YOST, JAMES A., AND PATRICIA M. KELLEY. 1983. "Shotguns, blowguns, and spears: The analysis of technological efficiency," in *Adaptive responses of native Amazonians*. Edited by Raymond B. Hames and William T. Vickers, pp. 189–224. New York: Academic Press.

Overlapping Species "Choice" by Italian Upper Pleistocene Predators[1]

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Work beginning in the 1940s on species sampling of living animal communities has elucidated a mathematical relationship between the number of taxa represented in nonselective samples and the number of individuals collected from the environment. Whether butterflies of the Malaysian lowlands (Fisher, Corbet, and Williams 1943) or Andean birds along a topographic gradient (Terborgh 1977), rare species can seem rarer or even invisible in small samples. The same relationship holds for the number of taxa (N-taxa) and the number of bones identifiable to taxon (NISP) preserved in archaeological sites (Grayson 1981, 1984). For archaeologists, however, eliminating the possibility of sampling bias is only half the battle, since we ultimately want to know what people were eating and how their choice of foods responded to the standing (but immeasurable) content of animal communities in the past.

Most zooarchaeological analyses of taxonomic abundance implicitly or explicitly assume that the species eaten will reveal important features of human ecology and evolutionary changes therein—once over the hurdle of numerical sampling effects. But can predatory adaptations be distinguished on the basis of the species consumed, or do humans and other predators respond directly to abundance? This question has been asked over and over by community ecologists working in modern settings. More often than not, data on predatory mammals and birds testify to the overwhelming influence of natural abundance on prey species selection *within* major trophic levels, such as among frugivores, insectivores, or carnivores (e.g., Schoener 1982, Terborgh 1977), despite most studies' having been directed to finding difference (e.g., Bertram 1979, Eisenberg 1990, Koehler and Hornocker 1991, Leopold and Krausman 1986, Major and Sherburne 1987, Skinner, Henschel, and van Jaarsveld 1986). Predators may vary in their relative emphases on certain prey species within a shared array, but there is much overlap even so, especially between predators of similar body size such as African lions and spotted hyaenas or leopards and cheetahs (Bertram 1979, Ewer 1973, Kruuk 1972, Schaller 1972).

There are many other ways for predators to partition the environment and the resources it contains than by simply taking different species. The potential for interspecific competition among trophically linked predators can be reduced, for example, through spatial segregation within habitats, differing biological apparatuses for processing and digesting food (Van Valkenburgh 1989), and/or different strategies and maneuvers for locating and capturing food (Gautier-Hion, Emmons, and Dubost 1980, Holmes, Bonney, and Pacala 1979, Jaksić, Greene, and Yañez 1981, Jaksić, Yañez, and Fuentes 1981, Landres 1983, Schoener 1982, Terborgh and Diamond 1970, and references cited above). Resource use may also be partitioned in time, especially by season (Wiens 1977).[2]

The ambiguous relationships between species choice and adaptations of modern coexisting predators raise some questions about what species representation might mean for archaeological studies of human ecology, independently of the problem of sample-size biases. We know without a shadow of a doubt that modern predators are different from one another; the animals they eat simply do not provide a very sensitive measure of adaptive variation. Yet many archaeologists have turned to species representation in faunal assemblages to evaluate hypotheses about foraging "specialization" as opposed to "generalist" strategies (for an analytical review, see Grayson 1984:131–51). And in archaeological research on early populations of *Homo sapiens*, apparent uniformity in taxa consumed has recently been called upon to support a variety of arguments about foraging adaptations across the Middle-to-Upper-Paleolithic transition in Eurasia (e.g., Clark and Lindly 1989*a*, *b*; Mellars 1989). Other researchers meanwhile are more inclined to look to climatic shifts (e.g., Tchernov 1981, 1989; Simek and Snyder 1988) or geographic isolation (Baryshnikov 1989) for explanations of the same general phenomena.

The problems of niche separation between contemporaneous taxa living in the same ecosystem and between populations of the same genus separated in time are not entirely equivalent. They are close enough, however, that it is relevant to ask what taxonomic abundance data really mean to research on the evolutionary history of

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2. Also relevant are observations that competition over a resource tends to be periodic rather than continuous (Wiens 1977). Thus, even where differences in prey species selection by predators are found, it remains to be established that the variation is not the product of short-term resource switching. This kind of behavior is very common among higher organisms; diversification is merely an adjustment to temporary scarcity of certain prey taxa (for general reviews, see Kitchener 1991:98–105; Schoener 1982).

human beings. The question is most relevant to pre-Holocene periods, when hominids were unlikely to have produced any of their own food and thus were more closely constrained by the ecological rules regulating all mammalian predators.

In this paper, I examine how interpretations of species representation of the sort used in human evolution studies hold up in the face of interspecific comparisons of a wide array of predators in Upper Pleistocene Italy. The analyses consider the extent to which relative abundances of taxa consumed might reflect differences in food niche among two noncontemporary but closely related subspecies of *H. sapiens* (Neandertals and anatomically modern humans) and two sympatric species of large social carnivore (spotted hyaenas and wolves). If species consumed can detect subtle changes in the niches of hominid subspecies through time, then the same criterion certainly should be capable of distinguishing hominid adaptations from those of other ungulate predators living in the same ecosystems. If, on the other hand, species consumed do not distinguish hominid from nonhuman predator adaptations, then taxonomic abundance data are not really telling us about foraging niche and evolutionary "continuity" at all. They instead are telling us about another (also very interesting) level of relationship higher in the food chain. It is significant for this study that substantial differences have already been documented in *other* aspects of foraging by the four predators—seasons of shelter use, food processing (Stiner 1990*a*), prey age selection (Stiner 1990*b*, 1991*c*), and food transport (Stiner 1991*b*, n.d.). These differences in turn relate to variable emphases on hunting and scavenging and, more important, ways of searching for food in space.

Analyses of taxonomic richness and relative emphases on key food species here are considered strictly in the context of natural shelters. It is an archaeological fact, lamented by some and capitalized upon by others, that Middle and Upper Paleolithic cave sites frequently contain carnivore occupations in addition to those of hominids (e.g., Brain 1981; Gamble 1983, 1986; Lindly 1988; Straus 1982). Shelters represent an interesting nexus for comparing the diets of coexisting predators because they often served as end points in food transport trajectories. While the roles of carnivores in Paleolithic cave sites sometimes cause interpretive problems for archaeologists, their contributions to depositional series can also be used to advantage.

THE STUDY SAMPLE

The full array of species represented in the Upper Pleistocene caves of west-central Italy (table 1) describes the maximum variation possible in these faunas, except for birds. It includes animals actually consumed by one or more of the four predators along with other (mostly smaller) taxa that entered the cave deposits through a variety of processes. Most prey species were present in the area throughout the Upper Pleistocene. Lowland ecosystems of this Mediterranean region consistently

TABLE 1
Italian Upper Pleistocene Species in Small-Mammal, Carnivore, Ungulate, and "Other" Categories

Common Name	Latin Name
Small mammals	
Insectivora	
Common mole	*Talpa europaea*
Roman mole	*T. romana*
Mole	*T. caeca*
Hedgehog	*Erinaceaus europaeus*
Chiroptera	
	Rhinolophus euryale
	R. ferrum-equinum
	Myotis emarginatus
	M. myotis
	M. oxygnathus
	Miniopterus schreibersii
	Barbastella barbastella
Lagomorpha	
Rabbit (European)	*Oryctolagus cuniculus*
Hare	*Lepus capensis/europeus*
Rodentia	
Common hamster	*Cricetus cricetus*
Common vole	*Microtus arvalis*
Water vole	*Arvicola terrestris*
Wood mouse	*Apodemus sylvaticus*
Marmot	*Marmota marmota*
Garden dormouse	*Eliomys quercinus*
Dormouse	*Muscardinus avellanarius*
Fat dormouse	*Glis glis*
Rat	*Epimys rattus*
Carnivores	
Wolf	*Canis lupus*
Red fox	*Vulpes vulpes*
Brown bear	*Ursus arctos*
Cave bear	*U. spelaeus*
Polecat	*Mustela putorius*
Weasel	*M. nivalis*
Pine marten	*Martes martes*
Wolverine	*Gulo gulo*
Badger (European)	*Meles meles*
Spotted hyaena	*Crocuta crocuta*
Wild cat (European)	*Felis silvestris*
Lynx	*Lynx lynx*
Lion	*Panthera leo*
Leopard	*P. pardus*
Monk seal	*Monachus monachus*
Ungulates	
Proboscidea	
Elephant	*Elephas antiquus*
Perissodactyla	
Horse	*Equus caballus*
Wild ass	*E. hydruntinus*
Rhinoceros	*Dicerorhinus/Rhinoceros* sp.
Artiodactyla	
Fallow deer	*Dama dama*
Roe deer	*Capreolus capreolus*
Red deer	*Cervus elaphus*
Giant deer	*Megaceros giganteus*
Aurochs	*Bos primigenius*
Chamois	*Rupicapra rupicapra*
Ibex	*Capra ibex*
Wild boar	*Sus scrofa*
Hippo	*Hippopotamus amphibius*
Other taxa	
Birds[a]	
Gray partridge	*Perdix perdix*
Dove/pigeon	*Columba* sp.
Quail	*Coturnix coturnix*

TABLE 1
(Continued)

Common Name	Latin Name
Reptiles	
European pond tortoise	*Emys orbicularis*
Spur-thighed tortoise	*Testudo graeca*
Mollusks	
Common mussel	*Mytilus galloprovincialis*
Clam (sand-dwelling)	*Callista (Meretrix) chione*
Clam (sand-dwelling)	*Glycymeris (Pectunculus)* sp.
Clam (sand-dwelling)	*Cardium* spp.
Limpet	*Patella* spp.
Scallop	*Pecten jacobaeus*
Oyster	*Ostrea* sp.

[a]Only taxa for which there is some evidence of use.

supported fairly high levels of species diversity, and animals with distinct habitat preferences existed alongside one another through all but the coldest oscillations in climate (Stiner n.d.; 1990*a*:97–113; see also Tchernov 1981:95 and, on mammals, particularly larger taxa, in the Middle East during the same period, 1989). Exceptions are hippopotamus and certain species of Chiroptera, whose food supplies were especially sensitive to temperature. Spotted hyaenas and pachyderms may have disappeared from the region very late in the sequence.

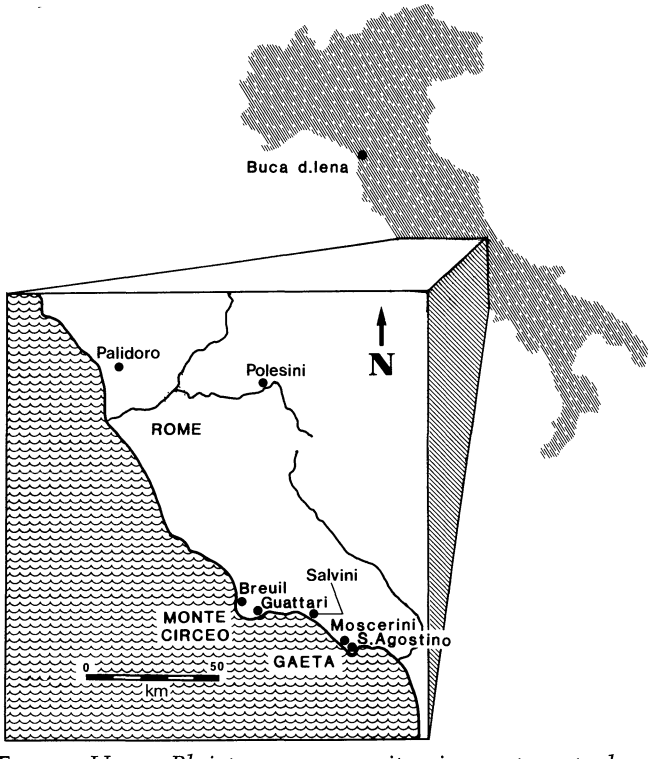

FIG. 1. *Upper Pleistocene cave sites in west-central Italy.*

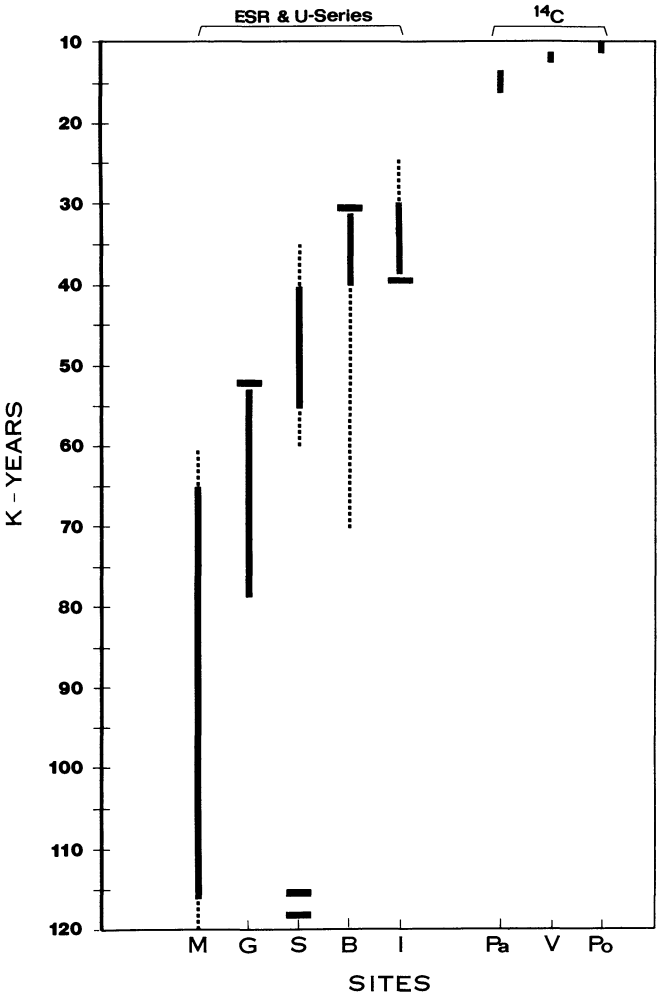

FIG. 2. *Time ranges represented by the cave faunas.* Solid vertical lines, *dated ranges as determined by electron-spin-resonance or* ^{14}C *technique;* horizontal bars, *U-series dates on calcite flowstone layer;* dashed lines, *estimated but undated extent of range.* B, *Breuil;* G, *Guattari;* I, *Buca della Iena;* M, *Moscerini;* Pa, *Palidoro;* Po, *Polesini;* S, *Sant'Agostino;* V, *Riparo Salvini.*

The cave sites discussed are situated at similar elevations on or near the modern coast of Latium and Tuscany (fig. 1). Grotta Polesini is the only exception, lying somewhat more inland on the Aniene River, a tributary of the Tiber. All assemblages are samples from incompletely excavated strata, although most represent substantial proportions of the deposits. Mousterian-aged caves include Grotta Guattari, Grotta Breuil, Grotta dei Moscerini, Grotta di Sant'Agostino, and Buca della Iena. Shelters of late Upper Paleolithic age include Grotta Palidoro, Riparo Salvini, and Grotta Polesini. Together, the faunas from these shallow caves span a time range beginning soon after the last interglacial, roughly 115,000 years ago, and ending around 10,000 years ago (fig. 2). Dates were obtained for the Middle Paleolithic caves by electron-spin-resonance and uranium-series

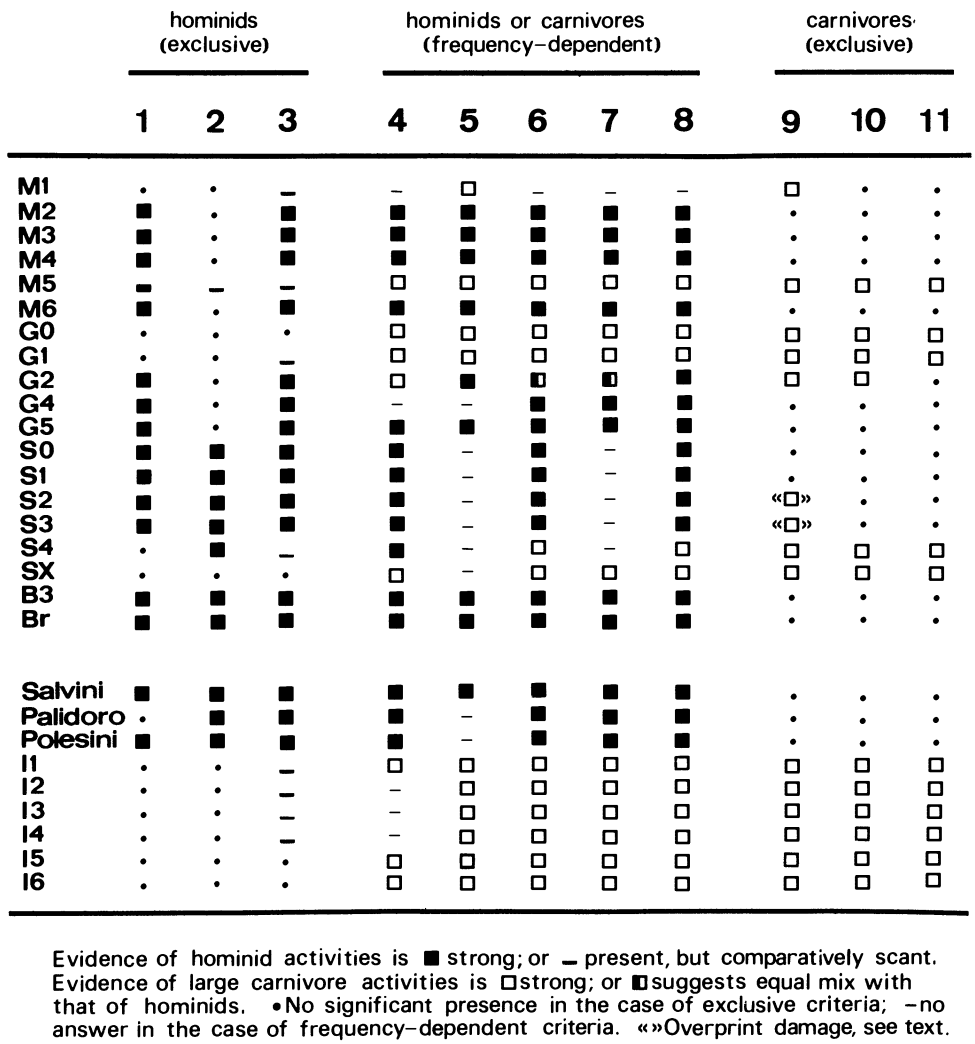

FIG. 3. *Cross-referenced evidence for hominid versus carnivore dominance in bone assemblage formation, based on mutually exclusive and frequency-dependent criteria.* 1, *burned bone;* 2, *cutmarks;* 3, *lithic artifacts;* 4, *cones (>6% versus ≤ 5%);* 5, *mean fragment length (low versus high);* 6, *fracture complexes (angular splits, toes usually opened, versus ragged "bows," toes usually unopened);* 7, *interior space use (light, open versus dark, cramped);* 8, *large-carnivore NISP:ungulate NISP (≤10% versus >10%);* 9, *gnawing (>10%);* 10, *latrine;* 11, *carnivore young.* M, *Moscerini;* G, *Guattari;* S, *Sant'Agostino;* B, *Breuil;* I, *Buca della Iena.*

techniques (for the Latium caves south of Rome, Schwarcz et al. 1990–91, 1991; for Buca della Iena, Fornaca Rinaldi and Radmilli 1968), aided by geochronological assessments (Blanc and Segre 1953, Segre 1982). Dates for the late Upper Paleolithic shelters were obtained directly or indirectly by ^{14}C technique (Avellino et al. 1989, Alessio et al. 1976–77, Radmilli 1974).

The presentation initially considers all species found in the caves, primarily ungulates, carnivores, and small mammals. Analyses are later narrowed to those of dietary significance. While most of the assemblages discussed were excavated by other researchers (e.g., Blanc and Segre 1953, Tozzi 1970), the data are my own unless stated otherwise. Ungulates were principal resources for the four predators while using the caves and hence receive the most attention. All ungulate remains were deliberately carried into the caves by one predator or another. In contrast, some of the other species arrived by their own means and happened to perish there—the usual situation for bears and insectivores (bats, moles, and hedgehogs). Most lagomorphs were prey of resident canids, whereas small rodents were introduced into the deposits by small carnivores or avian predators or simply died in their own burrows (Stiner n.d.; see also 1990*a*).

Each Upper Pleistocene faunal assemblage was attributed to a predator in advance of this study on the basis of taphonomic evidence. The taphonomic assessments use many categories of information, some of which are exclusive signatures either of hominids or of carnivores. Other signature categories instead distinguish on the basis of relative frequency; in other words, the signature is more frequent in assemblages generated by hominids

or by carnivores along a single continuum of difference (documented in Stiner n.d.). Figure 3 presents a synoptic matrix of taphonomic evidence for hominid versus carnivore roles in bone collection in the caves. The matrix combines mutually exclusive and frequency-dependent criteria to arrive at a synthetic assessment of which predator dominated assemblage formation in each vertical provenience. The major players in this study sample were hominids, spotted hyaenas, and wolves. I emphasize that my intent here is only to illustrate *how* bone collectors were identified in a general way. The extensive set of arguments, controlled comparisons, and other analyses that led to the creation of figure 3 cannot be presented economically (see, instead, Stiner n.d.). Taphonomic analyses of small-animal remains are similar in principle and in practice, except that shellfish were also examined for wave-caused abrasion and small mammals for digestive erosion damage.

Not every class of taphonomic information answers for every assemblage. The criteria, 11 in all, are weighted equally in the matrix. There are six exclusive signatures, three each for hominids and for large carnivores. Because only one or the other is able to produce them, exclusive signatures are primarily present or absent, although "present but rare" is further qualified in the illustration. Exclusive signatures of hominid activities are (1) burned ungulate bones, (2) cutmarks, and (3) lithic artifacts. Exclusive signatures of large-carnivore activities are (9) gnawing damage, (10) latrines evident from concentrations of hyaena coprolites or canid fecal bone, and (11) elevated frequencies of infant and juvenile individuals among the carnivore remains. Because virtually any archaeofauna, recent or ancient, will show *some* evidence of gnawing, frequencies must exceed 10% of ungulate bone NISP in this scheme to suggest collection by large carnivores. The significance of very elevated frequencies of young individuals among the carnivore remains is documented elsewhere (Stiner n.d.; see also 1991*a*); it connotes denning in social carnivores.

Frequency-dependent criteria, pointing to hominid activities at one end of the continuum and to the activities of large carnivores at the other, are (4) cone fractures, (5) mean bone fragment length (see Brain 1981), (6) distinctive fracture complexes involving the treatment of ungulate mandibles and toe bones, (7) interior space use, and (8) the ratio of *large*-carnivore bone NISP to ungulate bone NISP. The fracture complexes contrast the relative incidence of angular splits versus ragged "bows" on ungulate mandibles and the extent to which toe bones were fully opened to extract marrow (see Stiner n.d.). I acknowledge that the nutritional value of marrow and thus the incentive for any predator to open bones is mediated by season of death, food supplies, and prey health. Taking this into account, however, the basic contrast between what hominids and large carnivores do to mandibles and toe bones is generally upheld in modern control sets (see also Binford 1978, 1981). Interior space use refers to gross horizontal distributions of material relative to vault shape and dimensions, working from the general observation that denning carnivores generally prefer smaller spaces and hominids prefer larger ones.

The synopsis of taphonomic evidence in figure 3 should be read by row, beginning with the assemblage name in the first column. Reference cases from late Upper Paleolithic human and hyaena den sites in Italy are provided in the lower part of the figure, illustrating the visual appearance of assemblages collected by humans as opposed to hyaenas and wolves, the only other major bone collectors in evidence in the study sample. A row dominated by filled squares argues for hominid collectors, whereas a row dominated by open squares argues for large-carnivore collectors (hyaenas or wolves). The taphonomic indications are not always so clear-cut, sometimes showing significant influence by both sets of agencies. Equivocal rows reflect postdepositional mixing of hominid and carnivore components or, alternatively, contemporaneous damage "overprinting" of human refuse by canids (see Stiner n.d.).

In most cases there is only one dominant agency of large-mammal bone collection. The matrix attributes Moscerini 2–4 and 6, Guattari 4 and 5, Sant'Agostino 0–3, and Breuil 3 and 1 to Middle Paleolithic hominids, and all associated stone tools are Mousterian. It attributes Moscerini 5, Guattari 0 and 1, and Buca della Iena 1–6 principally or wholly to spotted hyaenas. The uppermost levels of Buca della Iena also contain scant quantities of Mousterian tools, but hominids' contribution to the overall character of the faunas was very minor (Pitti and Tozzi 1971; see also Stiner n.d., 1991*a*). The matrix attributes Sant'Agostino X to wolves exclusively. Riparo Salvini, Polesini (cuts 1–12, species counts from Radmilli 1974, taphonomic data mine), and Palidoro (33–34 my data, species counts from cuts 1–8 from Cassoli 1976–77) are clearly attributable to late Upper Paleolithic humans, and each assemblage is associated with Epigravettian tool industries.

A few of these assemblages are very small, making assessments of their origins difficult. However, this is less a problem for hyaena-collected cases than it is for those suspected to have been collected by hominids. Assemblages created by spotted hyaenas, even the small ones of Buca della Iena 1–4, typically display extensive and pervasive gnawing damage accompanied by an abundance of coprolites. Attributions to hominid activities are more problematic when assemblages are very small, because evidence of modification may be more lightly scattered among bone specimens. Guattari 4 and 5 are cases in point and should be viewed with some caution; they have been accepted as Mousterian only because evidence of carnivore modification is infrequent, whereas other kinds of damage point to hominid activities (see Stiner 1991*a*, n.d.). Assemblages whose taphonomic histories are severely scrambled (Sant'Agostino 4, Guattari 2) and those too small to be assessed (Moscerini 1, Guattari 3 and 7) are dropped from consideration after the first analysis below.

It is important to appreciate the extent of diversity embodied by the study sample, which represents three species of predator and two subspecies of one of them

(*H. sapiens*). Considerable variation also exists among the assemblages associated with each predator—except wolf, for which only one unmixed assemblage is available. The total sample includes material collected by ecologically dedicated hunters (late Upper Paleolithic humans and wolves) and hunter-scavengers (Middle Paleolithic hominids and spotted hyaenas), whose strategies varied at distinct spatial and temporal scales. The Middle Paleolithic sample is particularly heterogeneous in that it represents both hunted and scavenged prey in different sites (see Stiner 1990*b*, 1991*b*) collected over roughly 80,000 years (see fig. 2). In contrast, some of the late Upper Paleolithic faunal assemblages are quite large though formed in a comparatively short time.

Certain constants provided by the study sample lend important strengths to this comparison of predator diets. All of the bone assemblages occur in limestone caves situated at low elevations near the Mediterranean Sea. Obviously, hominids and other predators could have eaten any number of species while away from shelters: the cave faunas merely represent elements of diets filtered through the contingencies of transport, perhaps including only those resources sufficiently large or close by to make transport worthwhile. In the case of hominids, the caves appear to have served as some kind of residential hub. For spotted hyaenas and wolves, the shelters served as dens.

TAXONOMIC CLASSIFICATIONS AND NISP

Taxonomic classifications of mammals, reptiles, birds, and marine mollusks in the study sample are based on comparative collections housed at the Italian Institute of Human Paleontology (IIPU di Roma), the Zoological Museum (Rome), and the University of Pisa. Taxa are identified to the level of species for the purposes of this presentation; hence N-taxa is synonymous with number of species. Shellfish are exceptions to this rule, compared instead at the level of genus.

The analyses employ identifiable specimen counts (NISP) for bones, teeth, and shells, corresponding to the most basic catalog of identifiable fragmented and/or fully disarticulated units in each assemblage. The counts are used to gauge the relative importance of food species transported to shelters by each predator, analyzed according to major size and taxonomic divisions (e.g., ungulates, carnivores, small mammals). The definition of the NISP variable and the analytical methods used in this study follow those of Grayson (1984) with some modifications.

Of the many variables developed by zooarchaeologists, NISP is least prone to the ambiguities of data aggregation. It demands fewer assumptions about a data set than variables (including MNI) derived from it (but see Klein 1980, Klein and Cruz-Uribe 1984). Although problematic when used as a measure of taxonomic abundance for isolated cases, NISP is well-suited to comparisons of many faunal assemblages, provided that they involve the same potential array of species and the degrees of bone fragmentation are comparable. These criteria are met fairly well by the Italian sample: the caves have similar ecological, topographic, and geomorphic settings, and the depositional environments in the limestone caves are generally analogous (e.g., see Blanc and Segre 1953, Segre 1982, Pitti and Tozzi 1971, Stiner n.d.). As noted above, the overall composition of animal communities in west-central Italy appears to have been relatively stable throughout the period in question. The extent of bone fragmentation varies somewhat between assemblages generated by hominids and those created by hyaenas or wolves (Stiner 1991*b*:460–62), but this should not drastically alter the *relative* abundances of larger-prey taxa. Low levels of in situ bone attrition caused by chemical decomposition and the feeding habits of the predators are likely in all sites, despite soils favoring preservation. Within animal classes, however, the severity of in situ destruction in the subject assemblages varied most according to the major types of bone tissue, as anticipated by Brain (1981) and Lyman (1984, 1985, 1991). Trabecular structures of the axial skeleton are especially sensitive to decomposition, but these tissues are distributed similarly in skeletons within major mammalian groups and therefore should not prohibit interassemblage comparisons of taxonomic abundance.

Many of the assemblages come from old excavations, conducted between 1939 and 1955, when recovery practices were less than ideal from the modern point of view. However, the excavation teams used the same or very similar procedures at each site, systematically screening the excavated sediments and collecting all bones identifiable to species or genus. Indeed, the main purpose of collecting faunal remains at that time was to monitor changes in species content across periods; axial elements not diagnostic to species were sometimes discarded, but the excavators clearly recognized the potential of cranial and appendicular bone—in addition to teeth—for studies of species abundance.

Aspects of the way in which the NISP data are organized affect the way in which they should be read from the tables. The smallest components of composite skeletal units are counted as separate entities. For example, three articulated segments comprising part of an ungulate foot found intact in a deposit would be counted as three specimens. A distal radius with five carpals still attached would be counted as six specimens. A midsection of mandible in which two teeth remained fixed would be counted as three specimens. These anatomical units often enter archaeological deposits in articulated states but become disassociated by a host of small-scale postdepositional processes.

How best to count loose (isolated) versus "articulated" teeth emerges as a significant issue only in situations of good preservation and limited postdepositional disturbance, such as in many of the caves of west-central Italy. The Italian sample is comparatively unusual, however, and in archaeological records of many other parts of the world isolated teeth may be the rule rather than the exception. Teeth fall away from bone very easily because of differential rates of tissue shrinkage, sediment shifting, and perhaps chemical alteration. Yet

bone tissues surrounding the teeth are not always destroyed. In the Italian study sample, the relative proportions of isolated teeth to all teeth vary among the assemblages and even more among sites but show no consistent link to biological agency (Stiner n.d.); values range between about 15% (mostly articulated, as in Moscerini 4) and 97% (mostly isolated, as in Buca della Iena 1).

Variation in the extent of tooth disarticulation introduces a comparability problem for this study: if isolated teeth were counted as separate units and articulated teeth were not, then assessments of taxonomic abundance would depend at least in part upon the extent of postdepositional disturbance. In fact, the relationship between all (isolated and articulated) tooth NISP and bone NISP for ungulates (the largest subsets in each assemblage) is *linear* and highly significant ($r = .845$; $r^2 = .714$; N cases $= 26$; $P \ll .001$). In contrast, the relationship between isolated tooth NISP and bone NISP is *nonlinear*, an upwardly convex curve, and also highly significant ($r = .852$; $r^2 = .726$; N cases $= 26$; $P \ll .001$).[3] The hyaena and wolf den cases (e.g., from Buca della Iena) appear no different in this regard from the Mousterian faunas.

For the purpose of analyzing taxonomic abundance, isolated and articulated teeth should be counted by the same standard, preferably one in which the numerical relationship to bone NISP is (or is close to) linear. Otherwise, the distortion will be passed on to the relative species counts as a function of different body-size groups, sites, and regional fossil records. It is for these reasons that my NISP counting system treats all teeth *as if* they were isolated from bones, thereby circumventing comparability problems in the study sample and affording greater control over the *potential* effects of comminution and other postdepositional factors. While my procedure might seem to guarantee redundant counts with bone in the subject assemblages because some teeth are still fixed in bone, the quantitative effect is no different from what geological processes so commonly enforce; the procedure emulates the more common situation in archaeological records across regions and/or depositional settings.

ANALYTICAL STRATEGY

In the Italian assemblages, *tooth NISP* (loose and articulated) comprise roughly half of *total NISP* (bone plus tooth) but do not significantly change species lists as determined strictly from *bone NISP*. This assessment is feasible because numerous bony landmarks of the mammalian cranium and mandible are just as diagnostic to species as are teeth (for discussion, see Stiner 1991*b*: 459–62). The analyses presented below were conducted both on total NISP and, as an internal check for biases due to small samples, on bone NISP alone (half the data set). The presentation emphasizes the results for total NISP, but results for the bone subset are also summarized where pertinent. While determined independently of one another, the arrays of species based on these two classes of skeletal material completely overlap in each assemblage with very few exceptions (appendix 1).

Potential biases due strictly to numerical sampling are evaluated first through a simple regression analysis of "taxonomic richness" for mammals (*sensu* Grayson 1984). Broad patterns apparent from plotting N-taxa against log NISP are discussed in terms of expectations for hypothetical nonselective sampling. The procedure explores the potential influence of sample-size biases in the data, as well as affording a preliminary look at whether species choice by any of the four predators diverged from the overall slope of the distribution. Comparisons then turn to the question of relative emphases on the most common prey species (ungulates) in predator diets, an alternative approach that shows promise for elucidating shifts in human foraging ecology and land use in other recent studies (e.g., Grayson 1991) and is very important to this study in particular. The choice of statistical methods at this point specifically responds to the sample-size problems exposed by the regression plots: differences in ungulate species use are evaluated using a modified Robinson index (Robinson 1951; also known as the Brainerd-Robinson distance coefficient, discussed by Cowgill 1990). The Robinson-index analysis should circumvent most problems caused by differing assemblage sizes in the study sample because (1) the comparison considers variation only among common prey taxa, (2) the assemblages associated with each predator are lumped by site, greatly increasing NISP in most instances, and (3) the index of difference employs percentage values. Because it is possible that the four predators partitioned common resources according to taxonomy-related characteristics above the species level, a final kind of analysis compares the numbers of resource classes, including mollusks, reptiles, and small mammals, represented in predators' diets.

TAXONOMIC RICHNESS

The first analytical step is to see if the Upper Pleistocene bone assemblages from the Italian caves conform to expectations about the mathematical relationship between taxonomic richness and sample size and whether any predator-associated series diverge from the main regression slope. Figures 4 and 5 are plots of N-taxa and log total NISP for the two dominant mammalian groups, ungulates and carnivores. The Polesini (UP) faunas are excluded from consideration because they are vastly larger than the other assemblages (appendix 2). In each figure, the upper graph displays the data points by site and the lower graph identifies them according to the main agency of accumulation; question marks indicate assemblages whose origins are unknown or too scrambled to warrant further consideration (G2, G3, G7, S4, and M1). The N-taxa (vertical) axis is not logged because the ceiling values for mammalian subsets are relatively

3. This curvilinear relationship is best described by the second-order regression formula $Y = -7.14 + 3.16(X) - .0064(X^2)$.

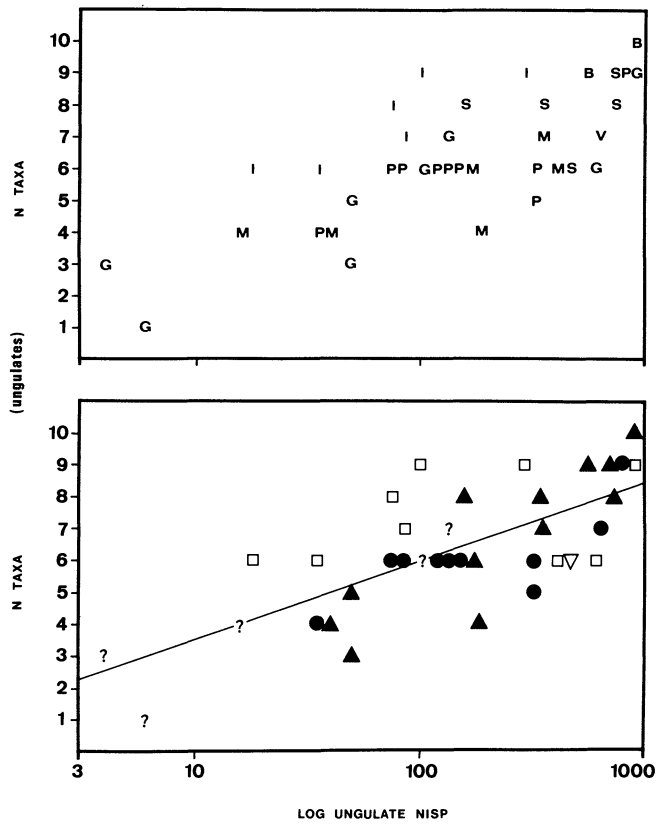

FIG. 4. *Ungulate NISP (logged) and ungulate N-taxa in the Italian Upper Pleistocene cave faunas, marked by* (top) *site name* and (bottom) *main agency of bone collection.* B, *Breuil;* G, *Guattari;* I, *Buca della Iena;* M, *Moscerini;* P, *Palidoro;* S, *Sant'Agostino;* V, *Riparo Salvini.*

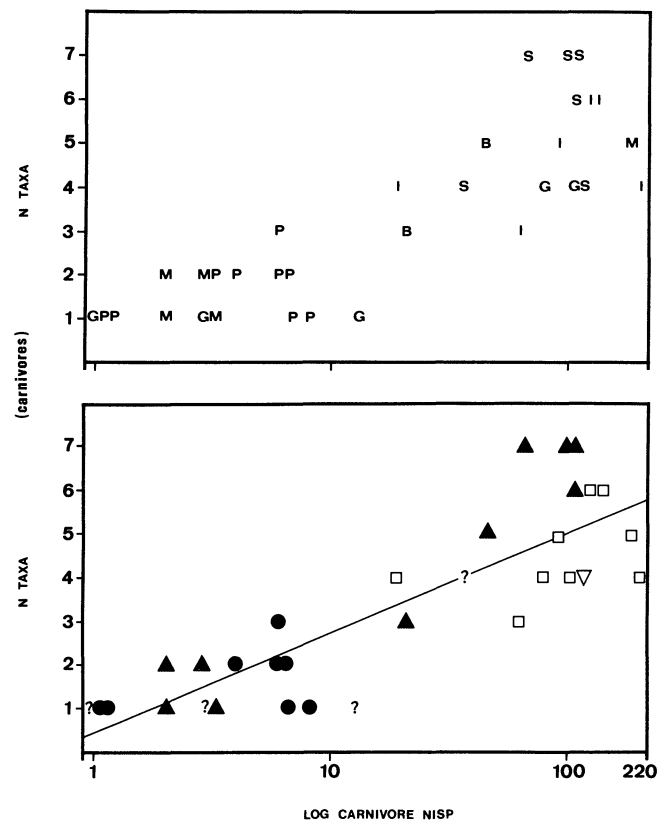

FIG. 5. *Carnivore NISP (logged) and carnivore N-taxa in the Italian Upper Pleistocene cave faunas, marked by* (top) *site name and* (bottom) *main agency of bone collection (symbols as in figure 4).*

low (maximum ungulate species = 10, maximum carnivore species = 7).

Regression statistics in table 2 indicate very significant relationships ($P < .001$) between N-taxa and total NISP for both the ungulate and the carnivore remains, and there are no obvious outliers. The plots testify to the overwhelming likelihood that much of the variation in numbers of species in these faunas *could* be due to numerical sampling bias—at least when compared in this way. The companion conclusion is that the Mousterian (and other) faunal assemblages tend to be small, an unfortunate fact of life.

It is interesting that substantial differences in chronology have no consistent effect on the distributions. A quick scan of figure 2 shows that the cave deposits yielding the assemblages represent disparate amounts of accumulation time, varying by site and by predator. Assemblages from Palidoro (UP), Riparo Salvini (UP), Breuil (MP), and the Sant'Agostino wolf den from layer X probably each formed within a thousand years, whereas each level group in the Moscerini series (MP) may have formed over several thousand years.

Because four bone-collecting predators are represented in the sample and human beings are more omnivorous as a rule, one might expect to see biases in species choice, possibly expressed as different slopes. All these four predators, however, emphasized ungulates and occasionally other large-mammalian prey such as one another. To the extent that their diets included meat, humans apparently behaved like classic carnivores in the number of game species consumed.

The potential effect of numerical sampling biases can

TABLE 2
Regression Statistics for Plots (N-taxa to Total NISP) of Ungulate and Carnivore Remains from All Sites and Proveniences

Trophic Group	Site and Provenience	*r* Value	r^2	*N* cases	*P*
Ungulates	all	0.733	0.537	37	$< .001$
Carnivores	all	0.843	0.711	32	$\ll .001$

TABLE 3
Regression Statistics for Plots (N-taxa to Total NISP) of Various Ungulate, Carnivore, and Small-Mammal Assemblages by Site

Site	Vertical Proveniences	*r* value	r^2	*N* cases	*P*
Buca della Iena	1–6	0.784	0.615	17	$.01 > P > .001$
Guattari	0–7	0.902	0.814	16	$\ll .001$
Moscerini	1–6[a]	0.769	0.591	15	$.05 > P > .01$
Sant'Agostino	0–4, X	.0641	0.411	18	$.1 > P > .05$[b]
Salvini and Palidoro	all cuts	0.948	0.899	25	$\ll .001$
Polesini	all cuts	0.277	0.077	36	$\gg .1$[b]

[a]By level group.
[b]Relationship is not significant.

also be explored at a finer level, for example, by site. Table 3 lists regression statistics for all mammals (not graphed) in sites yielding multiple assemblages, based on total NISP. The results are consistent with the general pattern described above. Only a weak relationship is found for Sant'Agostino, probably because the assemblages are consistently larger than most. As might be expected, the very large samples from Polesini (appendix 2) show no relationship between N-taxa and total NISP at all.

The regression comparisons obscure one interesting fact about species in the study sample, however. While the total number of carnivore species does not differ much between the Middle and late Upper Paleolithic periods in the Italian caves, the body sizes of carnivore species present and the relative abundance of carnivore to herbivore remains certainly do. As would be predicted by Gamble (1983, 1986), the hominid- and carnivore-collected faunas dating to the Mousterian period display more *large*-carnivore species, whereas those found in late Upper Paleolithic shelters are mostly small species and are uncommon relative to herbivores. Of course, taphonomic information segregates most carnivore remains from cultural components in Mousterian-aged caves, but the basic contrast between the Middle and late Upper Paleolithic holds: the alternating use by large carnivores and hominids so common during Mousterian times had all but ceased by the late Upper Paleolithic. Bears and wolves were still extant in the region but apparently were using different caves if they used caves at all.

Some subtle variation among predator series may also exist in relation to the main distribution for ungulate remains in figure 4. Spotted hyaena den faunas tend to fall on the high side of the line, Upper Paleolithic faunas occur on or below the line, and Middle Paleolithic faunas are scattered more widely. Such variation is not apparent for carnivore remains from the same sites (fig. 5). It would be pointless to make very much of the observation at this stage, but a few things pertaining to future research on this topic deserve mention. Because spotted hyaenas may scavenge nearly as much as they hunt, one might be tempted to suggest that scavenging will increase species richness in shelter faunas in general. While probably true for hyaenas, the expectation may not be borne out in the Middle Paleolithic assemblages. Species richness values for scavenged ungulate faunas in the Middle Paleolithic, interpreted on the basis of mortality and anatomical evidence, actually tend to be lower (Guattari and Moscerini, fig. 4) in relation to the regression line than those representing hunting (Breuil and Sant'Agostino). Perhaps scavenging opportunities exploited by hominids were more situationally limited than those utilized by hyaenas. Among modern predators that scavenge there are certainly contextual differences the consequences of which merit continued exploration.

Also of interest is that carnivore species richness values for faunas collected by denning spotted hyaenas (and bears) and by wolves in figure 5 tend to be slightly lower relative to the regression line than hominid-collected faunas overall. Exclusionary behavior associated with den defense may be responsible for this difference, but, if real, it is quite subtle and does not qualify as a compelling signature at the time scales considered here. High levels of interspecific violence, as documented in modern denning situations for the same kinds of predators (e.g., Kruuk 1972, Schaller 1972), may work against the formation of monospecific or species-poor carnivore faunas over the long term, especially since most paleontological records are palimpsests of many occupational events.

RELATIVE EMPHASES ON COMMON PREY SPECIES

Variation in the diets of the four predators may be examined by focusing on the relative frequencies of the most common prey taxa, first through a simple visual comparison and then through statistical analysis. Table 4 presents the full array of food species consumed by each predator, based on total NISP and groomed with the benefit of taphonomic information. The data for each predator are compiled by site, greatly enlarging the units of comparison. Assemblages whose taphonomic origins are ambiguous are now dropped from consideration, with the exception of Guattari 4 and 5. Only data for ungu-

TABLE 4
Dietary Data for the Four Predators in Italian Upper Pleistocene Shelters

Food Species by Descending Body Size	Middle Paleolithic Hominids				Wolves	Spotted Hyaenas			Late Upper Paleolithic Humans		
	M2–4, 6	G4–5	So–3	Br,3	SX	M5	Go–1	I1–6	Pal	Pol	Salv
Aurochs	14	54	146	188	4	22	358	97	503	980	14
Horse	1	5	38	25	0	14	125	225	98	1,250	78
Red/fallow deer[a]	574	38	1,086	793	36	245	863	225	902	29,785	458
Wild ass	0	0	3	3	0	0	0	0	411	2,262	37
Ibex	20	0	197	325	221	5	0	0	2	362	12
Wild boar	4	1	182	1	1	0	61	19	84	3,453	1
Chamois	0	0	0	1	0	0	0	0	0	694	4
Roe deer	105	2	332	162	211	137	53	35	13	3,167	49
Subtotal	718	100	1,984	1,498	473	423	1,460	601	2,013	41,953	653
Elephant	0	0	0	1	0	0	3	2	0	0	0
Hippopotamus	2	0	0	0	0	0	0	0	0	0	0
Rhinoceros	3	0	21	3	0	0	1	16	0	0	0
Monk seal	0	0	1	0	1	0	0	0	0	0	0
Marmot	0	0	0	0	14	0	0	1	0	10	0
Hare	0	0	0	1	0	0	0	0	5	365	2
Rabbit	0	0	0	0	175	0	0	0	0	0	0
Small rodents	0	0	0	0	0	0	0	0	0	0	0
Reptiles/amphibians	40	0	0	0	0	0	0	0	0	0	0
Birds[b]	0	0	0	0	0	0	0	0	25	514	?
Shellfish	613	0	0	0	0	0	0	0	0	0	0
Subtotal	658	0	22	5	190	0	4	19	30	889	2
Total NISP	1,375	100	2,006	1,503	663	428	1,464	615	2,043	42,842	655

NOTE: Based on bones, teeth, and shells and groomed on the basis of taphonomic evidence.
[a]The red/fallow deer category contains mostly red deer and only small quantities of fallow deer. Rare remains of *Megaceros* are also present in the Middle Paleolithic sites of Moscerini, Guattari, and possibly Buca della Iena.
[b]Avian species accepted as probable food in this study are ground-dwelling species: gray partridge, quail, and doves.

lates are analyzed in detail in this section, because their remains dominate the faunal assemblages by every conceivable measure. Pachyderms are excluded on grounds that they may not have been present in Italy by late Upper Paleolithic times.

Figure 6 summarizes the percentages of ungulate species (listed in descending order of body size) consumed by each predator at all sites combined. It suggests that the ungulate species taken by Mousterian hominids, late Upper Paleolithic humans, and spotted hyaenas were quite similar. Red deer was the principal prey, supplemented by much smaller quantities of large and small ungulates. The spotted hyaena prey profile appears slightly weighted toward the large-bodied end of the scale, indicating a slightly higher dependence on horse and aurochs. Conversely, the Mousterian profile appears slightly weighted toward the smaller end of the ungulate size scale. None of these differences are substantial, however.

Only the dietary profile for denning wolves shows a significant departure from the general red-deer pattern. The only one of its kind in the study sample, the wolf den assemblage introduces a valuable dimension to the comparisons. The denning period of modern wolves often corresponds to a temporary drop in average prey size (Peterson, Woolington, and Bailey 1984). Ungulates, vital resources for unencumbered wolves the world over, tend to avoid places where wolves concentrate for any amount of time (Mech 1977, Rogers et al. 1980). Denning imposes spatial restrictions on the food quest, and small prey, incapable of adjusting to wolf densities by moving away, become *short-term* staples. This point is of special relevance to later discussion of resource "specialization." The wolf den assemblage SX is entirely consistent with the expectations of denning, as the wolves focused on marmots and rabbits (Stiner n.d.) but also ate some ibex and the highly territorial roe deer. Ibex, for example, are important prey of modern nonreproducing wolves in other intact habitats with broken topography (e.g., Schaller 1977:140 on wolves in Afghanistan; see also Gamble 1986:104–10 for Eurasia during the last glacial). Decreases in average prey body size are no more apparent in spotted hyaena dens of Pleistocene Italy than in modern spotted hyaena dens. This is at least in part because of hyaenas' digestive capabilities and a rather different suite of foraging behaviors and transport objectives leading to bone accumulations in dens (e.g., Kruuk 1972). Also significant for this comparison, young hyaenas may occupy dens over periods of many months, making the switching tactics practiced by adult wolves less feasible.

The comparison portrayed in figure 6 makes three of the predator diets, those of spotted hyaenas and Middle Paleolithic and Upper Paleolithic hominids, look the same. The lumping of several of the assemblages generated by each predator to create it may, however, obscure

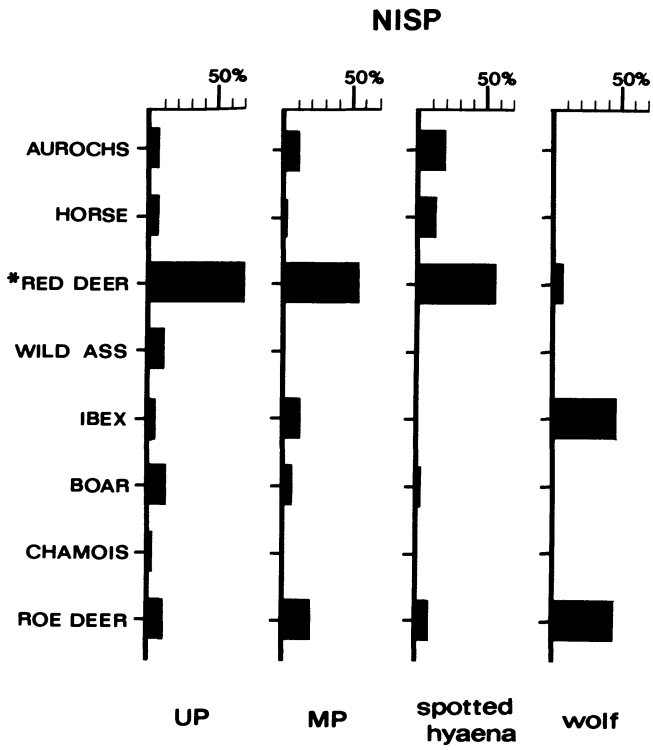

FIG. 6. *Composite frequency data on ungulate species (% of total ungulate NISP) in predator diets. *, including a small percentage of fallow deer in most cases.*

heterogeneity at the interassemblage level. This is an important issue, because other lines of evidence indicate that the ways in which Mousterian hominids procured ungulate resources in coastal Italy varied from site to site much more than was typical of late Upper Paleolithic foragers in the same region (Stiner 1990*b*, 1991*b*). The next problem is to ascertain whether uniformity in the relative emphases on ungulate prey species is upheld at a finer level, here examined statistically by predator and by site (as partitioned in table 4).

Table 5 contrasts ungulate species representation among predators and sites using a variant of the Robinson index of dissimilarity (Robinson 1951). The index is calculated by summing the differences in the percentages of each species for each pair of assemblage groups without regard to sign, and values vary between 0 (identical) and 200 (maximally different). Results for bone NISP and for total NISP are presented. Both versions of the matrix reveal fairly consistent levels of dissimilarity in the pairings for all predators except wolves. While only one wolf den is represented, the distances from other predators are consistently great (e.g., varying between 116 and 179). Distances among other predators at most reach the lower limit of those from wolves. The fact that the wolf case is a solitary example cannot fully account for its isolation from all other predator cases.

Relative emphases on ungulate taxa certainly vary among the other assemblages and predators, but this occurs within a narrower distance range, largely indepen-

TABLE 5
Robinson Coefficients of Dissimilarity for Assemblage Group Pairs by Site and Agency

	Mosc MP	Guat MP	SAgo MP	Breu MP	SX w	M5 sh	Go–1 sh	I1–6 sh	Pal UP	Pol UP	Salv UP
Bone NISP only											
Mosc MP	0										
Guat MP	109	0									
SAgo MP	52	96	0								
Breu MP	46	83	47	0							
SX w	138	175	124	138	0						
M5 sh	48	93	43	58	108	0					
Go–1 sh	60	52	70	35	172	65	0				
I1–6 sh	96	38	80	71	174	81	36	0			
Pal UP	105	67	85	80	185	90	55	55	0		
Pol UP	37	101	67	56	171	72	51	85	80	0	
Salv UP	38	84	81	54	170	69	43	71	85	21	0
Total NISP											
Mosc MP	0										
Guat MP	116	0									
SAgo MP	49	100	0								
Breu MP	63	92	32	0							
SX w	148	179	129	118	0						
M5 sh	47	103	39	55	116	0					
Go–1 sh	68	59	55	57	174	58	0				
I1–6 sh	108	77	89	85	170	96	62	0			
Pal UP	104	60	82	80	179	91	41	73	0		
Pol UP	36	107	49	69	166	56	54	96	79	0	
Salv UP	37	105	63	67	164	56	52	84	81	22	0

NOTE: *MP*, Middle Paleolithic; *w*, wolf; *sh*, spotted hyaena; *UP*, late Upper Paleolithic. Distance metric varies between 0 (identical) and 200 (maximally different).

TABLE 6
Differences in Distance between Assemblage Groups by Predator

Distance	MP Hominid	Spotted Hyaena	UP Human
Bone NISP only			
Minimum	46	36	21
Median	67	65	80
Maximum	109	81	85
Total NISP			
Minimum	34	58	22
Median	77	62	79
Maximum	115	96	81

dent of the time element (see fig. 2). Palidoro (UP), for example, is rather different from Moscerini (MP), but Moscerini is also different from Guattari (MP). In short, Middle Paleolithic assemblage groupings are about as different from one another as each is from various spotted hyaena den faunas or late Upper Paleolithic faunas. The results appear unaffected by differing assemblage sizes: total ungulate NISP for Guattari 4 and 5 is only 100, whereas most other samples range between 400 and about 2,000 and NISP for Polesini is just under 42,000.

The distances in the matrices can be summarized in a straightforward way by focusing on ranges and medians. These statistics are presented first by predator (table 6) and then between predator pairs (table 7), excluding wolves. Low, high, and median distances are remarkably similar, given the range of the distance metric; none of the three predators diverges significantly from the others in terms of relative emphasis on ungulate species, regardless of whether bone NISP or total NISP counts are considered. The predator-paired results (table 7) are of greatest interest because they involve a larger set of comparisons. Here, ranges and medians are even more alike, and there are no substantial differences in results between the bone NISP subsample and total NISP.

TABLE 7
Differences in Distance between Assemblage Groups between Predators

Distance	MP-sh	MP-UP	UP-sh
Bone NISP only			
Minimum	35	37	43
Median	59	73	69
Maximum	96	105	90
Total NISP			
Minimum	39	36	41
Median	63	68	56
Maximum	108	107	96

MP, Middle Paleolithic; *sh,* spotted hyaena; *UP,* late Upper Paleolithic.
NOTE: Distance metric varies between 0 (identical) and 200 (maximally different). Wolf is excluded from consideration because only one assemblage is available for comparison.

With the exception of the wolf case, then, the amount of difference among faunas collected by one kind of predator is about the same as between predators, irrespective of time. Ungulate species utilized do not distinguish the foraging niches of late Upper Paleolithic humans, Middle Paleolithic hominids, and spotted hyaenas in the context of cave occupations in coastal west-central Italy.

NUMBERS OF RESOURCE CLASSES IN PREDATOR DIETS

Somewhat more variation is apparent in the use of *small* prey by the four predators at coastal caves, if only because Mousterian hominids sometimes used shellfish and tortoises, wolves ate marmots, rabbits, and hares, and late Upper Paleolithic people took some ground-dwelling birds. Taking into account inequities of body size, small animals constituted relatively minor fractions of the total food volume carried into shelters (see table 4) or, in the case of wolves, defecated there (Stiner 1990*a*:311–19). On the other hand, the small species in the study sample certainly represent a more diverse array of habitats. Significantly different behaviors may have been required to obtain these small animals, making them interesting from the perspective of how diets were supplemented with alternative resources.

Food species are divided into ten classes (table 8) on the assumption that prey body size, anatomical and locomotor characteristics, and/or habitat preferences affected their accessibility and nutritional value to consumers. Dietary profiles are lumped by predator, combining all food species in assemblages from all sites to create a complete dietary profile. The comparison considers both the number of resource classes represented and the number of species per class. (Inclusion or deletion of teeth has absolutely no effect on numbers of large-mammal species.)

From this perspective, the overall Mousterian diet at shelters is more diverse than the diets of the other predators, even though huge quantities of material are available for Upper Paleolithic human cases. The Mousterian diet appears the least specialized, followed by that of the late Upper Paleolithic, spotted hyaenas, and finally wolves. All but two resource classes are represented in the Mousterian diet, and the total number of species is high relative to the maximum potential value for the study sample as a whole. The diets of denning spotted hyaenas and late Upper Paleolithic humans display fewer resource classes and are more similar to one another. The wolf den assemblage shows the least of all, consistent with foraging restrictions imposed by the reproductive strategies of this species and probably also the fact that only one assemblage can be considered.

Data grouped by resource class appear more useful than unstructured comparisons of N-taxa for distinguishing the adaptations of the four predators. Even here the differences are not very pronounced, however, and their significance may be further reduced by ambiguities inherent in the sample. The total Mousterian profile, for

TABLE 8
Number of Species in Each Resource Class in Diets of the Four Predators in Italian Upper Pleistocene Shelters

Resource Classes by Descending Body Size	Middle Paleolithic Hominids	Denning Wolves	Denning Spotted Hyaenas	Late Upper Paleolithic Humans
Pachyderms (3)	3	0	2	0
Large ungulates (2)	2	1	2	2
Medium-sized ungulates (5)	5	3	4	4
Small ungulates (3)	3	2	2	3
Phocids (seal) (1)	1	0	0	0
Lagomorphs (2)	1	2	0	1
Rodents (1)	0	1	1	1
Reptiles (2)	2	0	1	–
Birds (4)	0	0	0	4
Marine mollusks (7)	7	0	0	0
Total species	24	9	12	15
Total classes	8	5	6	6

NOTE: Results for bones only versus teeth and bones are identical. Value inside () indicates the maximum number of species possible (total = 30) for total combined food array. Pachyderms include elephant, rhinoceros, and hippopotamus; large ungulates include horse and aurochs; medium-sized ungulates include red deer, fallow deer, giant deer, ibex, and wild ass; small ungulates include roe deer, chamois, and boar; the rodent category includes marmot only. In the case of Polesini, small quantities of tortoise are reported by Radmilli (1974:29), but these individuals may have perished underground during hibernation rather than having fallen prey to humans. Taphonomic evidence shows that some individual carnivores were also eaten by the four predators considered (e.g., hominids ate bears and foxes at Polesini and some bears at Moscerini [Stiner 1990*a*]). Carnivores representing prey are not included in the dietary profiles because of the potential for confusing isolated instances of predation with deliberate entry into caves by the same species.

example, spans a much longer time range than those for the other predators—more time to recruit and accumulate rare species in the communitywide resource pool. Even so, Mousterian and late Upper Paleolithic diets diverge from those of the nonhuman predators only in the presence/absence of one or two small-prey classes; for example, from a small quantity of gnawed remains found in Moscerini 5 it is apparent that hyaenas also ate tortoises on occasion. The Mousterian differs from the Upper Paleolithic primarily in the mollusks and tortoises found at Moscerini and possibly also in the disappearance of pachyderms from the coastal Italian ecosystems by the later cultural period.

The late Upper Paleolithic shelters under discussion were probably farther from the Mediterranean shore when visited by people, and it is quite possible that truly littoral occupations and associated evidence of mollusk harvesting are now submerged (for related discussions on Middle and Late Stone Age faunas in South African caves, see Klein 1980 and Voigt 1982). Indeed, the Middle through Upper Paleolithic faunal sequence in Riparo Mochi, one of the Grimaldi caves on the coast near the Italian-French border, provides ample evidence of mollusk harvesting throughout the two cultural periods (my current research). The data presented above expand the hypothetical boundaries of Neandertal foraging. The Middle Paleolithic of Europe has been depicted as generally lacking evidence of aquatic exploitation or use of certain game species adapted to rocky terrain (e.g., Straus 1987, 1990). New information from Italy shows that Mousterian hominids clearly appreciated the benefits of gatherable aquatic prey and were wholly capable of hunting ibex (as at Breuil and in Sant'Agostino layers 0–3) but apparently scavenged at Moscerini (see Stiner 1990*a*). Use of ibex may have been confined, however, to periods when populations had expanded into lower areas and to relatively isolated coastal foothills (see also Gamble 1986:110 and, on chamois, Miracle and Sturdy 1991). New dates for the Circeo 1 fossil cranium from Guattari (Schwarcz et al. 1991) indicate that the hominids living in the study area prior to about 50,000 years ago were certainly Neandertals. Hominids thereafter, up to roughly 35,000–40,000 years ago, were probably also Neandertals, although verification is not currently possible (see, nonetheless, Manzi and Passarello, in Bietti et al. 1988, on probable Neandertal remains from Breuil). If anything, the Neandertals' diet was the most diverse of the predators considered; they ate nearly everything.

CONCLUDING DISCUSSION

The study sample holds region, topography, environment, and depositional context more or less constant, and predator diets are reconstructed from many assemblages (except for wolves) on the basis of taphonomic evidence. From the standpoint of a simple regression analysis (plots of N-taxa and log total NISP), nearly all variation in taxonomic richness among the Italian cave assemblages *could be* explained by sample-size effects. The slopes of the predator distributions are about the same as well. At least three of the predators, human or nonhuman, hunting or scavenging, fully carnivorous or omnivorous, had access to the same number of prey species. Comparisons focusing on the relative emphases on

common ungulate species and on total numbers of resource classes represented in diets show that all predators except denning wolves took similar ranges of prey in very similar frequencies. The results obtained for bone NISP, comprising only half the data set, are entirely consistent with those obtained for total NISP.

The bigger picture is one of uniform species choice by predators in the vicinity of the Latium caves in stark contrast to the variation documented for other aspects of foraging in the same predators (e.g., Stiner 1990*b*, 1991*b*, *c*). More than anything, the results show that spotted hyaenas and Middle and late Upper Paleolithic hominids in coastal Italy operated not only at the same trophic level but also within the same resource guild (see also Turner 1984 on biogeographic relationships between hominids and hyaenas in Middle Pleistocene Britain). That species collection in dens by spotted hyaenas, in turn, responds directly to real (living) species abundance is documented in modern situations (see, e.g., Skinner, Henschel, and van Jaarsveld 1986). Prey species "choices" may not have reflected choosiness at all—at least in the context of shelter use. Of course, caves are mere windows on larger patterns of land use in all of these social predators, but they were important to all of them and thus are an appropriate nexus of comparison. As did the large carnivores around them, hominids ate what was common. In environments of Upper Pleistocene Italy, their economies focused primarily on red deer, with smaller numbers of aurochs, horse, ibex, roe deer, and other species.

To understand what similarity or difference in prey taxa consumed might mean for archaeology, it is important to consider at least two scales at which predators interact with their environment. Of special interest are the concepts of guild and niche, two distinct levels in the hierarchy of resource relationships thought to structure animal communities. *Niches* are occupied by species, and the hypothetical boundaries between niches distinguish the adaptations of species to a large extent.[4] The niches of some species adjoin in a highly dynamic way, however, and the respective boundaries are fixed by some kind of subtle, long-term interaction; this certainly is true among many ungulate predators. *Guild* members exploit a resource—usually some broad class of food—in a similar manner (Jaksić 1981:399; see also MacArthur and Levins 1967, Pianka 1978, Root 1967). Guilds are assembled by nature, independently of taxonomy, and while guilds are usually composed of consumer species from the same trophic level, these nodes of relatively intense interaction must be found through research rather than defined in advance. The range of taxa consumed tells us who the guild members are, whereas the details of exploitation set members apart (e.g., Jaksić, Greene, and Yañez 1981; Jaksić, Yañez, and Fuentes 1981; Kitchener 1991:98–105; Landres 1983; MacMahon et al. 1981; Schoener 1982; Wiens 1977).

4. "Adaptation" and "niche" are not wholly equivalent terms, since the niche of a species can vary somewhat by environment, whereas adaptation characterizes the species throughout its total geographic range.

Thus, the similarity in species exploited may obscure the substantial differences in adaptation that normally define niches.

Understanding the difference between guild and niche is essential for isolating and developing appropriate measures of adaptive difference in human evolution research. Neandertal diet in Italy resembled that of modern humans, but then so did the diet of spotted hyaenas. We know very well that humans were different from spotted hyaenas in a multitude of other ways; humans were probably far more omnivorous, had technology, lacked spots, and so on. The data on prey species consumed merely provide evidence of ecological commonality among these predators at a higher level. Apart from the issue of sampling bias, similarities in the ranges of species consumed by different predators in Italy were a product of two things: (1) the linking of predators in a resource guild that focused primarily on ungulate prey and (2) guild members' responses to live abundance in utilizing these resources.

Guilds are of considerable evolutionary interest because nonrelated taxa can greatly affect one another through their use of the same resource (see also Foley 1984). Humans living in simple societies have often found themselves in the same guild as large carnivores, including wolves, cats, spotted hyaenas, and/or bears. Ungulate prey are very important to many simple human economies, although complemented by a variety of other foods, and this pattern extends far back into prehistory. What set the various predators apart—in Upper Pleistocene Italy at least—was the age-groups they most commonly extracted from ungulate populations, their relative reliances on live and scavenged prey, their strategies for offsetting needs for key nutrients (such as fats), food transport and processing habits, and the seasons of shelter use (Stiner 1990*a*, *b*, 1991*a*, *b*, *c*, 1992, n.d.; Stiner and Kuhn 1992).

This paper takes no position on the dynamics behind the Middle-to-Upper-Paleolithic transition, nor does it advocate abandoning efforts to understand the nature and causes of taxonomic diversity in archaeofaunas. Both are, for the moment, useful heuristic constructs, albeit of very different orders. Problems do exist, however, in what we consider to be valid tests of hypothesized evolutionary shifts in human ecology. Two issues in particular have emerged with the use of species abundance data in Paleolithic subsistence studies: (1) choice versus no choice and (2) generalized versus specialized foraging.

The question of choice versus no choice has been the main subject of this paper. Taxonomic abundance in death assemblages is interesting only in the context of knowledge about animal community structure and content, and it is important to distinguish between prey availability in the environment and selectivity on the part of predators. In Italy, the four predators responded in large part to the natural abundances of different types of ungulate prey. The evidence specifically argues against using continuity in species consumed by hominids as support for *evolutionary continuity* across the Middle-to-Upper-Paleolithic transition in Eurasia (cf.

Clark and Lindly 1989*a*; 1989*b*:644). In other words, finding "no difference" in species exploited across time does not include the possibility of "no change" in hominid adaptations. Species data appear to be inadequate to the task of *negating* the possibility of significant shifts in the human niche because, after all, they cannot distinguish between Mousterian (or Upper Paleolithic) hunters and spotted hyaenas in west-central Italy.

With regard to questions about resource specialization, it is clear that there are many reasons that humans might appear to concentrate on a resource. The question is whether cases dominated by one type of prey represent temporary foraging adjustments or real changes in human adaptation. Straus (1987, 1990) Rolland (1990), Kozłowski (1990), and many others cite faunas dominated by a single species as evidence of resource specialization in the late Upper Paleolithic. Chase (1987) and Mellars (1989) meanwhile point out that monospecific faunas can also be found in the Middle Paleolithic. That some faunas are dominated by one prey species is undeniable, but the behavioral significance of these observations for hominid hunting is far from clear.

Few if any animal species are distributed evenly in environments, and overall faunal diversity in an area will shrink or expand with changes associated with global cooling or warming respectively (e.g., Gamble 1986, Miracle and Sturdy 1991). To argue, for example, that very high percentages of reindeer remains in French Paleolithic sites are not wholly confined to the coldest of times (when only reindeer might have been available) assumes excellent temporal control over *both* climatic phases of the Pleistocene and relatively instantaneous, fine-grained distributions of animals across space, neither of which we really have at present.

By the same token, the only thing special about an ibex-dominated fauna in a Paleolithic site is that people may have ranged upland (or populations expanded downward) during one period but not so much during another. Such faunas in themselves imply nothing about hominids' hunting skills in relation to ibex wiles and speed (cf. Straus 1987, 1990). Virtually all foragers will make seasonal or local (i.e., short-term) adjustments to food availability. Grizzly bears may eat nothing but salmon in spring, but no one calls them specialists: by late summer they may be gorging on berries at another location. Because of the unique way in which shelter figures in the life history of wolves, prey taxa emphasized while using dens may be a poor descriptor of wolves' dietary profile overall. The single wolf den case in this study provides a fine example.

Site occupations by mobile peoples can also be relatively short-term events. Food may be brought in from the immediate vicinity or from farther away, depending on what is going on at that place as opposed to what generally goes on within a much larger territory. Regardless of what other behaviors might interest us, the possibility of short-term adjustment to food supply is foremost among *behavioral* explanations for variation in taxonomic abundance. It is also very difficult to refute archaeologically, because one needs very good temporal information for a *wide array* of archaeological cases distributed throughout a landscape. Any evidence that occupations were short-term (i.e., seasonal) as a matter of principle reduces the likelihood that a monospecific fauna represents ecologically specialized hunting. It is at least as likely to reflect the response of a generalist forager to a situation or locality in which few prey species are available.

No archaeologist can be faulted for trying to make the most of species abundance data: this is about all that paleontology-based faunal studies offered for nearly a century. It is also clear that individuals attempting major syntheses work largely at the mercy of what analytical specialists lay before them. Like questions about shifts in hominid niche through time, questions about resource specialization require both many cases for comparison and the scaling of the archaeological data against something that can be ascertained independently about the nature of animal community structure. We can never know the absolute composition of these ancient communities, since all records of them are biased in some way, but there are alternatives. One can set the archaeological evidence against longer-term climate-induced cycles in animal community content (e.g., Simek and Snyder 1988 in France; Tchernov 1981, 1989 in Israel) or against what is known about modern animal biogeography (e.g., Gamble 1983, 1986 on hominid-carnivore cave use across Pleistocene Europe and Grayson 1991 on the late Prehistoric period in the Great Basin) or, as in this study, against what other consumers with similar resource interests ate in the same situations.

Zooarchaeologists try to define their data categories according to some biological reality, usually an aspect of animal anatomy or phylogeny. The relation of most of these categories to higher-level questions about human adaptation remains unclear and is often taken for granted (see Dunnell 1989, Rindos 1989). The expectation that species representation in human diet will directly reflect adaptive change in humans is not an outcome of any kind of theoretical prediction from ecology (see also Stiner and Kuhn 1992), nor is it supported by the evidence from Upper Pleistocene Italy. It is part of a legacy—like old pictures and their more beautiful frames—built on a longer-standing interest in paleoclimate and on empirical generalizations describing some of the earliest data bases. Early "pictures" such as the contrast between the red-deer people of the French Mousterian and the reindeer people of the late Upper Paleolithic have long since been rejected, but their "frames" are still being widely used, even when they do not fit well. If the problem is mapping shifts in human adaptation (or niche) and the archaeological record proves too coarse, then there may be better places to look, such as in the changing ways in which hominids sought, obtained, and processed the very same classes of foods through time.

The data on species consumed at shelters demonstrate close trophic links among hominids, wolves, and spotted hyaenas in Italy during the Upper Pleistocene. Indeed, species representation data appear most informative about general patterns of hominid-carnivore coexistence (see also Gamble 1983, 1986). The data also show that

food choice determined from the variety of taxa represented in cave faunas is insufficient to distinguish predator adaptations *within* the guild centering on ungulate prey in this region. Foraging behaviors and the definition of resource niche more generally are not simply problems of the species eaten by a predator or even disparity in the kinds of sources exploited. Rather, niche boundaries of coexisting large predators may be better described by qualitatively different access procedures involving the same prey species, necessitated in part by the nature of inter- or intraspecific competition. Through the processes of natural selection, coexisting predators have arrived at different and sometimes complementary ways of exploiting the same prey species as other guild members. The same principle applies to comparisons of two variants of *H. sapiens* separated in time.

Appendix 1: NISP and N-taxa (Species) Counts, Italian Cave Sites

Site and Assemblage	Main Agency[a]	Ungulates		Carnivores		Small Mammals	
		NISP	N-taxa	NISP	N-taxa	NISP	N-taxa
Guattari							
0	sh	(414) 849	(5) 9	(63) 108	(3) 4	1	1
1	sh	(446) 615	(6) 6	(58) 80	(1) 4	6	2
2	MP/sh	(76) 104	(6) 6	(11) 13	(1) 1	2	1
3	?	(3) 4	(3) 1	(1) 0	(1) 0	0	0
4	MP	(35) 50	(5) 4	(2) 3	(1) 1	4	1
5	MP	(38) 49	(2) 3	(0) 0	(0) 0	6	2
7	?	(5) 6	(1) 1	(0) 0	(0) 0	0	0
Sant'Agostino							
0	MP	(459) 744	(8) 7	(36) 101	(4) 7	73	7
1	MP	(433) 752	(9) 7	(14) 105	(4) 7	148	10
2	MP	(181) 349	(8) 7	(16) 106	(4) 6	94	10
3	MP	(86) 160	(8) 7	(10) 66	(4) 7	71	12
4	w/MP	(71) 134	(7) 7	(10) 36	(4) 4	38	10
X	w	(160) 473	(5) 6	(34) 115	(4) 4	207	8
Breuil							
1	MP	(115) 928	(9) 10	(10) 21	(2) 3	no data	
3	MP	(277) 576	(8) 9	(38) 45	(5) 2	no data	
Moscerini							
1	?	(9) 16	(4) 3	(0) 0	(0) 0	15	4
2	MP	(16) 37	(2) 4	(0) 2	(0) 2	180	8
3	MP	(194) 358	(7) 7	(2) 3	(1) 1	0	0
4	MP	(115) 157	(6) 3	(1) 2	(1) 1	0	0
5	sh(+)	(204) 430	(5) 6	(58) 186	(5) 5	152	12
6	MP	(143) 184	(4) 3	(1) 3	(1) 2	12	4
Buca della Iena							
1	sh	(32) 87	(5) 7	(38) 63	(3) 3	0	0
2	sh	(4) 18	(2) 6	(8) 19	(2) 4	5	3
3	sh	(8) 36	(5) 6	(36) 92	(4) 5	6	2
4	sh	(13) 77	(5) 8	(58) 129	(4) 6	3	2
5	sh	(21) 102	(6) 9	(37) 129	(5) 6	5	2
6	sh	(151) 299	(7) 9	(136) 207	(4) 3	1	1
Riparo Salvini							
1988	UP	652	7	6	2	no data	
Palidoro							
33–34	UP	(235) 793	(5) 9	(1) 8	(1) 1	no data	
1	UP	76	6	1	1	1	1
2	UP	81	6	0	0	1	1
3	UP	127	6	3	2	0	0
4	UP	37	4	1	1	0	0
5	UP	330	6	6	2	1	1
6	UP	138	6	4	2	2	1
7	UP	326	5	7	1	1	1
8	UP	155	6	6	3	7	2

SOURCES: Stiner (1990*a*) and, for Palidoro 1–8, Cassoli (1976–77).

NOTE: NISP counts for teeth are listed separately (in parentheses) and together with large-mammal bone wherever possible (exceptions are data from other published studies). NISP counts for bone therefore can be derived by subtracting tooth NISP from the total NISP value in this table. Two values also are provided for N-taxa of ungulates and carnivores, the first derived from teeth only and the second derived only from bone. The arrays of taxa represented by the two counting methods overlap completely but were derived independently. The higher of the two N-taxa values is used for the analyses presented.

[a] *sh*, spotted hyaenas; *MP*, Middle Paleolithic hominids; UP, late Upper Paleolithic humans; *w*, wolves; (+), and some smaller carnivores. In seriously mixed cases, major and minor agencies are separated by a slash. The main collector seldom accounts for bear and may not account for small-mammal remains.

Appendix 2: NISP and N-taxa (Species) Counts, Grotta Polesini

Assemblage	Main Agency	Ungulates		Carnivores		Small Mammals	
		NISP	N-taxa	NISP	N-taxa	NISP	N-taxa
1	UP	3,291	8	127	5	108	7
2	UP	2,125	8	126	5	50	6
3	UP	3,413	8	76	5	69	8
4	UP	4,075	8	205	6	163	13
5	UP	6,750	8	345	8	228	11
6	UP	4,539	8	153	5	158	10
7	UP	4,230	8	148	6	108	9
8	UP	3,669	8	131	7	87	11
9	UP	4,095	8	110	6	114	9
10	UP	2,799	8	48	6	68	5
11	UP	683	8	21	4	90	8
12	UP	2,284	8	69	5	268	12

SOURCE: Radmilli (1974).
NOTE: Assemblages are from arbitrary layers 1–12. Agencies of collection for small mammals may differ from that for ungulates and carnivores.

References Cited

ALESSIO, M., F. BELLA, G. CALDERONI, C. CORTESI, AND S. IMPROTA. 1976–77. Carbon-14 dating of bone collagen from Upper Paleolithic Palidoro deposit. *Quaternaria* 19:181–85.

AVELLINO, E., A. BIETTI, L. GIACOPINI, AND A. LO PINTO. 1989. "A new Dryas II site in southern Lazio, Riparo Salvini: Thoughts on the late Epigravettian in middle and southern Tyrrhenian Italy," in *The Mesolithic in Europe.* Edited by C. Bonsall, pp. 516–32. Edinburgh: John Donald.

BARYSHNIKOV, G, 1989. Les mammifères du Paléolithique inférieur du Caucase. *L'Anthropologie* 93:813–30.

BERTRAM, B. C. R. 1979. "Serengeti predators and their social systems," in *Serengeti: Dynamics of an ecosystem.* Edited by A. R. E. Sinclair and M. Norton-Griffiths, pp. 221–48. Chicago: University of Chicago Press.

BIETTI, A., G. MANZI, P. PASSARELLO, A. G. SEGRE, AND M. C. STINER. 1988. The 1986 excavation campaign at Grotta Breuil (Monte Circeo LT). *Quaderno Archeologico Laziale* 16:372–88.

BINFORD, L. R. 1978. *Nunamiut ethnoarchaeology.* New York: Academic Press.

———. 1981. *Bones: Ancient men and modern myths.* New York: Academic Press.

BLANC, A. C., AND A. G. SEGRE. 1953. "Excursion au Mont Circé." *INQUA IVe Congrès International, Roma, Pisa.*

BRAIN, C. K. 1981. *The hunters or the hunted?.* Chicago: University of Chicago Press.

CASSOLI, P. 1976–77. Upper Paleolithic fauna at Palidoro (Rome): 1955 excavations. *Quaternaria* 19:187–95.

CHASE, P. G. 1987. Spécialisation de la chasse et transition vers le Paléolithique supérieur. *L'Anthropologie* 91:175–88.

CLARK, G. A., AND J. M. LINDLY. 1989*a*. Modern human origins in the Levant and Western Asia. *American Anthropologist* 91:962–85.

———. 1989*b*. "The case for continuity: Observations on the biocultural transition in Europe and Western Asia," in *The human revolution,* vol. 1. Edited by P. Mellars and C. Stringer, pp. 626–76. Princeton: Princeton University Press.

COWGILL, G. L. 1990. Why Pearson's *r* is not a good similarity coefficient for comparing collections. *American Antiquity* 55:512–21.

DUNNELL, R. C. 1989. "Diversity in archaeology: A group of measures in search of application?" in *Quantifying diversity in archaeology.* Edited by R. D. Leonard and G. T. Jones, pp. 142–49. Cambridge: Cambridge University Press.

EISENBERG, J. F. 1990. *Mammals of the northern neotropics.* Vol. 1. London: University of Chicago Press.

EWER, R. F. 1973. *The carnivores.* London: Weidenfeld and Nicholson.

FISHER, R. A., A. S. CORBET, AND C. B. WILLIAMS. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology* 12:42–58.

FOLEY, R. 1984. "Putting people into perspective: An introduction to community evolution and ecology," in *Hominid evolution and community ecology.* Edited by R. Foley, pp. 1–24. London: Academic Press.

FORNACA RINALDI, G., AND A. RADMILLI. 1968. *Datazione con il metodo Th^{230}/U^{238} di stalagmiti contenute in depositi musteriani.* Atti Società Toscana Scienza Naturale A 75(2).

GAMBLE, C. 1983. "Caves and faunas from Last Glacial Europe," in *Animals and archaeology,* vol. 1, *Hunters and their prey.* Edited by J. Clutton-Brock and C. Grigson, pp. 163–72. British Archaeological Reports International Series 163.

———. 1986. *The Palaeolithic settlement of Europe.* Cambridge: Cambridge University Press.

GAUTIER-HION, A., L. H. EMMONS, AND G. DUBOST. 1980. A comparison of the diets of three major groups of primary consumers of Gabon (primates, squirrels, and ruminants). *Oecologia* 45:182–89.

GRAYSON, D. K. 1981. The effects of sample size on some derived measures in vertebrate faunal analysis. *Journal of Archaeological Science* 8:77–88.

———. 1984. *Quantitative zooarchaeology.* Orlando: Academic Press.

———. 1991. Alpine faunas from the White Mountains, California: Adaptive change in the late Prehistoric Great Basin? *Journal of Archaeological Science* 18:483–506.

HOLMES, R. T., R. E. BONNEY, AND S. W. PACALA. 1979. Guild structure of the Hubbard Brook bird community: A multivariate approach. *Ecology* 60:512–20.

JAKSIĆ, F. M., 1981. Abuse and misuse of the term "guild" in ecological studies. *Oikos* 37:397–400.

JAKSIĆ, F. M., H. W. GREENE, AND J. L. YAÑEZ. 1981. The guild structure of a community of predatory vertebrates in central Chile. *Oecologia Berlin* 49:21–28.

JAKSIĆ, F. M., J. L. YAÑEZ, AND E. R. FUENTES. 1981. Assessing a small mammal community in central Chile. *Journal of Mammalogy* 62:391–96.

KITCHENER, A. 1991. *The natural history of the wild cats.* Ithaca: Comstock Publishing Associates (division of Cornell University Press).

KLEIN, R. G. 1980. "The interpretation of mammalian faunas from Stone Age archaeological sites, with special reference to sites in the southern Cape Province, South Africa," in *Fossils in the making.* Edited by A. K. Behrensmeyer and A. Hill, pp. 223–46. Chicago: University of Chicago Press.

KLEIN, R. G., AND K. CRUZ-URIBE. 1984. *The analysis of animal bones from archaeological sites.* Chicago: University of Chicago Press.

KOEHLER, G. M., AND M. G. HORNOCKER. 1991. Seasonal resource use among mountain lions, bobcats, and coyotes. *Journal of Mammalogy* 72:391–96.

KOZŁOWSKI, J. K. 1990. "A multiaspectual approach to the origins of the Upper Palaeolithic in Europe," in *The emergence of modern humans: An archaeological perspective.* Edited by P. Mellars, pp. 419–37. Ithaca: Cornell University Press.

KRUUK, H. 1972. *The spotted hyaena.* Chicago: University of Chicago Press.

LANDRES, P. B. 1983. Use of the guild concept in environmental impact assessment. *Environmental Management* 7:393–98.

LEOPOLD, B. D., AND P. R. KRAUSMAN. 1986. Diets of three predators in Big Bend National Park, Texas. *Journal of Wildlife Management* 50:290–95.

LINDLY, J. M. 1988. Hominid and carnivore activity at Middle and Upper Paleolithic cave sites in eastern Spain. *Munibe* 40:45–70.

LYMAN, R. L. 1984. Bone density and differential survivorship of fossil classes. *Journal of Anthropological Archaeology* 3:259–99.

———. 1985. Bone frequencies: Differential transport, *in situ* destruction, and the MGUI. *Journal of Archaeological Science* 12:221–36.

———. 1991. "Taphonomic problems and archaeological analyses of animal carcass utilization and transport," in *Beamers, bobwhites, and blue-points: Tributes to the career of Paul W. Parmalee.* Edited by J. R. Purdue, W. E. Klippel, and B. W. Styles, pp. 125–38. Illinois State Museum Scientific Papers 23.

MACARTHUR, R. H., AND R. LEVINS. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 191:377–85.

MACMAHON, J. A., D. J. SCHIMPF, D. C. ANDERSON, K. G. SMITH, AND R. L. BAYN. 1981. An organism-centered approach to some community and ecostystem concepts. *Journal of Theoretical Biology* 88:287–307.

MAJOR, J. T., AND J. A. SHERBURNE. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. *Journal of Wildlife Management* 51:606–16.

MECH, L. D. 1977. Wolf pack buffer zones as prey reservoirs. *Science* 198:320–21.

MELLARS, P. 1989. Major issues in the emergence of modern humans. CURRENT ANTHROPOLOGY 30:349–85.

MIRACLE, P., AND D. STURDY. 1991. Chamois and the karst of Herzegovina. *Journal of Archaeological Science* 18:89–108.

PETERSON, R. O., J. D. WOOLINGTON, AND T. N. BAILEY. 1984. Wolves of the Kenai Peninsula, Alaska. *Journal of Wildlife Management,* suppl., *Wildlife Monographs* 88.

PIANKA, E. R. 1978. *Evolutionary ecology.* New York: Harper and Row.

PITTI, C., AND C. TOZZI. 1971. La Grotta del Capriolo e la Buca della Iena presso Mommio (Camaiore, Lucca). *Rivista di Scienze Preistoriche* 26:213–58.

RADMILLI, A. M. 1974. *Gli scavi nella Grotta Polesini a Ponte Lucano di Tivoli e la più antica arte nel Lazio.* Firenze: Sansoni.

RINDOS, D. 1989. "Diversity, variation, and selection," in *Quantifying diversity in archaeology.* Edited by R. D. Leonard and G. T. Jones, pp. 13–23. Cambridge: Cambridge University Press.

ROBINSON, W. S. 1951. A method for chronologically ordering archaeological deposits. *American Antiquity* 16:293–301.

ROGERS, L. L., L. D. MECH, D. K. DAWSON, J. M. PECK, AND M. KORB. 1980. Deer distribution in relation to wolf pack territory edges. *Journal of Wildlife Management* 44:253–85.

ROLLAND, N. 1990. "Middle Palaeolithic socio-economic formations in western Eurasia: An exploratory survey," in *The emergence of modern humans: An archaeological perspective.* Edited by P. Mellars, pp. 347–88. Ithaca: Cornell University Press.

ROOT, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecology Monographs* 37:317–50.

SCHALLER, G. B. 1972. *The Serengeti lion.* Chciago: University of Chicago Press.

———. 1977. *Mountain monarchs: Wild sheep and goats of the Himalaya.* Chicago: University of Chicago Press.

SCHOENER, T. W. 1982. The controversy over interspecific competition. *American Scientist* 70:586–95.

SCHWARCZ, H. P., W. BUHAY, R. GRÜN, M. C. STINER, S. KUHN, AND G. H. MILLER. 1990–91. Absolute dating of sites in coastal Lazio. *Quaternaria Nova,* n.s., 1. In press.

SCHWARCZ, H. P., A. BIETTI, W. M. BUHAY, M. C. STINER, R. GRÜN, AND A. G. SEGRE. 1991. On the reexamination of Grotta Guattari: Uranium-series and electron-spin-resonance dates. CURRENT ANTHROPOLOGY 32:313–16.

SEGRE, A. G. 1982. "Considerazioni sulla cronostratigrafia del Pleistocene laziale." *Atti 24a Riunione Scientifica, Istituto Italiano di Preistoria e Protostoria,* pp. 23–30.

SIMEK, F., AND L. M. SNYDER. 1988. "Changing assemblage diversity in Perigord archaeofaunas," in *Upper Pleistocene prehistory of western Eurasia.* Edited by H. L. Dibble and A. Montet-White, pp. 321–32. University Museum Monograph 54.

SKINNER, J. D., J. R. HENSCHEL, AND A. S. VAN JAARSVELD. 1986. Bone-collecting habits of spotted hyaenas *Crocuta crocuta* in the Kruger National Park. *South African Journal of Zoology* 21:303–8.

STINER, M. C. 1990*a*. *The ecology of choice: Procurement and transport of animal resources by Upper Pleistocene hominids in west-central Italy.* Ann Arbor: UMI.

———. 1990*b*. The use of mortality patterns in archaeological studies of hominid predatory adaptations. *Journal of Anthropological Archaeology* 9:305–51.

———. 1991*a*. A taphonomic perspective on the origins of the faunal remains of Grotta Guattari (Latium, Italy). CURRENT ANTHROPOLOGY 32:103–17.

———. 1991*b*. Food procurement and transport by human and non-human predators. *Journal of Archaeological Science* 18:455–82.

———. 1991*c*. "An interspecific perspective on the emergence of the modern human predatory niche," in *Human predators and prey mortality.* Edited by M. C. Stiner, pp. 149–85. Boulder: Westview Press.

———. 1992. "The place of hominids among predators: Interspecific comparisons of food procurement and transport," in *From bones to behavior (Proceedings of the Eighth Annual Visiting Scholar's Conference, 1991).* Edited by J. Hudson. Carbondale: Southern Illinois University Press. In press.

———. n.d. Neandertal predatory niche: Taphonomy and zooarchaeology of Italian caves. MS.

STINER, M. C., AND S. L. KUHN. 1992. Subsistence, technology, and adaptive variation in Middle Paleolithic Italy. *American Anthropologist* 94(2). In press.

STRAUS, L. G. 1982. Carnivores and cave sites in Cantabrian Spain. *Journal of Anthropological Research* 38:75–96.

———. 1987. Upper Paleolithic ibex hunting in southwest Europe. *Journal of Archaeological Science* 14:163–78.

———. 1990. "The early Upper Palaeolithic of southwest Europe: Cro-Magnon adaptations in the Iberian peripheries, 40,000–20,000 B.P.," in *The emergence of modern humans: An archaeological perspective.* Edited by P. Mellars, pp. 276–302. Ithaca: Cornell University Press.

TCHERNOV, E. 1981. "The biostratigraphy of the Middle East," in *Préhistoire du Levant.* Edited by J. Cauvin and P. Sanlaville, pp. 67–97. Paris: Editions du CNRS.

———. 1989. "The Middle Paleolithic mammalian sequence and its bearing on the origin of *Homo sapiens* in the southern Le-

vant," in *Investigations in South Levantine prehistory (Préhistoire du Sud-Levant).* Edited by O. Bar-Yosef and B. Vandermeersch, pp. 25–38. British Archaeological Reports International Series 497.

TERBORGH, J. 1977. Bird species diversity on an Andean elevational gradient. *Ecology* 48:1007–19.

TERBORGH, J., AND J. M. DIAMOND. 1970. Niche overlap in feeding assemblages of New Guinea birds. *Wilson Bulletin* 82:29–52.

TOZZI, C. 1970. La Grotta di S. Agostino (Gaeta). *Rivista di Scienze Preistoriche* 25:3–87.

TURNER, A. 1984. "Hominids and fellow-travellers: Human migration into high latitudes as part of a large mammal community," in *Hominid evolution and community ecology.* Edited by R. Foley, pp. 193–218. London: Academic Press.

VAN VALKENBURGH, B. 1989. "Carnivore dental adaptations and diet: A study of trophic diversity within guilds," in *Carnivore behavior, ecology, and evolution.* Edited by J. L. Gittleman, pp. 410–36. Ithaca: Cornell University Press.

VOIGT, E. A. 1982. "The molluscan fauna," in *The Middle Stone Age of Klasies River Mouth in South Africa.* Edited by R. Singer and J. Wymer, pp. 155–86. Chicago: University of Chicago Press.

WIENS, J. A. 1977. On competition and variable environments. *American Scientist* 65:590–97.

Intensive Archaeological Survey in the Upper Santa Cruz Basin, Southern Patagonia[1]

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Several decades of archaeological research in various regions of Patagonia have focused mainly on cave sites, almost totally ignoring the surrounding archaeological landscapes. The purpose of this brief summary is to present the preliminary conclusions of recent regionally oriented research that addresses this perceived limitation by including a concern for open-air sites as well as for distributional data on archaeological, taphonomic, and lithic raw materials.

The region of southern Patagonia under study is the upper portion of the Santa Cruz Basin, including Lago Rico and Lago Argentino (fig. 1). Lago Argentino is encircled by strand lines attesting to higher lake levels during the late Pleistocene and throughout the Holocene (S. Stine, personal communication, 1990). Some of these higher-level strands contain reasonably well-preserved archaeological sites, most of them were probably formed after about 6,000 years ago. Previous archaeological research in this area, though limited, had occupied a central place in the discussion of supraregional technological patterns, with some researchers suggesting that the basin functioned as a cultural frontier. One of the objectives of our project was to test ideas about past interactions in Patagonia shared by members of the archaeological community, many of which were based on direct or disguised ethnographic projections. For example, archaeological wisdom considered the Santa Cruz River a geographic barrier to the dispersal of peoples, identifying a number of technological features expected to appear to the south and to the north of it (Vignati 1934, Orquera 1987). (This idea derives from the known distribution of the Tehuelche in historical times [Casamiquela 1967].) There is, however, theoretical support for the idea that rivers, which are in short supply in arid Patagonia, served as "concentrators" of people rather than as barriers (see Escalada 1958–59). We examined the distributional data to see whether there was in fact any marked difference between the areas north and south of the Santa Cruz. Another widespread idea concerning the occupation of the hinterland in Patagonia was that the lake region was used seasonally, primarily for spring and summer guanaco (*Lama guanicoe*) kills, and that the lakes themselves were used only very marginally. Theoretical support for winter use of the area may, however, be found in the occurrence of winter pastures around Lago Argentino and the presence of guanacos year-round. Furthermore, the year-round availability of huemul (*Hippocamelus bisulcus*) in the nearby forests may have been an added attraction. There is evidence of huemul consumption from sites in lacustrine settings to the north (Aschero 1981–82, Mena 1991). We hope to assess the degree of use of the lake region and of seasonality of human occupation.

Archaeological surveys should, in our opinion, be directed not only toward identifying "sites" (loci with a high density of archaeological remains) but also toward assessing the patterns of distribution of isolated and concentrated finds (Thomas 1975, Foley 1981, Wobst 1983, Dunnell and Dancey 1983). Systematically aligned 1,000-m^2 transects, set up under fixed compass readings, were intensively surveyed for archaeological as well as for natural taphonomic remains, and both sites and isolated finds were recorded. The taphonomic remains collected will allow the construction of a regional taphonomy to be used in evaluating the probability of discovery of guanaco bone beds and the degree of contamination of archaeological sites with natural bones in different settings in the lacustrine region (Borrero 1990). Preliminary results suggest that locations near lagoons