



# Mass Collecting and the Diet Breadth Model: A Great Basin Example

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The energetic return rates of many small animal and plant resources are often density dependent. When these resources are collected in mass, change in abundance can dramatically affect diet rank, and challenges the assumption that return rates are generally correlated with body size. When mass collecting is employed, as a result of either natural events (e.g. windrows) or technological developments (e.g. nets), population density may largely determine the overall return rate for a resource. Since a single food or resource type can be many prey types, an increase in the abundance of a food resource can change its diet rank. We examined this relationship at Lakeside Cave in northwestern Utah, and discovered that when the abundance of grasshoppers is high, and mass collecting is productive, the hunting of bighorn sheep and other large animal resources may have been abandoned, contradicting commonly held assumptions about prey size. In archaeological situations it may be necessary to determine what foraging technique was used before assuming that the presence of small animals and fish in the diet is a result of reduced foraging efficiency.

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## Introduction

Over the course of the last several decades, a variety of models, derived ultimately from economic theory through a filter of biological thought, have come to be an explanatory staple in anthropology generally, and archaeology particularly. Loosely grouped under the rubric of “Optimal Foraging Theory,” these models have been used to explain behaviour as diverse as differential transport (Jones & Madsen, 1989), field processing (e.g. Metcalfe & Barlow, 1992), differences in resource utilization (e.g. Hawkes, Hill & O’Connell, 1982) and the transition to agriculture (e.g. Layton, Foley & Williams, 1991). One model in particular, the Diet Breadth Model (together with the related Patch Choice Model), has become widely accepted, but is often misused or misapplied. It is not our purpose here to denigrate the use of the Prey Model, because we think it can provide an extraordinary explanatory mechanism when used in appropriate situations. Rather, we want to address problems in both the theoretical understanding and practical applications that have marked its use in some situations. Virtually all of these problems derive from the confusion of “prey types” with “food types,” and

from the broad range of return rates often associated with mass collecting.

The application of these models to human behaviour has been plagued both by the misuse of conceptually appropriate aspects of the models and by the limited ability of the models to distinguish between what constitutes a prey item and what constitutes a patch in which prey items are found. In biological studies of non-human animals, this latter conceptual problem has caused relatively few interpretive difficulties since the behavioural range of a particular species of non-human animal does not vary, from the pursuit of individual prey items to the simultaneous mass collection of multiple prey items, in the way that most human subsistence behaviour does. These interpretive problems are due primarily to a misunderstanding of how variation in the return rates of a particular food or resource type affects diet breadth. This variation requires some care in the application of two general predictions stemming from the Diet Breadth or Optimal Diet Model: (1) that changes in the abundance of lower ranked resources is irrelevant in determining diet breadth; and (2) that the body size of individual prey items is generally correlated with their return rate. These general rules are useful in relatively static

situations when identifying the procurement of individual prey items, but when dealing with dynamic situations and the mass collecting of resources these rules must be applied with some caution.

#### *The models*

The Diet Breadth, or Optimal Diet, model (sometimes called the Prey Model, [Stevens & Krebs, 1986](#)) has been discussed in a variety of forms (e.g. [MacArthur & Pianka, 1966](#); [Schoener, 1971](#); [Charnov & Orians, 1973](#); [Maynard Smith, 1974](#); [Pulliam, 1974](#); [Charnov, 1976](#); [Pyke, Pulliam & Charnov, 1977](#); [Krebs & Davies, 1978](#); [Winterhalder & Smith, 1981](#); [Kaplan & Hill, 1992](#)). This model predicts that a forager will pursue and take a prey type (that is, will include that type in its diet) only if the return rate (the amount of energy acquired minus the amount of energy necessary to attack and process the prey type) is as high or higher than the average return of searching for and handling other higher ranked potential prey types. More explicitly, the model predicts that a prey type will be included in the diet only when the abundance of higher ranked types (i.e. those with higher energy acquisition to energy cost ratios) decreases to the point where it is economically viable to take prey types with lower return rates. In short, “the inclusion of a type [in the diet] does not depend on its own encounter rate ([Stevens & Krebs, 1986: 23](#)),” but rather on that of higher ranked items.

#### *Constraints*

These models have been applied with difficulty in mass collecting situations because a number of assumptions of the Prey Model are not met when a forager preys on several resource items simultaneously. Mass collecting violates a number of the principles and/or constraints of the Prey Model ([Stevens & Krebs, 1986: 18–19](#)): (1) “A [prey] type is either always attacked upon encounter or always ignored upon encounter”, (2) “Searching and handling are mutually exclusive activities: prey are not encountered during handling” and (3) “Encounter with prey is sequential and is a Poisson process.”

In mass collecting, these constraints can be readily violated because an array of items is taken simultaneously rather than sequentially, and prey items that would normally not be attacked are collected along with those that do exceed the attack threshold in the sequential foraging of individual items. These violations of the Prey Model constraints can be resolved, as we discuss below, by treating the entire school or swarm, rather than its constituent members, as an individual prey item ([Steven & Krebs, 1986](#); see also [Steele & Baker, 1993](#)). Even assuming these violations can be overcome, however, it is easy to be confused about what constitutes a “prey type”.

#### *“Prey type” versus “food type”*

A “prey type” is a category of all prey items that have the same return rate ([Stevens & Krebs, 1986](#)). As such,

a single prey type may include food types as diverse as oranges, armadillos and beehives as long as the cost/benefit tradeoff for these different food items is the same. Technically (using energy as a common currency) all items with a return rate of 100 cal/h are one prey type, those with a return rate of 101 cal/h are another, and those with a return rate of 102 cal/h are yet another (although it is unlikely that a forager can discriminate in such detail). Conversely, a particular prey item can be in different prey type categories depending on its proximity to the forager, the time of day, weather conditions or any number of other variables or combination of variables which change the return rate for its collection. While the number of these variables is virtually infinite, two kinds of return rate-altering changes seem most important to us: change in abundance of a food or resource type (which affects all human and non-human foragers alike), and change in the technology with which a food type is procured (which affects primarily human foragers). As a result of change in these major variables, as well as change in innumerable minor ones, individual food types can have extensive return rate ranges. That is, a single food or resource type can be many prey types.

The distinction between food types and prey types has, unfortunately, often been ignored. We are aware, for example, of no anthropological application of a diet breadth ranking that employs a ranking of prey types. Rather, such rankings are uniformly comprised of foods (that is, they list the return rates of various floral and faunal species). Much of this is due to terminological confusion in the theoretical literature. [Kaplan & Hill \(1992: 171–172\)](#), for example, specifically conflate “food types” with “prey types”:

This model has three important implications. First, each individual prey type will always be ignored or always be exploited . . . , depending upon whether it is in the optimal set. If exploiting a food type will increase the average foraging return rate, there is no reason ever to ignore it. If, on the other hand, exploiting it would decrease the average return rate, it should always be ignored. Second, the food value of a resource type alone is not sufficient to determine whether a forager will pursue it; the costs must be considered as well. Thus, foods are ranked by their profitability (net energy gains divided by handling time) not by their food value. Third, the decision to exploit a food type does not depend on its abundance, but on the abundance of the more profitable alternative food types ([Kaplan & Hill, 1992: 171–172](#)).

This conflation of prey type, resource type, food type and prey item is relatively common in the description and use of Prey Models for archaeological purposes (see also, for example [Bettinger, 1992: 84–85](#)) and is one we have also made. Unfortunately, such

terminological confusion has led to a number of misconceptions about how changes in abundance affect diet breadth.

One of the basic predictions of the Prey Model is that “inclusion of lower ranked resources in the diet will depend *not on their own abundance, but on the abundance of higher ranked items*”. Emphasis, as in this quote from Simms (1987: 17), is nearly always given to this statement and it has become one of the more widely known predictions of Optimal Foraging Theory. Unfortunately, while technically correct when phrases like “ranked resources” and “ranked items” are understood to mean individual items, this prediction is easily misinterpreted because (1) return rate rankings are always given in terms of species or food types, and (2) in normal English usage a food “resource” is usually interpreted to mean a type of food rather than a return rate category. This terminological confusion, in turn, leads to the common misconception that changes in the abundance of lower ranked food types are irrelevant to the application of diet breadth models in a given anthropological situation. However, the post-encounter return rate of many resources, particularly those that can be collected in mass, is highly density-dependent, and as the abundance of those resources goes up, so too does their return rate and they change from one prey type to another. By “abundance” we mean the overall regional population density of particular resource types. These may occur either as randomly distributed individual items or as clumps of individual items. In the latter case, density changes can occur both in terms of the number of clumps and the number of individual items within each clump. In most cases the increase is due to a reduction in pursuit time, an important aspect of overall handling costs. For example, the experimentally derived return rates for cricket collecting range from as low as 618 cal/h to more than 33,156 cal/h, with most of that variance due to changes in the abundance of crickets within the foraging area (Jones & Madsen, 1991). Where processing costs constitute the large majority of overall handling costs, on the other hand, as in pickleweed seed collecting (e.g. Barlow & Metcalfe, 1996), changes in abundance have less impact on return rates. As a general rule of thumb, however, *when the abundance of many lower ranked resources increases, particularly mass collected resources, so too does their ranking in the diet as they become higher ranked prey types*. It follows then, that *higher ranked food types can be displaced from the diet with no change in their actual abundance*.

The problem here is not that the Prey Model is incorrect, but rather its inappropriate use and interpretation. Of particular concern is the suggestion that the abundance of low ranked food types is irrelevant. The problem is particularly egregious in many archaeological applications, where the relationship between return rates of “food types” and the diet ranking of “prey types” is often confused. They are

assumed to be the same, or at least very similar, because a resource with a low average return rate is often also included in lower ranked prey types. Return rates for many resources, however, are often highly variable, as in the cricket case cited above, and the rates of a number of food types overlap considerably.

One reason return rate rankings of food types have been used as an estimate of prey type rankings is that experimental and observed data on actual return rates have been so limited as to suggest that the return rate ranges for many resources are constrained sufficiently that they can be easily and reliably ranked as separate prey types. In nearly all cases, however, these return rates are based on only a few experiments or observations, in many cases on a single observation, carried out at a single time, in a single situation, in a single way (e.g. Simms, 1987). In the few cases where multiple return rate experiments or observations have been run on a particular food type, it often exhibits a substantial range of variation (e.g. Hawkes, Hill & O’Connell, 1982; Simms, 1987; Jones & Madsen, 1991). Moreover, the return rates for all food types actually overlap considerably because both experiments and observations of return rates typically ignore marginal situations where return rates will be low after encounter (e.g. Hawkes, Hill & O’Connell, 1982). Return rates for all resources start at 0 cal/h (or lower), since all food types are encountered in situations when and where it would be marginal to collect them. The mean/median return rate of these resources may be distinct, but their ranges overlap. Since a prey type is a return rate and not a food type, pine nuts and cattails are the same prey type for much of their return rate ranges. On average they may be different prey types, but much of the time they are the same prey type.

#### *Mass collecting and patches as prey*

Despite problems with violations of the Prey Model’s constraints, resources taken through mass collecting techniques have nearly always been included with individually collected resources in a variety of anthropological and archaeological situations (e.g. O’Connell & Hawkes, 1981; Winterhalder, 1981; Hawkes, Hill & O’Connell, 1982; Hill & Hawkes, 1983; Simms, 1987; Hawkes, O’Connell & Blurton Jones, 1989; Grayson, 1991a; Smith, 1991; Smith & Winterhalder, 1992; Broughton, 1994a, b). It has been possible to do this because the group of individual items being collected (e.g. seeds in a spikelet of grass collected with a seed beater, fish in a school collected with a weir, ground squirrels collected with a line of traps, oranges in a tree, a warren of rabbits collected in a net, etc.) has implicitly been treated as if the group as a whole was an individual prey item. Although rarely recognized as such (but see Stevens & Krebs, 1986; Smith, 1991; Steele & Baker, 1993), this approach implicitly treats a patch as a prey item, with resources which come in

groups analysed in terms of overall handling costs and energetic returns for the set of items collected as a unit. We think this patches-as-prey approach to treating resources collected in mass is entirely appropriate; a common problem has been the failure explicitly to recognize it as such. This, in turn, has led to a number of conceptual errors, particularly those concerning the relationship between body size and return rate.

Since it is not always possible to measure actual return rates directly, body size has often been used by animal ecologists and archaeologists as a proxy measure of return rates, and, hence, of prey rank (e.g. Griffiths, 1975; Bayham, 1979; Simms, 1987; Broughton, 1994b). This is generally true for the sequential encounter hunting of individual prey items (e.g. Hill & Hawkes, 1983; Hill *et al.*, 1987; Kaplan & Hill, 1992), but is not always a useful rule-of-thumb when applied to resources collected in mass (contra Broughton, 1994a). This is because when a patch (i.e. a group) is the prey, it is the biomass of that part of the group caught simultaneously in the net, weir or snare set that is the comparative unit, not the body size of individual components. For example, when netting birds from a flock, the appropriate comparative unit is the total body weight of all birds caught in a single netting episode, not the weight of an individual bird.

This failure to recognize the valid comparative unit can lead to a number of misconceptions, with one of the more important being that "Other things being equal . . . archaeological faunas dominated by larger-sized mammals should represent a higher level of mammalian predation efficiency compared to faunas dominated by smaller-sized mammals" (Broughton, 1994a: 376) (see also Jochim, 1983; Grayson, 1991a; Broughton & Grayson, 1993). This would only be true if all faunas were collected by the sequential hunting of individual animals. If mass collecting is involved, then faunas dominated by smaller animals (clearly birds, reptiles, fish and insects should be added to mammals in this comparative size list) may well involve more *efficient* predation (Steele & Baker, 1993). As a result, the foraging methods utilized must be identified when separate faunas are being compared to explore questions of diet breadth and resource intensification.

### "Large" versus "Small" Animal Foraging at Lakeside Cave

To explore the question of patches-as-prey and the interpretive implications for the mass collecting of small prey items in groups versus the individual foraging of large prey items, we compared the distribution of large and small animal remains in Lakeside Cave, a dry, stratified cave on the western margin of Great Salt Lake (Figure 1). The cave was excavated in 1984 and partially reported as part of an analysis of

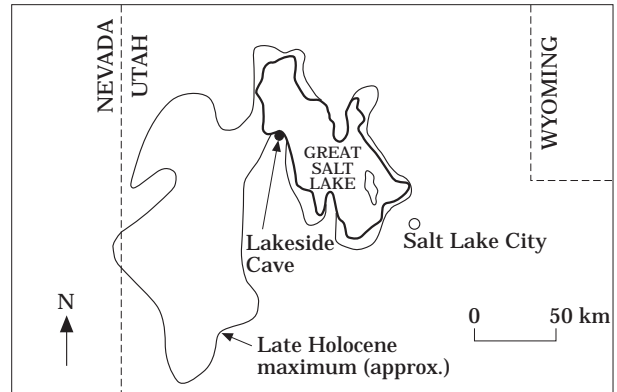


Figure 1. Location of Lakeside Cave in Northern Utah.

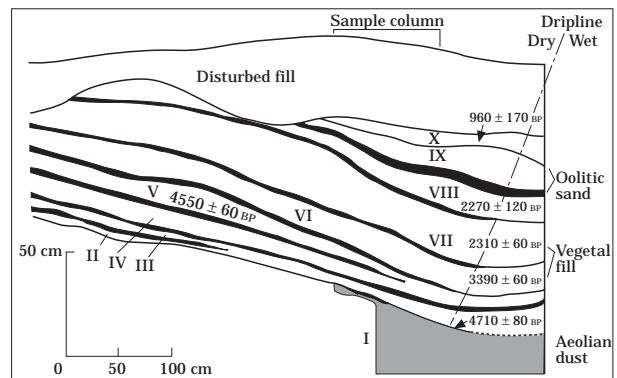


Figure 2. Stratigraphic profile of the Lakeside Cave deposits showing alternating layers of sand and vegetative fill and associated  $^{13}\text{C}$ -adjusted radiocarbon dates. Note vertical exaggeration in scale.

insect use at the cave (Madsen & Kirkman, 1988). Analyses are continuing and we are now able to evaluate this insect use in terms of all the faunal remains at the site.

Lakeside Cave, at an elevation of 1310 m, directly overlooks a series of oolitic sand beaches associated with late Holocene fluctuations of Great Salt Lake (Madsen, *in press*). Cultural deposits in the cave span the last 5000 years and consist of 18 alternating layers of vegetation and oolitic sand derived from these beaches (Figure 2). The oolitic sand layers are relatively thin (2–5 cm) compact deposits with well-defined upper surfaces. However, because the sand sifted down into the underlying vegetative layers (composed primarily of saltbush, greasewood, sagebrush and minor amounts of grass), it was impossible to separate the depositional layers accurately, and the 18 strata were combined into 9 sand/vegetation "sets" for comparative purposes. Fill from a ca. 12 m<sup>2</sup> area was excavated stratigraphically and passed through 6.4 mm (1/4") screen at the site. Bone and artefacts were removed and the remainder of the fill was discarded. The nature of small animal and plant remains was investigated by collecting a 1 m<sup>2</sup> sample column in its



Figure 3. Example of dried human faecal remains from Lakeside Cave. Glossy fragments are parts of grasshopper exoskeletons.

entirety and transporting it to the laboratory where all materials were hand-sorted and separated for analyses.

Large numbers of grasshopper parts (*Melanoplus sanguinipes*) were discovered during the analysis of the sample column and appear to have been a major part of the diet of people visiting the cave. This is not unusual, as a number of regional ethnographies and archaeological investigations document the common use of insects as a food resource (e.g. Stewart, 1942; Steward, 1943; Burgh & Scoggin, 1948; Kelly, 1964; Frison, 1968; Fowler & Walter, 1985; Sutton, 1985, 1995). The details of insect use specific to Lakeside Cave are reported elsewhere (Madsen & Kirkman, 1988), but briefly, the grasshoppers appear to have flown or been blown into the Great Salt Lake where they were then washed up in windrows along the oolitic sand beaches. Faecal remains (Figure 3) suggest that the prehistoric occupants of the cave collected these salted and sun-dried grasshopper windrows from the beaches and consumed them directly with very little, if any, processing. Experimental cost/benefit tests of energetic return rates associated with collecting grasshoppers from lake margin windrows (Madsen & Kirkman, 1988) indicate that return rates vary from approximately 4200–71,000 cal/h with a mean of 27,000 cal/h, but are possibly as high as 710,000 cal/h (measured return rates were arbitrarily reduced by an order of magnitude to compensate for several unknown processing and digestive variables).

We can now compare this insect use to that of large game animals (deer, bighorn sheep and pronghorn) that were also consumed at the cave. While the coarse screen size used in processing the majority of fill from the cave does not allow us to understand the entire array of animal species used by occupants of the cave (e.g. Thomas, 1969; Grayson, 1984), it does not affect the collection and analysis of large mammal specimens and we can accurately compare the distribution and use of large mammals (body weight >50 kg) with grasshoppers (body weight <5 g).

## The Lakeside Cave Animal Remains

Excavations at Lakeside Cave retrieved over 10,000 grasshopper parts (Madsen & Kirkman, 1988) and 4667 animal bones. Bones and bone fragments were quantified by the number of identified specimens (NISP; e.g. Grayson, 1984) per taxon or animal size class. Like most Great Basin caves and rock shelters, the assemblage contains a diverse suite of mammalian taxa (e.g. Aikens, 1970; Grayson, 1983, 1988), including the remains of leporids, small carnivores and a variety of rodents (Schmitt & Manion, in press). The assemblage of large mammal bones is dominated by small artiodactyls. Identified specimens include mule deer (*Odocoileus* cf. *hemionus*), pronghorn (*Antilocapra americana*) and bighorn sheep (*Ovis canadensis*). A large artiodactyl humerus shaft fragment also was recovered and represents either wapiti (*Cervus elaphus*) or, more likely, bison (*Bison bison*). Although taxonomically identified large mammal specimens are few in number, numerous cranial, vertebral and limb bone fragments clearly represent small artiodactyls (NISP=86). The remaining unidentifiable fragments were tallied simply as “large mammal,” but the abundance of small artiodactyls suggests that most represent the remains of deer, pronghorn and bighorn sheep.

Before quantifying and comparing human subsistence data at Lakeside Cave, it is necessary to investigate known and potential accumulating agents. Caves offer shelter for a variety of non-human predators and collectors (e.g. Brain, 1981; Andrews, 1990; Stiner, 1994) where prey remains and scavenged materials are often deposited in association with artefacts and human food refuse (Grayson, 1991b; Hockett, 1994; Schmitt & Lupo, 1995). Human faecal remains containing abundant grasshopper parts were recovered throughout excavations at Lakeside Cave and offer direct evidence of use by prehistoric foragers (Madsen & Kirkman, 1988). Similarly, limited excavations recovered thousands of grasshopper parts and most probably represent the remains of human food resources collected from nearby oolitic beaches. Butchered artiodactyl bones also provide direct evidence of large mammal utilization, but many associated specimens display evidence of carnivore attrition and we are concerned with distinguishing natural bone accumulations from human food refuse. In the following, we briefly examine the types, distribution and frequencies of non-human and human large mammal accumulations at Lakeside Cave. The frequencies of bones interpreted as human subsistence refuse are then compared with grasshopper abundance to investigate variability in hunter-gatherer subsistence strategies.

A total of 1372 large mammal bones was recovered (Table 1). Eighteen specimens possessed pits, furrows and/or scoring marks indicative of carnivore gnawing (e.g. Binford, 1981; Lyman, 1994 and references

Table 1. Attributes of large mammal specimens by NISP by stratum at Lakeside Cave. All tallies include taxonomically identified specimens

Attributes	Stratum									Total
	IX	VIII	VII	VI	V	IV	III	II	I	
Total large mammal	155	83	419	329	175	87	51	26	47	1372
Scat/gnawed	27	6	41	37	16	23	7	4	25	186
Non-scat/gnawed	128	77	378	292	159	64	44	22	22	1186
Butchered <sup>a</sup>	11	4	30	31	2	1	—	2	—	86
Burned/calced	28	7	57	49	19	9	2	2	4	177

<sup>a</sup>Includes cut and flake-scarred bone and percussion-produced bone flakes.

therein). Carnivore tooth-marked bone was collected from strata IX–IV and was especially abundant in stratum VI (NISP=12). We also identified 168 large mammal scatological bones, including numerous limb shaft fragments and foot bones (i.e. carpals, tarsals, astragali and phalanges) (Figure 4). These specimens are characteristically corroded, polished and/or stained as a result of partial digestion by terrestrial carnivores (Andrews & Evans, 1983; Klippel, Snyder & Parmalee, 1877; Schmitt & Juell, 1994). Small clusters of scatological bone were often found in unit/stratum aggregates and probably represent the remains of isolated scatological droppings.

The assemblage of non-scat/gnawed specimens offers evidence of human subsistence activities. Butchered large mammal bones include cut and flake-scarred specimens and a large assemblage (NISP=65) of percussion-produced bone flakes. Flake-scarred specimens (NISP=16) display one or more broad, crescent-shaped impact scars and associated negative flake scars within the medullary cavity (e.g. Johnson, 1985). Most of the flake scars occur on small artiodactyl limb bone shafts and are interpreted as a consequence of marrow extraction. A few flake-scarred bones with associated carnivore tooth marks were also identified and tallied as gnawed bone. Similarly, large bone flakes with broad and largely unmodified platforms (e.g. Blumenshine, Marean & Capaldo, 1996; Lyman, 1994: figure 8.7) were identified as hammerstone-produced bone detritus, while specimens

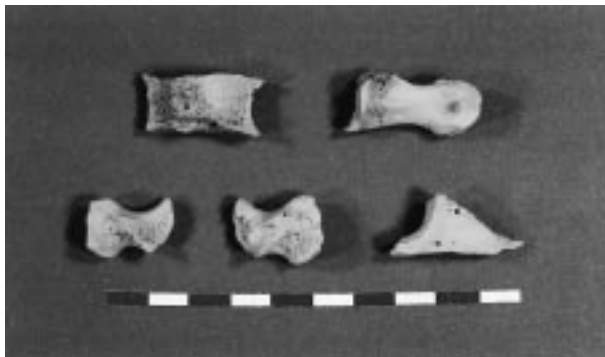


Figure 4. Selected large mammal foot bones showing extensive corrosion from partial digestion. Scale increment is 1 cm.

with carnivore tooth marks were recorded as scat/gnawed bone. Burned large mammal bones were also recovered throughout the deposits (Table 1) and range from partially carbonized limb bones to completely calcined small fragments. While bone accumulations may become burned by natural fires (Grayson, 1988) or inadvertent association with camp fires constructed by humans (Stiner *et al.*, 1995), the varying degrees of burning and context suggest that most of the Lakeside Cave large mammals were burned by human food preparation and/or refuse disposal. The rank order abundances of butchered and burned bone across strata are correlated (Table 1;  $r_s=0.87$ ,  $P=0.007$ ) and suggest that the extent of resource extraction, preparation and waste disposal were equivalent, and that these activities often occurred concurrently.

Cut bone, flake-scarred bone, bone flakes, and, to a lesser extent, burned bone indicate that a variety of human subsistence activities were undertaken at the site. The recovery of flake-scarred bone and bone flakes indicates that elements were often broken for marrow. The rank order abundances of butchered and burned bone are strongly and positively correlated with the remaining non-scat/gnawed specimens ( $r_s=0.933$ ,  $P=0.004$ ) and we assume that these specimens also manifest the by-products of human processing. Gnawed and scatological bone indicate that carnivores (probably canids) also inhabited the site. Whether or not these specimens represent the scavenged by-products of human activities or primary prey is ambiguous, but we believe that most represent carnivore prey accumulations. Recent research has demonstrated that carnivores tend to ignore bones that have been depleted of nutrients by human processing, specially bones that are boiled or exposed to fire (Lupo, 1995). Although domestic dogs have been reported in wetland sites in the eastern Great Basin (see Lupo & Janetski, 1994) and fresh bone acquired by the cave's human hunters may have been fed to and/or scavenged by domestic dogs, the frequencies of scat/gnawed bone by stratum are not correlated with the frequencies of butchered bone (Table 1;  $r_s=0.424$ ,  $P=0.12$ ) nor are they correlated with the aggregates of non-scat/gnawed bone ( $r_s=0.475$ ,  $P=0.10$ ). As a result, we interpret the scat/gnawed bone to be prey remains randomly deposited by wild canids during

Table 2. Numbers of large mammal bones and grasshopper parts by stratum at Lakeside Cave

Stratum <sup>a</sup>	Large Mammal NISP <sup>b</sup>	Grasshopper	
		NISP/1 m <sup>2</sup> <sup>c</sup>	NISP/12 m <sup>2</sup> <sup>d</sup>
IX	128	25	300
VIII	77	198	2376
VII	378	79	948
VI	292	40	480
V	159	3363	40,356
IV	64	3055	36,660
III	44	552	6624
I	22	3215	38,580
Totals	1164	10,527	126,324

<sup>a</sup>No grasshopper sample was collected from Stratum II.

<sup>b</sup>Non-scat/gnawed specimens recovered from 12 m<sup>2</sup> of excavations (6.4 mm mesh).

<sup>c</sup>Specimens from sample column (1.6 mm mesh; Madsen & Kirkman, 1988: Table 1).

<sup>d</sup>Estimated NISP across 12 m<sup>2</sup> of excavations based on 1 m<sup>2</sup> sample.

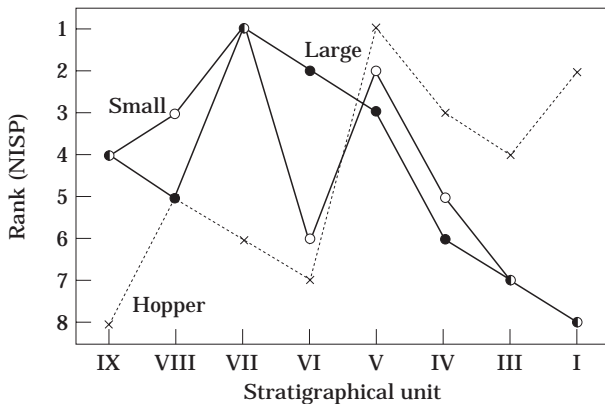


Figure 5. Rank order abundances of large and small mammal bones and grasshopper parts by stratum at Lakeside Cave.

episodes of human abandonment and we do not include scat/gnawed bone in our quantitative analyses.

### Variation in Human Subsistence Strategies

Table 2 presents the numbers of large mammal bones and grasshopper parts recovered from eight stratigraphic units that contained evidence of human habitation. Although each stratum contains the remains of both large and small animal resources, the frequencies of large mammal bones and grasshopper parts are markedly variable. The rank order abundances of large animal and grasshopper remains (Figure 5;  $r_s = -0.48$ ,  $P=0.11$ ) suggests that prominent shifts in human subsistence occurred at Lakeside Cave. During the Late Holocene occupations associated with strata VI and VII, foraging strategies for procurement of animal resources centred primarily on the pursuit of large game. Conversely, logistical hunting of large game was often ancillary to the mass collection of

grasshoppers. This was the case especially during the occupations associated with strata I–IV where grasshopper abundances often overshadow artiodactyl bone frequencies and logistical hunting of large game may have been ancillary to the mass collecting of smaller resources. When windrows of tens-of-thousands of salted and sun-dried grasshoppers accumulated on nearby oolitic beaches, human foragers may have largely abandoned the pursuit of “high-ranked” large prey and focused instead on patches of very small animals. The abundance, as well as the proximity (Madsen & Kirkman, 1988: 602; Jones & Madsen, 1989), of this resource would have significantly increased its ranking in the diet and the return rates from mass collecting would have exceeded those from hunting large mammals, especially when considering the associated search, transport, and processing costs. During occupations associated with the deposition of strata V and VIII, both large game and grasshoppers were collected, suggesting their return rates (and hence, their abundance) were such that they were within the same set of prey types.

While differences in large mammal and grasshopper-part frequencies reflect substantial changes in human subsistence strategies, there are additional cultural and environmental factors that may have affected the accumulation of faunas at Lakeside Cave and our subsequent interpretations. For example, the cave’s hunters may have acquired large mammal resources throughout the Holocene and the periodic decrease in artiodactyl bone frequencies may reflect gender-based differences in resource procurement and consumption, an increase in carcass processing and consumption at kill sites and/or variation in body-part transport (e.g. O’Connell, Hawkes & Blurton Jones, 1988, 1990). However, differences in transport costs (e.g. Jones & Madsen, 1989; Metcalfe & Barlow, 1992) and the presence of a large lake surrounding the site on three sides make this unlikely. Although the prospect of behavioural variability in carcass processing and transport cannot be resolved, numerous ethnohistoric accounts (Madsen & Madsen, 1987; Madsen & Kirkman, 1988) suggest that joint male and female collection of insects was common in the eastern Great Basin, particularly when they were abundant, so gender difference in procurement strategies seems an unlikely explanation.

It is also possible that the region witnessed intermittent environmental degradation where large mammals were rare or absent. Fortunately, the potential effects of environmental change on subsistence strategies can be examined by investigating the types and frequencies of other biotic resources. The most accessible comparative data sets at Lakeside Cave are the aggregates of small mammals. Caloric returns from hunting individual small mammals (i.e. leporids and rodents) are generally low-to-moderate in rank; they are below that of large game (see, for example Simms, 1985: 121–122 for animal return rates) but commonly exceed those

from collecting of individual insects (Jones & Madsen, 1991). If large game were scarce or unavailable, and assuming that humans did not venture to the Lakeside Mountains if conditions were so severe that all biotic communities were impoverished, leporids and rodents would have comprised the upper end of the diet breadth and the Lakeside faunas should exhibit an increase in small mammal frequencies as large mammals decline. Moreover, and of importance here, increases in grasshopper abundance that correspond with decreasing large and small mammal remains may reflect a narrow diet breadth that centred on the mass collection of high-ranked patches of small prey.

To investigate the nature of all animal resources and more fully examine human diet breadth, the Lakeside Cave small mammal frequencies (Total NISP=1418) were compared with frequencies of large game. As was the case with the large mammals, numerous small mammal bones (including ground squirrel [*Spermophilus* sp.], desert woodrat [*Neotoma lepida*], chisel-toothed kangaroo rat [*Dipodomys microps*], cottontail [*Sylvilagus* sp.], and jackrabbit [*Lepus*]) exhibited evidence of partial digestion by non-human predators. Schmitt & Manion (in press) excluded these specimens and found the rank order abundances of the non-scat/gnawed small mammal remains by stratum to be correlated with large mammal bone frequencies (Figure 5;  $r_s=0.74$ ,  $P=0.02$ ). Although there are numerous problems associated with distinguishing human versus non-human small mammal accumulations, the correlation between large and small mammal bone frequencies and their lack of correlation with grasshopper abundances is intriguing. If these data are correct, hunters appear to have periodically abandoned the pursuit of both large and small mammals and the cave's inhabitants engaged in the intensive collection and processing of dense patches of grasshoppers that accumulated on nearby beaches. This was the case especially during the occupations associated with strata I-IV where grasshopper abundances greatly exceed the remains of both large and small mammals and probably reflect the consequences of mass collecting.

## Discussion

At times, hunter-gatherers at Lakeside Cave seem to have given up the hunting of large mammals almost entirely in favour of grasshopper collecting, and, at first glance, the situation appears to be an exception to a number of predictions derived from foraging theory. Individually collected insects rank well below virtually all hunted mammal resources, as they should, given the disparity in size among the resources (Simms, 1987; Jones & Madsen, 1991). Unless the abundance of all mammals is reduced to extraordinary levels, insects should almost never enter into the diet. Why are they so obviously in the diet at Lakeside Cave?



Figure 6. Grasshopper windrows on the oolitic sand beaches of Great Salt Lake.

Given the association of oolitic beach sand and grasshopper parts in the dried human faecal material from Lakeside Cave, it is unlikely that grasshoppers were collected on the same individual encounter basis as were bighorn sheep and deer. When abundant, swarms of grasshoppers fly or are blow into the Great Salt Lake and are washed up by wave action into windrows reaching 1.5 m wide by 20 cm thick and containing up to 30,000 grasshoppers per metre. These windrows often stretch for tens of kilometres along the oolitic sand beaches which ring the lake margin (Madsen & Madsen, 1987; Madsen & Kirkman, 1988). It is this linear “patch” of salted and sun-dried grasshoppers which is the target prey, not individual grasshoppers within the windrows (Figure 6). They can be collected by merely scooping them up by the hundreds or thousands by hand or in winnowing trays. The size of these windrow “prey items” exceeds, by many orders of magnitude, the size of an individual deer or bighorn sheep, and it is mass collecting from this target prey which produces return rates which exceed those of individually hunted large Great Basin mammals (Simms, 1987) and which greatly exceed individually collected insects (Jones & Madsen, 1991). The return rates from mass collecting grasshoppers from windrows vary dramatically, with the variance in these return rates due almost entirely to changes in the abundance of grasshoppers within the windrows. Change in the numbers of grasshoppers within each windrow is, in turn, due to overall change in the regional population density of grasshoppers. The lake is a fixed mass collecting mechanism, similar in many respects to a fish weir, and as the general population of grasshoppers increases, more hoppers go into the lake and it collects higher numbers of grasshoppers in each windrow.

In short, as the abundance of grasshoppers goes up, so too does the return rate from mass collecting. Thin, narrow windrows with limited numbers of grasshoppers produce lower return rates, while thick, wider windrows with larger numbers of grasshoppers

produce substantially higher return rates. As the abundance of grasshoppers increases, their viability as a mass collected resource increases, and return rates change in relation to those of the relatively static return rates of individually hunted large game resources. As a result, the diet ranking of grasshoppers also increases and they begin to supplant both large and small game in the diet.

The case of grasshopper collecting and large mammal hunting at Lakeside Cave may seem extreme and due to very unusual natural events. As a result, there may be a temptation to discount the results described here as an exception to the general correlation between prey size and return rate, and to ignore the implications for the analysis of hunter-gatherer diets. We think the situation is just the opposite. The relationship between mass collecting, individual hunting and changes in the abundance of low ranked resources is obvious at Lakeside Cave only because it is so extreme. It does suggest, however, that we must look closely at situations where techniques (such as drives) or technologies (such as nets or weirs) have been developed to create mass collecting strategies, and makes obvious the necessity for understanding the method by which resources are collected.

The abundance of resources that are sequentially hunted on an individual basis is almost irrelevant, since abundance changes have only a modest effect on overall return rates. If the return rate of an individually collected item is sufficiently high to be included in the diet it will usually be pursued when encountered regardless of its overall abundance. When items are mass collected, however, it is the overall abundance of items which may largely determine the return rate, and, in turn, determine whether or not the resource will be pursued. Similarly, when using size as a guide to approximate return rates in analysing the remains of prehistoric diets, it is critical to know whether various resource types were taken individually or collectively, since the return rate of mass collected small items may exceed that of individually collected large items. Evidence of numerous "small" resources in the diet may as easily represent an increase or a decrease in foraging "efficiency" depending on whether or not they were collected one at a time or as a group. While the general predictions of the Prey Model remain valid, it is important to remember that "prey types" and "food types" are not the same, and that, unlike a prey type, *a food resource may be displaced from the diet, with no change in its own abundance or that of higher ranked resources, by abundance induced changes in the return rate of a previously low ranked food type and/or by the introduction of mass collecting technology.*

Careful analysis of archaeological faunas is beginning to reveal the utility of mass collecting other small resource items that commonly come in groups. In the Great Basin, for example, there are several cases in which the mass collecting of small fish with weirs or

nets seems to have been preferred over the taking of larger fish (e.g. Butler, 1996; Nauta, in press), and it is likely that the mass collecting of other small resources also made them more attractive (e.g. Drews, 1990; see also Bird & Bliege Bird, 1997). It is, of course, important to recognize that the mass collecting of large resources undoubtedly produces some of the highest overall return rates. While not yet measured experimentally, running a herd of buffalo or bighorn sheep off a cliff is likely to produce more calories per hour than will netting a bunch of jackrabbits. However, this only emphasizes the need to distinguish individually collected from mass collected resources. As a general rule of thumb, it is possible to assume that larger, individually foraged resources are more likely to have higher return rates than do smaller individually foraged resources, and that large items collected in mass probably produce higher return rates than do small items collected in mass. It is much less reasonable to assume that small items collected in mass have a lower return rate than large items collected individually, since abundance changes can produce a very high degree of variance in return rates.

It is this single factor which is the most critical when incorporating the array of mass collecting strategies into the application of foraging theory to human populations. Changes in the abundance of low return, and consequently low ranked, resources can alter the return rate and ranking of mass collected items to a much higher degree than can changes in those of individually collected resources, and the presence of abundant small animal remains in an archaeological site does not necessarily imply "resource intensification" or broad spectrum foraging. At Lakeside Cave, the hundreds of thousands of elements of very small animals at times reflect an extremely narrow diet breadth and the collection of a high return, high ranked resource. Similar situations may exist at other sites where nets, weirs, trap-lines and other similar means of mass collecting strategies are employed or where natural situations allow.

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