.03
Middle Archaic	305	.16

Note: Counts of Elko series points, which were likely used
during both the Middle Archaic period and the Maggie Creek
phase, are split evenly between these two time periods.

Figure 11. Comparison of LBB time-normalized projectile
point frequencies and Artiodactyl Index values (standard-
ized).

Several lines of artifactual evidence from the
LBB add further detail to this picture. One comes
from projectile points. At Hogup Cave, an index
measuring the abundance of projectile points rel-
ative to cordage closely tracks the Artiodactyl In-
dex, a pattern that is entirely predictable in light
of the "tech investment model." A similar index
cannot be calculated for the LBB because per-
ishable materials such as cordage are generally
absent at the open sites that comprise the archae-
ological record of this area. However, the relative
importance of projectile points among time peri-
ods can be measured by normalizing the number
of temporally diagnostic projectile points recov-
ered from LBB excavated sites by the amount of
time spanned by the period of which they are di-
agnostic (Table 8; see Cannon 2010). In normal-
izing the projectile point counts, calibrated cal-
endar years are used rather than uncalibrated
radiocarbon years (see Cannon 2010 for cali-
brated dates), and spans of 600 calendar years are
used for the Maggie Creek and Eagle Rock
phases, while a span of 1,900 calendar years is
used for the Middle Archaic period. Both the ab-
solute number of recovered projectile points and
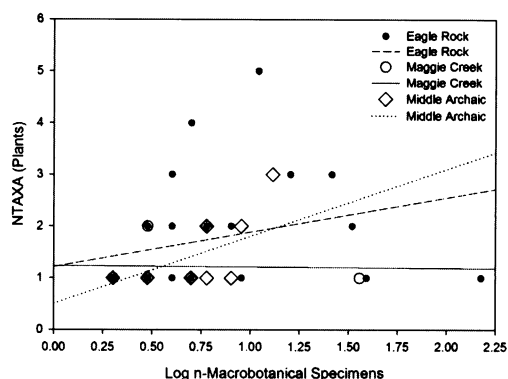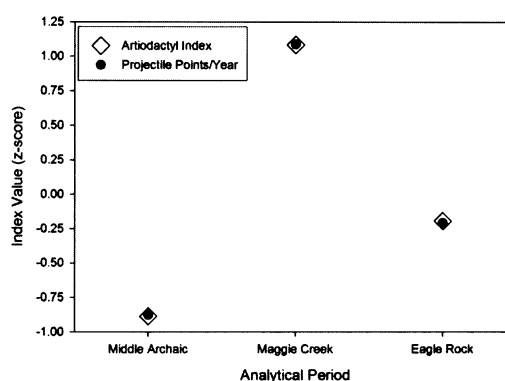the number of points per calendar year are far

higher for the Maggie Creek phase than for the
preceding and following periods. This pattern in
the abundance of hunting tools exactly mirrors the
pattern that occurs in the LBB Artiodactyl Index
(Figure 11), providing further support for the
proposition that late Holocene LBB hunter-gath-
erers experienced the highest artiodactyl en-
counter rates and highest foraging efficiency dur-
ing the Maggie Creek phase.

Whereas projectile points likely comprised an
important component of large mammal hunting
technology, grinding stones surely played a key
role in the processing of low-return plant foods.
Thus, as predicted by the "tech investment model"
and as demonstrated to some extent previously in
the LBB (Bright et al. 2002), measures of the de-
gree of investment in grinding stone technology
should vary inversely with the Artiodactyl Index.

Table 9. LBB Ground Stone Data by Time Period.

Period/Phase	Context	Number of Ground Stone Artifacts	Area (m²)	Number of GS Artifacts per m²	Shape Modified	Shape Unmodified	Shape Modification Index
Eagle Rock	Surface	4	7822	.00051	3	7	.30
	Excavation	6	860	.00698			
	Total	10					
Maggie Creek	Surface	0	30741	.00000	0	4	.00
	Excavation	4	340	.01176a			
	Total	4					
Middle Archaic	Surface	8	82681	.00010	5	39	.11b
	Excavation	40	291	.13746			
	Total	48					

Note: Includes only ground stone artifacts such as manos, metates and pestles that likely served a food processing function.
ᵃArea is not reported for one excavation block, so this is a maximum estimate.
ᵇOf the 48 Middle Archaic ground stone artifacts, 4 are not reported in a manner that allows determination of whether their shape has been modified.

Two such measures of investment in grinding stones can be calculated for the LBB (Table 9).

The first is based on the abundance of ground-stone artifacts, which, consistent with the patterns described to this point, is lowest for the Maggie Creek phase. Absolute artifact abundances, however, are somewhat problematic as an indicator of technological investment since they are as much a function of the amount of effort that archaeologists have expended at sites of a given age. To control for this factor, the ground-stone artifacts from each time period can be subdivided into those from surface and subsurface contexts, and artifact counts can then be normalized either by the total surface area of investigated sites or site loci, in the case of surface artifacts, or by the total area of excavation units, in the case of artifacts from excavation.[5] When this is done, the density of ground-stone artifacts from surface contexts varies in the manner predicted. The density of ground-stone artifacts from subsurface contexts does not do so, but because the area of one Maggie Creek phase excavation block cannot be determined from the relevant excavation report, the excavation density value derived for this phase may substantially overestimate the true value.

The second measure of investment in ground-stone technology that can be derived is a "shape modification index." This index reflects the abundance of ground-stone artifacts that are described in excavation reports as being formally shaped in some manner relative to those that are described as not being so shaped, and it should reflect the amount of time spent manufacturing food-processing implements. This index varies among the three LBB time periods in the manner that would be predicted based on the tech investment model, though due to small sample sizes, the differences are not statistically significant ($X^2 = 3.07$, $df = 2$, $p = .216$). Despite the lack of statistical significance, however, the shape modification index and ground-stone artifact density collectively present a consistent picture of lower investment in grinding technology during the Maggie Creek phase than either before or after this time (Figure 12). The ground-stone shape modification index (Table 9) also tracks aggregate plant richness (Table 7) quite well, suggesting that, in this case, the patterns observed in the ground stone data are reflecting patterns in foraging efficiency and the breadth of the plant component of the diet.

Little Boulder Basin: Summary

Additional lines of evidence reported elsewhere (Cannon 2010), particularly evidence relating to hearth features (see also Bright et al. 2002), provide further support for the conclusion that can be derived from the pattern in the Artiodactyl Index that artiodactyl encounter rates and foraging efficiency during the late Holocene in the LBB were highest, and diets narrowest, between about 1,300 and 650 B.P. It suffices to say here, however, that a variety of independent measures—including vertebrate and plant taxonomic richness, projectile point frequencies, and both the density and the degree of modification of ground-stone artifacts—
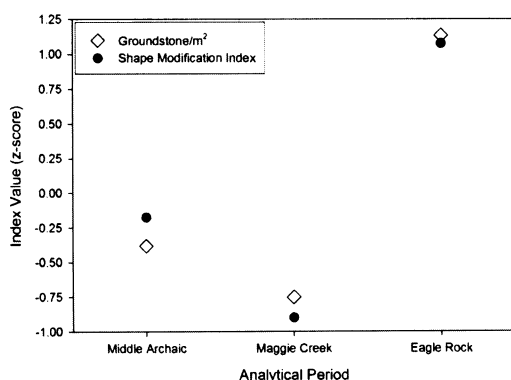
Figure 12. Density of LBB ground stone artifacts from surface contexts and ground stone shape modification index (standardized) by time period.

are all consistent with this conclusion. Thus, as with the Hogup Cave example, this case highlights the usefulness of a body size-based abundance index like the Artiodactyl Index as part of a comprehensive effort to track changes in foraging efficiency and important related behavioral variables. The degree of consistency among all of the various lines of evidence considered in both examples also strongly suggests that the body size-based Artiodactyl Index is a useful indicator of changes in prehistoric foraging efficiency, which in this case appears to be tightly linked to climatic variability.

Conclusion

The use of foraging theory to address issues related to prehistoric foraging efficiency and diet breadth represents one of the more prolific areas of the application of evolutionary ecology in archaeology. The success of this approach has been enabled by the derivation of proxy measures of key model parameters, a requirement in archaeological applications. One of the most widely applied such proxies has been the use of body size as a measure of prey rank, and research drawing on the foundation provided by this proxy has had far-reaching implications for our understanding of many other aspects of human behavior and evolution.

The use of the body-size proxy continues to be supported by the available ethnographic and experimentally derived return-rate data, information that we have summarized here. These data

uniformly show significant positive correlations between prey size and post-encounter return rate, with just a couple of exceptions that occur in cases where only a narrow range of smaller-sized prey are considered. Yet, as with all assumptions that are incorporated into the application of any foraging model, we emphasize that the body size–return rate rule of thumb should always be treated as a hypothesis to be tested rather than as an absolute or invariant claim about past human foraging behavior and prey choice. And because deviations from the general body size–return rate relationship certainly do occur, potential deviations must be considered on a case-by-case basis. In this regard, we note that there are many examples of archaeological applications of foraging theory in which considerable attention has been devoted to such potential deviations (e.g., Broughton 2004; Stiner et al. 2000; Ugan 2005a), and we also emphasize that our understanding of the variables influencing them continues to be enhanced by detailed analyses of contemporary foragers (e.g., Bird et al. 2009).

For artiodactyls and lagomorphs, taxa of particular importance in North American archaeofaunas, the available data show them to exhibit dramatically significant differences in return rates—even in data sets incorporating the costs of failed pursuits. Further, modeling presented here suggests that it is highly unlikely that pursuit success for lagomorphs could ever have been greater than that for artiodactyls to the extent that this might have offset the difference in return rate associated with the difference in body size between the two orders. Previous archaeological applications that have used the body size–return rate rule of thumb for these taxa are thus particularly well supported.

Finally, we also emphasize that most of the detailed analyses of archaeofaunal variability that have used the body size–return rate relationship—operationalized through an abundance index or similar measures—have not relied on this relationship alone. Instead, these studies have employed multiple lines of evidence, including richness and diversity indices, body-part representation, age structure, and measures of technological investment. Our analyses of archaeological faunal, floral, and tool assemblages from the Bonneville and Little Boulder basins represent examples of

this kind of approach. In each of these analyses we have employed at least half a dozen diet-breadth indices, each of which behaves as predicted from a consideration of paleoclimatic data from the northeastern Great Basin. In turn, the fact that such a diverse array of archaeological variables vary in tandem both with each other and with paleoclimatic variables strongly suggests that overall patterns in the archaeological record are reflecting climatically driven variability in foraging efficiency and diet breadth. Perhaps more important for purposes of this paper, the fact that the conclusions that can be derived from a body-size-based abundance index are so consistent with conclusions derived from so many other lines of evidence attests to the robustness of the body size–return rate relationship. Moreover, because the body size of a prey item is one of the few invariant referent properties of prey selection in archaeological contexts, this attribute and its relationship to prey rank can now even more confidently be used and employed to maximize the inferential potential of any prehistoric data set. We therefore conclude that, when used judiciously as one component of broader archaeological analyses geared towards testing hypotheses derived from foraging theory, the body-size proxy for prey rank must be considered more reliable than tenuous, and more robust rather than fragile.

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Notes

1. This formulation assumes for simplicity's sake that average handling time does not differ between successful and unsuccessful pursuits.

2. Insofar as particular spatiotemporal contexts during the early and middle Holocene were characterized by more equable climate, for instance, they may also have supported higher densities of artiodactyls. Primary migration corridors may also have contained relatively high densities (seasonally) of game during these times. In such contexts, increases in the proportional representation of artiodactyls would not be anticipated at the middle-late Holocene transition.

As we discuss elsewhere (Broughton et al. 2008:1931), several records seem to show just this pattern. We stress too that artiodactyl abundances appear to have been highly variable through time *within* the late Holocene, as the Bonneville Basin paleontological and archaeological records so clearly suggest. Thus, generating predictions about variation in artiodactyl abundances at any particular spot on the landscape requires careful attention to locally derived paleoclimatic data. And climatic conditions were, of course, not the only factors influencing the prehistoric abundances of artiodactyls in western North America. Despite generally favorable environmental conditions for artiodactyls across many stretches of the late Holocene, in certain contexts, human hunting pressure appears to have ultimately overtaken them, causing substantial population declines. Such anthropogenic depressions have now been documented in some detail in several areas of western North America. We also emphasize that variation in archaeological site function or the role that sites played in the regional settlement-mobility system can, of course, influence the energetics of prey choice and transport, and affect variation in the taxonomic composition of archaeological faunas, independent of any temporal trends in the abundances of artiodactyls on past landscapes (Bayham 1982; Broughton 1999, 2002; Cannon 2003). A shift in the regional settlement pattern in which the function of a site changed from a residential base to a hunting camp, would, for instance, have obvious implications for variation in the relative abundances of large game skeletal elements or hunting tools recovered from its sediments (see Bayham 1982; Byers and Broughton 2004). And insofar as there is a greater likelihood that large-packaged resources will be field processed, we anticipate kill sites to be biased towards the remains of large-sized prey, regardless of when they were deposited.

3. To maintain consistency with the published literature (e.g., Broughton et al. 2008; Grayson 2006; Madsen 2000), uncalibrated radiocarbon years before present is the time-scale used here.

4. Consistent trends in the Artiodactyl Index also occur at other sites with well-reported faunal assemblages in the upper Humboldt River region. At James Creek Shelter, located approximately 25 km to the southeast of the LBB, the abundance of artiodactyls relative to lagomorphs is also highest in deposits dating to the Maggie Creek phase (data in Grayson 1990). At Pie Creek Shelter, located approximately 65 km northeast of the LBB, the Artiodactyl Index is highest in deposits that date to between about 3,960 and 2,740 B.P. (Carpenter 2004; see discussion of the dating of this site in Cannon 2010). This largely pre-dates the earliest faunal assemblages from the LBB but, notably, corresponds to the earlier of the two late Holocene spikes in artiodactyl abundance observed at Hogup and Homestead Caves. The Artiodactyl Index then declines at Pie Creek Shelter in deposits that are roughly coeval with the LBB Middle Archaic assemblages. The Pie Creek Shelter faunal data are unfortunately not useful for exploring trends in artiodactyl relative abundance during the Maggie Creek and Eagle Rock phases because materials from these phases are stratigraphically comingled at the site (see Young 2004:45–46).

5. Due to very low rates of deposition during the Holocene, buried archaeological materials in the LBB generally occur within the first 20 cm below surface, and excavations routinely proceed no deeper than this. Therefore, excavation unit area, rather than volume, is an appropriate measure of excavation effort.