



Changing Diet Breadth in the Early Upper Palaeolithic of Southwestern France

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Archaeological applications of foraging theory models require that variables derived from ecological considerations be translated into archaeological terms. Here, we explore some of the potential difficulties that may exist in the archaeological measurement of diet breadth, a key variable in many foraging theory approaches. We then examine seven ungulate assemblages from the early Upper Palaeolithic site of Le Flageolet I (Dordogne, France) in this light, and show that these assemblages incorporate distinctly different relationships between numbers of specimens and numbers of taxa. While some of the differences involved may be caused by differential specimen fragmentation, the entire pattern of similarities and differences in richness appears to reflect changing maximum diet breadths through time.

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Introduction

During the past few decades, evolutionary ecologists have developed powerful quantitative models for understanding the decisions predators make in acquiring food (Stephens & Krebs, 1986; Kaplan & Hill, 1992; Smith, 1991; Kelly, 1995). Some of these models predict how long a predator will remain in a given part of its habitat, while others, termed prey-choice models, predict which prey types will be taken, and which ignored, on encounter. Foraging theorists have had a great deal of success in applying these models to contemporary human contexts, both in the sense that the models have been shown to have significant predictive power (e.g. O'Connell & Hawkes, 1981; Hawkes, Hill & O'Connell, 1982; Hill *et al.*, 1987), and in the sense that they have led to the precise formulation of novel questions about human behaviour (e.g. Hawkes, 1993).

The archaeological potential of foraging theory has been apparent for some time (Bayham, 1979; O'Connell, Jones & Simms, 1982; Simms, 1985, 1987; O'Connell, Hawkes & Blurton-Jones, 1988; Szuter & Bayham, 1989), but detailed and compelling applications have only recently begun to appear (e.g.

Broughton, 1994*a,b*, 1995). In these applications, concepts that are meant to apply in ecological time must be translated to archaeological time, and variables that are readily measured when they can be observed directly must now be estimated from very different kinds of information (O'Connell, 1995; Grayson & Cannon, 1998). For instance, while energy, measured in calories, is used to calibrate foraging theory models applied to living peoples, past energy returns have, up to this point, either been estimated from prey sizes (e.g. Bayham, 1979; Broughton, 1994*a,b*), or from experiments directed towards measuring return rates directly, under the assumption that those rates applied in the past as well (e.g. Simms, 1987; Madsen & Kirkman, 1988; Jones & Madsen, 1989, 1991; see the discussion in Grayson & Cannon, 1998).

Since prey-choice models are designed to predict that set of resources which will be included in a predator's diet, they are often referred to as "diet breadth" models, with diet breadth defined as "the total number of resources in the diet" (Kaplan & Hill, 1992: 171). In this formulation, resources, or prey types, are in theory defined according to their expected energetic return rates, and are thus not necessarily equivalent to biological species (see the discussion in Smith, 1991). In

Table 1. A summary of the contents and chronology of Le Flageolet I (from Rigaud, 1982, 1993)

Stratum	Cultural assignment	¹⁴ C dates
0-III	Late Perigordian	18,610 ± 440 (Ly-2185)
		22,240 ± 680 (Ly-1606)
IV	Perigordian	24,600 ± 700 (OxA-448)
		21,190 ± 920 (Ly-1607)
V	Perigordian	23,250 ± 500 (OxA-596)
		22,520 ± 500 (Ly-2721)
VI	Perigordian	25,700 ± 700 (OxA-447)
		24,280 ± 500 (Ly-2722)
VII	Perigordian	26,500 ± 900 (OxA-579)
		25,720 ± 610 (Ly-1748)
VIII	Late Aurignacian	26,150 ± 600 (Ly-2723)
		23,280 ± 670 (Ly-1608)
		24,800 ± 600 (OxA-597)
		26,800 ± 1000 (Ly-2724)
IX	Aurignacian	27,350 ± 1400 (Ly-2725)
		20,070 ± 1760 (Ly-1749)
XI	Early Aurignacian	33,800 ± 1800 (OxA-598)

practice, however, resources are often equated with species (e.g. Winterhalder & Goland, 1997), and we follow this equation here.

Some aspects of foraging theory models can be applied archaeologically without measuring diet breadth. However, many applications will require that this variable be quantified in such a way as to allow predictions derived from contemporary ecological considerations to be transferred to predictions that are archaeologically appropriate. Here, we discuss the obvious archaeological measure of diet breadth: the number of taxa incorporated in an archaeological assemblage, using an example drawn from the early Upper Palaeolithic faunal assemblages provided by the site of Le Flageolet I.

Le Flageolet I

Le Flageolet I is a small, well-stratified rockshelter overlooking the north side of the Dordogne River near the small town of Bézenac, southwestern France. Excavated under the direction of Jean-Philippe Rigaud, the site has provided substantial samples of both lithic and faunal material (Rigaud, 1982, 1993; Delpech, 1983; Simek, 1984, 1987; see also Enloe, 1992). These materials are distributed across a series of eight cultural strata deposited between about 34,000 and 20,000 ¹⁴C years ago (Rigaud, 1993). Analysis of the stone tools by Rigaud (1982) has allowed assignment of the Le Flageolet I lithic assemblages to both Aurignacian and Perigordian industries (Table 1).

Of these eight depositional units, one, composite Stratum 0-III, provided only 27 identifiable ungulate specimens. Because the analyses that we present below require samples larger than this, Stratum 0-III is not considered here. Numbers of identified specimens per ungulate and carnivore taxon for strata IV through XI are provided in Tables 2 and 3. Because the focus of our discussion is on the Le Flageolet I ungulates, and because there are many pathways by which ungulate

remains can be introduced into an “archaeological” site, we note that these ungulate assemblages are clearly of human origin. This issue will be treated in greater detail in the forthcoming Le Flageolet I monograph (Rigaud, 1997), but we note that while 219 (4.1%) of the ungulate specimens from this site show cut marks, only 25 (0.5%) show evidence of having been altered by carnivores. These and other indicators lead us to conclude that the Le Flageolet I ungulate assemblage has been overwhelmingly, and perhaps entirely, introduced by people.

Numbers of ungulate taxa at Le Flageolet I

A total of 12 ungulate taxa are represented in the Le Flageolet I faunal assemblages, but not all taxa are present in all assemblages. Not surprisingly, the number of taxa (NTAXA) varies across assemblages, and the number present in any given assemblage scales to the number of identified specimens (NISP) in that assemblage (see Grayson, 1991 for the protocol used to count non-overlapping taxa).

However, unlike many other faunal assemblages that have been analysed (e.g. Grayson, 1984), there are two distinct, and statistically significant, NISP–NTAXA relationships represented at Le Flageolet I (see Figure 1 and Table 4), with the slopes of these relationships significantly different (at $P < 0.05$) from one another. Importantly, “cultural” affiliation is unrelated to position in these relationships: Aurignacian and Perigordian faunal assemblages appear on both high-slope (upper) and low-slope (lower) curves.

Measuring the diet breadth of modern human populations may be time-consuming, but it is at least conceptually straightforward: one counts the resources that are included in the diet. Accordingly, given our equation of resources with species, the simplest interpretation of the two NISP–NTAXA relationships at Le Flageolet I is that these relationships reflect two different diet breadths. In this interpretation, the

Table 2. The Le Flageolet I ungulates: NISP by taxon*

Taxon	Couche							Totals
	IV	V	VI	VII	VIII	IX	XI	
<i>Bos/Bison</i>	4	4	12	124	41	34	38	257
<i>Capra</i> spp.	2	1	22	10	10	12	15	72
<i>Cervus elaphus</i>		29	115	1223	126	79	18	1590
<i>Rupicapra</i> sp.	3	16	6	14	15	10	3	67
<i>Capreolus</i> sp.		1	3	71	2	9		86
<i>Equus</i> spp.		2	3			1		6
<i>E. caballus</i>	4	21	45	28	22	50	66	236
<i>E. hydruntinus</i>				8		11		19
<i>Mammuthus</i> sp.						1		1
<i>Megaceros</i> sp.				1	1	1		3
<i>Rangifer tarandus</i>	132	1170	169	283	240	468	511	2973
Rhinoceros			1					1
<i>Sus</i> sp.				6	4	5		15
Totals	145	1244	376	1768	461	681	651	5326
NTAXA	5	7	8	10	9	11	6	

*Includes specimens identified as “cf.”.

Table 3. The Le Flageolet I carnivores: NISP by taxon*

Taxon	Couche							Totals
	IV	V	VI	VII	VIII	IX	XI	
<i>Canis lupus</i>		1	3	4	4	3		15
<i>Felis sylvestris</i>					1			1
<i>Lynx</i> sp.			1	8		1		10
<i>Lynx spelaea</i>				1				1
<i>Mustela erminea</i>					1			1
<i>Mustela cf. putorius</i>					1			1
<i>Panthera spelaea</i>				1				1
<i>Ursus</i> sp.						1		1
<i>Vulpes vulpes</i>				1				1
<i>Vulpes/Alopex</i>		3	4	10	8	18	5	48
Totals	0	4	8	25	15	23	5	80

*Includes specimens identified as “cf.”.

high-slope relationship resulted from broader diets than did the low-slope one. This is the case because, at any given sample size, the high-slope assemblages contain more taxa than the low-slope assemblages. For instance, at an NISP of 500, the low slope regression equation predicts the presence of 5.7 taxa, while the high-slope equation predicts the presence of 9.2 taxa.

Unfortunately, things are not this simple. First, diet breadths measured archaeologically are not comparable to those measured ethnographically. Second, it is possible that these curves do not measure diet breadth at all. We treat each of these issues in turn.

What do Archaeological Numbers of Taxa Mean?

Ethnographic applications of foraging theory are built from detailed observations of the results of activities that are generally archaeologically invisible: single hunting or gathering events, for instance. Although there are rare exceptions, archaeological faunal assem-

blages reflect the results of an uncontrolled number of indistinguishable collecting events distributed over an uncontrolled, but often long, period of time.

As a result, the number of taxa present in an archaeological faunal assemblage is not directly comparable to diet breadths measured ethnographically. Instead, and as has been argued elsewhere (Broughton & Grayson, 1993), the archaeological measure reflects the maximum diet breadth (in terms of the taxa being monitored—in our case, ungulates) of the human population whose activities accumulated that assemblage across the time period involved.

Effects of time-averaging

Consider, for instance, a human group living in an environment in the absence of significant climatic change. The potential diet of this group includes 10 species, each of which has a distinct return rate (and hence is a distinct “resource type”). Five of these species provide return rates sufficiently high that they are always taken when encountered, while the

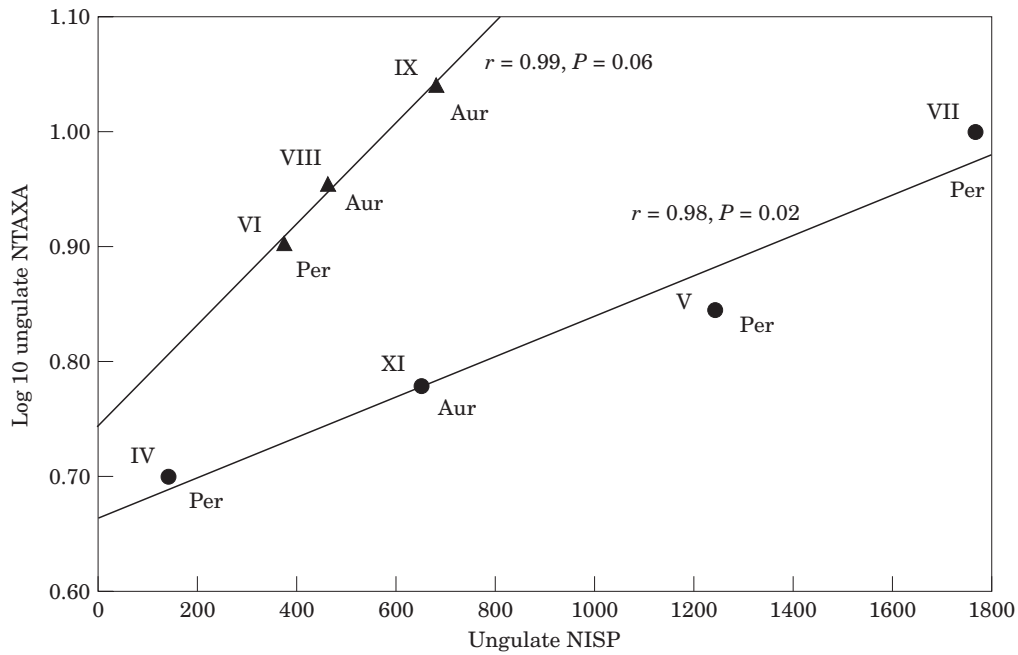


Figure 1. The relationship between ungulate NISP and (Log10) ungulate NTAXA in the Le Flageolet I faunal assemblages (Aur=Aurignacian; Per=Perigordian).

Table 4. Regression coefficients for the relationship between ungulate NISP and (Log10) ungulate NTAXA across the Le Flageolet I ungulate assemblages

Relationship	Intercept (SE)	Slope (S.E.)	Correlation
High slope	0.743 (0.023)	0.00044 (0.00004)	0.995 (P=0.06)
Low slope	0.662 (0.030)	0.00018 (0.00003)	0.978 (P=0.02)

S.E.=standard error; P=probability.

remaining five may or may not be taken depending on the rates at which the five highest-ranked taxa are encountered.

Every spring, the group returns to the same site, which it then uses as a base for collecting, and to which it returns to process all materials collected. Only once a century does the abundance of the five highest-ranked taxa decline to a point that all 10 potential food resources are actually included in the diet. In all other years, only the five highest-ranked resources are taken. The archaeological NTAXA provided by the resultant assemblage will be “10”.

Consider, on the other hand, a human group existing in an environment that provides the exact same set of resources, but in which the five highest-ranking resources have become rare, perhaps due to continued predation (see the discussion of resource depression by Charnov, Orians & Hyatt, 1976). In this context, all 10 resources are always in the diet. The archaeological NTAXA will again be “10”, although the resource structures, and resultant adaptive responses, that have led to these identical measures are quite different.

Finally, consider a situation in which these two contexts follow one another in time at the same site and produce two stratigraphically distinct faunal assemblages with identical NISP values. In both cases, NTAXA will be 10, and one might be tempted to conclude that average diet breadths were identical. This, of course, would be incorrect. Only maximum diet breadths are the same.

Two things follow from these considerations. First, similarities in NTAXA in archaeological faunal assemblages do not necessarily reflect similarities in average diet breadth. However, significant differences in these values might well be meaningful in terms of human adaptation (see Broughton & Grayson, 1993). Second, even if two faunal assemblages provide identical NTAXA values at a given sample size, differences in fine-scaled diet breadth might nevertheless be reflected in the distribution of specimens across taxa. Since high-ranked taxa will always be taken on encounter, their abundances should reflect encounter rates in the surrounding environment. Low-ranked taxa, on the other hand, will be taken only when encounter rates

with higher-ranked taxa decline. Accordingly, analyses of the distribution of specimens across taxa may help determine how frequently lower-ranked taxa were incorporated into the diet. There are a number of measures, both simple (e.g. relative abundances) and complex (e.g. evenness and diversity) that can be used to make such assessments. Of course, any such assessment assumes that dietary ranking can somehow be determined, as for instance, from the sizes of the resources involved (e.g. Broughton, 1994a).

Effects of differential time-sampling

While time-averaging can cause similar NTAXA values to result from different dietary usages, differential time-sampling can cause NTAXA values for the same population to suggest greater dietary differences than actually exist. Take, for instance, the situation described above, in which only five taxa are included in the local diet in 99 of 100 years. A faunal assemblage that incorporates only the first 99 years will provide an NTAXA of five. An assemblage that incorporates all 100 years will provide an NTAXA of 10. That is, the longer an assemblage takes to accumulate, the greater the chances that it will incorporate a low-probability dietary event. If that event incorporates taxa not otherwise represented in the assemblage, NTAXA will increase.

Comparing assemblages that differentially sample time in this way might, as a result, produce contrasts in NTAXA values that simply reflect these sampling differences. Indeed, even if all archaeological assemblages to be compared cover exactly the same amount of time—50 seasons, say—it is still possible that differences in NTAXA reflect nothing more than the incorporation of rare broad-diet events in one or more of these assemblages. Again, if the reasons for similarities and differences in NTAXA values are to be understood in dietary terms, comparisons of NTAXA must be combined with an analysis of the kinds of taxa represented in the assemblages and with an analysis of the distribution of specimens across those taxa.

These considerations by no means exhaust the potential causes of differences in NTAXA among archaeological faunal assemblages. Clearly, alterations in seasonal use, or even in the duration of use, of a site can also cause changes in NTAXA that do not reflect changing diets, but instead reflect changing site use (see the related discussion in Broughton, 1994a, 1995). More broadly, changes in climate and technology can also cause the numbers and kinds of taxa that enter the diet to change as well (Grayson & Cannon, 1998). We return to these matters below.

Mechanical effects

The simple fact of a correlation between sample size and numbers of classes across assemblages does not necessarily mean that changing sample sizes have caused the correlation (Grayson, 1984). In fact, it takes

no great insight to conceive of situations in which the numbers of specimens is the dependent variable in this relationship.

Consider a situation in which continued predation by hunter-gatherers on a set of high-ranked resources causes a severe decline in the abundance of, and hence encounter rates with, those taxa. In response, the human group involved broadens its diet to include a wider range of lower-ranked taxa, and takes more individuals of those taxa than it took of higher-ranked ones prior to the decline. In addition, it continues to take high-ranked taxa on encounter. The archaeological assemblages that result from this process will contain greater numbers of faunal specimens and contain greater numbers of taxa, but it is the dietary shift that has caused the increase in NISP. A stratified sequence containing the shift may reveal two NISP–NTAXA relationships, one high and one low in slope, with the differences in slope reflecting differences in diet breadth.

Unfortunately, purely mechanical factors can also cause different relationships between NISP and NTAXA. Consider a stratified set of faunal assemblages composed of identical suites of taxa based on initially identical numbers of specimens. For whatever reason, some of these assemblages have undergone greater fragmentation than the rest, but the specimens remain identifiable.

If these assemblages are sampled and the NISP–NTAXA relationships analysed, two relationships will result, with the slope of the relationship for the highly fragmented group of assemblages lower than that for the more intact group. This is the case for the simple reason that the highly fragmented set will contain larger numbers of specimens for a given NTAXA value than for the less fragmented set. Below, we refer to this possibility as the “NISP Increase Model”.

This situation may change, however, if fragmentation is differentially distributed across assemblages and fragmented specimens of selected taxa do not remain identifiable. If fragmentation proceeds to the point that certain taxa can no longer be identified at all (e.g. Marshall & Pilgrim, 1991), then those assemblages may appear to have fewer taxa for a given NISP value than was, in fact, the case. We will refer to this possibility as the “NTAXA Decrease Model”.

Accordingly, before NISP–NTAXA relationships can be analysed for their potential meaning in terms of diet breadth, it must be established that the differences involved have not been caused by differential fragmentation.

Differential bone transport and skeletal part representation

Ethnoarchaeological research has established that a wide variety of factors determine how many, and which, skeletal elements will be transported away from a kill site. O’Connell, Hawkes & Blurton-Jones (1988,

Table 5. Fragmentation index (shaft/proximal and distal [PD] specimens) and adjusted residual values for shaft specimens for the Le Flageolet I ungulate assemblages

Stratum	Shaft	PD	S/PD	Shaft adjusted residual
High-slope relationship				
VI	158	66	2.39	- 1.15 ($P>0.10$)
VIII	220	70	3.14	0.84 ($P>0.10$)
IX	362	72	5.03	4.87 ($P<0.001$)
Totals	749	212	3.53	
Low-slope relationship				
IV	92	18	5.11	2.39 ($P<0.02$)
V	863	119	7.25	11.83 ($P<0.001$)
VII	563	489	1.15	- 17.88 ($P<0.001$)
XI	327	84	3.89	2.83 ($P<0.01$)
Totals	1839	710	2.59	

1990), for instance, documented that bone transport among the Hadza of northern Tanzania is determined by a complex combination of variables, including animal size, the amount of meat removed at a kill or scavenging site, distance from the base camp, and the number of people involved in the transport episode (see the review in O'Connell, 1995). Bartram (1993) found no significant relationship between skeletal part utility and relative skeletal abundance in gemsbok (*Oryx gazella*) kill sites produced by the Kua of the eastern Kalahari. The reason, he observed, was simple: the Kua often stripped much of the meat from their prey and left the bones behind. Indeed, Bartram (1993) found a strong positive correlation between the amount of time spent processing animals at kill sites and the number of bones left at those sites.

Differential bone transport produced by such factors can readily produce different relationships between NISP and NTAXA in archaeological faunas. Consider, for instance, two groups of people preying on an identical set of taxa. Whenever any of these taxa is encountered, not only is it taken, but the same number of individuals is taken. If one of these groups always retrieves the entire skeleton, while the second group only retrieves a subset of that skeleton, the bone assemblages produced by these groups will show two distinct relationships between NISP and NTAXA. The relationship displayed by the assemblages produced by the group that always retrieves the entire skeleton will have a lower slope than the one retrieved by the second group. This is the case even though the number of species taken by the two groups is identical.

Indeed, it is not just differential bone transport that can cause this effect. Any process that causes the skeletons in a given set of assemblages to be better represented than skeletons in a second set of assemblages will result in differences in slope in the resultant NISP-NTAXA relationships. This possibility must also be eliminated if those slopes are to be interpreted in terms of diet breadth. Fortunately, this effect should be readily detected as long as differences in skeletal representation are not randomly distributed across skeletal elements.

The NISP-NTAXA Relationship at Le Flageolet I

Differential fragmentation

We first consider whether the two different NISP-NTAXA relationships at Le Flageolet I could be caused by differential fragmentation. To investigate this possibility, we follow Todd & Rapson (1988; see also Lyman, 1994 and the important discussion in Marean, 1991) and use a very simple fragmentation index: the ratio of proximal and distal ends to shafts for all long bones and ribs. We presume, with Todd & Rapson (1988), that greater degrees of fragmentation will differentially increase the number of shaft fragments in this ratio, and hence trace degree of breakage.

If differential fragmentation has increased NISP counts for the assemblages that define the low-slope curve (the NISP Increase Model), then these assemblages should have higher fragmentation ratios than do those assemblages that define the high-slope relationship. The NTAXA Decrease Model is more difficult to deal with, since we currently lack ways to detect taxa that have been so heavily fragmented as to be unidentifiable (but see Hardy, Raff & Raman, 1997). Nonetheless, if this has occurred, then it is again the low-slope relationship that should have higher fragmentation ratios, since it is the low-slope relationship that has undergone sufficient fragmentation to cause certain taxa to become completely unidentifiable. Table 5 provides the relevant raw data and ratios.

We note two aspects of the relationship between degree of fragmentation and position on the high- and low-slope relationships at Le Flageolet I. First, taken as a composite, the four assemblages that form the low-slope relationship have a lower composite fragmentation index (2.59) than do the four assemblages that form the high-slope relationship (3.53), opposite to the prediction of both NISP Increase and NTAXA Decrease Models. Second, chi-square analysis shows that the low-slope relationship has significantly fewer shafts, and significantly more proximal and distal specimens, than does the high-slope curve

Table 6. NISP of major skeletal elements by high- and low-slope assemblages

Skeletal part	High-slope	Low-slope
Phalanges	95*	351**
Metapodials	358*	1051**
Podials	49	117
Tibia	102	299
Femur	84**	158*
Innominate/Sacrum	20	45
Vertebrae	67	157
Scapula	12	48
Ribs	201**	326*
Humerus	57	146
Radius/Ulna	96*	314**
Skull/Mandible	120	289

*Element significantly underrepresented ($P < 0.05$).

**Element significantly overrepresented ($P < 0.05$).

(chi-square=12.23, $P < 0.01$). These relationships suggest that differential fragmentation has not produced the NISP–NTAXA relationships that mark the Le Flageolet I assemblages.

While this is the case, it is also true that there is no fully consistent relationship between degree of fragmentation and position on the two curves. For instance, Stratum VII has the lowest fragmentation index of all eight assemblages, but is on the low-slope curve. Similarly, Stratum IX, with a high fragmentation index, is on the high-slope curve. These positions are also opposite those predicted by both of the fragmentation models considered here.

A more precise view of the relationship between degree of fragmentation and location on the Le

Flageolet I curves can be gained by examining the adjusted residuals for numbers of shafts across all eight assemblages (Table 5). Adjusted residuals are read as standard normal deviates (Everitt, 1977), and thus provide the probability that the cell values in question could have occurred by chance; negative values indicate instances in which the value in question occurs less often than chance allows. According to the fragmentation models we have discussed, shafts should be over-represented in all low-slope assemblages and under-represented in all high-sloped ones. However, as Table 5 shows, they are not.

We conclude that while differential fragmentation may account for some of the patterning in the Le Flageolet I NISP–NTAXA relationships, it cannot account for all of it. We are, as a result, led to seek other causes.

Differential skeletal part representation

Table 6 presents NISP values for major skeletal parts by high-slope and low-slope assemblages for the Le Flageolet I ungulates. Chi-square and adjusted residual analyses show that there are, in fact, significant differences in skeletal part representation across these two groups of assemblages (chi-square=55.76, $P < 0.001$). In particular, phalanges, metapodials, and radioulnae are significantly under-represented in the high-slope assemblages.

Why this has occurred—for instance, whether this pattern represents differential bone transport or some other mechanism—is not important here. What is important is that it is precisely this kind of under-

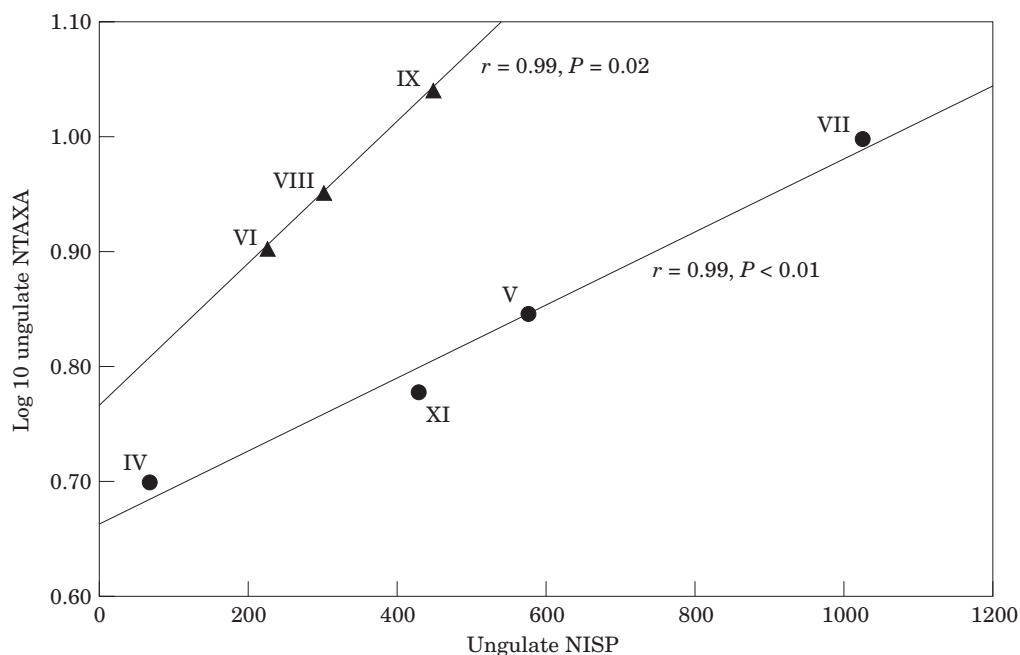


Figure 2. The relationship between ungulate NISP and (Log10) ungulate NTAXA in the Le Flageolet I faunal assemblages with phalanges, metapodials, and radioulnae excluded from the analysis.

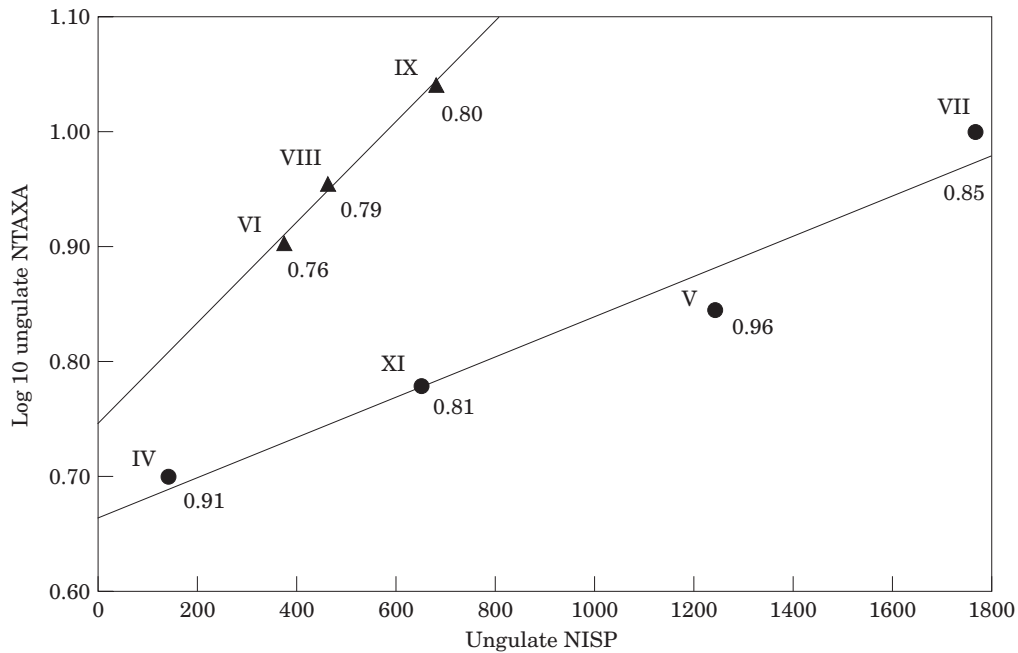


Figure 3. Red deer–reindeer dominance in the Le Flageolet I ungulate assemblages.

representation that can drive NISP–NTAXA slopes up or down and give the impression of differences in diet breadth when none exists. If this has occurred, however, then the effect should disappear when the under-represented body parts are dropped from the analysis. Figure 2 replots the data presented in Figure 1, with phalanges, metapodials, and radioulnae removed. Clearly, the dual relationships between NISP and NTAXA represented at Le Flageolet I remain. The same results occur if over-represented elements are also excluded from the analysis. We conclude that differential body part representation, whether caused by differential bone transport or by some other mechanism, cannot account for these patterns. Note, however, that our analysis assumes that any such differential representation would not be randomly scattered across skeletal elements. Were it so distributed, our approach could not detect it.

Diet breadth

It is, in fact, fairly evident that these curves are primarily reflecting the degree to which the Le Flageolet I assemblages are dominated by two taxa: red deer (*Cervus elaphus*) and reindeer (*Rangifer tarandus*). Figure 3 (see also Table 7) plots the fraction of each assemblage that is accounted for by these two taxa. Those assemblages most dominated by red deer and reindeer form the low-slope relationship.

In addition, the assemblages that form this curve strongly tend to be dominated by either red deer or reindeer, but not both (Figure 4). Because the low-slope assemblages are dominated by a single taxon, they are also less even than the high-slope assemblages

(Table 7; evenness has been calculated as the Shannon Index/ $\ln(\text{NTAXA})$, and varies from 0 to 1; when evenness=1, all taxa are equally common: see Magurran, 1988). While there are significant correlations between NISP and both evenness and red deer–reindeer dominance in the high-slope relationship, there are no such correlations in the low-slope relationship. Not surprisingly, there is a very high correlation between evenness and red deer–reindeer dominance across all assemblages: the greater the dominance, the less even the assemblage (Figure 5).

We thus conclude that the high-slope and low-slope relationships at Le Flageolet do, in fact, reflect diet breadth, even if some of the variability in the NISP–NTAXA relationships can be accounted for by differential fragmentation. The low-slope relationship describes assemblages that are dominated by red deer or reindeer, and hence are less even than those that

Table 7. Red deer–reindeer dominance and evenness values for the Le Flageolet I ungulate assemblages

Stratum	Red deer–reindeer dominance	Evenness
High-slope relationship		
VI	0.755	0.661
VIII	0.794	0.604
IX	0.803	0.485
Low-slope relationship		
IV	0.910	0.262
V	0.964	0.154
VII	0.852	0.454
XI	0.813	0.446

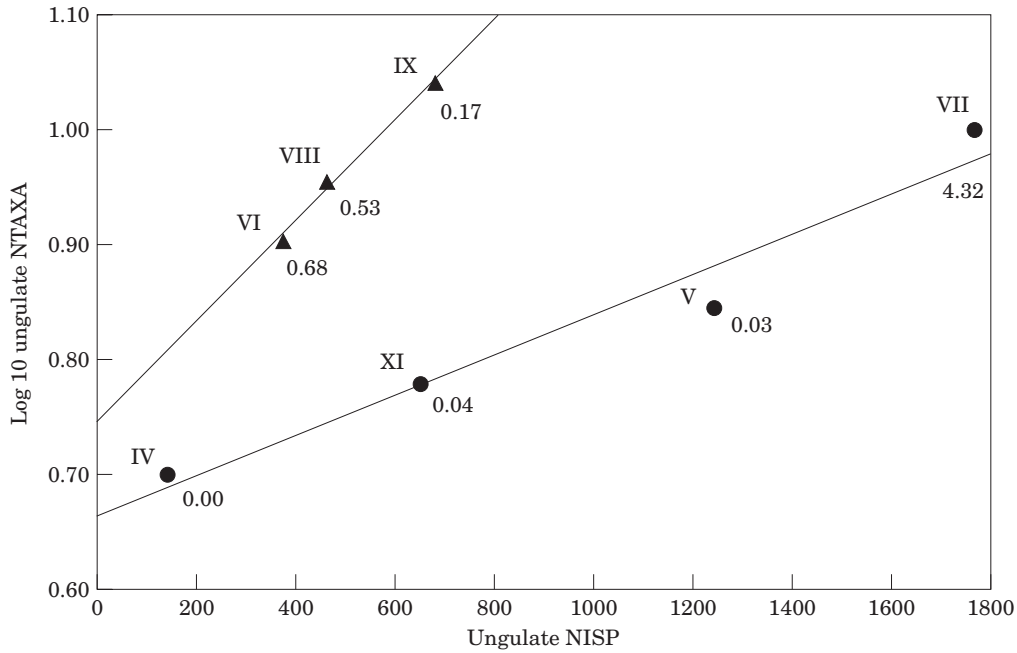


Figure 4. The ratio of red deer to reindeer in the Le Flageolet I ungulate assemblages.

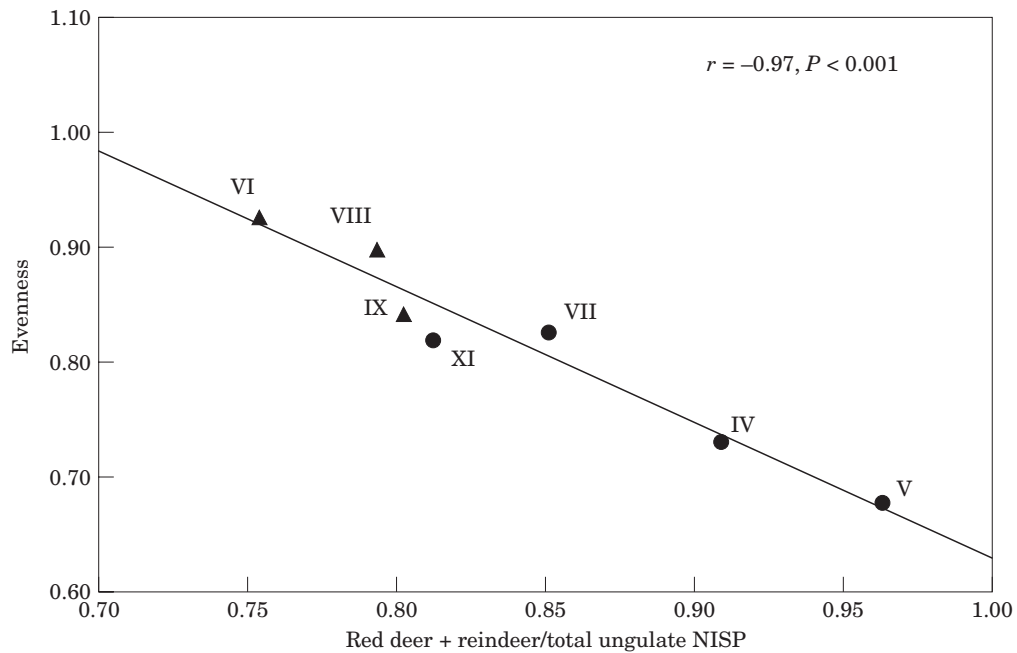


Figure 5. The relationship between evenness and red deer–reindeer dominance across the Le Flageolet I ungulate assemblages; high-slope assemblages are indicated by triangles, low-slope assemblages by closed circles.

form the high-slope relationship. Accordingly, the high-slope relationship contains greater numbers of taxa at a given NISP value than does the low-slope one. The low-slope assemblages reflect maximum diet breadths that were lower during the periods sampled by these assemblages than were the maximum diet breadths during the periods that the high-slope assemblages accumulated.

The question remains, of course, as to why did diet breadth change the way it did through time at Le Flageolet I? This is an issue we do not address here. We do, however, note that the reasons for these changes do not appear to reflect technological innovations. This possibility is made extremely unlikely by the fact the Perigordian and Aurignacian assemblages lie on both curves. On the other hand, we are currently unable to

control for different seasonal uses of the site through time. The information that is available suggests that the red deer or Stratum VII were taken between fall and late spring, but comparable information is not available for other taxa and other strata (Pike-Tay, 1991, 1993). As we argue elsewhere, however, the changes in richness that we have detected appear to have been driven by changes in the nature of the environments that surrounded Le Flageolet I (Delpech & Grayson, 1997).

Conclusions

Archaeological data can be used to test hypotheses drawn from foraging theory models, and thus to aid in the development of those models, or the validity of current foraging models can be assumed and then used to further our understanding of prehistoric land use and diet. We are aware of no instances of the former approach, even though the archaeological record would seem to provide a powerful source of information on the predictive strength of foraging theory models. Indeed, uses of foraging theory models to understand past settlement and subsistence change are themselves very much in their infancy (Grayson & Cannon, 1998).

In either approach, variables that are critical to the models need to be translated into archaeological terms. In this paper, we have examined one of these key variables, diet breadth, and have discussed a series of issues that can complicate the simple use of numbers of taxa in faunal assemblages as a diet breadth measure. However, even though numbers of taxa per assemblage may be problematic in this context, combined analyses of numbers of taxa, numbers of specimens, fragmentation and the distribution of specimens across body parts and taxa can provide strong evidence that diet breadth has, or has not, changed through time.

At Le Flageolet I, the two very different relationships that exist between ungulate NISP and ungulate NTAXA cannot be fully explained as a simple function of differential bone fragmentation or of differential skeletal representation. Instead, we argue that these relationships reflect distinctly different maximum diet breadths at distinctly different times as monitored at this site. These differences, we suggest, do not reflect changing technologies, but instead represent dietary responses to changes in the environments that surrounded Le Flageolet I during the early Upper Palaeolithic.

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