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Eagles, owls, and coyotes (oh my!): Taphonomic analysis of rabbits and guinea pigs fed to captive raptors and coyotes

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ABSTRACT

There is the potential for multiple accumulating agents of small mammals (<4.5 kg body weight) at fossil sites, however, the lack of diverse predator and prey experimental and actualistic studies often makes it difficult to attribute the accumulator(s) of small mammals. I report the results of experimentally created assemblages of rabbits (*Oryctolagus cuniculus*) and guinea pigs (*Cavia porcellus*) fed to a bald eagle (*Haliaeetus leucocephalus*), great horned owl (*Bubo virginianus*), and coyote (*Canis latrans*). The analysis provides a taphonomic assessment of two small mammal taxa that differ in size and build and are broadly representative of small mammals recovered from archaeological sites. The ingested and non-ingested portions of the prey remains were analyzed for skeletal-, digested-, deleted-, and fractured-part representation, bone breakage, and bone surface modifications. The rabbit and guinea pig samples are compared and taphonomic differences between predators and prey taxa are observed. The predators produced variable and distinctive intra- and interspecific skeletal-, digested-, deleted-, and fractured part profiles. Bone surface modification frequency differences between the samples show a mixture of significant and non-significant intra- and interspecific comparisons. This study expands the range of small mammal experimental and actualistic studies to include prey of underrepresented size and build (guinea pigs) and characterizes the signatures of predator accumulations of small mammals. Often archaeological assemblages feature a mixture of accumulators, this analysis of raptor and mammalian carnivore predation on rabbits and guinea pigs will aid in the differentiation of predation between raptors, mammalian carnivores, and humans in the archaeological record.

1. Introduction

In recent years the role of small prey in human subsistence strategies has received considerable attention, particularly in relation to the increase in dietary breadth around the Middle and Upper Paleolithic transition in Eurasia (Cochard et al., 2012; Fa et al., 2013; Lloveras et al., 2011; Stiner, 2009, 2013; Stiner et al., 2000; Tortosa et al., 2002) and modern human origins research in Africa (Clark and Kandel, 2013; Dusseldorp, 2010, 2012; Thompson, 2010; Steele and Kein, 2009). In addition to dietary breadth, the study of small prey has the potential to inform us about paleodemography (Stiner, 2001, 2004; Stiner et al., 1999, 2000), population mobility and landscape use (Hockett and Haws, 2002; Langejans et al., 2012; Stiner et al., 1999; Thompson and Henshilwood, 2014), division of labor (Bird et al., 2005), site occupation intensity (Hockett and Haws, 2002; Lupo and Schmitt, 2005; Rodríguez-Hidalgo et al., 2013a; Stiner, 2013), socioeconomic status (Schmitt and Lupo, 2008), environmental and economic stress (Langejans et al., 2012; Lupo, 2007; Stiner, 2004, 2013; Stiner and Munro, 2011), technological complexity (Backwell et al., 2008; Hockett and Bicho, 2000; Jones, 2006; Steele and Kein, 2009; Wadley, 2010), and the experimentation and transition to domesticatable resources (Munro, 2004a,b). However, the attribution of small prey accumulations are especially challenging as there is potential for multiple accumulating agents: anthropogenic, intrusive, mammalian carnivore, and/or raptor derived (Lloveras et al., 2010). The taphonomic hurdle for faunal analysts rests in distinguishing between these possible bone accumulation origins in order to correctly attribute the fossil accumulator(s).

Central to the challenge of interpreting small mammal (mammals <4.5 kg adult body weight) assemblages is taphonomic attribution. There is the lack of diverse predator and prey experimental, actualistic, and ethnoarchaeological studies such as those that have been essential in establishing the taphonomic criteria underpinning the study of large mammal fossil remains. However, small mammal taphonomy has been strong in two areas: the predator acquisition and bone modification of (1) leporids (Álvarez et al., 2012; Armstrong and Avery, 2014; Avery, 1990; Cochard, 2004a,b, 2008; Cruz-Uribe and Klein, 1998; Hockett, 1991, 1995, 1996; Lloveras et al., 2008a,b, 2009, 2010, 2012a,b, 2014; Pavao and Stahl, 1999; Rodríguez-Hidalgo et al., 2013b; Sanchis Serra, 2000; Schmitt, 1995; Schmitt and Juell, 1994) and (2) primates (McGraw et al., 2006; Mitani et al., 2001; Pobiner et al., 2007; Sanders

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et al., 2003; Tappen and Wrangham, 2000; Trapani et al., 2006) by raptors and mammals. The leporid studies have been instrumental in the interpretation of faunal assemblages and forager life-ways around the Mediterranean basin (Bicho et al., 2000; Cochard et al., 2012; Fa et al., 2013; Hockett and Bicho, 2000; Hockett and Haws, 2002; Hockett, 2009; Munro, 2009; Stiner and Munro, 2011; Stiner et al., 1999, 2000), while studies of primate remains have been critical in establishing the role of raptors and mammalian carnivores in the accumulation of hominin and primate fossils (Berger and Clarke, 1995; Berger and Clarke, 1996; Gilbert et al., 2009; Hendenstrom, 1995; McGraw and Berger, 2013).

Collectively, these and other studies (Andrews, 1990; Andrews and Evans, 1983; Elkin and Mondini, 2001; Erlandson et al., 2007; Hockett, 1999; Landt, 2007; Lupo and Schmitt, 2002, 2005; Mondini, 2004; Munro and Bar-Oz, 2005; Schmitt and Lupo, 2008; Tagliacozzo and Fiore, 1998; Yellen, 1991a,b, and others) form the core of small mammal comparative taphonomy. Yet the criteria used to characterize the signatures of predator involvement in small mammal accumulations and the range of variability within those signatures remain less-well defined. For instance, some raptor predation studies (Bochenski et al., 2009; Erlandson et al., 2007; Hockett, 1995, 1996; McGraw et al., 2006; Sanders et al., 2003; Schmitt, 1995; Trapani et al., 2006) have documented minimal levels of prey anatomical part patterning and bone surface damage while others (Andrews, 1990; Bochenski et al., 1997; Brain, 1981; Cruz-Uribe and Klein, 1998; Hoffman, 1988; Lloveras et al., 2008a; Msuya, 1993) have recognized extensive bone modification and patterning.

Small mammal (or prey) is an extraordinarily broad category that groups taxonomically disparate organisms into a single class usually based on size. Stiner et al. (2000) discussed the distinct biological properties of small prey, noting that they differ greatly in their morphology and predator avoidance adaptations among other characteristics. Because of these differences, it cannot be assumed that the taphonomic pattern of one small mammal taxon will resemble the pattern of another (Armstrong and Avery, 2014). It stands to reason that leporids and primates are not representative of the variety of small mammal archaeofaunas. In addition to the range in taphonomic variability between different prey taxa, variation is also introduced by the acquisition, transport, and modification tendencies of the particular predator responsible for accumulation. For instance, Andrews (1990) described the different prey skeletal-part and bone surface modification (BSM) patterns of various diurnal and nocturnal raptors as well as differences between specific predator taxa within those broad divisions. The taphonomic variation produced by diverse predators and prey points to the fact that more actualistic and experimental studies are needed, studies that include a wider variety of small mammals and their predators in order to refine the criteria essential to identifying the accumulator(s) of small mammal assemblages.

Towards this objective I describe and compare the taphonomic profiles of experimentally created assemblage of rabbits (*Oryctolagus cuniculus*) and guinea pigs (*Cavia porcellus*) accumulated by a bald eagle (*Haliaeetus leucocephalus*), great horned owl (*Bubo virginianus*), and coyote (*Canis latrans*). Distinguishing between the bones accumulated by different agents and documenting the range of variation inherent to diverse prey is essential to interpreting small mammal faunal assemblages. The predators featured in this study are native to the Western Hemisphere but are representative of the diurnal and nocturnal raptors and small/medium canids that are often responsible for the accumulation of small mammal fossil remains in multiple locales. The guinea pig (GP) is similar in body plan and size to other small mammals that frequently occur in fossil and archaeological assemblages, such as bathyergids, cavids, scuirids, and larger-bodied muroids (among others), of which there are few taphonomic studies. The rabbit is analogous to other leporid taxa that are often recovered at fossil and archaeological sites. The two prey species differ greatly in terms of body plan and size, and comparisons between these experimentally derived assemblages provide a taphonomic assessment of different sized small mammals collected by a variety of predators.

Predators such as eagles, owls, and canids often live and feed in or around locations that attract humans such as rock shelters and caves. It stands to reason that prey remains accumulated by these predators and humans can become interspersed, and it is often these locales which feature archaeological deposits. Therefore, differentiating between human and predator accumulated prey remains is crucial for interpreting human subsistence behaviors and site formation processes. Towards this end, the taphonomic profiles described and compared for each prey and predator in this study include the following: skeletal-part representation, bone breakage, and BSMs for ingested, non-ingested, and where possible deleted bone. The aims of this paper are as follows: (1) to extend the range of small mammal taphonomic studies to include prey of underrepresented size and morphology, (2) to elucidate the taphonomic differences between accumulations of small prey of different sizes (rabbits and GPs) recovered from the non-ingested and ingested prey remains of a variety of typical accumulators (eagles, owls and canids), and (3) to better develop the diagnostic features that can be used to identify small mammal accumulators in archaeological bone accumulations.

2. Materials and methods

For this study, 10 adult rabbits and GPs each were fed to a captive bald eagle (BE), great horned owl (GHO), and coyote, totaling 30 rabbit and 30 GPs. The raptors used in this study are housed at the University of Minnesota College of Veterinary Medicine Raptor Center, which specializes in raptor veterinary services and the rehabilitation of injured birds. The coyote is housed at the Carlos Avery Wildlife Science Center of Minnesota, which focuses on wildlife education, conservation, and rehabilitation of injured animals. Twenty rabbits and all GPs used in this study were purchased from Rodent Pro, a distributor specialized in supplying feeder animals to zoos and institutions that house carnivorous animals. The 10 rabbits that were fed to the coyote were donated by a local farmer who raises meat rabbits. The average weights of the rabbits fed to the BE, GHO, and coyote were as follows: 3.8 kg, 3.5 kg, and 4.0 kg, and for the GPs: 1.3 kg, 1.3 kg, and 1.6 kg respectively.

The study sample comprises six assemblages: (1) BE–rabbit, (2) BE–GP, (3) GHO–rabbit, (4) GHO–GP, (5) coyote–rabbit, and (6) coyote–GP. Each of these assemblages consists of an ingested portion (raptor pellets and coyote scat) and a non-ingested portion that may have been chewed but was not ingested by the predators. In all there were 18 BE–rabbit, 24 BE–GP, 56 GHO–rabbit, and 62 GHO–GP pellets recovered; the majority of pellets contained bone specimens. The coyote samples consisted of 49 and 42 scats containing rabbit and GP bones respectively; the majority of scats contained bone specimens.

2.1. Feeding protocol and sample preparation

Before each feeding episode, the predators' enclosures were cleaned of previous meals, pellets, and scats. Each rabbit and GP was fed individually to a single predator. The predators were allowed to free feed until the carcass was completely consumed or the predator lost interest and ceased feeding on the remains for at least three days. Throughout the feeding phase of the experiment the raptors were fed only mice and the coyote was fed only boneless meals to avoid contamination of the rabbit and GP scat samples.

For the raptors, feeding typically lasted between three and five days. At the end of each day, the carcass was removed, weighed, and introduced again to the bird the next morning. Over the course of the feedings, the raptors consumed at least 50% of each carcass by weight. After feeding, the enclosures were cleaned of all non-ingested and ingested prey remains — including fur, bones, pellets, and tissues. Over the next five days, all pellets were collected and associated with the previous feeding episode.