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Expansion of the referential framework for the rabbit fossil accumulations generated by Iberian lynx

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ABSTRACT

The Iberian lynx is an endemic predator of the Iberian Peninsula currently restricted to southern Spain. It is one of the primary predators of rabbits in Iberian ecosystems and probably an important taphonomic agent. Few experimental taphonomic research has focused specifically on this aspect because the Iberian lynx is currently the world's most endangered feline. During the late Pleistocene and early Holocene its home range spread to the whole Iberian Peninsula and Southern France. From an anthropological point of view, Southwestern Europe is one of the major areas of interest for studies of leporid fossil accumulations because some archaeological sites show a clear anthropogenic exploitation of rabbits and hares by Neanderthals and Anatomically Modern Humans. This research is framed within the study of variability in the taphonomic signal of the Iberian lynx. In this paper a set of rabbit bones eaten by a female lynx and her cubs during the denning season which takes around two months has been studied. The experimental assemblage has been characterized using the anatomical representation of the remains, breakage patterns and damage modifications preserved on bone surfaces. The taphonomic data are discussed along with data from the literature of the ethology of the Iberian lynx. The characteristics of the taphonomic modifications are very similar in non-ingested remains altered by adults documented in previous works, and non-ingested remains modified by the litter, in terms of anatomical profile, breakage and tooth mark frequency. The main difference is the presence of specific small tooth marks caused by infant individuals. It is concluded that the Iberian lynx may be a significant source of rabbit bone accumulations in caves and shelters, but exclusively during its breeding season. The presence of bones of mixed origin in the final set (non-ingested and ingested) is inferred as a taphonomic signal feature of Iberian lynx. The expansion of the referential framework will allow us to strongly discriminate the role of hominids and lynxes in fossil accumulations of rabbits, especially when this kind of preys was usually exploited and accumulated by the hunter–gatherers in caves and shelters.

1. Introduction

Fossil leporid accumulations are a central topic of zooarchaeological studies in certain areas, such as the North American Great Basin, the Mediterranean Basin and Southwest Europe (Hockett, 1994, 1995; Villaverde et al., 1996; Quirt-Booth and Cruz-Uribe, 1997; Stiner et al., 1999; Hockett and Haws, 2002; Jones, 2006, 2012, 2013). The interest aroused by these small mammals mainly stems from their relationship with the development of the broad-spectrum revolution (Binford, 1968; Flannery, 1969; Zeder, 2012), the emergence of modern human behavior and the composition of the diets of prehistoric populations (Stiner et al., 2000; Stiner and Munro, 2002). In recent years, these animals have been the subject of renewed interest as the recurrent exploitation of leporids and other small prey by archaic hominids has become more evident (Blasco, 2008; Sanchis and Fernández-Peris, 2008; Blasco et al., 2011; Cochard et al., 2012). However, the timing and causes of specialization in the exploitation of these resources remain under discussion (Fa et al., 2013).

The advancement of research has brought with it the clear need to establish reference models to interpret the origin of rabbit accumulations, because the ecosystems in which these mammals abound are often key prey for many predators. As a result, leporid accumulations may stem from a number of different origins (Schmitt and Juell, 1994; Hockett, 1999; Lloveras et al., 2010, 2011; Rodríguez-Hidalgo et al., 2013a). The most widely studied taphonomic agents are raptors

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(Andrews, 1990; Hockett, 1996; Lloveras et al., 2008a, 2009a, 2012a, 2014a; Sanchis, 2000; Schmitt, 1995), carnivorous mammals (Andrews and Evans, 1983; Sanchis, 2000; Lloveras et al., 2008b, 2012b; Mallye et al., 2008; Sanchis and Pascual, 2011; Krajcarz and Krajcarz, 2012; Rodríguez-Hidalgo et al., 2013b) and humans (Lloveras et al., 2009b; Ugan, 2010; Sanchis et al., 2011).

The experimental taphonomic work undertaken to study the abovementioned agents have focused most closely on two topics: skeletal representation and taphonomic modifications. Taphonomists have very successfully highlighted the importance and complexity of predator feeding behavior (including hominins) as a natural phenomenon. Variability in taphocoenoses has therefore not only been studied as a result of different predators, but also in terms of differences in the origins of the remains (non-ingested *vs.* scat/pellets) (Schmitt and Juell, 1994; Lloveras et al., 2008b, 2012b; Rodríguez-Hidalgo et al., 2013b), age and size/weight of prey (Lloveras et al., 2012a), health status of the predator (Rodríguez-Hidalgo et al., 2013b), spatial organization of dens (Cochard, 2008; Mallye et al., 2008; Krajcarz and Krajcarz, 2012), and the validity of methods used (Lloveras et al., 2014b). Although the issue of leporid predators has not been specifically addressed, the status of freedom (captive *versus* free-ranging) is also a variable to consider in neo-taphonomic research (Gidna et al, 2013; Sala et al., 2014).

Regarding the problem of variability, little is known about the age of the predators involved in modification and deposition events, although in most cases, such accumulations are associated with the use of caves and shelters as dens or lairs, or with locations in which raptors tend to have nests or perches.

One of the top predators of rabbits on the Iberian Peninsula is the Iberian lynx (*Lynx pardinus*) (Delibes, 1980; Delibes and Hiraldo, 1981; Calzada and Palomares, 1996). In two previous papers, the lynx was explored as a taphonomic agent (Lloveras et al., 2008b; Rodríguez-Hidalgo et al., 2013b). Both works analyzed rabbit remains eaten by adult lynxes. Therefore, taphonomic data generated by infant individuals has been unavailable until now.

Our goals in this paper are to expand the referential framework of the taphonomic signal of the Iberian lynx to include rabbit leftovers after meals consumed by a litter formed by the female and her cubs during the denning season, improve studies of variability for a relevant agent for leporid research, and to discuss aspects of the Iberian lynx as a taphonomic modifier and bone accumulator.

2. Feeding behavior of *L. pardinus*

The Iberian lynx, *L. pardinus* (Temminck, 1827), is a medium-sized feline endemic to the Iberian Peninsula. On average, the males of the species reach a weight of 13 kg while the females are somewhat smaller (Rodríguez and Delibes, 1990; Beltrán and Delibes, 1993; Blanco, 1998; Rodríguez and Delibes, 2002). The range of the Iberian lynx extended to central and southern France from the Late Glacial to the Iron Age (Guilaine et al., 1986; Kurtén and Granqvist, 1987; Vigne, 1996; Vigne and Pascal, 2003). Currently, the species is restricted to two isolated breeding populations in the southern Iberian Peninsula, comprising fewer than 200 individuals. Thus, conducting experiments aimed at characterizing the taphonomic signal of this predator before its range is reduced any further is especially important.

The habitat of the living Iberian lynx is the Mediterranean forest, with a preference for a mosaic environment of patches of scrub, scattered trees, herbaceous grasses and rocky areas. The Iberian lynx is a specialist predator of the European rabbit (*Oryctolagus cuniculus*), a species which makes up between 85 and 100% of its diet, regardless of season or geographic area (Delibes, 1980). The Iberian lynx generally preys on adult rabbits, although young rabbits are also hunted especially in late spring. There is evidence of co-evolution between the Iberian lynx and the European rabbit, the lynx adapting both its weight and its energy needs (the consumption of one adult rabbit per day being, about 600 kcal) to coincide with the supply of these lagomorph populations in the Mediterranean area (Aldama et al., 1991). However, their diet may be supplemented with other small mammals, reptiles, birds and small ungulates usually of less than 50 kg (Delibes, 1980; Blanco, 1998; Gil-Sánchez et al., 2006). This high degree of prey specialization has been suggested as the main cause of the Iberian lynx's decline as a species, in keeping with the decline of its primary prey, the rabbit (Rodríguez and Delibes, 1990; Delibes et al., 2000).

3. Materials and methods

The rabbit remains used in this study come from the Iberian lynx breeding center of Granadilla (Extremadura, Spain). During the spring of 2013, a pregnant female (called Fárfara) was chosen as the subject for our study. This female bore three fully healthy cubs in mid-March, which have survived to the present. Fárfara and her cubs were isolated in a naturalized enclosure of 150 m^2 during the first part of the breeding season. The enclosure has a small cubbing box with a drawer for breeding, which simulates a birthing den, where the cubs spend the first weeks of life. The enclosure and cubbing were constantly monitored by the staff of the Granadilla Center *via* closed circuit video. This monitoring allowed to document the processes described below in detail.

The female and the cubs were fed *ad libitum* with live rabbits and other prey beyond the scope of this study. The rabbit leftovers not ingested during feeding by the female and her cubs from the moment the female first provisioned them with meat to two months after their birth were collected. This time period attempts to reproduce approximately the phase of the cubs' lesser mobility around the breeding den (Fernández et al., 2002). It took fifteen days from the time the prey was first provisioned until the time the cubs were first observed feeding. From that time, the cubs gradually increased the amount of meat in their diets. They were 40 days old at the time they started to have contact with the prey. They were provided 40 live rabbits during the observation period. The rabbits were wholly or partially eaten by the mother and the cubs. The team members at the Granadilla Center went around the enclosure collecting the non-ingested rabbit leftovers with comprehensive controls regarding delivery dates, ages and weights of the rabbits, date of collection and collected weight. Unfortunately, the remains left by the mother from those left by the cubs could not be separated. The average weight of the delivered rabbits was 1015 g and the average age of the prey was 47.3 days (Table 1).

The rabbit remains were processed by boiling them in water with non-enzymatic soap. After the soft parts were eliminated, the bone collections were washed with tap water and dried before analysis. In order to be able to compare the taphocoenosis of the Iberian lynx with that of other leporid predators, the analytical methodology used broadly in this study follows the same criteria applied by Lloveras and colleagues in previous works (Lloveras et al., 2008a, 2008b), with the exception of the degree of digestion, which was irrelevant in this case because it is dealt solely with undigested remains. The variables considered within each of the analytical parameters studied are presented below.

3.1. Anatomical representation

The number of skeletal elements identified (NISP) was counted and relative abundance was calculated (Dodson and Wexlar, 1979; Andrews, 1990). The proportions of the skeletal elements were also evaluated using several indices: postcrania in relation to crania (PCRT/

Table 1
Basic statistics of delivered rabbits involved in the experiment. (NID) Number of individuals delivered.

	Minimum	Maximum	Mean	SD
Age (days)	36	62	47.3	7.9
Weight (g)	840	1350	1015	148
NID	1	3	–	–