

## **Taphonomic and Methodological Perspectives of Leporid Hunting During the Upper Paleolithic of the Western Mediterranean Basin**

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*Leporid (rabbit and hare) bones have been shown to yield important information about subsistence practices, mobility patterns, and demographic trends during the Paleolithic of the western and eastern Mediterranean regions. Studies of Spanish Paleolithic caves rich in rabbit bones suggest that residential mobility patterns influence the degree of leporid hunting through time. Studies of Paleolithic sites in the eastern Mediterranean suggest that leporids were hunted in large numbers only after population sizes and densities reached certain thresholds. This paper reviews and critiques these studies based on current taphonomic and ecologic information about leporids. Leporid hunting during the Upper Paleolithic of central Portugal is then discussed and compared to these existing models. These latter data suggest that rabbit hunting in central Portugal does not conform to any existing model, suggesting that local factors of leporid density and environmental conditions likely influenced the nature and timing of small game acquisition during the Upper Paleolithic.*

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**KEY WORDS:** rabbits; hunting; Portugal; Paleolithic.

### **INTRODUCTION**

Rabbits and hares have been important to many human societies throughout the world for food, clothing, and more recently companionship. During glacial stages of the Pleistocene, Iberia was the refuge for leporids, namely the European rabbit (*Oryctolagus cuniculus*). As such, rabbits were a ubiquitous and often highly

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abundant resource, especially during warm, temperate periods. Not surprisingly, rabbit bones often dominate faunal assemblages from Paleolithic sites in Spain and Portugal. As Hockett and Bicho (2000) recently argued, leporids provide as many nutritional benefits as larger terrestrial mammals—they just come in smaller packages. In addition to meat and marrow, rabbit fur was vital to some prehistoric human foragers for both winter clothing and insulation, commodities that were every bit as important as food to their survival.

This paper explores methodological and theoretical approaches to the study of leporid remains in Paleolithic archaeology. These include taphonomy, subsistence and demographic trends, mobility patterns, and regional comparisons of faunal remains. A comprehensive review of the importance of leporids to Paleolithic foragers across the Old World is not possible in this forum. Instead, we focus on Upper Paleolithic (ca. 30,000–10,000 B.P.) rabbit hunting in the Iberian Peninsula (Spain and Portugal) and the greater Mediterranean region (Fig. 1). The paper is organized in four sections: (1) a taphonomic perspective on the deposition of leporid bones in Paleolithic caves and rockshelters; (2) a review of leporid taxonomy, evolution, and ecology to understand the context of leporid hunting during the Paleolithic; (3) an evaluation of models that explain changes in Paleolithic diets, mobility patterns and demographics based partly on frequencies of leporid bones; and (4) a discussion of rabbit hunting during the Upper Paleolithic of central Portugal in order to illustrate temporal and spatial variability in leporid exploitation between ca. 30,000 and 10,000 B.P. in southern Europe.

The recognition of extensive leporid exploitation by people throughout the Paleolithic has been hampered by theoretical biases until recently. Most early investigators dismissed these bones as human refuse and attributed their presence to nonhuman predators (e.g., Roche, 1982). This was mainly due to the lack of an appropriate taphonomic framework through which archaeologists could determine whether or not humans had eaten the rabbits found in European caves and rockshelters. Many argued that rabbits could not have been significant human



**Fig. 1.** General relationship between Mediterranean region (Iberia) and the eastern Mediterranean region (Levant).

dietary components because of their small size (e.g., Davidson, 1976). This bias stemmed from a big-game focus which was perpetuated by oversimplistic models grounded in formal economic theory. Recently, archaeologists have developed new methodological and theoretical frameworks to explain prehistoric mobility and demography based on the timing of rabbit and hare hunting (e.g., Hockett and Bicho, 2000; Stiner *et al.*, 2000; Villaverde *et al.*, 1996). Because the establishment of human agency is critical to understanding leporid exploitation, we begin with a review of taphonomic studies necessary to separate human and nonhuman predation.

### TAPHONOMY OF LEPORID BONES

Distinguishing leporid bones modified by humans from those modified by nonhuman predators should be among the first stages of zooarchaeological analysis. A large number of taphonomic studies have been published that outline methods to distinguish leporid bones modified and deposited on the landscape by humans from those of nonhuman predators (Cruz-Uribe and Klein, 1998; Hockett, 1989, 1991, 1994, 1995, 1996, 1999; Hockett and Bicho, 2000; Pérez Ripoll, 1992, 1993; Schmitt, 1990, 1995; Schmitt and Juell, 1994; Serra, 2000). Human butchering patterns may leave specific traces on leporid bones that are rarely duplicated by the actions of carnivore teeth, raptor beaks and talons, or the digestive enzymes of these nonhuman predators. Put another way, leporid bone assemblages created by human foragers often can be distinguished from those created by nonhuman predators. It also may be important, however, to identify the specific type or species of predator that deposited leporid bones into a Paleolithic cave or shelter. These latter studies may be important in models that place prehistoric foragers within a regional predator niche, or in answering questions such as "What predator niche did ancient humans occupy within their ecosystem?" In order to answer this type of question, it would be useful to determine the numbers and types of nonhuman predators that deposited leporid bones along with ancient humans during the Paleolithic. Two important studies which recently sought answers to this type of question were Stiner's and Mussi's research into the predator niche occupied by Neanderthals in Italy (Mussi, 1999; Stiner, 1994). Although these researchers came to different conclusions after analyzing the same set of data, these studies underscore the need for taphonomic research to look beyond the human vs. nonhuman distinction toward a more detailed research program of distinguishing among types of nonhuman predators that may have damaged leporid bones and accumulated those bones in Paleolithic sites.

Current taphonomic methods cannot identify every species of nonhuman predator that preyed upon rabbits and hares. Additionally, archaeologists cannot assume a priori that leporid bone assemblages created by humans during the Lower and Middle Paleolithic will look precisely like those created by humans utilizing

Upper Paleolithic technology. Yet, much research has been completed on distinguishing human from nonhuman-modified leporid bone assemblages, as well as distinguishing leporid bone assemblages accumulated by small carnivores from those accumulated by eagles and owls. It is this research, in relation to understanding the taphonomy of leporid remains recovered from Paleolithic caves and rockshelters, that is reviewed below.

### Characteristic Taphonomic Traces of Eagles, Owls, and Carnivores

Large carnivores such as wolves (*Canis lupus*) are capable of consuming all portions of leporid carcasses. Wolves and other large carnivores that preyed on rabbits and hares probably accumulated leporid bones in Paleolithic caves and rockshelters primarily by defecating scats full of bones in these sites. Many of these bones will be fractured but identifiable to the genus level, and show characteristic damage caused by strong gastric digestive enzymes, such as staining, pitting, thinning, and polishing (Andrews and Evans, 1983; Schmitt and Juell, 1994).

Smaller carnivores such as the fox (*Vulpes vulpes*) and lynx (*Lynx pardina*), as well as raptors such as the eagle owl (*Bubo bubo*) and the golden eagle (*Aquila chrysaetos*) generally do not consume entire leporid carcasses (Hockett 1989, 1995, 1996; Pérez Ripoll, 1993; Schmitt, 1995; Serra, 2000); bones not swallowed are generally deposited at kill sites or at secondary feeding sites, such as caves and rockshelters. Thus, small carnivores, eagles, and owls were more likely to accumulate relatively intact leporid bones in Paleolithic caves and rockshelters than were large carnivores.

Table I compares the relative frequencies of leporid elements that were recovered from modern and fossil bone assemblages. The relative frequencies are based on minimum number of leporid elements (MNE) except the eagle owl pellet assemblage, which is based on number of identified specimens (NISP). The assemblages from columns 2–7 were recovered from modern eagle nests, owl pellets, and carnivore scats, while those from columns 8–11 were recovered from fossil contexts.

Leporid bones from four eagle nests have been combined in the second column of Table I because the element patterning was nearly identical in each of the individual nesting sites. These assemblages consisted of three golden eagle (*Aquila chrysaetos*) nests located in the Great Basin of North America (Hockett, 1993, 1995) and one martial eagle (*Polemaetus bellicosus*) nest from Africa (Cruz-Urbe and Klein, 1998). The eagle owl (*Bubo bubo*) pellets were collected in Spain (Serra, 2000). Serra (2000) reports NISP values but not MNE values, so the relative frequencies reported in column 3 were taken from raw NISP counts. The barn owl (*Tyto alba*) pellet assemblages were collected in Nevada (Hockett, 1991, 1995).

The rabbit (*Oryctolagus cuniculus*) bones from Picareiro Cave (Hockett, 1999) and Buraca Glorioso were collected in central Portugal. These are relatively

**Table I.** Quantitative Summary of Characteristic Taphonomic Traces Left on Leporid Bones by Carnivores, Eagles, Owls, and Humans

Element	Golden eagle nest	Eagle owl pellets	Barn owl pellets	Buraca Glorioso	Surface Picareiro	Coyote scats	Mineral Hill Cave	Hogup Cave	Picareiro Cave	26NY3393
Mandible	0.23	0.54	0.83	0.39	0.48	1.0	0.66	1.0	0.72	1.0
Maxilla	0.14	0.64	0.66	0.56	0.58	—	0.47	0.35	0.51	0.42
Scapula	0.06	0.59	0.57	0.11	0.19	0.40	0.04	0.56	0.73	0.81
Humerus	0.18	1.0	1.0	0.28	0.33	0.37	0.47	0.39	0.69	0.40
Radius	0.22	0.77	0.43	0.00	0.25	0.37	0.41	0.13	0.81	0.28
Ulna	0.19	0.91	0.88	0.17	0.31	0.50	0.57	0.17	0.84	0.34
Sacrum	0.41	0.53	0.13	0.11	0.19	—	0.08	0.03	0.02	0.01
Innominate	0.60	0.41	0.46	1.0	0.73	0.33	0.73	0.42	1.0	0.30
Femur	0.51	0.58	0.56	0.67	0.67	0.63	0.29	0.15	0.57	0.11
Tibia	1.0	0.57	0.51	0.89	1.0	0.23	1.0	0.18	0.60	0.81
Vertebra	2.3	—	5.9	2.9	5.7	—	2.1	1.2	1.2	0.5
NISP/MAU										
MNE/NISP	0.83	—	0.68	0.95	0.95	0.57	0.75	0.75	0.63	0.66
NISP Total	647	2482	1385	76	259	203	669	12503	8981	616
MNE Total	535	—	941	72	246	115	505	9409	5646	404
Percent bones punctured	0.02	—	0.03	0.24	20.24	0.03	0.05	0.03	0	0

*Note.* Percentages are expressed as relative frequencies unless otherwise noted in the text.

recent rabbit bones collected from the mouth of caves. They were accumulated by small carnivores, possibly the fox (*Vulpes vulpes*) and the Iberian lynx (*Lynx pardina*). The coyote (*Canis latrans*) scat assemblage was collected from Nevada and California (Schmitt and Juell, 1994).

Mineral Hill Cave is a Pleistocene-aged paleontological site located in central Nevada (Hockett, 2000). More than 50 AMS dates extracted from bone collagen indicate that the majority of bones predate ca. 30,000 B.P. The assemblage is dominated by bones of the lower limbs and feet of large herbivores such as camel (*Camelops hesternus*), large-headed llama (*Hemiauchenia macrocephala*), horse (*Equus occidentalis* and *Equus conversidens*), bison (*Bison bison*), mountain deer (*Navahoceros fricki*), mountain sheep (*Ovis canadensis*), and pronghorn (*Antilocapra americana*). The site served as a den for a variety of large and small carnivores, including bobcat (*Lynx rufus*), the extinct North American cheetah (*Miracinonyx trumani*), bear (*Arctos* or *Arctodus*), wolf (*Canis lupus*), coyote, and fox (*Vulpes vulpes*). Bones of mustelids such as badger (*Taxidea taxus*) and six species of weasels and skunks were also recovered. Approximately 2000 cottontail rabbit (*Sylvilagus* spp.) and hare (*Lepus americanus* and *Lepus californicus*) bones were recovered as well, which represent 20% of the identifiable bones from the site.

The leporid bones from Hogup Cave represent 8500 years of faunal accumulation primarily by humans and owls. The vast majority of these bones were from hares (Hockett, 1994). The rabbit bones from the subsurface deposits of Picareiro Cave were recovered from a large, Magdalenian-aged hearth feature dating between 11,800 and 12,300 B.P. (Hockett and Bicho, 2000). The cottontail rabbit bones from site 26NY3393 represent human food waste deposited within and just outside the confines of a well-defined, open-air hearth dating to ca. 300 B.P. in southern Nevada (Hockett, 1995).

The latter three assemblages represent sites where leporid bones were discarded by modern humans wielding an Upper Paleolithic toolkit. Leporid carcasses may have been processed differently during the Lower Paleolithic and Middle Paleolithic, and this may render the recognition of leporid bone assemblages accumulated during earlier time periods more difficult to identify. If that is the case, then inductively driven research will continue to play an important role in deciphering who or what deposited leporid bones in these assemblages.

### *Owls and Eagles*

Table I indicates that owl pellets tend to contain higher percentages of leporid forelimb bones compared to hindlimb bones. In contrast, leporid hindlimb bones generally outnumber forelimb bones at eagle nesting sites where young are fledged (compare column 2 with columns 3 and 4). Owl pellets full of leporid bones may be regurgitated directly onto the floor of a cave. Bones that are not swallowed by eagles may be carried to a nest and either dropped below the nest or incorporated

directly into the nest itself. These latter bones may be deposited on the floor of a cave or shelter after the nest deteriorates. This would result in the deposition of weathered and unweathered leporid bones side-by-side in caves and rockshelters, possibly leading to erroneous interpretations about the degree of time-averaging which occurred at individual sites (e.g., Behrensmeyer, 1983).

Table I shows that leporid bones deposited under eagle nests generally contain relatively few skulls and mandibles. Decapitated hare carcasses have been observed lying in golden eagle nests with eaglets present (Hockett, 1995). In contrast, owl pellet assemblages may contain two to four times the relative frequency of leporid skulls and mandibles than do eagle nest assemblages. Additionally, owl pellet assemblages may contain three times the number of vertebrae per individual leporid carcass than do eagle nest assemblages. The eagle nest assemblages have a vertebra-NISP/MAU ratio of 2.3, indicating that there were approximately two vertebrae recovered for each individual leporid carcass represented in the nests. The barn owl pellet assemblages contained about six vertebrae for each leporid carcass represented in the pellets.

Eagle nest assemblages tend to contain greater numbers of adult leporid bones than do owl pellet assemblages (Hockett, 1995). Eagle nests contain predominantly adult leporid bones despite the fact that these bones accumulate primarily during the spring season when higher numbers of young leporids are available to predators.

Approximately 2 and 3% of the leporid bones from both the eagle nest and owl pellet assemblages displayed beak or talon puncture marks (Table I). Thus, it would be inappropriate to state that raptors had little to do with the deposition of leporid bones to a Paleolithic site because "only" 2% of the bones displayed puncture marks. Eagles and owls generally create single beak or talon puncture marks on leporid bones, and the posterior side of the innominate tends to be punctured more often than other bones (Hockett, 1991, 1995). In the relatively few cases in which eagles and owls create multiple punctures on leporid bones (less than 10% of all bones punctured), these marks generally occur on only one side of a bone.

It is clear that there are significant differences between eagle nest and owl pellet assemblages in the patterning of leporid elements present and in the number and location of punctures. In order to recognize fossil leporid bone assemblages that were deposited mainly or solely by eagles and owls, faunal analysts should pay particular attention to element patterning, and publish NISP and MNE counts for individual bones. These data, however, are currently rarely published by zooarchaeologists analyzing Paleolithic faunal assemblages.

### *Carnivores*

Columns 5–7 in Table I represent three modern small carnivore assemblages, while column 8 represents a fossil carnivore den. The element patterning of the non-scatological carnivore assemblages (surface of Picareiro Cave, Buraca Glorioso,

and Mineral Hill Cave) are remarkably similar to one another. Each assemblage contains high relative frequencies of innominates and hind limb bones, fewer front limb bones, and moderate numbers of mandibles and skulls. In many respects, this patterning is similar to that documented for eagle nest assemblages. The number of vertebrae present per individual carcass ranges from two to six. The MNE/NISP ratio is identical and very high at both Picareiro and Buraca Glorioso (0.95), while this ratio is 0.75 at Mineral Hill Cave. This indicates that high numbers of complete bones are typical of leporid bone assemblages accumulated by small carnivores where evidence is lacking for the presence of large numbers of degraded scats.

The leporid element patterning of the small carnivore scatological assemblage is very different from the three nonscatological assemblages. In this assemblage, the relative frequency of mandibles is high, while the remaining elements are approximately equally represented. There is no clear differentiation in relative frequencies of hindlimb and forelimb bones, although the overall relative frequency values for the majority of these elements is low. Additionally, as might be expected from an assemblage of bones which has been swallowed and passed through the digestive tract of a small carnivore, the MNE/NISP ratio is much lower in the scatological assemblage (0.57). Although an accurate determination of the minimum number of vertebrae present in the coyote scats cannot be determined to give a vertebrae MNE/MAU ratio, it is worth noting that this assemblage produced nearly 160 identifiable fragments of vertebrae (Schmitt and Juell, 1994, p. 255).

Only 3.5% of the scatological bones and 4.5% of the leporid bones from Mineral Hill Cave show evidence of puncture marks. One-quarter of the leporid bones from the surface of Picareiro Cave and Buraca Glorioso, however, displayed at least one puncture mark. In contrast to the eagle nest and owl pellet assemblages, the vast majority of these bones display multiple puncture marks, some of which display as many as 10 punctures on a single bone. These punctures generally are not restricted to one side of bones as they are in owl and eagle assemblages.

The scatological assemblage is characterized by bones displaying staining, thinning, and polishing traces (Schmitt and Juell, 1994). Leporid bones displaying these taphonomic traces can also be found in the pellets of diurnal raptors (Hockett, 1996; Mayhew, 1977).

### **Taphonomy of Leporid Processing by Humans**

Column 9 displays the element patterning of leporid bones that were deposited in a cave by humans and owls (Hogup Cave), while columns 10 and 11 display the element patterning of leporid bones solely left behind by humans at two sites located on either side of the Atlantic. The leporid bones from Picareiro Cave and site 26NY3393 show similarities and differences. Both of these assemblages contain high relative frequencies of mandibles. At Picareiro Cave, there are no clear differences in the relative frequencies of hindlimb and forelimb bones, and



the relative frequency values of individual bones is high. This pattern undoubtedly results from human hunters butchering and discarding rabbit carcasses in the same place. Nevertheless, only a single vertebra was recovered per individual carcass represented at Picareiro Cave. At site 26NY3393, scapulae and tibiae also occur in high numbers, while the remaining elements are all about equally represented, although in lower frequencies than at Picareiro Cave. Similar to Picareiro Cave, there are few vertebrae present per individual carcass represented. At 26NY3393, the lack of vertebrae probably resulted from the grinding of the vertebral column with milling stones, a practice ethnographically documented in the Great Basin of North America (see Hockett, 1995, for a review). Although this behavior cannot be conclusively demonstrated to have occurred at Picareiro Cave, it is possible that some Upper Paleolithic peoples pounded the vertebral column of rabbits into bone meal. Grinding stones are known from Gravettian and Solutrean contexts at Vale Boi in southern Portugal (Bicho *et al.*, 2001), and from the Magdalenian at Cabeço do Porto Marinho in the Rio Maior valley of central Portugal (Bicho, 1994; Marks *et al.*, 1994). No grinding stones were recovered from Picareiro Cave.

There are taphonomic traces that human hunters in both the Old World and the New World sometimes left on leporid bones that are rarely duplicated by carnivores and raptors. One of these is the creation of rabbit long bone cylinders by breaking or snapping the ends of long bones to extract marrow (Drews and Schmitt, 1986; Hockett, 1991, 1994; Hockett and Bicho, 2000; Pérez Ripoll, 1992, 1993; Schmitt, 1990; Vila *et al.*, 1985). Jones (1983) observed that the Ache of Paraguay often snapped or bit off the ends of monkey long bones to extract marrow. This created faunal assemblages containing high percentages of small mammal long bone cylinders. Several years later, Drews and Schmitt (1986) identified large numbers of hare tibiae cylinders recovered from prehistoric house floors at the Vista site near Reno, Nevada, dating between 550 and 850 B.P. They concluded that the inhabitants of the Vista site probably extracted marrow from the tibiae of jackrabbits. Subsequent to these pioneering studies, large numbers of leporid long bone cylinders have been identified in North American sites ranging in age from 150 B.P. to 8500 B.P. (Hockett, 1991, 1994; Schmitt, 1990), and in Upper Paleolithic sites in Spain and Portugal (Hockett and Bicho, 2000; Pérez Ripoll, 1992, 1993; Vila *et al.*, 1985). Although small carnivores, eagles, and owls sometimes create leporid long bone cylinders, these bones, in and of themselves, are not diagnostic of human activity. Nevertheless, the vast majority of leporid long bones recovered from modern eagle nests and owl pellets still have at least one epiphysis attached, whereas hundreds of rabbit or hare long bone cylinders may be present in culturally accumulated faunal assemblages (Hockett, 1994; Hockett and Bicho, 2000; Pérez Ripoll, 1992, 1993).

Leporid bones also may be cut by stone tools during carcass processing (Blasco, 1995; Hockett, 1994; Pérez Ripoll, 1992) and subsequently burned if the carcasses were roasted over or within hot coals, as was the case at the Epipaleolithic site Cingle Vermell in Catalunya (Vila *et al.*, 1985), and in the Magdalenian hearths

at Picareiro Cave, Portugal (Hockett and Bicho, 2000). Cut marks are sometimes inflicted less frequently on bones during the processing of small animal carcasses compared to the processing of large mammal carcasses. For this reason, the identification of a minimal number of cut-marked leporid bones from Paleolithic sites does not necessarily mean that humans had a minimal role in their taphonomic history. As examples, an examination of almost 20,000 leporid bones deposited over an 8500-year-period at Hogup Cave yielded only 14 cut-marked bones (Hockett, 1994). At Picareiro Cave, none of the nearly 10,000 culturally accumulated rabbit bones show definitive evidence of a cut mark made by a stone tool. On the other hand, Valente (2000) observed cutmarks on 15% of a rabbit bone sample from Levels 8 and 9 at Lapa do Suão in Portugal. At Santa Maira in Spain, Pérez Ripoll (1992) found that up to 60% of all rabbit bones from the Magdalenian levels displayed cut marks. He cautioned, however, that percentages of rabbit bones displaying cut marks in Spanish Paleolithic contexts can be highly variable even within archaeological levels of individual sites depending on, among other variables, bone preservation and whether or not the faunal analyst took the time to examine the bones under a microscope. Although cut-marked rabbit bones can provide important information they are not a prerequisite to determine human agency in the deposition of rabbits into Paleolithic caves.

Roasting leporid carcasses tends to differentially burn specific elements. In particular, bones of the feet and the ends of long bones may be burned more frequently than other bones or other bone portions (Hockett and Bicho, 2000; Vila *et al.*, 1985). It is therefore crucial that zooarchaeologists publish details of the patterning of burned leporid bones when arguing that rabbits or hares were cooked by Paleolithic hunters, especially since Hockett (1993) identified a number of burned hare bones at Hogup Cave which also displayed raptor beak or talon puncture marks. These latter bones were likely damaged and deposited in the cave by eagles or owls, and subsequently burned by humans starting fires within unprepared hearths on the surface of the cave.

### Summary

The taphonomic data outlined above are summarized in Table II. The characteristics analyzed here by no means exhaust the agents and processes that may modify leporid bones between the time of death and recovery by archaeologists (Behrensmeier and Hill, 1981; Binford, 1981; Brain, 1981; Efremov, 1940; Lyman, 1994; Voorhies, 1969; Weigelt, 1927). In addition, there are few taphonomic traces which result from human behavior that are not duplicated by noncultural processes. Nevertheless, excluding specific cases of bone diagenesis (e.g., Stiner *et al.*, 2001), the four agents that modified and deposited leporid bones in Paleolithic caves and shelters more frequently than others are probably those analyzed here: small carnivores, eagles, owls, and humans.

**Table II.** Qualitative Summary of Characteristic Taphonomic Traces Left on Leporid Bones by Carnivores, Eagles, Owls, and Humans

	Carnivores			Raptors			Humans
	Not swallowed	Scats	Not swallowed	Not swallowed	Pellets		
Staining, polishing, thinning	Not present	Common	Not present	Uncommon in owls, common in eagles	Uncommon in owls, common in eagles	Not present	
Forelimb or hindlimb bones more common	Hindlimb	Relatively equal	Hindlimb (eagles)	Forelimb (owls)	Forelimb (owls)	Relatively equal	
Mandibles/skulls	Moderately common	Common	Uncommon	Moderately common	Moderately common	Common	
Vertebrae	Moderately common	Common broken spinal processes	Moderately common	Common 6.0/carcaass	Common 6.0/carcaass	Uncommon <1/carcaass	
MNE/NISP ratio	4-5/carcaass	Low (0.50)	High (0.80)	Moderate (0.70)	Moderate (0.70)	Moderate (0.70)	
Long bone cylinders	Uncommon	Uncommon	Uncommon	Uncommon	Uncommon	May be common—in the hundreds	
Percent punctured bones	Common—up to 0.25	Uncommon—up to 0.03	Uncommon—up to 0.02	Uncommon—up to 0.03	Uncommon—up to 0.03	Not present	
Number/placement of punctures	Multiple; on opposite sides of the bone; distal femur/proximal tibia commonly punctured	Single, because of intense mastication	Single, posterior innominate commonly punctured	Single, posterior innominate commonly punctured	Single, posterior innominate commonly punctured	Not present	
But-marked bones	Not present	Not present	Not present	Not present	Not present	Highly variable—0-0.60	
Burnt bones	Not present	Not present	Not present	Not present	Not present	Probably uncommon to absent before 50,000 B.P., roasting tends to burn foot and long bone ends more frequently than other bones	

Careful and detailed taphonomic analysis can begin to tease out the agents responsible for the deposition of leporid bones into Paleolithic sites. Taphonomic analysis must constitute a first-order of analysis before interpretations are offered about how those bones accumulated in a site in the first place, and what their significance may hold for early human behavior. In the absence of taphonomic analysis, behavioral models that utilize leporid remains should be considered tantalizing propositions in need of further evaluation.

### LEPORID TAXONOMY, EVOLUTION, AND ECOLOGY IN RELATION TO PALEOLITHIC HUNTING STRATEGIES

Knowledge of the taxonomy, evolution, and ecology of prey available to Paleolithic hunters may assist in the development of subsistence models that describe or explain ancient behavior patterns. These data are also important in reviewing the logic of existing models that utilize leporid bones.

All known rabbits and hares are classified under the family Leporidae. The hares of Europe and the eastern Mediterranean are classified under the genus *Lepus*, while the old world rabbit is classified under the genus *Oryctolagus*. Pikas are classified under the family Ochotonidae, and together with Leporidae these two families form the order Lagomorpha. The term "lagomorph" refers to rabbits, hares, and pikas, while the term "leporid" refers only to rabbits and hares. "Leporid" is preferred in this paper rather than "lagomorph" because there is no evidence that pikas ever formed even a minor component of human diets at any time during the Pleistocene in Europe or in the eastern Mediterranean.

Dawson (1967, 1981) reviewed the evolution of modern leporids. The oldest representatives of the Order Lagomorpha occur in late Paleocene deposits in modern-day Mongolia and China. The earliest records of the Order in Europe are pikas from the late Oligocene. Pikas underwent an adaptive radiation in many parts of Europe and Asia throughout the succeeding Miocene. Since that time, the number of species of pika have steadily declined while members of the family Leporidae have flourished. Leporids, represented by the extinct genus *Hypolagus*, reached eastern Europe in the Pliocene, and reached western Europe by the late Pliocene.

Cladistic analysis reveals that a "Lepus pattern of P<sub>3</sub>" developed earliest in the Holarctic during the late Pliocene or early Pleistocene from advanced forms of the genus *Hypolagus*. The European rabbit (*Oryctolagus cuniculus*) probably evolved from that central stock during the Villafranchian Land Mammal Age of the early Pleistocene. Biogeographically, both *Lepus* and *Oryctolagus* spread southward from the Holarctic, where *Oryctolagus* was able to extend its range into northern Africa, while *Lepus* extended its range into southern Africa. There is currently no evidence for human occupation of the European continent prior to the Pleistocene (Gamble, 1999), so at least one species of leporid probably was available to human

hunters in most places in Europe and the eastern Mediterranean since the onset of hominid occupation of those regions.

At least five species of hares and one species of rabbit potentially were incorporated into European and eastern Mediterranean Paleolithic diets during specific time periods and in specific subregions. Species designations follow Wilson and Reeder (1993). The mountain hare (*Lepus timidus*) occupied large regions of northern Europe and some of the mountainous regions further south during the Pleistocene. Bones of the mountain hare are abundant, for example, at Gravettian-aged sites such as Pavlov I in modern Czech Republic (Musil, 1994). The Don hare (*Lepus tanaiticus*) is commonly found in early Upper Paleolithic assemblages in the southern East European Plain, such as at Kostenki VIII and XIV (Hoffecker, 2002). The brown hare (*Lepus europaeus*) was available to many Paleolithic hunters in central and southern Europe outside of Iberia. In Spain and Portugal, the Iberian hare (*Lepus granatensis*) was available to Paleolithic hunters in appropriate habitats. The Cape hare (*Lepus capensis*) was hunted during the Paleolithic in the eastern Mediterranean region, although the brown hare was also present. Bones of the European rabbit (*Oryctolagus cuniculus*) most frequently occur in large numbers in Paleolithic sites in central and southern Mediterranean Spain, in central and southern Portugal, and portions of southern France (e.g., Callou, 1995; Fontana, 1999; Hockett and Bicho, 2000; Pérez Ripoll, 1992).

Hares and rabbits evolved a number of different survival strategies which may have influenced the methods used by Paleolithic peoples to hunt these animals. Hares, for example, give birth to precocial young in shallow depressions on the ground surface. They are generally solitary animals throughout much of the year although they are known to congregate in large numbers during periods of subsistence stress. The European rabbit, on the other hand, gives birth to altricial young deep within burrows. Male European rabbits seek to maintain a harem of females and keep them within a well-defined territory often referred to as a "warren" (Garson, 1981; Southern, 1940).

Rabbit hunting probably returned a greater ratio of calories and other nutritional benefits in relation to the energy expended than did the hunting of hares because rabbit warrens are relatively easy to identify on the landscape and generally consist of a dense concentration of animal nutrition. Whenever Paleolithic peoples decided to hunt rabbits, multiple animals were likely taken by ambushing individuals along their well-worn trails, by digging them out of their burrows, and by trapping and snaring when this technology was available. The successful hunting of large numbers of rabbits undoubtedly required intimate knowledge of the location of warrens and the foraging habits of these animals.

Paleolithic hunters probably encountered hares individually most of the time, but occasionally groups of hundreds of these animals would have been seen migrating across the landscape. Hunting individual hares need not have required the use of special equipment or hunting practices. While hares are built for, and are capable of rapid bursts of speed, hares often "freeze" in place as their first line of

defense. The pelage of hares is designed for camouflage, displaying the recurring natural pattern of darker fur above the belly against a lighter background near the skyline combined with lighter fur below the belly and on the feet against a darker background nearest to the ground. Because hares use their camouflage and freeze in place before “bolting,” any predator with sharp enough eyes can often approach quite close before it flees. The flight distance is highly variable among individual animals, but Angerman (1972) cites 3 m as the average flight distance of the European brown hare. Paleolithic groups engaged in encounter hunting as they foraged across the landscape potentially could have approached within 3 m of a hare and dispatched the animal with simple spears, darts, or throwing sticks.

Hares are also known to gather by the hundreds to migrate to more favorable microenvironments during periods of severe weather (Angerman, 1972). Mass migrations have been particularly documented for the mountain hare (Angerman, 1972). During mass migrations hares could have been ambushed and taken in large numbers in much the same manner as large herd animals, providing a small group of Paleolithic hunters with considerable nutritional resources. Hare gatherings and migrations may help to explain the ubiquitous nature of leporid bones recovered from a number of Paleolithic sites in northern Europe beginning as early as the Gravettian, such as at Pavlov I in modern Czech Republic (Musil, 1994). It also must be acknowledged, however, that some northern European groups may have been manufacturing nets as early as the Gravettian, and some authors have suggested that these nets were used to capture small game such as hares during the early Upper Paleolithic (Adovasio *et al.*, 2001). Nets certainly would have aided in the capture of large numbers of mountain hares aggregating and migrating across the northern European landscape.

### **MODELS OF EARLY HUMAN BEHAVIOR BASED ON LEPORID BONES: A REVIEW AND CRITIQUE**

Leporid bones have been used for the past three decades in models that interpret human subsistence patterns on both sides of the Atlantic (Davidson, 1972; Elston, 1982; Szuter and Bayhem, 1989). In Europe and the eastern Mediterranean leporid hunting during the Paleolithic has received considerable attention in the past few years. Most prominently, rabbit hunting in Paleolithic Spain has been the subject of research by Davidson (1972, 1976), Aura Tortosa and Pérez Ripoll (1992), Pérez Ripoll (1992, 1993), Blasco (1995, 1997), Catalan and Muñiz (1995), Villaverde Bonilla and Martínez-Valle (1992), Villaverde *et al.* (1996), Aura *et al.* (1998), Morales *et al.* (1998), Olaria (1999), and Serra (2000). Rowley-Conwy (1992), Hockett and Bicho (2000), Valente (2000), Haws and Valente (2001), and Hockett (2001) discussed details of rabbit hunting during the Paleolithic in central Portugal. Jullien and Pillard (1969), Pillard (1972), and Fontana (1999) reported on leporids from southern France. Leporids were included in studies of small

mammals by Stiner (1994) and Tagliacozzo and Fiore (1998) in Italy. Recently, Stiner *et al.* (1999, 2000), Bar-El and Tchernov (2001), and Stiner (2001) discussed the diachronic use of rabbits and hares in the Paleolithic of the Levant. These studies demonstrate the importance of leporid bones in the Paleolithic archaeological record. The following sections review and critique models built to explain the role of leporids in Paleolithic diets, human mobility, and demography.

### Paleolithic Subsistence and Meat Weight Data

For eastern Spain, Davidson (1972, 1976) argued that the European rabbit was a minor and relatively unimportant food source for Upper Paleolithic people despite the fact that rabbit bones greatly outnumbered all other mammal bones at La Cueva del Volcán del Faro (see Fig. 2). He based the argument on the estimated amount of meat represented by the bones of rabbits compared to horse (*Equus spp.*) and red deer (*Cervus elaphus*). Since 100–150 rabbits would be needed to equal the meat from a single red deer, rabbits would not have been a significant food resource. Davidson (1976) later expanded on these ideas, noting that rabbit bones were also very common in other Upper Paleolithic sites in east-central Spain, including Parpalló and Les Mallaetes. He then discussed at length and ultimately rejected the possibility of a Paleolithic economy in east-central

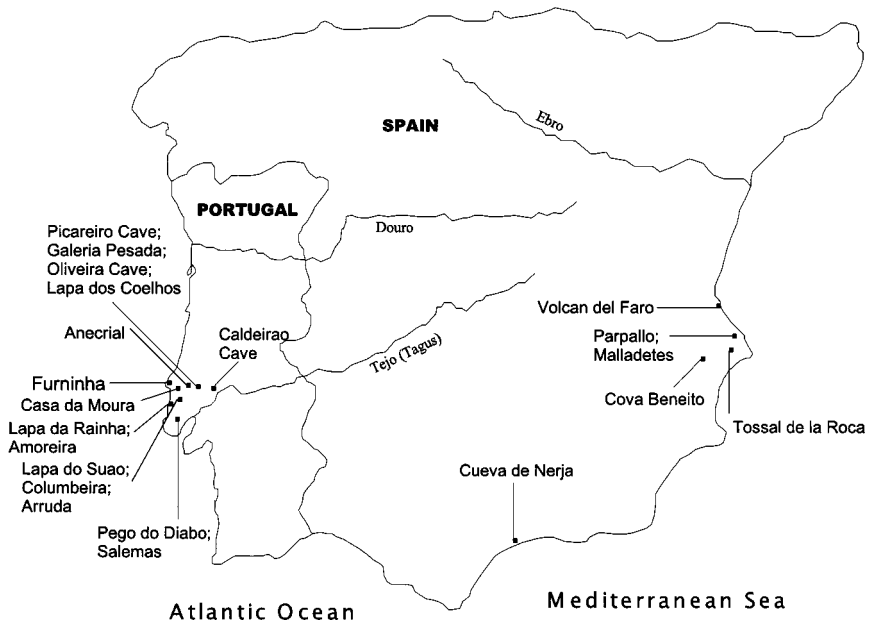


Fig. 2. Location of key sites mentioned in text.

Spain based on rabbit hunting, with large game providing supplemental nutrition. At Les Mallaetes, for example, Davidson (1976) argued that the amount of meat represented by the number of rabbit bones in comparison to large game such as the Spanish ibex (*Capra pyrenaica*) and red deer suggested that rabbits never contributed more than 3% of the total amount of meat consumed at the site during the entire Upper Paleolithic sequence. He estimated that a success rate of 0.5 rabbits procured per person per hour for a group of 20 Paleolithic hunters would require 5-h work per person per day in order to procure the calorie requirements of the entire group for an entire year. Similar to the earlier study of the faunal remains from Volcán, Davidson (1976) argued that although rabbit bones were very common at Les Mallaetes, large game constituted the bulk of the animal calories consumed throughout the Upper Paleolithic of east-central Spain.

A similar conclusion was reached by Morales *et al.* (1998) after analysis of the Late Magdalenian faunal remains from Cueva de Nerja in southern Spain. Rabbit bones dominate the faunal assemblage in the late Magdalenian deposits of Nerja, where four times as many rabbit bones were identified than Spanish ibex bones, and 25 times as many rabbit bones were identified than red deer bones. Yet Morales *et al.* (1998) concluded that both ibex and red deer were the most important mammals in the diet of the late Paleolithic occupants of Nerja. Similar to Davidson (1972, 1976), they compared the amount of meat represented by the bones of each of these animals, and concluded that rabbit was a negligible component of the diet for the Paleolithic inhabitants of Nerja.

As a result of these and other studies, a consensus is still held that rabbits were insignificant dietary components despite their abundance in Iberian Upper Paleolithic sites (e.g. Villaverde and Valle, 1992). There are a number of potential problems, however, with using “dressed meat weight” comparisons between large and small game to interpret prehistoric subsistence practices. These types of studies probably lead to misleading interpretations about the importance of small game to Paleolithic diets. For example, if rabbits were only a minor component in the Paleolithic diets of east-central and southern Spain, then they simply would be neither abundant nor ubiquitous at these sites, providing that the majority of them were accumulated by humans. Taphonomic studies by Pérez Ripoll (1992, 1993) clearly show that the thousands of rabbit bones frequently recovered from Upper Paleolithic caves in Spain were in fact a result of human hunting rather than nonhuman predation. The fact that rabbit bones are both ubiquitous and extremely abundant probably indicates that rabbits formed a substantial part of the economic *package* in the day-to-day lives of Paleolithic hunters in east-central and southern Spain, even if they did not contribute the largest amount of animal calories consumed.

The conclusion that rabbits were unimportant in the Paleolithic diets of Spain despite their abundance begs the question, “Did the meat provided by each large game kill provide sustenance for an entire group until the next successful large game kill?” It could be argued that the presence of thousands of rabbit bones



in site after site may imply just the opposite conclusion from those reached by Davidson (1972, 1976) and Morales *et al.* (1998)—rabbits formed an important part of the economic package in the day-to-day quest for food. This conclusion is bolstered by ethnographic research. A study of Hadza hunting and gathering practices by Hawkes *et al.* (2001), for example, concluded that although the Hadza live in an environment with one of the densest concentrations of terrestrial large game on earth, their success rate of procuring large game would not sustain individual groups from one kill to the next. Plant foods and small game form the bulk of the day-to-day diet for the Hadza, supplemented by an occasional influx of large quantities of nutritional resources from large game animals.

Of equal importance regarding the Upper Paleolithic caves of Spain are the issues of seasonality and excavator bias. In their paper on site exploitation territories in east-central Spain, Bailey and Davidson (1983) argued that Parpalló and Les Mallaetes were seasonal bases within a single site exploitation territory during the Gravettian and Solutrean. Parpalló, excavated in the 1940s by Pericot, is situated on the south face of a mountain at 450 m asl. Rabbit bones were noted by Pericot as “abundantísimo en todos los niveles” (Pericot, 1942, p. 268 cited in Davidson, 1989, p. 67). He later wrote that hundreds of mandibles were found in each excavated level (Pericot, 1968 cited in Davidson, 1989, p. 67). Given the total NISP of 123 rabbit bones studied by Davidson (1989), the majority of specimens probably were not kept by the excavator, a fact acknowledged by Davidson (1989, p. 67). Les Mallaetes is located on the north face of the same mountain at 600 m asl, and exposed to winter winds. Bailey and Davidson (1983) argued that this site was a summer base for exploiting red deer and ibex in their summer pastures. As Bicho *et al.* (2000) and Hockett and Bicho (2000) showed, adult-dominated rabbit mortality profiles likely indicate fall or winter kills because spring/summer ones probably would have large numbers of subadults, provided hunters were not selecting prime-age trophy rabbits. With high proportions of juveniles, and thus smaller packages of nutritional resources available, rabbit populations may not have been attractive to human hunters during spring and summer as opposed to fall and winter. If so, one might not expect large numbers of rabbit bones from summer sites like Les Mallaetes, where rabbit NISP totaled only 279 in the entire Upper Paleolithic sequence. Parpalló was probably a better example of the scale of rabbit hunting in the Upper Paleolithic, but unfortunately the majority of rabbit bones were not kept by the original excavator.

### **Leporid Bones and Paleolithic Mobility Patterns**

Recent studies in east-central and southern Spain suggest that changes in the nature and timing of the acquisition of small game such as leporids and various coastal resources may signal changes in Paleolithic mobility patterns. After careful taphonomic study, Villaverde *et al.* (1996) proposed a model to explain differences

between the Middle and Upper Paleolithic using leporid hunting as an indicator of human mobility. They noted that Middle Paleolithic levels in caves in eastern Spain (Cova Negra and Cova Beneito) contained large numbers of subadult leporid bones that displayed evidence of gastric etching and carnivore marks. Since few showed anthropogenic marks, they concluded that the eagle owl (*Bubo bubo*) probably deposited the majority of rabbit bones in Middle Paleolithic levels. In contrast, the Upper Paleolithic sequences in these same caves contained large numbers of adult leporid bones, many of which exhibited cut marks made by stone tools. The frequency of rabbit bones displaying gastric etching damage significantly decreased from the Middle to the Upper Paleolithic deposits. Villaverde *et al.* (1996) also noted a shift from hunting several species of medium and large herbivores during the Middle Paleolithic to the hunting of predominantly red deer, ibex, and rabbits during the Upper Paleolithic. The Upper Paleolithic diet became more specialized than Middle Paleolithic diets. Villaverde *et al.* (1996) related this phenomenon to a change in mobility patterns rather than to technological innovations or demographic pressure during the Upper Paleolithic. They concluded that the Middle Paleolithic in east-central Spain was a period of high mobility amongst human societies (large niche width), which fostered the hunting of a variety of species the most common of which were large herbivores. By the Upper Paleolithic, human hunters in east-central Spain had decreased their mobility patterns (reduced their niche width), and changed their hunting patterns toward a focus on rabbits and medium-sized herbivores. Villaverde *et al.* (1996) argued that the successful hunting of large quantities of rabbits could only be accomplished in foraging societies which restricted their mobility patterns because rabbits do not migrate or occupy large territories.

Aura *et al.* (1998) also discussed the nature and timing of the acquisition of rabbits, as well as aquatic resources, during the Paleolithic of east-central and southern Spain. They argued rabbits and red deer were the main animals included in the diet during the Magdalenian in east-central Spain (ca. 14,000 B.P.). The major change in the diet of Paleolithic foragers in southern Spain took place at the end of the Pleistocene with the increased importance of aquatic resources (see also Morales *et al.*, 1998; Villaverde *et al.*, 1998). Caves located close to shorelines during the Magdalenian displayed meager evidence for the acquisition of aquatic resources by humans but there was ample evidence for a diet based primarily on rabbits and red deer. In contrast, caves located further from the coastline during the early Holocene indicated increased acquisition of estuarine and marine resources. At Cueva de Nerja (which was close to the shore regardless of sea level changes) in southern Spain, fish bones were five times more abundant during the Magdalenian and 10 times more abundant during the Epipaleolithic than they were during the early Upper Paleolithic (Aura *et al.*, 1998). Curiously, rabbit abundance decreased throughout the region during the Epipaleolithic at a time when dietary diversity and, presumably, regional populations densities were rising (Aura Tortosa and Pérez-Ripoll, 1992). Aura *et al.* (1998) did not propose whether

changes in climate, mobility patterns, demographic patterns, technological innovations, or a combination of these factors were responsible for these patterns.

Similar to Villaverde *et al.* (1996), Bar-El and Tchernov (2001) emphasized the role of mobility patterns in understanding changes in Paleolithic diets in the eastern Mediterranean. They argued that the shift from ephemeral to more sedentary occupations at Levantine sites resulted in the exploitation of a wider array of animals, particularly small game such as hares, birds, reptiles, and land snails. Bar-El and Tchernov (2001) also noted the possible role of new technologies in the late Upper Paleolithic such as traps and snares which may have increased the effectiveness of capturing hares.

Whether rabbit hunting should coincide with reductions in human mobility patterns, as Villaverde *et al.* (1996) and Bar-El and Tchernov (2001) suggested, is an open question. It seems possible that groups practicing relatively high residential mobility patterns could have targeted a series of closely spaced rabbit warrens for several days and then moved on to another foraging locale. It is also possible, however, that the “paths and tracks” between “locales and gatherings” (Gamble, 1999) of highly mobile groups did not lead to the kind of intimate knowledge of the landscape that fostered the exploitation of microhabitats that included rabbit warrens. Each of these possibilities has not been adequately demonstrated for the Paleolithic, and it is possible that both strategies were in operation at the same time in different places.

### Paleolithic Demography

Stiner and colleagues recently proposed a model to track population pulses in the Paleolithic (Stiner, 2001; Stiner *et al.*, 1999, 2000). They argued that slow-moving small game such as tortoises and shellfish were exploited first during the Middle Paleolithic in Italy and the Levant, and only in the Late Upper Paleolithic did quick-moving small game such as rabbits and birds become mainstays of the diet (Stiner, 2001; Stiner *et al.*, 1999, 2000). Their model assumes that Middle Paleolithic societies optimized their foraging strategies in terms of the caloric return rate of individual species as measured by archaeological applications of optimal foraging theory (e.g., Grayson and Cannon, 1999; Simms, 1987; Winterhalder and Smith, 1981). According to this model, shellfish and tortoises outranked rabbits, hares, and birds in terms of their individual caloric return rates, or the amount of calories remaining after subtracting the costs in calories to pursue, acquire, transport, and process individual carcasses from the total calories available. The implication is that those small game species that were easiest to catch (tortoises and shellfish) outranked ones that were presumed to be harder to catch (leporids and birds). More specifically, shellfish and tortoises outranked leporids and birds during much of the Middle and Upper Paleolithic because it was assumed that high pursuit costs precluded the effective use of the latter. People included them in the

diet only after the invention of specialized technology such as traps and snares, which enabled hunters to lower pursuit costs and raise caloric return rates. Thus, tortoises and shellfish were exploited in large numbers first during the Middle Paleolithic, while rabbits and birds were eaten in large numbers only during the late Upper Paleolithic (after ca. 12,000 B.P.). In contrast to the data from east-central and southern Spain, then, the eastern Mediterranean model argued that aquatic resources were exploited there in large numbers thousands of years before leporids, and that this change occurred not during the earliest Upper Paleolithic but during the late Upper Paleolithic. The assumptions of resource ranking in optimal foraging models explain the chronological sequence of small game acquisition in this region.

Although comparatively few leporids were hunted during the Middle or Upper Paleolithic in the Levant, Stiner *et al.* (1999, 2000) and Stiner (2001) attributed increases in numbers of leporid bones in the Upper Paleolithic and Epipaleolithic to human demographic pressure on animal resources. Population pressure was argued to affect small game resources in two principle ways: (1) overexploiting slow-moving tortoises and shellfish reduced their numbers and caused diminution in the average size of these animals, thereby lowering their caloric return rates; and (2) the consequences of these end-effects was a greater reliance on quick-moving small game such as leporids and birds.

The hunting of quick-moving small game such as leporids and birds is argued to be an independent variable with which to track demographic pulses in the Paleolithic record. The model predicts that Paleolithic societies relied more extensively on slow-moving small game such as shellfish and tortoises when population densities were low, but a concomitant reduction in their numbers coupled with an increasing reliance on quick-moving small game such as leporids and birds signal increases in human population densities.

Armed with a possible method to track general population increases during the Paleolithic, the model tested Flannery's Broad Spectrum Revolution (BSR) model (Flannery, 1969). Binford (1968) argued that population pressure probably was a key factor pressuring human societies to extend their range of ecological niches into niches which remained unoccupied until the end of the Pleistocene, namely the food producing niche of agricultural societies. Flannery's subsequent BSR model explained that in the face of ever-increasing population densities human groups in the eastern Mediterranean diversified their diet near the end of the Pleistocene, just prior to the domestication of plants and animals (Flannery, 1969). More recently, Neeley and Clark (1993) pointed out the importance of developing methods to independently test the two main variables of the BSR model: population pressure and the diversification of Paleolithic diets. They scaled the number of sites recorded in the Levant per a standardized unit of time and found there was a gradual increase in site density through time in the region with several "spikes" in human population, including a threefold increase in site densities from the Epipaleolithic to the Neolithic. Stiner and colleagues offered another independent

test of both variables. They concluded that late Pleistocene societies in the eastern Mediterranean did not diversify their diet compared to earlier societies. Instead, they switched from consuming larger frequencies of shellfish and tortoises during the Middle Paleolithic to hares and birds near the end of the Pleistocene, which signaled increasing population densities through time.

The pattern of leporid and aquatic resource exploitation in eastern Mediterranean region stands in stark contrast to the data available from Iberia. For the most part, rabbits are ubiquitous in Iberian cave and rockshelter faunal assemblages. No region on earth has consistently yielded leporid remains numbering in the thousands as have the Paleolithic caves of the Iberian Peninsula, except perhaps in North America's Great Basin and Southwest regions. For example, a single hearth feature in Picareiro Cave, central Portugal (Hockett and Bicho, 2000), spanning a period of no more than a few centuries produced over 10,000 leporid bones, a number that rivals the total number of leporid bones that were recovered from several key sites in the Levant spanning a period of 200,000 years (Bar-El and Tchernov, 2001; Stiner *et al.*, 2000; Tchernov, 1997). Leporids probably contributed a relatively minor component to many eastern Mediterranean diets during the Paleolithic. The effects, if any, that the consistent availability of large concentrations of leporids had on the nature and timing of small faunal exploitation during the Paleolithic remains largely unexplored, but may be the key to understanding differences in regional histories.

## The Nature and Timing of Rabbit Hunting in Central Portugal

### *Background*

Until recently, studies of rabbit remains from Paleolithic contexts in Portugal were unmethodical and unsystematic. Historically, rabbits were interpreted as intrusive because of their burrowing habits, as evidence of small carnivore meals or as human refuse. For central Portugal, these possibilities were discussed early on by Delgado (1867) in his report on excavations at the Upper Paleolithic cave site Casa da Moura. In his subsequent examination of the fauna, Harlé (1910–11) simply noted the presence of numerous remains of rabbits. Breuil (1918) later attributed “the rabbit bones layers” from Casa da Moura to the Magdalenian. Lithic analyses by Roche (1951) also concluded that the site was Magdalenian but a Solutrean component was also recognized (França *et al.*, 1961; Roche, 1974). Unfortunately, the majority of the faunal assemblage was destroyed by fire before it could be studied further (Zilhão, 1995). Recent work by Straus *et al.* (1988) and Zilhão (1995) suggests the site dates to the early Upper Paleolithic. The rabbit bones were assumed by the latter authors to be either recent intrusives or carnivore refuse because of the identification of several large and small carnivores in the remaining assemblage.

**Table III.** Pleistocene Cave Sites With Rabbit Bones Listed in Roche (1972)

Sites	Cultural period	Absolute dates (B.P.) (from Cardoso, 1995)
Algar do João Ramos	Paleontological	14,170
Furninha	Middle Paleolithic	80,000
Gruta Nova de Columbeira	Middle Paleolithic	26–28,000
Lapa da Rainha	Early Upper Paleolithic	20–25,000
Gruta das Salemas	Solutrean	20–24,000
Algar de Cascais	Solutrean	18,000

Roche (1972), writing about Pleistocene faunas from central Portugal, listed the presence of rabbit bones in every site examined in his report (Table III) but gave no discussion of their remains. Later, he did not list rabbit remains in his preliminary report on the cave site Lapa do Suão (Roche, 1982) despite the fact that over 5000 rabbit bones recently were identified by Valente (2000) and Haws and Valente (2001) for the Upper Paleolithic levels. Reasons for this omission are unclear though it is likely due to the idea that rabbits were either too small to have provided significant food to Paleolithic humans or were deposited by nonhuman predators. Roche's work preceded the beginning of taphonomic research on leporids and it may be that he lacked the methodological and theoretical framework to evaluate their remains.

The first acknowledgment of rabbit consumption by prehistoric people in Portugal comes from Lentacker (1986) for the Mesolithic. This work followed the Davidson (1976) meat weight argument. For example, in the Amoreira and Arruda *concheiros*, or shell middens, rabbits made up 74.2 and 86.8% of the identified mammalian bone assemblages, respectively (Lentacker, 1986, Table 8). When meat weight was taken into consideration these proportions dropped to 3.3 and 5.1%, respectively, rendering the dietary contribution of rabbit insignificant. Lentacker (1986) wrote that "the importance of wild rabbit was in fact much smaller" . . . than that of larger game, but no doubt it was easier to come by, with the use of snares or digging the animals out of their holes." (p. 22).

Rowley-Conwy's study of the Neolithic fauna from Caldeirão Cave represents the first taphonomic study of rabbit bones from cave contexts in Portugal (Rowley-Conwy, 1992). He concluded that the remains of rabbits in Caldeirão were deposited almost exclusively by humans in the Neolithic and Magdalenian levels. Analyses of the remaining Upper Paleolithic assemblage are still in preparation but likely result from human consumption as well (Zilhão, 1995), particularly in the Solutrean and Magdalenian levels (Sally Newton, personal communication).

While these examples offer tantalizing evidence to support the possibility of early rabbit exploitation in central Portugal, the discussion here will be limited to those Paleolithic assemblages that have been studied from a taphonomic standpoint. Unfortunately, no studies of late Middle Paleolithic rabbit-bearing

assemblages have been published, and the bones from the sites in Roche's list were not kept (Roche, 1982). Hockett (2001) has reported on a substantial Middle Pleistocene collection of rabbit bones from Galeria Pesada, and they are present in low numbers in the important Middle Paleolithic cave site Oliveira Cave (Zilhão, 2001). These two sites represent the only available Middle Paleolithic-aged leporid samples for Portugal, and analyses of both samples is currently in progress as excavations extend into the 2002 field season at both caves (e.g., Marks *et al.*, 2001, in press; Zilhão, 2002). However, several Upper Paleolithic sites have been analyzed. These include Lapa do Picareiro (Bicho *et al.*, 2000; Hockett and Bicho, 2000), Lapa do Suão (Haws and Valente, 2001; Valente, 2000), Lapa dos Coelhos (this report), Anecrial (Brugal, in press), and Pego do Diabo (Valente, 2001). Additionally, preliminary numbers from the Upper Paleolithic levels of Caldeirão Cave (Sally Newton, personal communication) offer important information in interpreting variations in rabbit numbers through time in central Portugal.

### *Rabbit Hunting in Central Portugal*

Table IV displays the general technological and chronological framework established for the Upper Paleolithic of central Portugal. Table V lists the sites analyzed here, their elevation above sea level, their associated technological phase, and the number of leporids recovered from each chronological phase. These data are similar to the general pattern outlined from east-central Spain; in both regions, leporids were a targeted resource since the early Upper Paleolithic. In central Portugal and east-central Spain, the Upper Paleolithic record is scarce prior to the Gravettian, beginning at 26,000 B.P. (Marks, 2000; Marks *et al.*, 1994; Straus *et al.*, 2000). Aurignacian artifacts in central Portugal are argued to be present in the cave site Pego do Diabo, with an associated C-14 date of approximately 28,000 B.P. (Zilhão, 1995), and from a handful of open-air sites in the Rio Maior region (Marks *et al.*, 1994; Thacker, 2001), including the important site Vale de Porcos (Zilhão, 1995). Of these sites, only Pego do Diabo contained faunal remains (Valente, 2001). Rabbits are common in Pego do Diabo, but a recent taphonomic analysis by Valente (2000, 2001) convincingly shows that these bones were deposited mainly by small carnivores. Thus, the food resources eaten during the earliest Upper Paleolithic

**Table IV.** Chrono-Stratigraphic Sequence for the Upper Paleolithic of Central Portugal

Technological sequence	Chronology (B.P.)
Epipaleolithic	10,500–8,500
Magdalenian	16,500–10,500
Solutrean	21,000–16,500
Gravettian	26,000–21,000
?Aurignacian	28,000–26,000

**Table V.** Number of Identified Remains of Leporids From Upper Paleolithic Caves in Central Portugal

Site	Cultural period	Leporid NISP	Climate	Elevation (m)
Picareiro <sup>a</sup> (E)	Epipaleolithic	1333	Cool	520
Suão	Magdalenian	5152	Warm	100
Picareiro (F, G)	Magdalenian	7408	Warm	520
Coelhos <sup>b</sup>	Magdalenian	1051	Warm	127
Caldeirão <sup>c</sup> (F)	Solutrean	8815	Cool	120
Picareiro (I)	Solutrean	182	Cool	520
Anecrial	Gravettian <sup>d</sup>	1601	Warm	340
Pego do Diabo	Aurignacian/ paleontological	931	Warm	250

<sup>a</sup>Through the 1999 field season.

<sup>b</sup>Through the 2000 field season.

<sup>c</sup>Numbers for the Magdalenian levels of Caldeirão are not yet available, but they number in the thousands.

<sup>d</sup>Stratum J in Picareiro, located below stratum I, contains a hearth full of burned leporid bones although these bones have yet to be counted; this feature likely dates to the Gravettian, thus this feature indicates high altitude use of the central Portuguese uplands during this warm period.

occupation of central Portugal are not well known, nor are they well known for the preceding Middle Paleolithic, and they are completely unknown for the Lower Paleolithic occupation of the region.

However, by the late Gravettian rabbits appear to have been a focused target of exploitation at particular places, as the data from Anecrial and stratum J in Picareiro Cave suggest. It is also noteworthy that at the earliest stage of targeted leporid exploitation during the Gravettian, marrow was already being systematically extracted from the long bones of rabbit carcasses. All of the Gravettian to Epipaleolithic-aged sites analyzed exhibit dozens or hundreds of rabbit long bone cylinders, the result of systematic marrow extraction. There is no evidence for an increasingly intensified use of rabbit carcasses between the Early Upper Paleolithic and Epipaleolithic of central Portugal.

Rabbit continued to be an important resource during the Solutrean of central Portugal, as almost 9000 remains were recovered from levels dating between 21,500 and 18,000 B.P. at Caldeirão. However, rabbit numbers fell dramatically at this time in higher altitude sites such as Picareiro Cave.

The exploitation of rabbits is a clear focus of subsistence activity during the Magdalenian at both upland and lowland sites. Picareiro, Suão, Coelhos, and Caldeirão all contain abundant quantities of rabbit bones that were clearly deposited by humans. A dramatic decline in rabbit bone numbers after 11,000 B.P. in Picareiro Cave does not, however, correspond to any significant changes in technology.

The data from central Portugal may not conform to any of the models described previously for the eastern Mediterranean or east-central Spain. Leporid hunting does not appear to signal population pulses in either east-central Spain



or central Portugal as it seems to in the eastern Mediterranean. The evidence from Cova Beneito in Spain suggests an increase in rabbit hunting during the Aurignacian, a time of sparse human occupation (Villaverde *et al.*, 1998). An increase in site numbers during the Gravettian in central Portugal would not necessarily imply dense regional populations (Straus *et al.*, 2000). In central Portugal the increase in site numbers during the Gravettian could be due largely to geomorphological factors effecting site preservation, and to changes in human use of the landscape rather than to large-scale population increases (Zilhão, 2001). The best evidence for population increases may be during the Solutrean when the Iberian Peninsula is thought to be a refugium for human populations (Straus, 1991a,b, 1996, 2000; Straus and Winegardner, 2000). However, as discussed in more detail below, a population pulse during the Solutrean would coincide with cooler, drier conditions in central Portugal that probably decreased the natural populations of rabbits available in specific microhabitats, thereby changing hunting patterns in the region. In addition, while rabbit numbers are high in Magdalenian levels, they drop rather dramatically in Epipaleolithic levels when there is no evidence for decrease in regional human population densities. This same pattern is seen in the Epipaleolithic occupations of east-central Spain (Table VI).

The timing of large-scale use of shellfish resources in central Portugal is also similar to east-central Spain, where large-scale shellfish gathering appears to be a post-Pleistocene phenomenon (Bicho, 1993, 1994, 2000; Bicho and Haws, 1996; Clarke, 1976). The earliest site that could be considered a true *concheiro* is Pedra do Patacho on the Alentejo coast, dated 10,400 B.P. (Bicho, 1994). By 10,000 B.P., shellfish appears in caves and rockshelters up to 40 km from the contemporary coast. Marine resources have been utilized in central Portugal since at least the Middle Paleolithic at sites such as Figueira Brava (Antunes, 1991) and possibly earlier (Breuil *et al.*, 1942). Solutrean-aged sites located near paleocoastlines currently would be submerged under 100–150 m of water, so the possibility exists

**Table VI.** Summary of NISP of Fauna From Late Upper Paleolithic and Mesolithic Sites in Mediterranean Spain (Adapted From Aura Tortosa and Pérez Ripoll, 1995)

	MSM <sup>a</sup> (Late Magdalenian)	EMM <sup>b</sup> (Epipaleolithic)	EGM <sup>c</sup> (Mesolithic)
Equus sp. + Bos sp.	86	39	8
Cervus elaphus	1543 (6%)	2381 (16%)	379 (10%)
Capra pyrenaica	1227 (5%)	1430 (9%)	1057 (37%)
Rupicapra + Capreolus	11	39	18
Sus scrofa	1	70	45
Leporids	23,162 (87%)	11,005 (72%)	1327 (46%)
Carnivores	64	81	23
Birds	537	272	18

<sup>a</sup>Magdalenian Superior Mediterráneo (13,000–11,000 B.P.).

<sup>b</sup>Epipaleolítico Microlaminar Mediterráneo (11,000–9000 B.P.).

<sup>c</sup>Epipaleolítico Geométrico Mediterráneo (9000–7500 B.P.).

that our knowledge of shellfish exploitation in central Portugal is extremely biased. The data at hand, however, suggest that rabbits were exploited in large numbers thousands of years before large-scale shellfish exploitation in central Portugal.

Rabbit hunting also may not have been related to changes in mobility patterns in central Portugal. Bicho (1993, 1997, n.d.) and Thacker (1996, 2001) studied mobility patterns in central Portugal by tracking the movement of raw materials, and concluded that the Gravettian was a period of high residential mobility. Residential mobility decreased through time, particularly during the Magdalenian when logistical foraging strategies likely prevailed (Bicho, n.d.; Thacker, 2000). Despite changes in residential mobility, both Gravettian and Magdalenian hunters targeted rabbit for sustenance. For central Portugal, then, the degree of rabbit hunting during the Upper Paleolithic may not reflect changes in mobility patterns.

#### *A Climate-Based Land Use Model for Central Portugal*

If rabbit hunting declined in upland habitats in central Portugal during the Solutrean and Epipaleolithic, what caused these declines? The model suggested here is that the number and density of rabbits available on the landscape naturally fluctuated during the Pleistocene due to climatic phases that effected local ecological conditions. Specifically, rabbit numbers probably increased in number near the upland caves such as Picareiro during warmer, more temperate periods, but decreased during cooler, drier periods. Paleoenvironmental data suggest that the climate of central Portugal as a whole was always relatively mild and temperate during the Pleistocene, even during general periods of extreme cold such as LGM (ca. 21,500–18,000 B.P.) and the Younger Dryas (ca. 11,000–10,500 B.P.). These cold periods probably effected the productivity of the highest uplands of central Portugal, such as near Picareiro Cave at an altitude of 510 m asl. Ecological conditions near lowland sites such as Caldeirão and Suão were probably only minimally effected by these climatic phases, and hence rabbit populations likely remained stable. These locales remained attractive to human hunters throughout the period between 26,000 and 10,000 B.P. In central Portugal rabbits were exploited at both lowland and upland sites in the warmer periods associated with the Gravettian and Magdalenian occupations. During cooler periods of the Solutrean and the Epipaleolithic, land use patterns shifted from a more eclectic use of the landscape to a more restricted pattern of use of lowland habitats.

Broadly similar patterns occurred in east-central Spain. Sites such as Cova Beneito contain Middle Paleolithic, Aurignacian, Gravettian, and Solutrean levels. Rabbit numbers steadily increased in number at Cova Beneito from the Middle Paleolithic to the Gravettian, and then showed a sharp decrease in abundance during the Solutrean (Aura Tortosa *et al.*, 2002). Table VI indicates that rabbit numbers decreased rather dramatically in east-central Spain during the Younger-Dryas as well. These data all suggest that fluctuations in the abundance of rabbit

bones during the middle and late Upper Paleolithic in the Iberian Peninsula may have been influenced by climatic factors. European rabbits in Iberia currently display bimodal peaks in breeding coinciding with the rainy seasons in Spring and Fall, which also coincides with the growth of new vegetation (Soriguer and Rogers, 1981). Conditions during the LGM and Younger-Dryas in some upland environments probably were not optimal for the successful and consistent survival of young rabbits, and this would have negatively affected population densities of rabbits during these cold periods. Conversely, warm, temperate Mediterranean climates would have fostered successful breeding of rabbits during two seasons of each year, even in the highest uplands of central Portugal, so many rabbits would have been available to human foragers. As a result, large quantities of rabbit remains represented in both upland and lowland caves in central Portugal probably are indicative of a warm, temperate climate. Interpretations that relate fluctuations in patterns of rabbit hunting by Paleolithic populations to demographic or residential mobility trends must take natural fluctuations in the availability of rabbits on the landscape into consideration.

## CONCLUSION

This paper was written to outline some of the problems in the study of leporid use in the Paleolithic. Three areas stand out as especially critical to understanding prehistoric leporid hunting: taphonomy, leporid ecology, and paleoclimate. Archaeologists must consider the taphonomic processes by which leporids are incorporated into Paleolithic sites. Many predators leave characteristic signatures on rabbit and hare assemblages. The review of past research designed to recognize various nonhuman and human traces should serve as a starting point for further research and model-building. More actualistic studies are needed, especially for the Iberian lynx. Some feeding studies are in preparation and will yield added perspectives on assemblage formation.

In addition, the behavioral ecology of leporids must be considered. The models proposed by Villaverde *et al.* (1996) and Stiner *et al.* (2000) both illustrate the potential for modeling leporid exploitation during the Paleolithic. The former model showed after careful taphonomic analysis how rabbit behavior may have affected human mobility patterns. The latter used a wider range of animal behaviors to expand the power of optimal foraging theory beyond the previous economic models based on caloric energy yield. The Portugal case study offers a contrasting view to the general applicability of the two models in regions of heavy leporid exploitation.

As paleoenvironmental reconstructions become more detailed further back in the Pleistocene, archaeologists will be able to understand fluctuations in leporid exploitation more accurately. Even subtle climatic shifts probably affected rabbit and hare populations and therefore impacted human subsistence and settlement

patterns. This appears true for the Upper Pleistocene in Portugal. Ongoing and future work in central and southern Portugal may help clarify the climatic model proposed here.

A great deal more Paleolithic sites in Portugal and Spain, as well as other areas within the Mediterranean Basin, need to be investigated through careful excavation, taphonomic, and paleoecological study in order to adequately test existing models and develop new models to explain subsistence, mobility, and demographic patterns. Leporids will factor prominently in the development of these models. Local histories of leporid density and ecological conditions are likely to play significant roles in subsistence patterning. Not surprisingly, perhaps, faunal data from Paleolithic contexts indicate that small game such as rabbits and hares have been exploited the earliest and most extensively in areas where they were most abundant.

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