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Taphonomic signature of golden eagles (Aquila chrysaetos) on bone prey remains

Lluís Lloverasa, Alessandra Cossob, Jaume Soléc, Bernat Claramunt-Lópezde and Jordi Nadala

aSERP, Secció de Prehistòria i Arqueologia, Facultat de Geografia i Història, Universitat de Barcelona, Barcelona, Spain; bDipartimento di Storia, Scienze dell'Uomo e della Formazione, Università degli Studi di Sassari, Sassari, Italy; 'MN Consultors en Ciències de la Conservació, Tarragona, Spain; d'CREAF, Universitat Autònoma de Barcelona, Bellaterra, Spain; eUnitat d'Ecologia, Departament de Biologia Animal, Biologia Vegetal i Ecologia, Universitat Autònoma de Barcelona, Bellaterra, Spain

ABSTRACT

The golden eagle (Aquila chrysaetos) is one of the most important birds of prey in the Northern Hemisphere. This raptor is used to building large nests in high cliffs to which they return for several breeding years accumulating important amounts of their prey skeletal remains. This makes the golden eagle one of the major predators able to accumulate faunal remains in archaeological sites. Despite this fact, the taphonomic signature of golden eagles has not been properly characterized. Here we present the analysis of ingested and non-ingested faunal remains predated and accumulated by this raptor in two different nesting areas from the Iberian Peninsula. Results show how the faunal taxonomic record may vary depending on the ecological zone. Leporids and terrestrial carnivores are the best represented. The observed anatomical representation, breakage and bone surface modification patterns are discussed for different taxa. The taphonomic pattern varies depending on the type of prey and the origin of skeletal materials (non-ingested vs. pellets). Finally, after comparing our results with marks left by other predators, several characteristic features are noted to recognise golden eagles as agents of animal bones accumulations in the fossil record.

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Taphonomy; Aquila chrysaetos; bone accumulator agents: small prey; anatomical representation; breakage; beak marks; digested bones

Introduction

The golden eagle (Aquila chrysaetos) is one of the most important birds of prey from the Northern Hemisphere. It is the most widely distributed species of eagle, still nowadays being present in sizeable areas of Eurasia, North America and parts of North Africa (Watson 2010). Golden eagles show a preference for open landscapes such as montane grassland, rocky habitats and scrublands, avoiding heavily forested zones, however they inhabit very diverse areas, including mountains, uplands and also lowland forests or wetland terrains (Cramp & Simmons 1980; Tucker & Evans 1997; Arroyo 2003).

Golden eagles are large raptors (75-85 cm in length and a mass of 3.5-6 kg [Watson 2010]) that use their agility and speed combined with powerful feet and sharp talons to catch a large variety of prey. They have been reported to feed upon medium sized birds and mammals such as hares, rabbits, grouse, crows, partridges, foxes, young deer, marmots or squirrels (Cramp & Simmons 1980). Diet varies with local differences in prey availability and habitat. For example, in Mediterranean environments European rabbits (Oryctolagus cuniculus) are the most common prey (30–65% of the total prey items) (Delibes et al. 1975; Fernández & Purroy 1990; Gil-Sánchez et al. 1994; Moleón et al. 2002) and in some coastal areas breeding eagles prey upon seabirds (Watson 2010). Golden eagles also use to consuming regularly ungulates; actively hunting juvenile individuals throughout its whole distribution range (Schweiger et al. 2014), but also in the form of carrion that have been especially documented in northern latitudes and during cold seasons (Watson et al. 1993; Sánchez-Zapata et al. 2010).

Golden eagles normally breed in holes in crags and cliffs rock shelters where the raptors build large stick nests (Cramp & Simmons 1980). Crag ledges need to be large enough to accommodate a substantial nest and often have an overhang that provides shelter during severe weather (McGrady et al. 1997). The main feature of nesting places is their relative openness, so providing easy access to nests. The average altitude of nesting is of 950 m, with a range that oscillates between 160 and 2,150 m, in calm zones with little human interference (Arroyo et al. 1990; Del Hoyo et al. 1994). Some eagles can also nest in the large open crowns of trees but they normally stand less than 10% of pairs (McGrady et al. 1997; Arroyo 2003).

It is well known that a large amount of prey remains in regurgitated food pellets and unswallowed portions of animal carcasses accumulate in golden eagles' nests and below feeding or roosting sites (Watson 2010). Besides, Pleistocene-aged remains of these raptors have been found in many archaeological deposits from different regions throughout the eagle's habitat range (Tyrberg 2008). This raises the possibility that they were active bone-accumulating agents in prehistoric caves and shelters. Their nests can therefore occur in the same spaces frequented by prehistoric hunter-gatherer populations and the food remains of

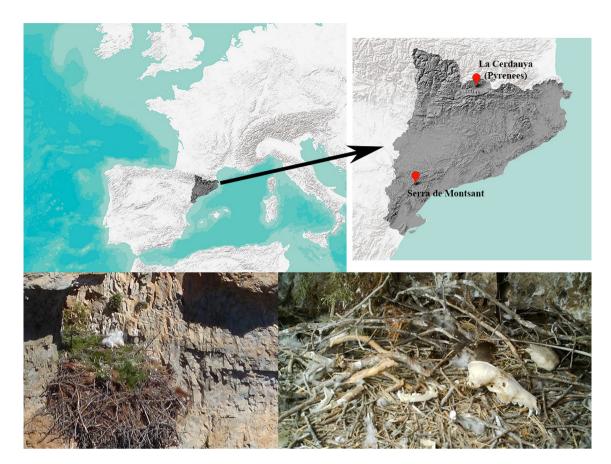


Figure 1. Locations from which golden eagles nests samples were collected. Note: Examples of two of the nests analysed in this study.

both may become intermingled. For this reason, establishing the taphonomic signature of golden eagles is necessary to distinguish between human and eagle archaeological accumulations.

In recent years, assessment of the origin of small prey bone accumulations from archaeological sites has become an important line of taphonomic research. In order to identify the agent responsible for accumulations of small prey, several actualistic studies have been conducted for terrestrial carnivores and raptors (e.g. Hockett 1991, 1995; Schmitt & Juell 1994; Sanchis 2000; Laroulandie 2002; Cochard 2004a; Mallye et al. 2008; Lloveras et al. 2008a, 2008b, 2009, 2012a, 2012b, 2016; Rodríguez-Hidalgo et al. 2013; Lloveras, Nadal, et al. 2014; Sanchis Serra et al. 2014; Armstrong 2016; among others). Some prey remains accumulated by golden eagles have also been studied. In North America, Hockett (1995, 1996) analysed a small sample of leporid and bird bones recovered from pellets and Schmitt (1995) characterized a sample of leporid remains obtained from the ground surface below the eagles' nests. In Europe, Bochenski et al. (1999, 2009) studied a sample of uneaten bird bones collected from several nests from Finland.

It is necessary to obtain information provided by these taphonomic studies in order to understand the formation processes at archaeological and palaeontological sites, and distinguish human and other animal agents of accumulation. However, the research conducted up until now is scarce and it appears that a characteristic taphonomic signature of golden eagles on small prey which can be successfully recognised in archaeological deposits, has not been properly registered yet.

The aim of our study is to elucidate the taphonomic patterns of prey remains recovered from modern nests and pellets of golden eagles and to establish diagnostic features that can be used to evaluate their role as contributors of bone accumulations in archaeological assemblages.

Material and methods

The osteological material used in this study consists of remains of prey recovered from ten golden eagle nests located in two different areas, both in Catalonia, in the northeast of the Iberian Peninsula (Figure 1): 2 nests from La Cerdanya region in the eastern Pyrenees (henceforth Pyrenees sample) and 8 nests from Serra de Montsant, Gaià and Prades, all of them mountain chains in the Catalan Pre-Coastal Range (henceforth Montsant sample). All materials were collected by the authors (JS and BC) between 1990 and 2012 after the breeding season to avoid disturbing the birds. Each sample comprises non-ingested remains and pellets (Figure 2) collected from the surface of nests and in the surrounding areas beneath them. The nests were situated in protected cliffs and materials were not exposed to the weather for a long time, for this reason remains accumulated did not display any sign of weathering or having been disturbed by scavengers.

Pellets were disaggregated while dry to separate the bones and teeth contained, then osteological materials were sorted under a magnifying glass to prepare for analysis. Skeletal remains were anatomically determined, sided, and identified to taxon whenever possible. Identifications were carried out

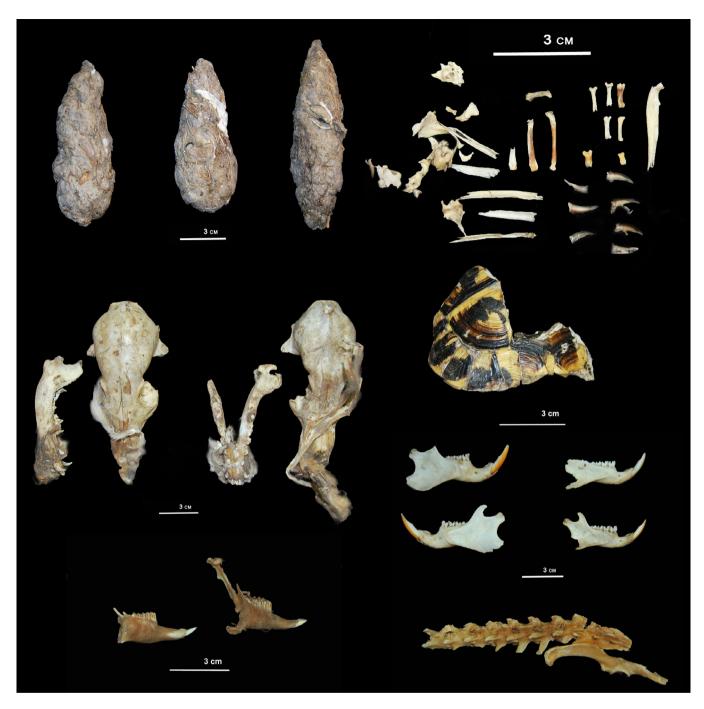


Figure 2. Examples of pellets and non-ingested remains recovered from golden eagle nests.

using the animal bone reference collection of the Secció de Prehistòria i Arqueologia from the University of Barcelona and the Museu de Ciències Naturals of Barcelona. The Number of skeletal elements (N), Number of Identified Specimens Present (NISP), Minimum Number of Elements (MNE) and Minimum Number of Individuals (MNI) were calculated as well as relative frequencies.

Determination of the age at death of the prey mammals was estimated taking into account the epiphyseal fusion state of long bones (humeri, radii, ulnae, femora and tibiae), metapodials, scapulae, calcanei and innominates (Taylor 1959; Barone 1976; Rogers 1982). Only two age categories were considered, adult and immature. On birds, the maturity of the animals was estimated

using relative porosity of the bone. It is assumed that a clearly porous texture belongs to an immature bird, from the time of hatching to nearly fledging age (Serjeantson 2009).

To facilitate comparison of the taphonomic signature of golden eagles with other predators, the analytical methodology follows the same criteria applied in previous works (Lloveras et al. 2008a, 2008b, 2009, 2012a, 2012b; Lloveras, Nadal, et al. 2014; Lloveras, Thomas, et al. 2014):

Anatomical representation

Relative abundance was calculated using the formula advocated by Dodson and Wexlar (1979): $RA_i = MNE_i/MNI \times E_i$

 $(RA_i = the relative abundance of element i; MNE_i = the minimum number of skeleton element i; MNI = the minimum number of individuals based on the highest number of any single element in the assemblage; <math>E_i = the number of element i$ in the prey skeleton).

In addition, proportions of skeletal elements in mammalian prey were evaluated using the following ratios (Andrews 1990):

- PCRT/CR the total number of postcranial elements (limb elements, vertebrae and ribs) compared with the total number of cranial elements (mandibles, maxillae and teeth).
- (2) PCRAP/CR the total number of limb elements (long bones, scapulae, innominates, patellae, metapodials, carpals, tarsals and phalanges) compared with the total number of cranial elements (mandibles, maxillae and teeth).
- (3) PCRLB/CR the total number of postcranial long bones (humeri, radii, ulnae, femora and tibiae) compared with the total number of cranial elements (mandibles and maxillae).

Loss of distal limb elements was shown by two indices (Lloveras et al. 2008a):

- (4) AUT/ZE autopodia (metapodials, carpals, tarsals and phalanges) compared with zygopodia and stylopodia (tibiae, radii, ulnae, humeri, femora and patellae).
- (5) Z/E zygopodia (tibiae, radii and ulnae) compared with stylopodia (femora and humeri).

A further index compared anterior to posterior limb elements:

(6) AN/PO – scapulae, humeri, radii, ulnae and metacarpals compared with innominates, femora, tibiae and metatarsals.

The following ratios were calculated for birds:

- (1) To assess the differential representation of wings and legs (following Ericson 1987), the number of wing elements (humeri, ulnae, carpometacarpi) was divided by the sum of wing and leg elements (femora, tibiotarsi, tarsometatarsi), and expressed as a percentage.
- (2) To evaluate the presence of proximal and distal elements (Bochenski & Nekrasov 2001), the number of proximal elements (scapulae, coracoids, humeri, femora, tibiotarsi) was divided by the sum of proximal and distal fragments (ulnae, radii, carpometacarpi, tarsometatarsi), and expressed as a percentage.
- (3) To appraise the proportions of core and limb elements (Bochenski 2005), the number of core elements (sterna, pelves, scapulae, coracoids) was divided by the sum of core and limb elements (humeri, ulnae, radii, carpometacarpi, femora, tibiotarsi, tarsometatarsi), and expressed as a percentage.

All the ratios were calculated using the MNE.

Chi-square test and Z-test were used to evaluate the significance of differences in survivorship of particular skeletal elements or their fragments.

Breakage

The breakage pattern was described by the maximum length of all identified skeletal elements. Percentages of complete elements, isolated teeth (for mammals) and articulated elements were also calculated (Andrews 1990). Fragmentation of bones was analysed using separate categories for mammals and birds. For all mammals, bone fragments were categorised depending on bone type:

- (1) Patellae, carpals, tarsals and ribs were classified as complete (C) or fragmented (F).
- (2) Phalanges were recorded as complete (C), proximal (P) or distal (D) fragments. When the distinction between proximal or distal was not possible, they were recorded as fragment (F).
- (3) Vertebrae were registered as complete (C), vertebral body (VB), vertebral epiphysis (VE) or spinous process (SP).
- (4) Breakage of teeth was calculated separately for isolated and *in situ* elements (Fernández-Jalvo & Andrews 1992) and they were classified as complete (C) or fragmented (F).
- (5) Breakage categories for long bones, metapodials, mandibles, crania, scapulae and innominates follow those proposed by Lloveras et al. (2008a) and applied in subsequent studies (Lloveras et al. 2008b, 2009, 2012a, 2016; Lloveras, Nadal, et al. 2014; Lloveras, Thomas, et al. 2014).

Breakage of bird bones was analysed using the methodology proposed by Bochenski et al. (1993).

Digestion

Damage to the bone surface was observed under light microscope ($\times 10-\times 40$ magnification). Different categories of digestion damage were applied to bones and teeth (Fernández-Jalvo & Andrews 1992; Lloveras et al. 2008a, 2008b; Lloveras, Moreno-García, et al. 2014). Five categories of digestion were distinguished: null (0); light (1); moderate (2); heavy (3); and extreme (4).

Beak/talon marks

Damage to bone surfaces caused by beaks or talons was noted and counted. Following the methodology used in previous studies (e.g. Lloveras et al. 2008a) beak/talon marks were classified as scoring, notches, tooth punctures/tooth pits and crenulated/fractured edges (Binford 1981; Brain 1981; Andrews 1990). Punctures and pits were also classified by their number (isolated or multiple) and distribution (unilateral – i.e. located on one surface – or bilateral) (Sanchis Serra et al. 2014).

Results

A total of 2.695 skeletal remains was analysed, 1.025 from the Pyrenees and 1.670 from Montsant. Taxonomic data is presented separately for each area. However, for the taphonomic analysis the data from all nest sites have been combined and analysed as a single assemblage. Since the accumulating agent is the same



Table 1. NISP (Number of Identified Specimens), MNE (Minimum Number of Elements) and MNIs (Minimum Number of Individuals) by taxon recovered in the Pyrenees, the Montsant and in the whole samples.

| | Pyrenee | s sample | Montsan | t sample | | Whole | sample | |
|-------------------------|---------|---|---------|----------|------|---|--------|------|
| Taxa | NISP | % | NISP | % | NISP | % | MNE | MNIs |
| Leporids | | | | | | | | |
| Oryctolagus cuniculus | 352 | 34.3 | 792 | 47.4 | 1144 | 42.4 | 949 | 13 |
| Lepus europaeus | 387 | 37.8 | 12 | 0.7 | 399 | 14.8 | 361 | 6 |
| Rodents | | | | | | | | |
| Marmota marmota | 46 | 4.5 | _ | _ | 46 | 1.7 | 48 | 3 |
| Scirius vulgaris | _ | _ | 136 | 8.1 | 136 | 5 | 123 | 2 |
| Apodemus sylvaticus | _ | _ | 54 | 3.2 | 54 | 2 | 46 | 5 |
| Small mammals | | | | | | | | |
| Crocidura sp. | _ | _ | 45 | 2.7 | 45 | 1.7 | 43 | 3 |
| Unidentified | _ | _ | 159 | 9.5 | 159 | 5.9 | 140 | 4 |
| Carnivores | | | | | | | | |
| Vulpes vulpes | 53 | 5.2 | 394 | 23.5 | 447 | 16.6 | 436 | 8 |
| Genetta genetta | 15 | 1.5 | _ | _ | 15 | 0.6 | 15 | 1 |
| Martes foina | 32 | 3.1 | 21 | 1.3 | 53 | 2 | 53 | 3 |
| Martes martes | 19 | 1.9 | | _ | 19 | 0.7 | 19 | 1 |
| Martes sp. | 14 | 1.4 | _ | _ | 14 | 0.5 | _ | _ |
| Meles meles | 23 | 2.2 | _ | _ | 23 | 0.9 | 23 | 1 |
| Unidentified | _ | _ | 3 | 0.2 | 3 | 0.1 | _ | _ |
| Domestic mammals | | | _ | | - | | | |
| Sus sp. | 21 | 2 | 7 | 0.4 | 28 | 1 | 27 | 2 |
| Ovis aries | 4 | 0.4 | _ | _ | 4 | 0.1 | 3 | 2 |
| Ovis/Capra | 4 | 0.4 | _ | _ | 4 | 0.1 | 3 | 1 |
| Birds | · | • | | | · | • | | • |
| Phalacrocorax sp. | 2 | 0.2 | _ | _ | 2 | 0.1 | 1 | 1 |
| Ardea cinerea | 12 | 1.2 | _ | _ | 12 | 0.4 | 12 | 1 |
| Aquila chrysaetos | _ | _ | 6 | 0.4 | 6 | 0.2 | 5 | 1 |
| Alectoris rufa | 3 | 0.3 | _ | _ | 3 | 0.1 | 2 | 1 |
| Gallus domesticus | 4 | 0.4 | _ | _ | 4 | 0.1 | 4 | 1 |
| Columba sp. | 26 | 2.5 | 3 | 0.2 | 29 | 1.1 | 28 | 4 |
| Buteo buteo | 1 | 0.1 | _ | - | 1 | 0.05 | 1 | 1 |
| Small passeriforme | _ | - | 28 | 1.7 | 28 | 1 | 26 | 2 |
| Unidentified | 7 | 0.7 | 2 | 0.1 | 9 | 0.3 | _ | _ |
| Reptiles | , | 0. , | - | 0.1 | | 0.5 | | |
| Malpolon monspessulanus | _ | _ | 5 | 0.3 | 5 | 0.2 | 5 | 1 |
| Hemorrhois hippocrepis | _ | _ | 1 | 0.06 | 1 | 0.05 | 1 | 1 |
| Testudo hermanni | _ | _ | 2 | 0.1 | 2 | 0.05 | 2 | i |
| Total | 1025 | | 1670 | 0.1 | 2695 | 0.03 | _ | 1 |

for each sample it was assumed that the taphonomic pattern would be identical.

Taxonomic representation

The taxa recovered from the samples are presented in Table 1. Different species of mammals (including leporids, carnivores, rodents and other small mammals), birds and reptiles were identified. In both areas, leporids and terrestrial carnivores are the best represented taxa, followed by rodents, birds and domestic mammals (Figure 3). However, the faunal taxonomic record varies depending on the ecological zone. For instance, the European wild rabbit (Oryctolagus cuniculus) was the most abundant taxon in Montsant whilst, in the Pyrenees, hares (Lepus europaeus) outnumbered rabbits. Marmots were only present in the Pyrenees, in turn; other species of smaller rodents such as the Eurasian red squirrel (Scirius vulgaris) and the wood mouse (Apodemus sylvaticus) were uniquely represented in the Montsant area. Among carnivores, the red fox (Vulpes vulpes) was the main prey in both regions but in the Pyrenees they were less abundant, the diversity of carnivore taxa being much greater in this area including the presence of the genet (Genetta genetta), the beech marten (Martes foina), the European pine marten (Martes martes) and the badger (Meles meles). Among domestic mammals, suids were present in both areas but caprines only in the Pyrenees. The only common species of birds was the pigeon (*Columba* sp.), other bird taxa varied in both samples. The birds recovered include cormorant (*Phalacrocorax* sp.), grey heron (*Ardea cinerea*), golden eagle (*Aquila chrysaetos*), red-legged partridge (*Alectoris rufa*), domestic chicken (*Gallus domesticus*), common buzzard (*Buteo buteo*) and some unidentified passerine remains. Reptiles were recorded only in Montsant, the Montpellier snake (*Malpolon monspessulanus*), the horseshoe whip snake (*Hemorrhois hippocrepis*) and the Hermann's tortoise (*Testudo hermanni*) were identified.

From the whole sample, the most abundant taxon was the European rabbit, which made up 42.4% of the total sample, followed by the red fox (16.6%) and the European hare (14.8%). Among birds, pigeons were the best represented (1.1%), (Table 1). The most abundant taxa when quantified by MNI did not vary: European rabbit (13), red fox (8) and European hare (6).

Age at death

Age at death estimated for rabbits and hares revealed a preponderance of adult individuals (83.5%). Among carnivores, red foxes were mostly represented by young individuals (94.3%), whilst martens and the badger were adults. All skeletal remains of domestic mammals belonged to young individuals. Regarding birds, no immature individuals were registered in the assemblage.

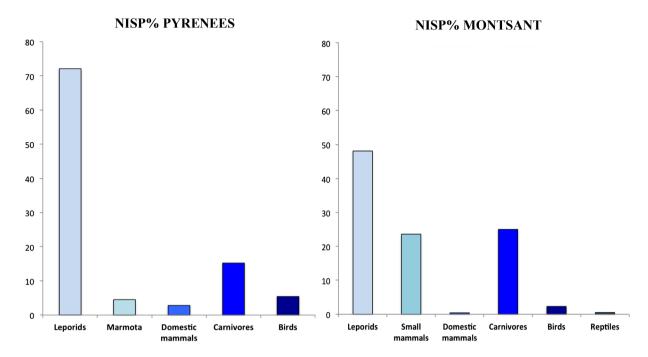


Figure 3. Relative abundance of prey taxa (%NISP) in each region analysed.

Table 2. Leporid skeletal elements recovered from golden eagle nest accumulations.

| | | Wł | nole samp | le (MNI = | 16) | | | Non-in | gested (N | 1NI = 13) | | | Pe | llets (MNI | = 9) | |
|----------|------|------|-----------|-----------|-----|------|-----|--------|-----------|-----------|------|-----|------|------------|------|------|
| Leporids | N | N% | MNE | RA% | MNI | C% | N | N% | MNE | RA% | C% | N | N% | MNE | RA% | C% |
| cra | 37 | 2.4 | 11 | 68.8 | 11 | 8.1 | 14 | 1.6 | 5 | 38.5 | 21.4 | 23 | 3.4 | 2 | 22.2 | 0 |
| man | 28 | 1.8 | 19 | 59.4 | 10 | 14.3 | 17 | 1.9 | 15 | 57.7 | 23.5 | 11 | 1.6 | 4 | 22.2 | 0 |
| Inc. | 63 | 4.1 | 61 | 63.5 | 11 | 87.3 | 40 | 4.6 | 41 | 52.6 | 100 | 23 | 3.4 | 20 | 37 | 65.2 |
| u mol | 149 | 9.7 | 149 | 77.6 | 13 | 98 | 105 | 12 | 107 | 68.6 | 100 | 44 | 6.6 | 42 | 38.9 | 93.2 |
| l mol | 103 | 6.7 | 101 | 63.1 | 13 | 72.8 | 73 | 8.4 | 77 | 59.2 | 76.7 | 30 | 4.5 | 24 | 26.7 | 66.7 |
| mol ind | 15 | 1 | 9 | _ | _ | 23.5 | _ | - | _ | - | 57.1 | 15 | 2.2 | 9 | - | 0 |
| SC | 17 | 1.1 | 12 | 37.5 | 7 | 32 | 7 | 0.8 | 5 | 19.2 | 88.9 | 10 | 1.5 | 7 | 14.6 | 0 |
| hum | 25 | 1.6 | 13 | 40.6 | 7 | 33.3 | 9 | 1 | 8 | 30.8 | 71.4 | 16 | 2.4 | 5 | 27.8 | 0 |
| rad | 15 | 1 | 10 | 31.3 | 6 | 27.8 | 7 | 0.8 | 7 | 26.9 | 71.4 | 8 | 1.2 | 3 | 16.7 | 0 |
| uln | 18 | 1.2 | 12 | 37.5 | 7 | 85.3 | 7 | 0.8 | 7 | 26.9 | 100 | 11 | 1.6 | 5 | 27.8 | 37.5 |
| mtc | 34 | 2.2 | 34 | 21.3 | 4 | 67.6 | 26 | 3 | 26 | 20 | 92.6 | 8 | 1.2 | 8 | 8.9 | 0 |
| inn | 37 | 2.4 | 32 | 100 | 16 | 24.4 | 27 | 3.1 | 26 | 100 | 61.5 | 10 | 1.5 | 5 | 27.8 | 7.1 |
| fem | 41 | 2.7 | 21 | 65.6 | 11 | 100 | 13 | 1.5 | 12 | 46.2 | 100 | 28 | 4.2 | 9 | 50 | 100 |
| pat | 6 | 0.4 | 6 | 18.8 | 4 | 23.5 | 1 | 0.1 | 1 | 3.8 | 66.7 | 5 | 0.7 | 5 | 27.8 | 0 |
| tib | 68 | 4.4 | 29 | 90.6 | 15 | 68.8 | 24 | 2.7 | 21 | 80.8 | 100 | 44 | 6.6 | 8 | 44.4 | 0 |
| mts | 77 | 5 | 77 | 60.2 | 10 | 53.1 | 53 | 6.1 | 53 | 51 | 90.9 | 24 | 3.6 | 24 | 22.2 | 33.3 |
| cal | 32 | 2.1 | 30 | 93.8 | 16 | 54.5 | 11 | 1.3 | 11 | 42.3 | 91.7 | 21 | 3.1 | 18 | 100 | 10 |
| ast | 22 | 1.4 | 19 | 59.4 | 11 | 93.8 | 12 | 1.4 | 12 | 46.2 | 96.5 | 10 | 1.5 | 7 | 38.9 | 75 |
| c/t | 65 | 4.2 | 65 | 16.9 | 4 | 90.7 | 57 | 6.5 | 57 | 18.3 | 100 | 8 | 1.2 | 8 | 3.7 | 70.2 |
| mt ind | 12 | 8.0 | 6 | - | - | 93.5 | - | - | _ | - | 100 | 12 | 1.8 | 6 | - | 90.8 |
| phal1/2 | 150 | 9.7 | 147 | 27 | 5 | 53.2 | 103 | 11.8 | 103 | 23.3 | 87.2 | 47 | 7 | 40 | 13.1 | 3.3 |
| phal3 | 169 | 11 | 169 | 58.7 | 10 | 78 | 39 | 4.5 | 39 | 16.7 | 93.9 | 130 | 19.4 | 130 | 80.2 | 0 |
| ver | 301 | 19.5 | 221 | 49.3 | 8 | 8.1 | 179 | 20.5 | 154 | 41.8 | 21.4 | 122 | 18.2 | 67 | 26.2 | 0 |
| rib | 59 | 3.8 | 57 | 14.8 | 3 | 14.3 | 49 | 5.6 | 49 | 15.7 | 23.5 | 10 | 1.5 | 8 | 3.7 | 0 |
| Total | 1543 | | 1310 | | | | 873 | | 836 | | | 670 | | 464 | | |

Notes: N - number of skeletal elements; N% - percentage of skeletal elements; MNE - minimum number of elements; RA% - relative abundance; C% - percentage of complete skeletal remains. Abbreviations: cra - cranium; man - mandible; Inc. - incisors; u mol - upper molar; I mol - lower molar; mol ind - indeterminate molar; sc - scapula; hum - humerus; rad - radius; uln - ulna; mtc - metacarpal; inn - innominate; fem - femur; pat - patella; tib - tibia; mts - metatarsal; cal - calcaneum; ast astragalus; c/t - carpal/tarsal; mt ind - indeterminate metapodial; phal - phalanges; ver - vertebrae; rib - rib.

Taphonomic analysis

Most body parts were represented in the samples, though their presence and frequency varied by taxonomic group. Observation of breakage patterns revealed that most remains were complete with an average percentage of 70% complete bones. Additionally, a total of 48.3% of the remains measured less than 10 mm in length, 41% of bones were articulated and 60.4% of teeth remained in situ. Damage from digestion affected 24.4% of the remains and most (56.8%) showed a heavy degree of corrosion. Beak or talon marks occurred on 166 remains (8.2%), fractured edges (53.5%) and beak/talon punctures (12.8%) were the most common form.

Henceforth, each group was treated separately in the analysis to account for the potential that different taxa might exhibit different taphonomic patterns.

Leporids RA%

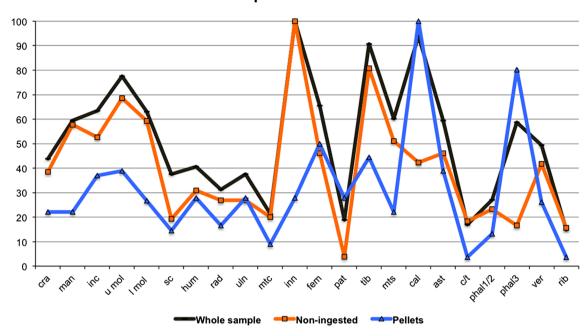


Figure 4. Relative abundance of different parts of the skeleton for leporid remains. Note: For abbreviations see the caption for Table 2.

Table 3. Proportions of different parts of the skeleton for leporids.

| Indices (%) | Leporids sample |
|-------------|-----------------|
| PCRT/CR | 53.8 |
| PCRAP/CR | 55.3 |
| PCRLB/CR | 85 |
| AUT/ZE | 73.6 |
| Z/E | 100 |
| AN/PO | 41.3 |
| | |

Leporids

The total number of recovered leporid remains was 1543, of which 873 belonged to non-ingested remains and 670 were extracted from pellets.

Anatomical representation. The anatomical composition of the identified remains in the leporid sample is presented in Table 2. The entire skeleton was represented – vertebrae (19.5%), upper and lower molars (9.7 and 6.7%), phalanges (9.7%) and metatarsal bones (5%) were the most numerous elements (N%). The relative abundance of skeletal elements (RA%) is also shown in Table 2 and Figure 4. The mean value (52.5%) was low indicating a loss of bones in the assemblage. The best-represented elements were the innominate (100%), calcaneum (93.8%) and tibia (90.6%), whilst ribs and carpal/tarsal bones were uncommon (14.8 and 16.9% respectively).

Relative proportions of skeletal elements are shown in Table 3. Results indicate that there was a deficiency in the numbers of:

- (1) postcranial compared to cranial remains;
- (2) lower compared to upper limb elements, indicating a loss of distal elements (especially the smallest ones, i.e. third phalanges and carpal/tarsal bones) and;
- (3) anterior compared to posterior limb elements.

Analysis of the leporids by the origin of remains (non-ingested and pellets), reveals that the absolute numbers of scapulae, long bones and third phalanges were higher in pellets, whereas cranial remains, metapodials, vertebrae and innominates were better-represented in non-ingested remains (Table 2). Relative abundance profiles show that almost all skeletal elements are better represented in the non-ingested remains sample, especially the innominate. Exceptions to this norm are calcanea and third phalanges that were much more common in pellets (Table 2, Figure 4). The differences in anatomical representaion observed between both samples are statistically significant ($\chi^2 = 197.5$, p < 0.01, df = 21).

Breakage. The size of leporid bone fragments ranges between 1.3 and 152.4 mm; the average maximum length was 23.4 mm and 44.7% of the rabbit remains had length values under 10 mm. The percentage of complete elements was 68.2%. Values vary according to bone size, with the highest percentages obtained for the smallest bones: carpals/tarsals, patellae, phalanges and teeth (Table 2). Long bones were complete in 45.3% of cases.

A total of 345 (28.4%) remains within the entire leporid sample were articulated and 70.6% of teeth were recovered *in situ*. Breakage categories (Table 4) show that:

- crania were complete in 8.1% of cases and their fragments were mostly identified by parts of the maxilla (M);
- (2) mandibles were complete in 14.3% of cases and their fragments were represented by body portions (including MB, MBI and MBB);
- (3) 94% of teeth located *in situ* were complete and isolated teeth were complete in 62.9% of cases;



Table 4. Number and percentage of parts of the skeleton included in each breakage category for leporids.

| | | | | | | | | | SDE | | | |
|------------------------|-----|--------|---------|------|------|------------|-----|-------|---------|--------|------|--------|
| Long bones and metapo- | | С | P | E | | PES | | S | SI | DE | D | E |
| dial | N | % | N | % | N | % | N | % | N | % | N | % |
| Humerus | 8 | 32 | 2 | 8 | 2 | 8 | 11 | 44 | 2 | 8 | 0 | 0 |
| Radius | 5 | 33.3 | 0 | 0 | 2 | 13.3 | 7 | 46.7 | 0 | 0 | 1 | 6.7 |
| Ulna | 5 | 29.4 | 0 | 0 | 3 | 17.7 | 8 | 47.1 | 1 | 5.9 | 0 | 0 |
| Femur | 10 | 24.4 | 0 | 0 | 3 | 7.3 | 25 | 61 | 2 | 4.9 | 1 | 2.4 |
| Tibia | 16 | 23.5 | 0 | 0 | 8 | 11.8 | 33 | 48.6 | 6 | 8.8 | 5 | 7.4 |
| Metacarpus | 29 | 85.3 | 0 | 0 | 0 | 0 | 4 | 11.8 | 1 | 2.9 | 0 | 0 |
| Metatarsus | 53 | 68.8 | 0 | 0 | 5 | 6.5 | 19 | 24.7 | 0 | 0 | 0 | 0 |
| Mandible | N | % | Cranium | N | % | Innominate | N | % | Scapula | N | % | |
| С | 4 | 14.3 | С | 3 | 8.1 | С | 25 | 67.6 | С | 4 | 23.5 | |
| IP | 2 | 7.1 | IB | 4 | 10.8 | Α | 4 | 10.8 | GC | 2 | 11.8 | |
| MBI | 8 | 28.6 | IBM | 2 | 5.4 | AIS | 1 | 2.7 | GCN | 5 | 29.4 | |
| MB | 7 | 25 | M | 16 | 43.2 | AISIL | 2 | 5.4 | NF | 2 | 11.8 | |
| MBB | 5 | 17.9 | ZA | 2 | 5.4 | AIL | 0 | 0 | F | 3 | 17.6 | |
| PC | 2 | 7.1 | NC | 10 | 27 | IS | 2 | 5.4 | | | | |
| | | | | | | IL | 3 | 8.1 | | | | |
| | | | | | | Phalanges | | | | | | |
| Vertebrae | N | % | Ribs | N | % | 1/2 | N | % | Phalai | nges 3 | N | % |
| C | 160 | 53.2 | C | 46 | 78 | C | 136 | 90.7 | | C | 158 | 93.5 |
| VB | 64 | 21.3 | F | 13 | 22 | Р | 3 | 2 | | F | 11 | 6.5 |
| VE | 58 | 19.3 | | | | D | 11 | 7.3 | | | | |
| SP | 19 | 6.3 | | | | | | | | | | |
| Patella | N | % | Car/tar | N | % | Cal | N | % | Ast | N | % | |
| С | 6 | 100 | С | 61 | 93.8 | С | 17 | 53.1 | С | 12 | 54.5 | |
| F | 0 | 0 | F | 4 | 6.2 | F | 15 | 46.9 | F | 10 | 45.5 | |
| | | | 'In s | itu′ | | | | | Isola | ated | | |
| | | cisors | Upper | | | er molars | | isors | | molars | | molars |
| Teeth | N | % | N | % | N | % | N | % | N | % | N | % |
| С | 40 | 95.2 | 115 | 100 | 66 | 86.9 | 15 | 71.4 | 31 | 91.2 | 7 | 26 |
| F | 2 | 4.8 | 0 | 0 | 10 | 13.2 | 6 | 28.6 | 3 | 8.9 | 20 | 74.1 |

Notes: Long bones, metacarpal and metatarsal bones were classified as: complete (C); proximal epiphysis (PE); proximal epiphysis + shaft (PES); shaft (S); shaft + distal epiphysis (SDE); and distal epiphysis (DE). Mandible as: complete (C); incisive part (IP); mandible body + incisive part (MBI); mandible body (MB); mandible body + branch (MBB); and condylar process (CP). Cranium as: complete (C); incisive bone (IB); incisive bone + maxilla (IBM); maxilla (M); zygomatic arch (ZA); and neurocranium (NC). Innominate as: complete (C); acetabulum (A); acetabulum + ischium (AlS); acetabulum + ischium + ilium (AlS)L); acetabulum + ilium (AlL); ischium (IS); and illium (IL). Scapula as: complete (C); glenoid cavity (GC); glenoid cavity + neck (GCN); neck + fossa (NF); and fossa (F). Vertebrae as: complete (C); vertebral body (VB); vertebral epiphysis (VE); and spinous process (SP). Phalanges as: complete (C); proximal fragment (P); distal fragment (D); and fragment (F). Patella, carpal/tarsal, calcaneum, astragalus, ribs and teeth as: complete (C); and fragment (F).

- (4) vertebrae were complete in 53.2% of cases, their fragments were mainly represented by the vertebral body (VB);
- innominates were complete in 67.6% of cases, most fragments were represented by portions containing the acetabulum (A, AISIL, AIS);
- scapulae were complete in 23.5% of cases and most fragments comprised the glenoid cavity and neck (GCN);
- (7) long bones were mostly represented by shaft fragments and complete elements;
- metapodials were well preserved; metacarpals and metatarsals were complete in 85.3 and 68.8% of cases respectively.

Non-ingested remains were clearly less affected by breakage than bones from pellets. The size of the leporid remains differs noticeably; in the non-ingested remains sample the average maximum length was 23.4 mm and 44.7% of the rabbit remains had length values under 10 mm, whereas those in the pellets had an average maximum length of 10 mm and 76.6% of remains had length values under 10 mm. The percentage of complete elements was also distinct: 89.2% in non-ingested

remains compared with 39.8% in pellets. Differences were mostly concentrated in large skeletal elements (Table 4) such as: long bones (70% vs. 1.9%), innominates (92.6% vs. 0%) or metatarsi (100% vs. 0%).

Digestion and beak/talon marks. Digestion damage was present in 32% of the overall leporid sample. Different degrees of digestion damage were observed on the surface of skeletal remains; specifically, 1.4% of the elements were altered to a light degree, 4.3% to a moderate degree, 8.1% to a heavy degree and 18.2% to an extreme degree of corrosion (Figure 5).

No digested remains were recovered in the non-ingested sample. Considering the pellet sample, the percentage of remains affected by digestion was considerably higher (73.6%). In this sample, the percentage of elements included in each degree of digestion damage was: 3.1% light, 9.9% moderate, 18.7% heavy and 41% extreme (Figure 5). Different skeletal elements were altered in similar proportions although patellae, carpals/tarsals, metapodials and third phalanges were less corroded than other remains (Table 5). Whole surfaces of bones or bone fragments were often affected by digestive corrosion, but the most altered areas were fractured or articular surfaces (Figure 6). A high proportion of teeth were corroded (Table 5).

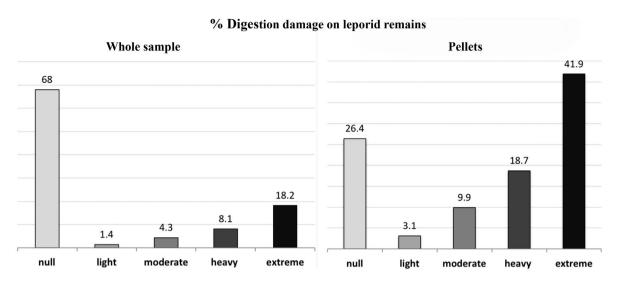


Figure 5. Percentage of leporid remains from the whole sample and the pellets sample included in each digestion category.

Table 5. Number and percentage of leporid bones and teeth included in each digestion category. For abbreviations see the caption for Table 2.

| | | | Digestio | n damage on | leporid rema | ins (whole san | nple) | | | |
|---------|------|------|----------|-------------|--------------|----------------|-------|------|-----|------|
| | N | lull | Li | ght | Мос | derate | Н | eavy | Ext | reme |
| | N | % | N | % | N | % | N | % | N | % |
| cra | 17 | 1.6 | 1 | 4.8 | 2 | 3 | 4 | 3.2 | 13 | 4.6 |
| man | 18 | 1.7 | 0 | 0 | 2 | 3 | 0 | 0 | 8 | 2.8 |
| lnc. | 43 | 4.1 | 2 | 9.5 | 3 | 4.5 | 3 | 2.4 | 12 | 4.3 |
| u mol | 105 | 10 | 0 | 0 | 14 | 21.2 | 17 | 13.6 | 13 | 4.6 |
| l mol | 73 | 7 | 2 | 9.5 | 5 | 7.6 | 8 | 6.4 | 15 | 5.3 |
| sc | 9 | 0.9 | 0 | 0 | 0 | 0 | 4 | 3.2 | 4 | 1.4 |
| num | 13 | 1.2 | 1 | 4.8 | 1 | 1.5 | 2 | 1.6 | 8 | 2.8 |
| rad | 9 | 0.9 | 0 | 0 | 1 | 1.5 | 0 | 0 | 5 | 1.8 |
| uln | 11 | 1 | 0 | 0 | 0 | 0 | 3 | 2.4 | 4 | 1.4 |
| mtc | 26 | 2.5 | 0 | 0 | 2 | 3 | 3 | 2.4 | 3 | 1.1 |
| nn | 27 | 2.6 | 0 | 0 | 0 | 0 | 2 | 1.6 | 8 | 2.8 |
| fem | 15 | 1.4 | 0 | 0 | 2 | 3 | 7 | 5.6 | 17 | 6 |
| oat | 1 | 0.1 | 0 | 0 | 2 | 3 | 3 | 2.4 | 0 | 0 |
| tib | 35 | 3.3 | 1 | 4.8 | 0 | 0 | 12 | 9.6 | 20 | 7.1 |
| mts | 55 | 5.2 | 1 | 4.8 | 5 | 7.6 | 7 | 5.6 | 9 | 3.2 |
| cal | 12 | 1.1 | 0 | 0 | 2 | 3 | 6 | 4.8 | 12 | 4.3 |
| ast | 12 | 1.1 | 1 | 4.8 | 1 | 1.5 | 2 | 1.6 | 6 | 2.1 |
| c/t | 58 | 5.5 | 0 | 0 | 1 | 1.5 | 3 | 2.4 | 3 | 1.1 |
| ohal1/2 | 119 | 11.3 | 8 | 38.1 | 5 | 7.6 | 8 | 6.4 | 10 | 3.6 |
| ohal3 | 154 | 14.7 | 2 | 9.5 | 8 | 12.1 | 1 | 0.8 | 4 | 1.4 |
| /er | 187 | 17.8 | 0 | 0 | 6 | 9.1 | 22 | 17.6 | 86 | 30.6 |
| rib | 49 | 4.7 | 0 | 0 | 1 | 1.5 | 3 | 2.4 | 6 | 2.1 |
| Гotal | 1050 | | 21 | | 66 | | 125 | | 281 | |

A total of 97 specimens (8% of the bones sample) presented evidence of alterations caused by the eagles' beak. Marks were mostly situated on the vertebrae (37), innominates (21), tibiae (11), mandibles (8), humeri (4), femora (4), ulnae (3), radii (3), scapulae (2) and ribs (3). The most common forms of damage were fractured and crenulated edges (72) followed by punctures (13), notches (10) and pits (5) (Figure 6). Pits and punctures were present on 18 bones (1.5% of the sample) and most of them (50%) were situated in different parts of the innominate. Some leporid remains (11) displayed different types of beak/talon damage (i.e. punctures and notches) on the same specimen. Talons may have inflicted some of the recorded marks; however, there are no reliable criteria by which these might be separated.

Rodents and other small mammals

All marmot remains are part of the non-ingested remains. The total number of other rodent and small mammal specimens was 394, of which 198 belonged to non-ingested remains and 196 were from pellets.

Marmots are much larger animals than the other small mammal species considered within this group, for this reason, their taphonomic features will be commented on separately.

Anatomical representation. Marmots were only represented by mandibles (10.4%), lower teeth (52.1%), vertebrae (35.4%) and innominate (2.1%), (Table 6).

In the small mammals sample the best represented elements were cranial remains, phalanges and vertebrae. However, the

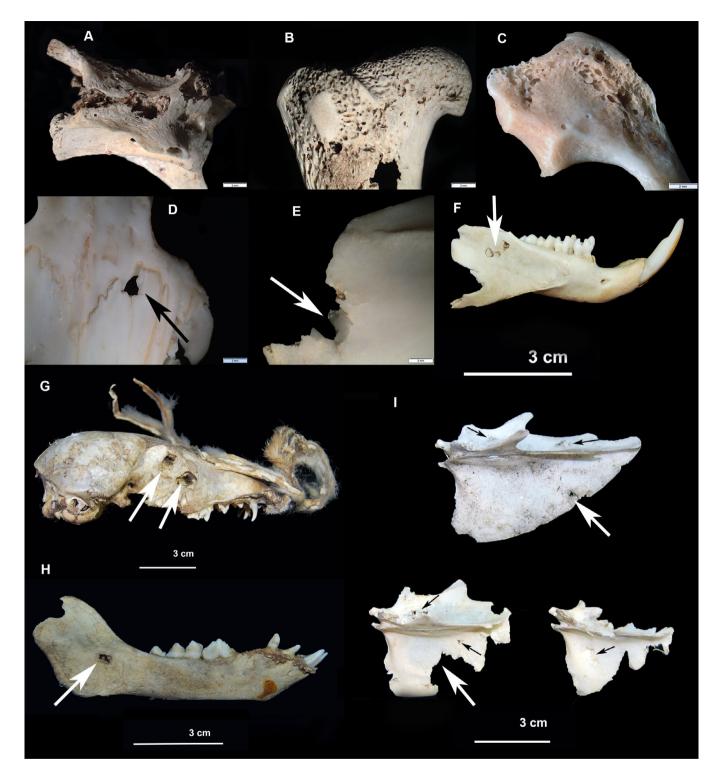


Figure 6. Examples of different type of prey bones displaying digestion damage and beak/talon marks caused by golden eagles. A, B and C: digestion corrosion on leporid remains. D-I: beak/talon pits and punctures, notches and crenulated edges on rabbits (D, E), marmot mandible (F), red fox crania (G), suid mandible (H) and avian sterna (I).

highest value of relative abundance was for tibiae, showing that the most abundant parts are long bones, cranial remains, scapulae and innominates. A large loss of autopudium and axial skeleton elements was observed (Table 6).

Breakage. The average maximum length of marmot remains was 81.2 mm and all remains were anatomically connected. Almost all remains were complete (89.6%).

In the small mammal group the average maximum length was 8.5 mm (values range 1.2-46.2 mm). The average percentage of complete elements was 54.3%. The majority of the recovered remains which were complete were teeth, phalanges and carpal/ tarsal bones. Scapulae and innominate were never complete and in the case of the long bones the frequency of complete remains was 5.3% (Table 6). Proportions of different bone fragments are represented in Table 7. Long bones and metapodials were mostly



Table 6. Number (N), percentage (N%), Minimum Number of Elements (MNE) and percentage of complete elements (C%) of skeletal elements of marmots, small mammals, carnivores, domestic mammals and reptiles recovered from golden eagle nest accumulations.

| | | Marmo | ts | | Sma | ıll mam | mals | | | C | arnivor | es | | Do | mestic | mamm | als | | Reptile | s |
|-----------|----|-------|-----|-----|------|---------|------|------|-----|------|---------|------|------|----|--------|------|------|----|---------|-----|
| | N | N% | NME | N | N% | NME | RA% | C% | N | N% | NME | RA% | C% | N | N% | NME | C% | N | N% | NME |
| cra | 0 | 0 | 0 | 16 | 4.1 | 9 | 64.3 | 12.5 | 10 | 1.7 | 5 | 55.6 | 20 | 1 | 2.8 | 1 | 0 | 0 | 0 | 0 |
| man | 5 | 10.4 | 5 | 19 | 4.8 | 13 | 46.4 | 5.3 | 16 | 2.8 | 15 | 83.3 | 75 | 2 | 5.6 | 2 | 100 | 0 | 0 | 0 |
| Inc. | 5 | 10.4 | 5 | 25 | 6.3 | 25 | 44.6 | 88 | 75 | 13.1 | 75 | 69.4 | 96 | 5 | 13.9 | 5 | 100 | 0 | 0 | 0 |
| can | _ | - | _ | _ | _ | _ | - | - | 28 | 4.9 | 28 | 77.8 | 100 | 2 | 5.6 | 2 | 100 | 0 | 0 | 0 |
| pmol | _ | _ | _ | - | _ | _ | - | - | 87 | 15.2 | 87 | 60.4 | 97.7 | 5 | 13.9 | 5 | 100 | _ | _ | - |
| mol | _ | _ | _ | - | _ | _ | - | - | 34 | 5.9 | 34 | 37.8 | 100 | _ | - | - | - | 0 | 0 | 0 |
| upper mol | 0 | 0 | 0 | 23 | 5.8 | 23 | 27.4 | 100 | - | _ | _ | - | - | _ | - | - | - | _ | _ | _ |
| lower mol | 20 | 41.7 | 20 | 31 | 7.9 | 31 | 36.9 | 93.5 | _ | _ | _ | - | - | _ | - | _ | - | _ | _ | _ |
| SC | 0 | 0 | 0 | 9 | 2.3 | 8 | 28.6 | 0 | 3 | 0.5 | 2 | 11.1 | 33.3 | 1 | 2.8 | 1 | 100 | _ | _ | _ |
| hum | 0 | 0 | 0 | 10 | 2.5 | 7 | 25 | 0 | 6 | 1 | 5 | 27.8 | 50 | 4 | 11.1 | 4 | 25 | _ | _ | _ |
| rad | 0 | 0 | 0 | 9 | 2.3 | 9 | 32.1 | 11.1 | 5 | 0.9 | 5 | 27.8 | 80 | 0 | 0 | 0 | _ | _ | _ | _ |
| uln | 0 | 0 | 0 | 13 | 3.3 | 13 | 46.4 | 15.4 | 5 | 0.9 | 5 | 27.8 | 80 | 0 | 0 | 0 | _ | _ | _ | _ |
| mtc | 0 | 0 | 0 | 10 | 2.5 | 8 | 5.7 | 20 | 15 | 2.6 | 15 | 16.7 | 86.7 | 0 | 0 | 0 | - | _ | _ | _ |
| inn | 1 | 2.1 | 1 | 10 | 2.5 | 7 | 50 | 0 | 12 | 2.1 | 12 | 66.7 | 91.7 | 0 | 0 | 0 | _ | _ | _ | _ |
| fem | 0 | 0 | 0 | 9 | 2.3 | 7 | 50 | 0 | 5 | 0.9 | 5 | 27.8 | 100 | 1 | 2.8 | 1 | 0 | _ | _ | _ |
| pat | 0 | 0 | 0 | 1 | 0.3 | 1 | 3.6 | 100 | 2 | 0.3 | 2 | 11.1 | 100 | 0 | 0 | 0 | - | _ | - | _ |
| tib | 0 | 0 | 0 | 14 | 3.6 | 10 | 71.4 | 0 | 8 | 1.4 | 8 | 44.4 | 100 | 3 | 8.3 | 3 | 33.3 | _ | - | _ |
| fib | 0 | 0 | 0 | _ | _ | _ | _ | _ | 6 | 1 | 6 | 33.3 | 66.7 | 1 | 2.8 | 1 | 0 | | | |
| mts | 0 | 0 | 0 | 5 | 1.3 | 5 | 3.6 | 0 | 29 | 5.1 | 29 | 40.3 | 66.7 | 0 | 0 | 0 | _ | _ | _ | _ |
| mt | _ | _ | _ | _ | _ | _ | _ | _ | _ | _ | _ | _ | _ | _ | _ | _ | _ | _ | _ | _ |
| cal | 0 | 0 | 0 | 3 | 8.0 | 3 | 10.7 | 0 | 8 | 1.4 | 8 | 44.4 | 87.5 | 1 | 2.8 | 1 | 100 | _ | _ | _ |
| ast | 0 | 0 | 0 | 2 | 0.5 | 2 | 7.1 | 50 | 7 | 1.2 | 7 | 48.9 | 100 | 0 | 0 | 0 | _ | _ | _ | _ |
| c/t | 0 | 0 | 0 | 2 | 0.5 | 2 | 0.5 | 100 | 16 | 2.8 | 16 | 14.8 | 100 | 0 | 0 | 0 | _ | _ | _ | _ |
| phal | 0 | 0 | 0 | 121 | 30.7 | 116 | 21 | 70.7 | 109 | 18.9 | 109 | 23.2 | 97.1 | 0 | 0 | 0 | _ | - | _ | _ |
| ver | 17 | 35.4 | 17 | 51 | 16.0 | 43 | 45 | 96.8 | 54 | 9.4 | 48 | 11.9 | 100 | 10 | 27.8 | 8 | 30 | 53 | 86.9 | 53 |
| rib | 0 | 0 | 0 | 11 | 12.9 | 11 | 10.6 | 49 | 0 | 0.0 | 0 | 0 | _ | 0 | 0 | 0 | _ | 8 | 13.1 | 8 |
| TOTAL | 48 | | 48 | 394 | | 353 | | | 574 | | 560 | | | | | | | 61 | _ | 61 |

Note: For abbreviations see the caption for Table 2.

represented by fragments of proximal epiphysis plus shaft and by shaft fragments. The majority of mandible fragments contained part of the mandible body. Innominate was represented by fragments containing the acetabulum, ischium and ilium. Almost all fragments of scapulae included the glenoid cavity and neck.

Digestion and beak/talon marks. Skeletal remains of marmots did not show evidence of digestion damage. Beak/talon marks were observed on nine specimens (18.8%). Most of them occurred on mandibles (5) and vertebrae (3), the rest being located on the innominate (1). Crenulated/fractured edges were the most common damage (9), followed by beak punctures (3), notches (3) and beak pits (1) (Figure 6). In three cases, different types of damage caused by beaks/talons were observed on the same specimen.

The surface of 117 (29.7%) small mammal bones displayed signs of digestion. The degrees of damage registered were: light (1.5%), moderate (4.3%), heavy (7.1%) and extreme (16.8%). Any type of beak or talons damage was registered on the sample.

Carnivores

The carnivore's sample was composed of 574 skeletal remains, of which 539 were non-ingested leftovers. This assemblage mostly consisted of red fox remains (77.9%, Table 1).

Anatomical representation. With the exception of the ribs all parts of the carnivores skeleton were recovered (Table 6). Phalanges (18.9%), premolars (15.2%), incisors (13.1%) and vertebrae (9.4%) were the most numerous elements. The mean value of relative abundance of skeletal elements was low (36.9%)

indicating an important loss of bones in the assemblage. The best-represented elements were mandibles (83.3%), teeth and the innominate (66.7%) (Table 6 and Figure 7). In contrast, scapulae (11.1%), patellae (11.1%) and vertebrae (11.9%) were rare.

Comparison of relative proportions of skeletal elements from crania and postcrania indicate that there was a deficiency in the number of postcranial compared to cranial remains (PCRT/CR = 32.4).

Breakage. The average maximum length of the recovered remains was 54.4 mm, with values ranging between 3.1 and 203 mm, and 25% of the carnivore remains had length values under 10 mm. Almost all elements were complete (93%), but crania (only 20% were complete) and scapulae (33.3%) were the most fragmented (Table 6). Long bones were complete in 82.8% of cases. Besides, 90.9% of bones within the entire carnivore sample were articulated and 95.5% of teeth were recovered in situ. Breakage categories are shown in Table 7.

Digestion and beak/talon marks. Digestion damage on the surfaces of the carnivore skeletal remains was observed in only 19 specimens (3.3%). The degrees of damage registered were: light (1), heavy (3) and extreme (15). (Figure 6).

Traces left by beaks or talons of golden eagles were observed on 21 bones (6%). They occurred on vertebrae (7), crania (4), mandibles (4), innominate (4), scapulae (1) and ulnae (1) and the damage registered on them was in the form of fractured/crenulated edges (77.2%), punctures (11.4%), pits (8.6%) and notches (2.9%).



Table 7. Number and percentage of parts of the skeleton included in each breakage category for small mammals and carnivores. For abbreviations see the caption for Table 4.

| Small mammals | | | | | | | | | | | | | | |
|----------------|----|------|------------|------|------|------------|----------|------|---------|-----|---------|--------|------|-----|
| Long bones and | | C | PE | | | PES | | 5 | SE | DE | D | E | | |
| metapodial | Ν | % | N | % | Ν | % | N | % | N | % | N | % | | |
| Humerus | 0 | 0 | 0 | 0 | 2 | 20 | 2 | 20 | 5 | 50 | 1 | 10 | | |
| Radius | 1 | 11.1 | 0 | 0 | 7 | 77.8 | 1 | 11.1 | 0 | 0 | 0 | 0 | | |
| Ulna | 2 | 16.7 | 0 | 0 | 10 | 83.3 | 0 | 0.0 | 0 | 0 | 0 | 0 | | |
| Femur | 0 | 0.0 | 1 | 11.1 | 3 | 33.3 | 3 | 33.3 | 0 | 0 | 2 | 22.2 | | |
| Tibia | 0 | 0.0 | 1 | 7.1 | 2 | 14.3 | 10 | 71.4 | 0 | 0 | 1 | 7.1 | | |
| Metapodial | 2 | 13.3 | 0 | 0.0 | 1 | 6.7 | 9 | 60.0 | 3 | 20 | 0 | 0.0 | | |
| Mandible | Ν | % | Cranium | N | % | Innominate | N | % | Scapula | N | % | | | |
| С | 1 | 5.3 | C | 1 | 6.3 | C | 0 | 0 | C | 0 | 0 | | | |
| IP | 4 | 21.1 | IB | 4 | 25 | Α | 0 | 0 | GC | 1 | 11.1 | | | |
| MBI | 2 | 10.5 | IBM | 1 | 6.3 | AIS | 1 | 10 | GCN | 7 | 77.7 | | | |
| MB | 5 | 26.3 | M | 4 | 25 | AISIL | 2 | 20 | NF | 1 | 11.1 | | | |
| MBB | 6 | 31.6 | ZA | 0 | 0 | AIL | 0 | 0 | F | 0 | 0 | | | |
| PC | 1 | 5.3 | NC | 6 | 37.5 | IS | 3 | 30 | | | | | | |
| | | | | | | IL | 4 | 40 | | | | | | |
| Vertebrae | N | % | Ribs | N | % | Pł | nalanges | | Teeth | Ir | ncisors | Molars | | |
| С | 25 | 49 | С | 1 | 9.1 | | N | % | | N | % | N | % | |
| VB | 12 | 23.5 | F | 10 | 90.9 | C | 102 | 83.6 | C | 22 | 88 | 52 | 96.3 | |
| VE | 9 | 17.6 | | | | F | 20 | 16.4 | F | 3 | 12 | 2 | 3.7 | |
| SP | 5 | 9.8 | | | | | | | | | | | | |
| Carnivores | | | | | | | | | | | | | | |
| Long bones and | | C | PE | | | PES | | 5 | SE | DE | D | E | | |
| metapodial | N | % | N | % | N | % | N | % | N | % | N | % | | |
| Humerus | 3 | 50 | 1 | 16.7 | 0 | 0 | 1 | 16.7 | 0 | 0 | 1 | 100 | | |
| Radius | 4 | 80 | 0 | 0 | 0 | 0 | 1 | 20 | 0 | 0 | 0 | 0 | | |
| Ulna | 4 | 80 | 0 | 0 | 1 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| Femur | 5 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| Tibia | 8 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| Fibula | 4 | 66.7 | 0 | 0 | 1 | 16.7 | 0 | 0 | 0 | 0 | 1 | 16.7 | | |
| Metacarpus | 13 | 86.7 | 0 | 0 | 0 | 0 | 2 | 13.3 | 0 | 0 | 0 | 0 | | |
| Metetarsus | 29 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| Mandible | N | % | Cranium | N | % | Innominate | N | % | Scapula | N | % | | | |
| С | 12 | 75.0 | С | 2 | 20 | С | 11 | 91.7 | С | 1 | 33.3 | | | |
| IP | 1 | 6.3 | IB | 0 | 0 | A | 0 | 0 | GC | 0 | 0 | | | |
| MBI | 3 | 18.8 | IBM | 4 | 40 | AIS | 0 | 0 | GCN | 1 | 33.3 | | | |
| MB | 0 | 0.0 | M | 0 | 0 | AISIL | 0 | 0 | NF | 0 | 0 | | | |
| MBB | 0 | 0.0 | ZA | 0 | 0 | AIL | 0 | 0 | F | 1 | 33.3 | | | |
| PC | 0 | 0.0 | NC | 4 | 40 | IS | 0 | 0 | | • | | | | |
| | | | | | | IL | 0 | 0 | | | | | | |
| Vertebrae | N | % | Ribs | N | % | Teeth | Inc | isor | Can | | Prem | nolar | Mol | |
| С | 45 | 83.3 | С | 0 | 0 | | N | % | N | % | N | % | N | % |
| VB | 3 | 5.6 | F | 0 | 0 | C | 72 | 96 | 28 | 100 | 85 | 97.7 | 34 | 100 |
| VE | 5 | 9.3 | | | | F | 3 | 4 | 0 | 0 | 2 | 2.3 | 0 | 0 |
| SP | 1 | 1.9 | | | | | | | | | | | | |
| Calcaneum | N | % | Astragalus | N | % | Carpals | N | % | Tarsals | N | % | | | |
| С | 7 | 87.5 | С | 7 | 100 | С | 16 | 100 | С | 33 | 97.1 | | | |
| F | 1 | 12.5 | F | 0 | 0 | F | 0 | 0 | F | 1 | 2.9 | | | |

Domestic mammals

Within this small sample, 29 specimens belonged to non-ingested remains and only seven were from pellets.

Anatomical representation. The best represented skeletal elements were teeth and vertebrae. Other elements present were cranial and mandible fragments, scapula and long bones (Table 6). Innominates, autopodial elements and ribs were not recovered.

Breakage. The size of the recovered remains varied with maximum lengths between 8.1 and 129.2 mm (average 54.3 mm) and only 5% of remains measured less than 10 mm. The average percentage of complete elements was 58.3%, which mainly corresponds to teeth and mandibles (Table 6).

Breakage categories show that: Crania were never complete and they were identified on parts of the neurocranium; all mandibles were complete; all teeth were recovered *in situ* and they were always complete; vertebrae were complete in 30% of cases, the most common fragments being vertebral bodies; scapulae were represented by only one complete element; long bones were complete in 22.2% of cases, while different breakage categories included fragments of proximal epiphysis, shaft and distal epiphysis.

Articulated elements were not found in this sample.

Digestion and beak/talon marks. Digestion corrosion was observed on the surface of six remains (16.7%), 5 vertebrae and one fibula fragments. The degree of damage registered was: moderate (1) and heavy (5).

Carnivores RA%

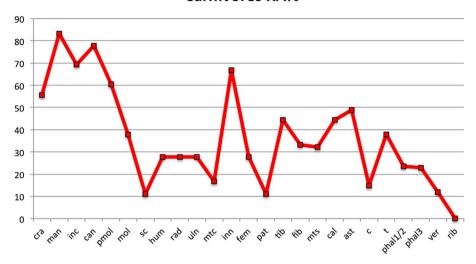


Figure 7. Relative abundance of different parts of the skeleton in the carnivore remains sample. Note: For abbreviations see the caption for Table 4.

Table 8. Bird skeletal elements recovered from golden eagle nests.

| | | Whole | sample | (MNI = 12) | | Colu | mba sp | p. (MNI | = 4) |
|-------|----|-------|--------|------------|------|------|--------|---------|------|
| BIRDS | N | N% | MNE | RA% | C% | Ν | N% | MNE | RA% |
| cra | 2 | 2.1 | 1 | 8.3 | 0 | 0 | 0 | 0 | 0 |
| man | 0 | 0.0 | 0 | 0 | | 0 | 0 | 0 | 0 |
| fur | 3 | 3.2 | 2 | 16.7 | 0 | 0 | 0 | 0 | 0 |
| SC | 3 | 3.2 | 3 | 12.5 | 66.7 | 0 | 0 | 0 | 0 |
| cor | 6 | 6.4 | 6 | 25 | 83.3 | 2 | 6.9 | 2 | 25 |
| hum | 5 | 5.3 | 5 | 20.8 | 80 | 2 | 6.9 | 2 | 25 |
| rad | 1 | 1.1 | 1 | 4.2 | 0 | 0 | 0 | 0 | 0 |
| uln | 2 | 2.1 | 2 | 8.4 | 50 | 0 | 0 | 0 | 0 |
| cmc | 1 | 1.1 | 1 | 4.2 | 100 | 0 | 0 | 0 | 0 |
| C | 1 | 1.1 | 1 | 4.2 | 100 | 0 | 0 | 0 | 0 |
| fem | 4 | 4.3 | 4 | 16.8 | 50 | 1 | 3.4 | 1 | 12.5 |
| tbt | 3 | 3.2 | 3 | 12.5 | 33.3 | 1 | 3.4 | 1 | 12.5 |
| tmt | 2 | 2.1 | 2 | 8.4 | 50 | 1 | 3.4 | 1 | 12.5 |
| str | 8 | 8.5 | 8 | 66.7 | 37.5 | 4 | 13.8 | 4 | 50 |
| pel | 8 | 8.5 | 5 | 41.7 | 12.5 | 4 | 13.8 | 2 | 25 |
| phal | 17 | 18.1 | 17 | 5.1 | 88.2 | 12 | 41.4 | 12 | 10.7 |
| ver | 28 | 29.8 | 28 | 7.8 | 21.4 | 2 | 6.9 | 2 | 2.5 |
| rib | 0 | 0.0 | 0 | 0 | _ | 0 | 0 | 0 | 0 |
| Total | 94 | | 89 | | | 29 | | 27 | |

Notes: N – number of skeletal elements; N% – percentage of skeletal elements; MNE – minimum number of elements; RA% – relative abundance; C% – percentage of complete elements. Abbreviations: cra – cranium; man – mandible; fur – furcula; sc – scapula; cor – coracoid; hum – humerus; rad – radius; uln – ulna; cmc – carpometacarpus; c – carpal (carpi radial, carpi ulnare); fem – femur; tbt – tibiotarsus; tmt – tarsometatarsus; str – sternum; pel – pelvis; phal – leg phalanges; ver – vertebrae; rib – rib.

Traces left by beaks or talons were observed in seven bones (24.1%) from this sample (Figure 6). Most were on mandibles (2) and long bones (3); the rest were located on the scapula (1) and vertebrae (1). Crenulated/fractured edges (10) and beak/talon punctures (4) were the most common traces, followed by scoring (2).

Birds

The total number of recovered bird remains was 94, of these 75 came from non-ingested remains and only 17 were from pellets.

Anatomical representation. All parts of the avian skeleton with the exception of mandibles and ribs were recovered, most of them in very scarce numbers (Table 8). Vertebrae (29.8%) and phalanges (18.1%) showed the highest values. Sterna (8.5%), pelvis (8.5%), coracoides (6.4%), humeri (5.3%) and femora (4.5%) were also common. Relative abundance varied by skeletal element (Table 8, Figure 8): fragments of the trunk (sternum and pelvis) were the best represented (66.7 and 41.7% respectively) followed by wing and leg bones. In the main, all elements showed low values of relative abundance, the average value was 13.9 indicating a great loss of skeletal remains.

Relative abundance was calculated separately for *Columba* spp. because these were the best represented taxa. Results should be viewed with caution because the sample is too small to be significant, however they show that anatomical representation is similar to that observed in the whole sample, the sterna and pelves were the most frequent elements followed of humeri and coracoides (Table 8, Figure 8).

Wing bones account for 40% of the sum of wing and leg bones evidencing a slightly higher representation of leg bones. The deviation from the expected 50% (1:1 proportion) is not statistically significant (Z=0.55, p>0.05). The ratio of proximal to distal portions shows a higher representation of the first (77.8%). Deviation from the expected percentage (50%) is statistically significant (Z=0.24, p<0.05). The ratio of the core to limb elements was 55%; the low predominance of core elements is not statistically significant (Z=0.45, p>0.05).

Breakage. The size of the recovered avian remains ranged between 2.3 and 224 mm (average maximum length 39.2 mm) and 41% of bones had length values under 10 mm. The degree of fragmentation was moderate; on average 45.7% of the elements were complete. Long bones were complete in 63% of cases, coracoids and humeri were the best preserved (Table 8). Crania, furcula and radii were never complete.



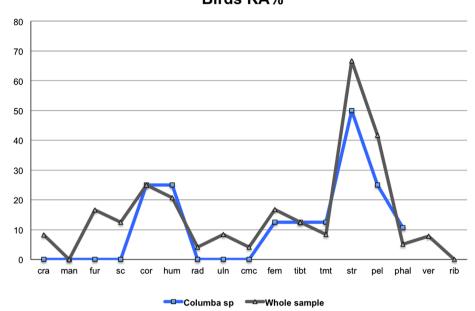


Figure 8. Relative abundance of different parts of the skeleton in the bird remains sample. Note: For abbreviations see the caption for Table 8.

Table 9. Number and percentage of parts of the skeleton included in each breakage category for birds.

| Skull | N | % | Pelvis | N | % | Sternum | N | % |
|---|----|------|-------------------------------------|------|------|--------------------------|----|------|
| Whole | 1 | 4.2 | Synsacrum + ilium-is- chii-pubis | 7 | 50 | More 1/2 with rostrum | 4 | 33.3 |
| Beak + brain case without back part | 1 | 4.2 | llium-ischii-pubis | 5 | 35.7 | Less 1/2 with rostrum | 7 | 58.3 |
| Brain case with- out back part | 0 | 0 | Synsacrum | 1 | 7.1 | Fragment without rostrum | 1 | 8.3 |
| Brain case | 15 | 62.5 | Acetabulum | 1 | 7.1 | | | |
| Beak | 7 | 29.2 | | | | | | |
| | W | hole | Proximal pa | rt | | Distal part | Sh | aft |
| _ | N | % | N | % | N | % | N | % |
| Scapula | 1 | 6.3 | 13 | 81.3 | 0 | 0 | 2 | 12.5 |
| Coracoid | 3 | 23.1 | 9 | 69.2 | 1 | 7.7 | 0 | 0 |
| Humerus | 1 | 10 | 3 | 30 | 5 | 50 | 1 | 10 |
| Radius | 1 | 7.1 | 7 | 50 | 1 | 7.1 | 5 | 35.7 |
| Ulna | 2 | 16.7 | 1 | 8.3 | 2 | 16.7 | 7 | 58.3 |
| Carpometacarpus | 6 | 35.3 | 4 | 23.5 | 2 | 11.8 | 5 | 29.4 |
| Femur | 0 | 0 | 6 | 42.9 | 4 | 28.6 | 4 | 28.6 |
| Tibiotarsus | 0 | 0 | 2 | 11.8 | 6 | 35.3 | 9 | 52.9 |
| Tarsometatarsus | | 26.3 | | 10.5 | 8 | 42.1 | 4 | 21.1 |

A notable number of skeletal remains were articulated (N = 38, 40.4%); most being leg bones (tibiotarsi, tarsometatarsi and phalanges, 42.1%) and vertebrae (26.3%).

Breakage categories (Table 9) show that:

- all breakage categories occurred on long bones, scapulae and coracoids; most bones were complete (68%), proximal and distal ends and shaft (with missing articular ends) were all represented (8, 12 and 12% respectively);
- (2) skulls were represented by brain case and beak fragments;
- (3) most pelves fragments included ilium-ischium-pubis bones (62.5%);

(4) all of the sternae fragments included the rostrum, but most were less than half complete (62.5%).

Digestion and beak/talon marks. Digestion corrosion was evident in 19.1% of the whole bird sample. Most bones showed extreme (44.4%) and heavy corrosion (33.3%) whereas it was moderate on 22.2% of the elements and no light damage was found.

Vertebrae were the skeletal remains most affected by digestion, exhibiting substantial damage.

Traces left by beaks or talons were observed on 29 bones, 30.9% of the sample (Figure 6). Most of them occurred on sterna (8), the pelves (6), coracoids (2), scapulae (2), humeri

and vertebrae (2). The rest were located on crania (1), radii (1), carpometacarpi (1), tibiotarsi (1) and tarsometatarsi (1). Crenulated/fractured edges (62.5%) were the most common form of damage, followed by punctures (14.6%), notches (14.6%), pits (14.6%) and scoring (2.1%). Four sterna, one pelvis and one phalanx displayed several simultaneous pit/ puncture marks; pits and punctures were isolated in all other specimens.

Reptiles

Anatomical representation. The skeletal profile of the snakes was uniquely based on the presence of vertebrae (N = 6). No cranial remains or ribs were found.

Tortoises were represented by two shell fragments, both from the dorsal face of the carapace. The larger fragment included different bony plates: the third neural, peripherals and pleurals.

Breakage. The maximum length of colubrid remains was between 3.8 and 12.2 mm (average maximum length 7.4 mm). All the remains were complete being two vertebrae articulated.

The maximum lengths of the tortoise shell fragments were 54.4 and 36.3 mm.

Digestion and beak/talon marks. Only one vertebra of Hemorrhois hippocrepis presented digestion damage, the degree of corrosion was light. Reptile remains did not show any beak damage.

Discussion

The diversity of prey taxa identified in our samples is characteristic of golden eagles and it is related to the availability of optimal prey in the landscape and the heterogeneity of their habitat. Studies of the diet of this large avian raptor have shown that it is a highly opportunistic hunter with a diverse diet. Prey selection is largely determined by the local availability and abundance of prey species (Watson 2010). According to the feeding studies (e.g. Delibes et al. 1975; Gil-Sánchez et al. 1994; Moleón et al. 2002; Whitfield et al. 2009; Watson 2010), in Eurasia preferred prey of golden eagles include four prey families: Leporidae (rabbits and hares), Sciuridae (squirrels and marmots), Tetraonidae (grouses) and Phasianidae (pheasants and partridges). Our results are consistent with this assertion. The most common representatives of these families in our study are rabbits, hares, squirrels and marmots. Leporids are clearly the most important contribution to the eagle's diet in both of our samples. Regarding avian prey and Phasianidae family, grouses were not found and only a few remains of red-legged partridge were recorded. Another important group of prey in the assemblage analysed were carnivores, especially red foxes, whose remains accounted for 16.6% of the whole assemblage (Table 1). Foxes are also considered one of the eagle's preferred prey, usually as juveniles though foxes of any age, including adult males heavier than the eagles themselves, may be hunted (Hoffmann et al. 2004).

Considering the age of prey, in our samples foxes were mostly young individuals, as were domestic mammals. However, smaller prey such as leporids and small carnivores were generally adults (83.5 and 100% respectively).

Body part representation in the golden eagle nests varied with taxonomic group or species. Most taxa were transported whole to the nest and all skeletal remains were found with the exception of the ribs that are fragile and difficult to preserve, especially if they were swollen.

Small mammals showed a different taphonomic pattern, which is related to their small size. Whole carcasses were transported to the nest, however a great loss of autopudium and axial skeleton elements is observed. The average maximum length was less than in other taxonomic groups (8.5 mm), they and leporids displayed the highest percentage of digested remains (29.7%) that was mostly present in an extreme degree of damage and beak/ talon marks were not registered on the sample.

This study has also shown that a large number of carnivore bones and teeth (especially of red foxes) can also be accumulated by golden eagles. Despite this type of prey seeming to be abundant in golden eagle prey assemblages (Ellis et al. 2000; Schweiger et al. 2014), there are no previous data about the taphonomic features of this type of assemblages, thus comparisons are not possible. It is clear that whole carcasses were transported to nest by the eagles and that all skeletal remains were present. Carnivore remains have also been recorded on Egyptian vultures (Neophron percnopterus) nest accumulations. In these cases, despite the vulture being able to transport complete carcasses to the nest, samples normally show a bias in anatomical representation, which is consequence of his scavenging feeding behaviour (Lloveras, Thomas, et al. 2014; Sanchis Serra et al. 2014). Regarding breakage, the average maximum length of the recovered remains (54.4 mm) and the high percentage of complete elements (93%) are similar to the parameters recorded for carnivores from Egyptian vulture assemblages (60.4 mm and 80%, Lloveras, Thomas, et al. 2014). Digestion damage was observed on only a low percentage of remains (3.3%) however, they were mostly affected by an extreme degree of damage (79%). This differs from Egyptian vulture accumulations, where digestion was not recorded on carnivore remains. Traces left by beaks/talons of golden eagles were abundant (6% of bones), their number and location is consistent with observations registerd on carnivores accumulated by Egyptian vultures (Lloveras, Thomas, et al. 2014; Sanchis Serra et al. 2014).

Domestic mammal remains were rare in our samples and skeletal representation indicates that only part of the animal carcasses were transported to the nest. This is probably because they belong to animals that were scavenged by the eagles. Other taphonomic features indicate that most remains were over 10 mm (95%) and the percentage of complete elements was high (58.3%); digestion corrosion affected 16.7% of remains most of them on a heavy degree of damage (83.3%); and traces left by beaks/talons were abundant (24.1%), 13.8% of bones displayed beak or talon punctures. A similar taphonomic pattern has been described for domestic mammal remains accumulated on Egyptian vulture nests. The main difference between both samples lies in the presence of butchery marks on the vulture accumulations because these raptors usually scavenge on rubbish remains from human consumption (Lloveras, Thomas, et al. 2014; Sanchis Serra et al. 2014).

It is manifest that the taphonomic pattern obtained is strongly related to the prey/predator size, to the type of prey and to the feeding behaviour of the predator.



Table 10. Anatomical representation, breakage, digestion, teeth/ beak/talon marks and age at death for leporid remains accumulated by different types of predators (raptors and terrestrial carnivores) compared with the results obtained for golden eagles in the present study.

| | , , , , , , , , , , , , , , , , , , , | | | <u>'</u> | |
|------------------------------------|---------------------------------------|---------------------------------------|--|------------------------------------|-----------------------------------|
| Raptors | Eagle owl Bubo bubo | S. Imperial eagle Aquila adalberti | Egyptian vulture Neophron percnopterus | Bonelli's eagle Aquila fasciata | Golden eagle Aquila chrysaetos |
| Reference | Lloveras et al. (2009) | Lloveras et al. (2008b) | Lloveras, Nadal, et al. (2014) | Lloveras, Thomas, et al. (2014) | Present study |
| Origin | Nest | Pellets | Nest | Nest | Nest |
| N | 1808 | 824 | 133 | 438 | 1543 |
| RA% > values | cal-inn-fem | phal 3-u mol-tib | man-cra-teeth | cr-u mol-inn | inn-cal-tib-u mol |
| RA% < values | mtc-c/t | rib-fem-rad | phal-c/t-long bone- ver | mtc-rib | rib-c/t- pat |
| PCRT/CR | +postcranial | +cranial | +cranial | +cranial | +postcranial |
| P/D | +proximal | +distal | _ | +proximal | +distal |
| AN/PO | +hindlimb | +hindlimb | _ | +hindlimb | +hindlimb |
| Complete elements (%) |) | | | | |
| Mean value long bones | 14.6 | 0 | - | 51.7 | 45.3 |
| Mean value total Length (in mm) | 53.9 | 27 | 81.2 | 74.7 | 68.2 |
| Average | 14.5 | 8.4 | 52.5 | 19.7 | 23.4 |
| % <10 mm | 49 | 73 | 7.8 | 54.9 | 44.7 |
| % Digested remains | 68.8 | 98 | 0.8 | 31.2 | 32 |
| % Digested long bones | 88.9 | 100 | - | 31 | 50.3 |
| Degree Null | 21.2 | 2 | 00.3 | 60.0 | 60 |
| | 31.2 | 2 | 99.2 | 68.8 | 68 |
| Light | 40.2 | 18.2 | 0 | 2.3 | 1.4 |
| Moderate | 19.8 | 46.8 | 0.8 | 7.9 | 4.3 |
| Heavy | 8 | 27.4 | 0 | 14.4 | 8.1 |
| Extreme | 0.7 | 5.6 | 0 | 6.5 | 18.2 |
| Teeth/beak pits & punctures | 2 | 0.5 | 7.5 | 0.8 | 1.1 |
| Age – % of adults | 50 | - | 100 | 41.4 | 83.5 |
| | lbe | rian lynx | | Fox | European wildcat |

| Terrestrial carnivores | Lynx | pardinus | Vu | lpes vulpes | Felis silvestris | | |
|-----------------------------|----------------------------|------------------------------------|--------------|-------------------|------------------|---------------|--|
| Reference | Lloveras et al. (2008a) | Rodríguez-Hidalgo et al. (2013) | Llovera | as et al. (2012a) | Lloveras e | al. (2016) | |
| Origin | Scats | Non-ingested | Scats | Non-ingested | Scats | Non-ingested | |
| N | 1522 | 9564 | 265 | 639 | 87 | 1457 | |
| RA% >values | man-teeth-cra | tib-cal-mts | long bone-sc | mts-ast-tib | sc-hu-ra-ul-cr | cr-fe-mts-cal | |
| RA% < values | c/t-ver-rib | sc-ver-hum | mtc-c/t-inn | cr-sc-rib | teeth-hindlimb | sc-rib-hu-ver | |
| PCRT/CR | +cranial | +postcranial | = | +postcranial | +postcranial | +cranial | |
| P/D | +proximal | +distal | +proximal | +distal | +proximal | +distal | |
| AN/PO | +forelimb | +hindlimb | +hindlimb | +hindlimb | +forelimb | +hindlimb | |
| Complete elements % | | | | | | | |
| Mean value long | 2.5 | 37.6 | 0 | 5.4 | 0 | 23.7 | |
| bones | | | | | | | |
| Mean value total | 43 | 73-78 | 12 | 89.4 | 11.5 | 92.3 | |
| Length (in mm) | | | | | | | |
| Average | 7.1 | 17.4 | 9.3 | 19.3 | 5.4 | 21.5 | |
| %<10 mm | 80 | 19.7 | 61 | 28 | 98.8 | 35 | |
| % Digested remains | 97.2 | _ | 99.5 | _ | 98.6 | _ | |
| % Digested long | 100 | _ | 100 | _ | 100 | _ | |
| bones | | | | | | | |
| Degree | | | | | | | |
| Null | 2.8 | _ | 0 | _ | 1.4 | _ | |
| Light | 12 | _ | 6 | _ | 1.4 | _ | |
| Moderate | 22 | _ | 26 | _ | 9.6 | _ | |
| Heavy | 43.8 | _ | 43 | _ | 39.7 | _ | |
| Extreme | 19.3 | _ | 25 | _ | 47.9 | _ | |
| Teeth/beak pits & punctures | 0.3 | 0.9 | 3 | 9.5 | 0 | 1.2 | |
| Age – % of adults | 21.4 | _ | 87 | - | _ | _ | |

The taphonomic signature of golden eagles on leporid remains

To facilitate comparisons, we present a summary of results obtained from different leporid predators, where the data have been collected using the same methods (Table 10).

In relation to the age at death, our results show that golden eagles prefer to prey on adults (83.5%). Hockett (1995, 1996) and Schmitt (1995), in their studies on leporid remains recovered from golden eagle nests, also commented that most of the specimens were adults, however, values of representation were not provided. The percentage of adults here recorded is higher than

those found for other raptors such as eagle owls (50%) or Bonelli's eagles (41.4%). However different studies have suggested that the percentage of adult individuals can be variable, not only on raptors but also in terrestrial carnivores (Lloveras et al. 2012b; Lloveras, Thomas, et al. 2014), implying that leporid age is not a sufficiently distinctive characteristic to separate accumulations generated by different predators.

The main taphonomic features observed in the leporid sample point to anatomical representation characterized by an abundance of innominates, calcanei, tibiae and cranial remains (specially upper molars); a low frequency of ribs and carpal/tarsal and a greater presence of hindlimbs relative to forelimbs. Some differences were observed between non-ingested remains and pellets. Crania and long bones were more abundant in non-ingested samples whilst calcanei and phalanges prevailed in pellets. Hockett (1995, 1996) and Schmitt (1995) reported that the most common skeletal elements in leporid assemblages accumulated by golden eagles were hindlimb bones, specifically tibiae, femora and calcanei. Innominates were also well represented but in lower frequencies, whilst forelimbs and skulls were rare. Our results agree with the importance of these skeletal elements, but in different position. In our study innominates are the best represented and skulls and autopodia are more abundant. This reflects the fact that despite similar trends being found, variability also occurs and should be taken into account when considering anatomical representation.

Comparisons with other diurnal raptors reveal that the taphonomic signature of golden eagle accumulations is distinctive. In Bonelli's eagle leporid assemblages Lloveras, Thomas, et al. (2014) found that innominates were also the best represented element, however, crania were much more abundant than in golden eagle nests; whilst tibiae, femora and calcanei were rare. Comparisons with the taphonomic signature of Spanish imperial eagle (Aquila adalberti) pellet samples also show some differences. This eagle tends to accumulate larger numbers of third phalanges and cranial remains (Lloveras et al. 2008b); though calcanei and femora were more abundant in our golden eagle pellet sample. Differences are also found with nocturnal raptors, such as the European eagle owl (Bubo bubo), in which the anatomical profile is characterized by lower percentages of cranial remains (specially teeth) and third phalanges (Sanchis 2000; Cochard 2004b; Lloveras et al. 2009). With regard to terrestrial carnivores, both Iberian lynx (*Lynx pardinus*) and red fox (*Vulpes vulpes*) leporid assemblages of non-ingested remains are characterised by lower frequencies of cranial remains, scapulae or femora; whilst other elements, such as metapodials, are much more abundant than in our study (Lloveras et al. 2008a, 2012a; Rodríguez-Hidalgo et al. 2013). Otherwise, almost all skeletal elements, with the exception of the scapula are better represented in non-ingested remains accumulated by wildcats (Lloveras et al. 2016). The scat accumulations of all these carnivores display higher percentages of scapulae and forelimb bones; but fewer calcanei and third phalanges (Lloveras et al. 2008a, 2012a, 2016).

As far as breakage patterns are concerned, the percentage of complete elements in our study (68.2%) was much higher than the 38-32.3% obtained with golden eagle accumulations by Schmitt (1995). This value can vary depending on the percentage of remains coming from pellets in the sample, however this large difference is probably related to other causes. In fact, in his study Schmitt noted that the majority of the leporid remains were incomplete but much of the fragmentation resulted from post-depositional weathering. Considering that our samples were not affected by weathering, this could explain the differences observed on breakage. Comparisons with other raptors show similar values to Bonelli's eagle nest accumulations (74.7%) but a higher percentage than that recorded in European eagle owl nest assemblages (53.9-45.9%) (Lloveras et al. 2009). In the pellets sample, the percentage of complete bones was 39.8%, lower than the 59.6% recorded for Bonelli's eagles and higher than the values recorded for Spanish imperial eagles (27%). The percentage of complete long bones (45.3%), again is lower than the percentage recorded in Bonelli's eagle pellets (51.3) but higher than the percentages recorded for other raptors or for terrestrial carnivore scat accumulations (Table 10). These results indicate that leporid bones accumulated by golden eagles are slightly more fragmented than those accumulated by Bonelli's eagles but less-fragmented than those generated by other raptors or by terrestrial carnivore scats. This is also confirmed when the percentage of remains under 10 mm is observed (Table 10).

It is well known that prey remains coming from diurnal raptor pellets are usually affected by important corrosion caused by digestion. Hockett (1996) reported that the majority of leporid bones recovered from the golden eagle pellets were extensively corroded and thinned and that jagged ends of fractured bone specimens were often polished. The same alterations have been found in this study. The percentage of digested remains in our golden eagle samples is similar to that obtained in the Bonelli's eagle analysis (32 and 31.2% respectively) and lower than those recorded for other predators. Values obtained for the pellets sample (73.6%) are lower than those recorded for Spanish imperial eagle pellets (98%) and for Iberian lynx, red fox and wildcat scat accumulations (97.2, 99.5 and 98.6%). Even in eagle owl nest accumulations, the percentage of digested remains is higher (68.8%). However, digested remains in golden eagle samples, as occurs with other diurnal raptors, were damaged to a very high degree. This clearly distinguishes golden eagles from European eagle owls, which are characterised by high percentages of light corrosion. Digestion damage was also more pronounced than in Bonelli's eagles and Spanish imperial eagle pellets but slightly lower than those of terrestrial carnivores (Table 10).

The percentage of bones with beak or talon marks (1.5% of remains displayed BPU/BPI) is consistent with the values recorded by Hockett (1995). This researcher counted between 1 and 2% of punctured bones and stated that one of the most frequently punctured bones was the innominate. In this study, innominate was also the most affected bone; however, punctures were randomly located in different parts of the skeletal element (ilium, ischium, acetabulum). In contrast, the majority of punctured innominates in the Hockett samples displayed a single puncture mark directly behind the acetabular fossa.

The percentage of beak/talon marks found is also similar to those recorded in Bonelli's eagle and European eagle owl nest accumulations but clearly lower than those obtained for other raptors such as the Egyptian vulture, which reached values of 7.5–10.4% (Lloveras, Nadal, et al. 2014; Sanchis Serra et al. 2014). Iberian lynx and wild cats also produce similar percentages of damaged bones in non-ingested remains (0.9 and 1.2%), while the percentage of tooth damage in red fox leporid accumulations



was much higher (9.5%). Nevertheless, the lack of gnawing and location of the puncture marks is not typical of the action of carnivores but of birds of prey (Sanchis Serra et al. 2014).

In summary, leporid assemblages accumulated by golden eagles are characterised by:

- a body part representation with an abundance of cranial remains, upper molars, innominates and hindlimb bones:
- (2) a moderate degree of breakage, with high percentages of complete bones;
- a moderate percentage (around 30%) of digested remains but mostly with a heavy and extreme degree of corrosion;
- a large number of beak/talon marked bones;

Some of these features are shared with other leporid predators, especially with other diurnal raptors such as Bonelli's eagles. However, considering all of them together, it is possible to distinguish golden eagles taphonomic signature.

The taphonomic signature of golden eagles on bird remains

Among the bird remains recovered, sterna and pelves were the most abundant elements. The same bones were also the best represented in Bonelli's eagle nest accumulations (Lloveras, Thomas, et al. 2014). The sternum was similarly the most frequent element in non-ingested assemblages from diurnal raptors such as Spanish imperial eagle, golden eagle, gyrfalcon (Falco rusticolus), crested caracara (Caracara plancus) and Egyptian vulture (Bochenski et al. 1998, 1999, 2009; Bochenski 2005; Montalvo et al. 2011; Lloveras, Nadal, et al. 2014; Sanchis Serra et al. 2014). Regarding long bones, coracoids and humeri were the best represented in our study. The same bones were the most abundant in golden eagle nest accumulations studied by Bochenski et al. (1999) and they usually are the most frequent elements in non-ingested remains of diurnal raptors (Bochenski 2005).

Results from the wing/leg ratio indicated a slight preponderance of leg elements in the sample. Conversely, a slight superiority of wing bones was found by Bochenski et al. (1999) in golden eagle nest accumulations. This means that some variability is possible and that these values should be considered with caution, especially when the predominance of a determined part is low. When comparing these data with other studies (Bochenski et al. 1997; Laroulandie 2002; Bochenski 2005; Montalvo et al. 2011; Lloveras, Thomas, et al. 2014), it is clear that most diurnal raptors showed a higher proportion of wing elements. The preponderance of leg bones has only been recorded for Spanish imperial eagles in the pellets sample (Bochenski et al. 1997). The ratio of proximal to distal elements indicated that proximal elements outnumbered distal bones to a much larger extent (77.8%). This high value fits well with the expected rate established for non-ingested remains of golden eagles (Bochenski & Nekrasov 2001; Bochenski 2005) and distinguishes this predator from other raptors. The abundance of core elements detected here is also consistent with other golden eagle studies (Bochenski et al. 1999; Bochenski 2005).

Golden eagles fragment bird bones to a similar extent to other diurnal birds of prey. The percentage of complete long bones was 63%, which is comparable with values above 60% reported by Bochenski (2005) for non-ingested remains of diurnal raptors. The average value of complete bones (45.7%) is also very similar to the 49.9% recorded on birds accumulated on Bonelli's eagles' nests (Lloveras, Thomas, et al. 2014).

The percentage of digested remains in the golden eagle sample (19.1%) is under the 60.4% recorded with Bonelli's eagle (Lloveras, Thomas, et al. 2014). However, these values are not comparable because they vary depending on the number of remains coming from pellets in the sample. What is striking about digestion damage is the high percentage of extreme and heavy digested elements (44.4 and 33.3%). These values are clearly higher than those recorded for the European eagle owl (Laroulandie 2002), Snowy owl (Bubo scandiacus) (Bochenski et al. 1997), crested caracara (Montalvo et al. 2011), Egyptian vulture (Lloveras, Nadal, et al. 2014), Bonelli's eagle ((Lloveras, Thomas, et al. 2014) and gyrfalcon (Bochenski et al. 1998).

The percentage of remains affected by beak/talon marks was higher for golden eagles (14.6%) than for Bonelli's eagle (6.2%), but lower than for Egyptian vulture (28.3%, Lloveras, Nadal, et al. 2014; Lloveras, Thomas, et al. 2014). The location of most beak/ talon marks on sterna (100%) and pelves (75%) is replicated on non-ingested assemblages left by other diurnal birds of prey: Bochenski et al. (2009) found punctures on 70% of sterna and 38% of pelves in white-tailed eagle (Haliaaetus albicilla) assemblages; punctures were observed on 39% of sterna and 51% of pelves in golden eagles; Lloveras, Thomas, et al. (2014) recoded punctures on 75% of sterna and 71.4% of pelves in Bonelli's eagles nests. Coracoids, scapulae and humeri were the most affected long bones in our study. Similar results have also been recorded for other raptors (Bochenski et al. 2009; Lloveras, Thomas, et al. 2014).

In summary, the taphonomic signature observed on bird remains accumulated by golden eagles nests is characterised by:

- an abundance of sterna and pelves; among long bones coracoids and humeri are the most frequent;
- a low degree of breakage, with more than 60% complete long bones.
- (3) a high percentage of heavily and extremely digested remains (44.4 and 33.3% respectively);
- (4) a high percentage of beak/talon marked bones (> 14%), most on pelves, sterna and long bones.

Comparisons show clear differences to nocturnal birds of prey. Although many features are shared with other diurnal raptors, especially with Bonelli's eagles, differences are apparent nevertheless.

Conclusions

This study provides detailed taphonomic observations of prey remains accumulated by golden eagles on their nests. These raptors may accumulate large quantities of animal bones and teeth that could result in the formation of faunal deposits mixed with human or other predator-derived assemblages. Results from our analysis help to identify and classify the most important characteristics of bones accumulated by the raptors.



Golden eagle's diet is focused on a wide range of species. Leporids, rodents, birds and carnivores are normally present in their nest assemblages. The species represented vary according to the ecological region. The observations and results obtained through this study showed that damage caused by golden eagles to leporids and birds differs sufficiently from other predators. However, more studies are needed to go deeper in other taxonomic groups, such as small carnivores or large rodents. The use of the criteria presented in this study can help to assess the potential contribution of golden eagles in accumulating prey remains on archaeological sites.

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