International Journal of Osteoarchaeology

WILEY

RESEARCH ARTICLE OPEN ACCESS

Non-Ingested Scapulae and Mandibles Accumulated in Nests by Bearded Vultures (*Gypaetus barbatus*) in Corsica: A Neo-Taphonomic Analysis

Montserrat Sanz[1] | Isabelle Attard[2] | Joan Daura[1] | Jean-Denis Vigne[2]

[1]Grup de Recerca del Quaternari, GRQ-SERP. Department of History and Archaeology, University of Barcelona, Barcelona, Spain | [2]Archaeozoology, Archaeobotany: Societies, Practices and Environment (UMR 7209), CNRS - Muséum National d'Histoire Naturelle, Paris, France

Correspondence: Montserrat Sanz (montsesanzborras@ub.edu)

Received: 31 October 2024 | **Revised:** 3 February 2025 | **Accepted:** 6 February 2025

Funding: This work was supported by the Ministerio de Ciencia e Innovación Government of Spain (PID2020-113960GB-100/AEI), Ministerio de Ciencia e Innovación and the European Union NextGenerationEU, Ramon y Cajal postdoctoral grant (RYC2021-032999-I), CNRS-INEE International Research Network program (Grant No. IRN0871TaphEN), and AGAUR Generalitat de Catalunya (SGR2021-00337).

Keywords: bearded vulture | bone consumption | mandible | nest | Pleistocene | scapula | scavenger

ABSTRACT

The bearded vulture (*Gypaetus barbatus*) is a scavenger and bone-eating vulture that also transports bones to the nest to feed the nestlings. Bones found at nests are characterized by the accumulation of small- to medium-sized ungulates, a high number of third and second phalanges and digestive corrosion marks on regurgitated bones. This actualistic study explores the taphonomic signatures of modern free-ranging bearded vultures left on mandibles and scapulae bones transported and abandoned at nests. The assemblage was recovered on the island of Corsica (France), and its findings are crucial for identifying bearded vulture signatures on bones found in eyries. While mandibles and scapulae are less nutritious as food and exhibit lower handling efficiency, they can be transported to the nests. Nevertheless, a distinct diagnostic pattern of consumption is observed on both skeletal elements, as described in this study. This pattern is essential for discerning the activities of other biological agents, such as hyenas and humans in Pleistocene sites.

1 | Introduction

Bearded vulture (*Gypaetus barbatus*) is a scavenger and bone-eating vulture capable of ingesting bones of up to 30 cm in length, which are digested because of their high stomach acidity. Accordingly, the most diagnostic features to identify this agent in taphocenosis accumulations are the characteristic corrosion left on bones regurgitated, their scats or coprolites, the skeletal part frequencies with a high proportion of phalanges, long bones complete in circumference, rare bone flakes, and predominance of small- to medium-sized ungulate bones (Attard Robert 2010; Frey and Walter 1986; Laroulandie et al. 2024; Marín Arroyo et al. 2009; Robert and Reumer 2009; Robert and Vigne 2002a, 2002b; Sanz and Daura 2023; Sanz et al. 2023). In particular, hooves are the most common items found in modern nests, as in Corsica (Vigne 1995). However, they do not preserve well in fossil assemblages due to the chemical degradation of keratin, which explains the high preservation rate of third phalanges in modern and prehistoric bearded vulture nests (Robert and Vigne 2002b).

This scavenger bird presents similar behavioral features in common with Paleolithic humans and hyenas (Brugal et al. 1997; Cruz-Uribe 1991; Davis et al. 2007). Thus, the three agents consume mostly ungulates, accumulate bones, and dwell in caves and rock shelters; bearded vultures in openings and fissures in or above cavities, but remains can be mixed with human or hyenid occupancies. Detailing the taphonomic and zooarchaeological characteristics of bearded vulture activity on bones becomes essential due to these features, aiding in distinguishing their influence from that of other biological agencies (Marín-Arroyo and Margalida 2012; Robert and Vigne 2002a). Although bearded vultures could accumulate ungulate bones, there is still a limited amount of research dedicated to this agent. Recently, attention has also been drawn to the potential of Egyptian vultures (*Neophron percnopterus*) for bone accumulations on archaeological sites. This vulture primarily feeds on carrion but is also opportunistic, capable of consuming birds, reptiles, and small mammals (Milchev et al. 2012) and transports, accumulates, and modifies bones in nests (Lloveras et al. 2014; Sanchis Serra et al. 2014). The scavenging lifestyle of other vultures in other areas, such as America, has also attracted attention and requires further consideration of their potential role as accumulators, scatterers, and modifiers of bone remains (Pokines et al. 2021). Although American vultures and condors (family Cathartidae) have a different evolutionary history from Old World vultures (subfamilies Aegypiinae and Gypaetinae), both lineages are obligate scavengers, relying almost entirely on carrion rather than hunting live prey for food (Ogada et al. 2012). Most of the carcasses scavenged by birds are left at the original death site. However, some large mammal bones can be regurgitated as pellets and accumulated elsewhere. For instance, the pellets of the American black vulture (*Coragyps atratus*) are characterized by a predominance of medium-sized vertebrates, with autopodial elements being highly represented and phalanges often exhibiting pronounced digestion marks (Ballejo et al. 2012, 2016). The abundance of skeletal elements in Paleolithic assemblages is widely examined by scholars to establish the relation of nutritional utilities and transport choices from kill sites to the camps. These patterns are usually compared with ethnoarchaeological works that developed several established indices to apply to past assemblages (Binford 1978, 1981; Schoville and Otárola-Castillo 2014; White 1952). Dietary preferences of bearded vultures are widely known, choosing the most fatty and nutritive bones to enhance the nutritional benefits and energy acquisition while optimizing their foraging efficiency (Brown and Plug 1990; Margalida 2008a; Thibault et al. 1993). Appropriately to this anatomical preference, a Bearded Vulture Bone Utility Index (BVBUI) was proposed to identify this agent in archaeological sites (Marín-Arroyo and Margalida 2012) and discern by other agents, humans included. The index is determined by within-bone nutrients, the contents of fatty acids, and the maximum length of the bones. According to this index, phalanges are the most valuable, coinciding with the greatest number of skeletal elements ingested. By contrast, the sternum, scapula, and mandible are the skeletal elements with a lower utility. Even though their low nutritional value, bearded vultures also transport some of these bones to the nest and consume them, as observed in the Pleistocene deposits of Luri-Grítulu cave (Robert and Vigne 2002a), and El Miron cave (Marín Arroyo et al. 2009).

Another variable examined by scholars to determine the different agencies involved in assemblages are the modifications and fractures observed on bones, because they could be distinctive of the kind of predator or scavenger (Behrensmeyer and Hill 1988; Fernández-Jalvo and Andrews 2016; Haynes 1983; Sala and Arsuaga 2013; Stiner et al. 2012; Yravedra et al. 2014), even though damage inflicted to bones by a specific predator can exhibit features that resemble those caused by other agents. Certain modifications may be more closely associated with specific biological agents, while in many cases, it is a combination of damages that forms a diagnostic pattern or indicates the progression of feeding intensity (Binford 1981; Stiner 1994) combined with behavior and context, such as interactions and competition among carnivores, seasonality, and availability of prey (Fosse et al. 2012; Haynes 1982). Some damage inflicted by vultures, such as punctures on flat bones and pits, is similar to those produced by carnivores, and the marks with parallel micro-striations probably caused by the beak are often mimicked by trampling alterations, which complicates taphonomic evaluation (Domínguez-Solera and Domínguez-Rodrigo 2011; Fernández-Jalvo and Andrews 2016). However, some elements, such as scapulae and mandibles, show distinctive features that deserve further description.

The taphonomic signature of bearded vultures from Corsican nests is characterized by the accumulation of small-sized ungulates, skeletal frequencies clearly disproportionate, with a high number of phalanges, digestive corrosion marks on bones that should have been regurgitated, and a few indeterminate bones, some of them exhibiting green fractures (Robert and Vigne 2002a, 2002b; Vigne 1995). In light of this context, we introduce fresh observations on the scapulae and mandibles accumulated by the bearded vultures at modern Corsican nests. Thus, we present the study of the actualistic sample of modern free-ranging bearded vultures to examine the taphonomic signatures left on these skeletal elements transported to the nests but not ingested.

2 | Samples, Study Area, and Project Background

The study sample was derived from free-ranging bearded vultures in the Mediterranean island of Corsica (Figure 1). Items—horns, hooves, feathers, hair, skin, scats, bones, and teeth—have been exhaustively collected between 1985 and 2000 from 11 nesting eyries of bearded vultures and two bone-breaking sites located in different subalpine valleys of this island (Thibault et al. 1993). During that period, the population size in Corsica was stable with around eight breeding pairs (Seguin et al. 2010). The foraging area of bearded vultures during the breeding season was mostly above 1000 m in the mountains. When snow covered these high areas, the vulture exploited other cliff areas and middle-altitude regions without snow coverage. Other scavengers on the island were rare, such as the golden eagle (*Aquila chrysaetos*), common buzzard (*Buteo buteo*), raven (*Corvus corax*), and only a mammalian carnivore, the fox (*Vulpes vulpes*), together with the absence of other vultures, such as the griffon vulture (*Gyps fulvus*) (Thibault et al. 1993).

Related to feeding traits, a variation within regions is observed according to species availability; thus, diet agrees with the biocenosis within each territory. In general trends, bearded vultures from Corsica mostly feed on domestic species, mainly caprines but also calf bones—cattle is a very small size on the island (Vigne 1988)—with less mouflons and suids. Other small mammals, such as dogs, foxes, cats and hares, are testimonial,

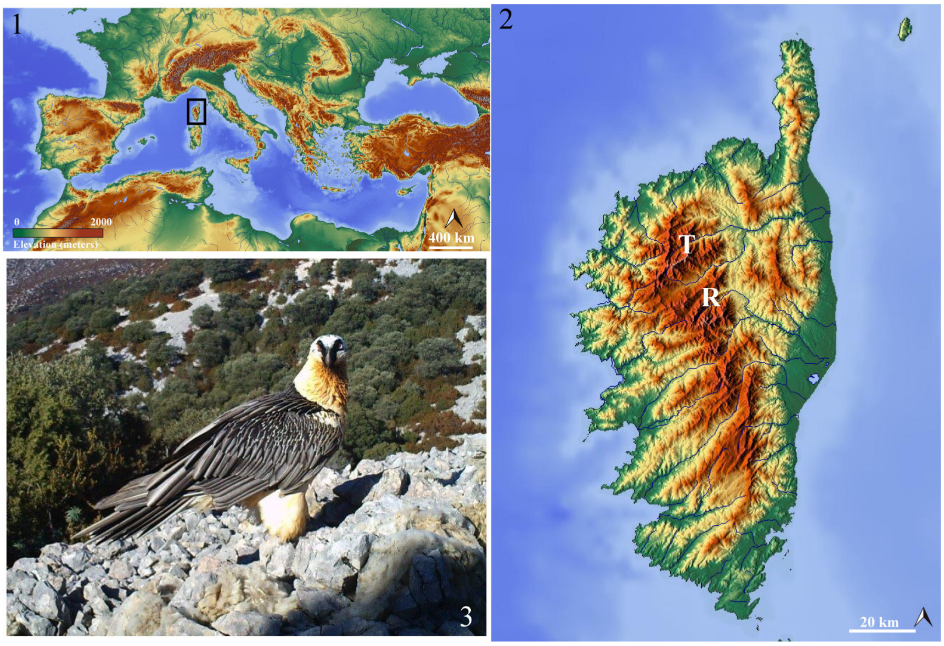

FIGURE 1 | (1) Location of the island of Corsica in the western Mediterranean basin. (2) Location of the two areas of study, where scapulae and mandibles from nests were recovered (after Thibault et al. 1993). (3) Adult bearded vulture in a breaking-bone area (image courtesy of Fundación para la Conservación de los Quebrantahuesos). [Colour figure can be viewed at wileyonlinelibrary.com]

probably related to their bone fragility (Thibault et al. 1993). Several feathers were also recovered in the nests, also evidencing bird consumption. According to Thibault et al. (1993), five categories of items have been determined related to features and young consumption: (i) uneatable elements, (ii) scats, (iii) regurgitated semi-digested bones and hooves, (iv) food portions not consumed, and (v) incompletely eaten bones (i.e., bones that were not swallowed), such as scapulae as the remaining parts of ingested limbs, broken fragments of skulls and mandibles, and distal parts of limbs. The percentage of skeletal representation in Corsican nests is dominated by short and compact ungulate bones (tarsals, carpals, sesamoids, and phalanxes), representing 75% of the assemblage, with third phalanxes being the most common (Robert and Vigne 2002b). All the material is housed in the National Museum of Natural History (Paris, France), and the material has been studied and published previously (Attard Robert 2010; Robert and Vigne 2002a, 2002b; Thibault et al. 1993; Vigne 1995).

3 | Materials and Methods

The present study has been focused on scapulae and mandibles found in the different nests from Corsica. From the nests revised, only T (1985, 1991, and 1995) and R (1986) present a total of 20 elements (Figure 1). The number refers to the year of collection and the letter to the area (Thibault et al. 1993). This indicates that not every nest contained these two bones. Scapulae and mandibles were taxonomically identified previously by J.-D. Vigne (Thibault et al. 1993). Most part of these materials are small-sized ungulates, such as sheep, mouflon, and goats, and medium-sized, such as mostly young cattle.

Bones were analyzed following standard taphonomic methods (Fernández-Jalvo and Andrews 2016; Lyman 1994). To determine the effects of bearded vultures as breakage type and bone modification, surfaces were scrutinized at both macro and microscopic levels under a Dino-Lite digital microscope; detailed images and dimensions of marks were made using the DinoCapture 2.0 software. The variety of modifications noted in the sample has been classified using the nomenclature commonly employed in avian taphonomy (Bochenski et al. 2009; Fernández-Jalvo and Andrews 2016; Laroulandie 2005; Sanchis Serra et al. 2014): puncture (hole or perforation of the bone), notch (cup-shaped depressions accompanied by bone loss along the fracture edge), pit (superficial marks on the surfaces of bone with semi-circular shape), peeling (type of breakage with featuring heavily jagged edges), and crenulated edges (a sequence of punctures or indentations at the edge of the bone).

Geographic Information System (GIS) was used to illustrate the distribution of pits produced by bearded vultures and the skeletal overlapping portions, only applied to scapulae due to the scarce number of mandibles. This methodology has been previously applied in archaeology by several authors (Marean et al. 2001; Parkinson et al. 2014; Stavrova et al. 2019). Previous authors primarily used ArcGIS software; however, we opted for the public domain software QGIS Version 3.34 Prizrern under CC BY-SA 3.0 DEED.

To process the scapulae and mandibles in QGIS software, we used the Corsican material and Marean's image (Marean et al. 2001) and vectorized them using Inkscape software. Then, we scaled the polygons and images to conform to standardized measurements compatible with QGIS software. As bone specimens are non-geographical, we assigned arbitrary coordinates, considering the compatibility scale required for GIS analysis. For both bones, we analyzed only one side; as such, we mirrored the images of the opposite side to overlap seamlessly with the corresponding side for comparison. The images and vectorizations of the analyzed bones show slight variations due to differences in age, size, and image capture methods. To enable accurate comparison and layer overlay within the QGIS software, all images underwent standardization procedures.

The "raster" images were georeferenced using the Georeferencing tool, employing a Polynomial—1st degree—transformation type and the Nearest Neighbour resampling method. This was facilitated by the inclusion of 20 landmarks to ensure accuracy and precision. Following this, the layer and scapula profiles were defined in QGIS software. The vector shape files were then converted to "raster" format with a resolution of 200 × 200 pixels. The "rasterized" images have been merged into a single figure using r.series from the GRASS GIS repository (Version 8.4.1dev). This function assigns each output cell value based on the corresponding values in the input "raster" map layers. The SUM function was used for this process. To calculate bone survivorship, the area of each scapula was calculated using the r.report command available in the GRASS module.

Finally, pits were plotted on the scapula and mandible images and analyzed using heat maps with a triangular kernel shape. To ensure consistency in processing raster and point data in the QGIS software environment, a kernel radius of 30° was used.

4 | Results

4.1 | Scapulae

A total of 17 not-swallowed scapulae from nests have been studied (Figure 2). The extent of damage in the scapulae is light overall. Small ungulates scapulae #1 to #6 are totally complete and undamaged; however, #6 presents some notches on both sides of the cranial angle. Scapula #7 shows a crenulated edge and light damage at the cranial angle, followed by #8, which has damage at both the cranial and caudal angles, while the proximal rim of the scapular blade remains intact. The following scapula #9 exhibits more significant damage in the cranial angle and in the infraspinous fossa of

FIGURE 2 | Range of variability of damage observed on scapulae at bearded vulture nests. Dorsal and ventral sides of each specimen. (1–14) Small ungulates (sheep, goat, and mouflon). (15–17) Medium ungulates (cattle). Photos and CAD M. S. [Colour figure can be viewed at wileyonlinelibrary.com]

the scapular blade, with crenulated edges. The caudal border, however, remains undamaged. Several pits and linear marks are observed near two notches in the ventral proximal part of this scapula (Figure 3, 4a), likely associated with efforts to consume the proximal rim. The proximal edge of the scapula is absent in the other elements (#10 to #14), where it has been completely hollowed out, showing a stepped profile created by punctures at the edge, i.e., a crenulated edge, together with

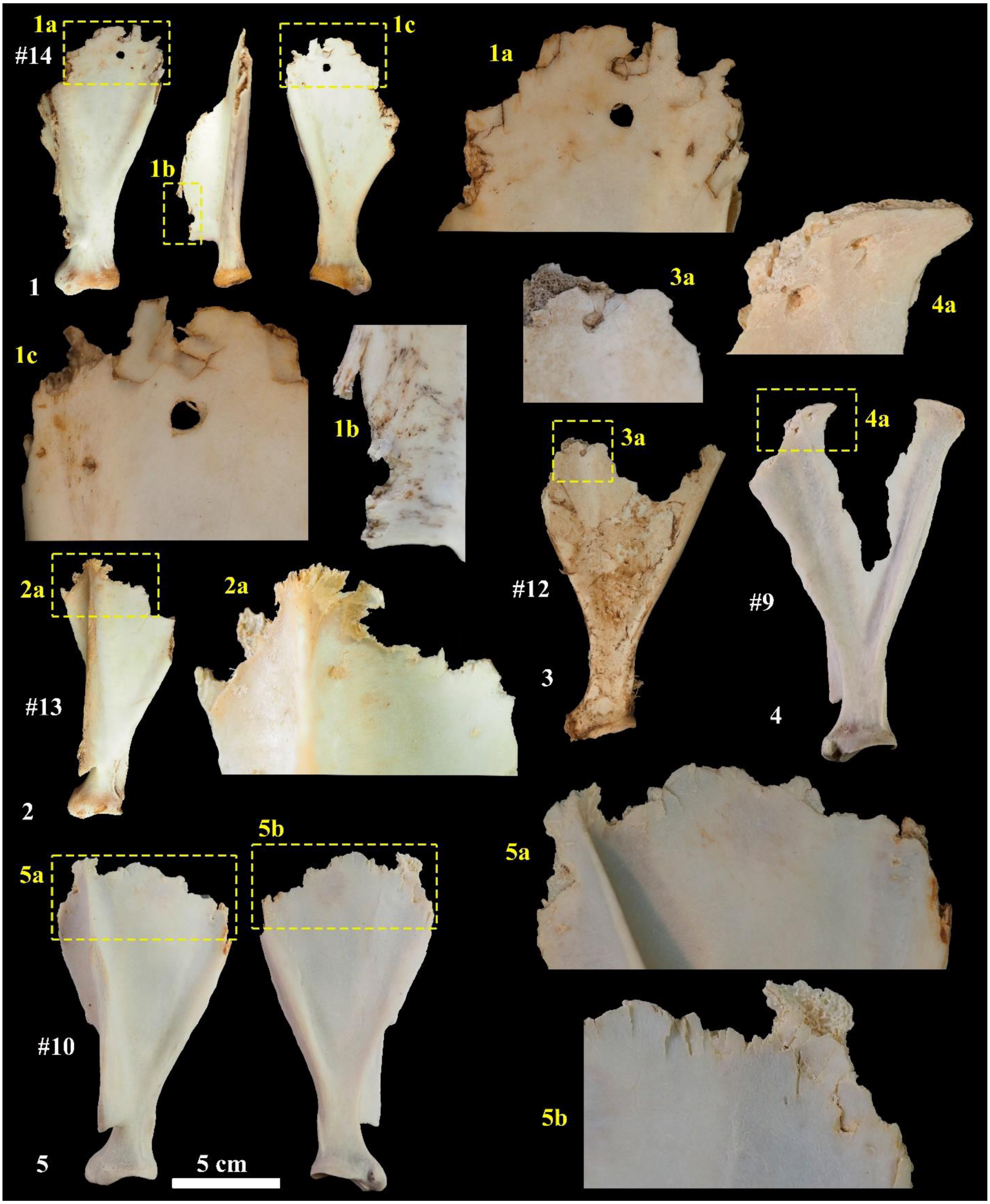

FIGURE 3 | (1) Scapula #14, (1a and 1c) crenulated edges, punctures, and detailed views of the strong damage at the proximal rim of the blade, (1b) peeling and punctures on the spine. (2) Scapula #13, (2a) crenulated edge at the rim and pits at the blade. (3) Scapula #12, (3a) detailed view of a notch. (4) Scapula #9, (4a) pits and linear marks at the proximal part. (5) Scapula #10, (5a and 5b) crenulated edge, notches, and pits together with linear marks at the proximal area. Photos and CAD M. S. [Colour figure can be viewed at wileyonlinelibrary.com]

pits and notches located at the proximal portion (Figure 3, 3a). The proximal U-shape corresponds to the consumption of the most brittle and thin areas, avoiding the spine and edges. Some of them present peeling and punctures on the spine and acromion (#11 to #14) (Figure 3, 1b). The distal end is not damaged, except for #13. Pits and notches are also present together with a few linear marks (#10, #13, and #14) and a perforation in #14 with a diameter of 13.4 mm, a length of 4.58 mm, and a width of 3.89 mm (Figure 3, 1a and 1b). Three scapulae (#15 to #17) pertaining to medium ungulates, such as cattle, also present damage. The immature scapula (#15) presents some pits and notches on the distal end but also on the proximal edge. The scapula #16 presents a crenulated edge in the proximal rim, together with the incipient consumption of the acromion. Finally, the last scapula, #17, is a fragment of the caudal border and the blade with some pits and notches.

A cartographic representation generated using QGIS software is provided (Figure 4). The green regions indicate high concentrations of scapulae, with the resulting analysis showing lower rates of bone destruction and an overall survival rate of 83% across the 14 samples. Only one case exhibits a survival rate below 50%, while three cases fall below the 75% threshold. Most samples exceed the 75% threshold. Bone plotting showed that the caudal and cranial angles from the proximal edge of the scapula were the most consumed area (Figure 4, 2).

4.2 | Mandibles

Three mandibles not swallowed by bearded vultures have been studied (Figure 5); however, in the collection, there is a fox mandible showing signs of strong digestion (Robert and Vigne 2002b). Two of them correspond to small ungulates (#1 and #2), and the third (#3) is a young cattle mandible. One mandible bears a notch on the basal corpus near the angle in the lateral face (#1). The second one exhibits longitudinal splitting along the basal corpus without any other visible damage (#2). The third one exhibits a crenulated edge limited at the inferior angular process associated with pits and linear marks (#3) (Figure 4,5).

5 | Discussion

Bearded vultures use their talons and beaks to carry food to the nest, as unlike other vultures, they do not feed their young by regurgitation (Brown and Plug 1990; Margalida and Bertran 2000; Margalida 2008a). Moreover, this bird drops freshly scavenged bones from the air when they are too long to ingest at specific locations, known as bone-breaking sites—used to reduce bone size for later ingestion but also for storing food—where indeterminate flakes or diaphysis fragments dominate (Robert and Vigne 2002a). The bones found in ossuaries are probably the result of the rejection because of their low nutritive value, whereas handling efficiency may also play a secondary role in food selection (Margalida 2008a). Ungulate scapulae and mandibles are bones with shapes that cannot be swallowed whole by bearded vultures (Margalida 2008b). Thus, handling efficiency is required to consume these elements because they must be crushed against rocks before ingestion or require an extra effort to prepare them. Accordingly, both elements are frequently found in ossuaries or bone-breaking areas. Together with these elements, other skeletal bones with less oleic acid are abundant at these bone-breaking areas, such as vertebrae, skulls, tibias, ribs, and humeri (Margalida 2008a, 2008b), when they are rare or absent from the modern eyries (Robert and Vigne 2002a, 2002b). Digestion marks were not observed on these bones accumulated at ossuaries; half of the bones exhibit weathering marks resulting from exposure, and some bear marks produced by carnivore scavenging (Robert and Vigne 2002a). Thus, the choice to transport to the nest some of these elements characterized by low nutritional value and the difficulty to handle could be related to other variables, such as carcass availability, seasonality, and snow coverage. It seems that other variables are less relevant, such as carnivore or scavenging pressure that is practically absent in Corsica, because only a few scavenger birds are present and only a mammalian carnivore species, the fox. Although these elements could be brought to nest as isolated bones, as documented in Cazorla (Cano and Valverde 1959), they can also be brought as articulated limbs or segments. In fact, the foot morphology of the bearded vulture allows its digits to function like a vice, enabling the bird to cut through tough joint ligaments and tendons (H. Frey, pers. comm.).

Although scapulae and mandibles are less represented in Corsican nests compared with phalanges, other contexts show different patterns. For example, the nest documented in the protohistoric shelter of Baume du Houx shows an overrepresentation of phalanges, especially the third. However, it is noteworthy that among the bones with digestion marks, the isolated teeth (~40%) are more common than the third phalanges (~20%) (Valensi et al. 2011), whereas no isolated teeth with digestion marks were identified at El Mirón (Marín Arroyo et al. 2009).

Gnawing patterns and bone damage are useful criteria to determine the intensity of bone consumption and to identify the biological agents involved in an assemblage (Delaney-Rivera et al. 2009; Domínguez-Rodrigo and Piqueras 2003; Haynes 1983). The damage observed in scapulae modified by bearded vultures indicates that the caudal and cranial angles are often removed. According to Attard Robert (2010), 37% of the scapulae examined from the Pyrenees and Corsica show this pattern, a high proportion indicating that this fragmentation should be considered as a taphonomic feature of the bearded vulture. This contrasts with the damage typically caused by terrestrial carnivores, which tend to focus on consuming the entire proximal rim. For example, hyenas and wolves cause severe damage to the shoulder blade, ranging from furrowing or complete destruction of the proximal rim—resulting in a stepped profile—to partial destruction of the spine and complete destruction of the acromion, often accompanied by numerous tooth marks primarily located at the edges (Fourvel and Mwebib 2011; Sala et al. 2014). Red fox activity on scapulae primarily results in gnawing along the proximal rim, as documented also for mountain lion (Stiner et al. 2012), sometimes leading to the complete consumption of the acromion. Scapulae are among the skeletal elements with the highest frequency of gnawing marks (Yravedra et al. 2014). For instance, damage inflicted by other vultures to scapulae was recorded mostly as

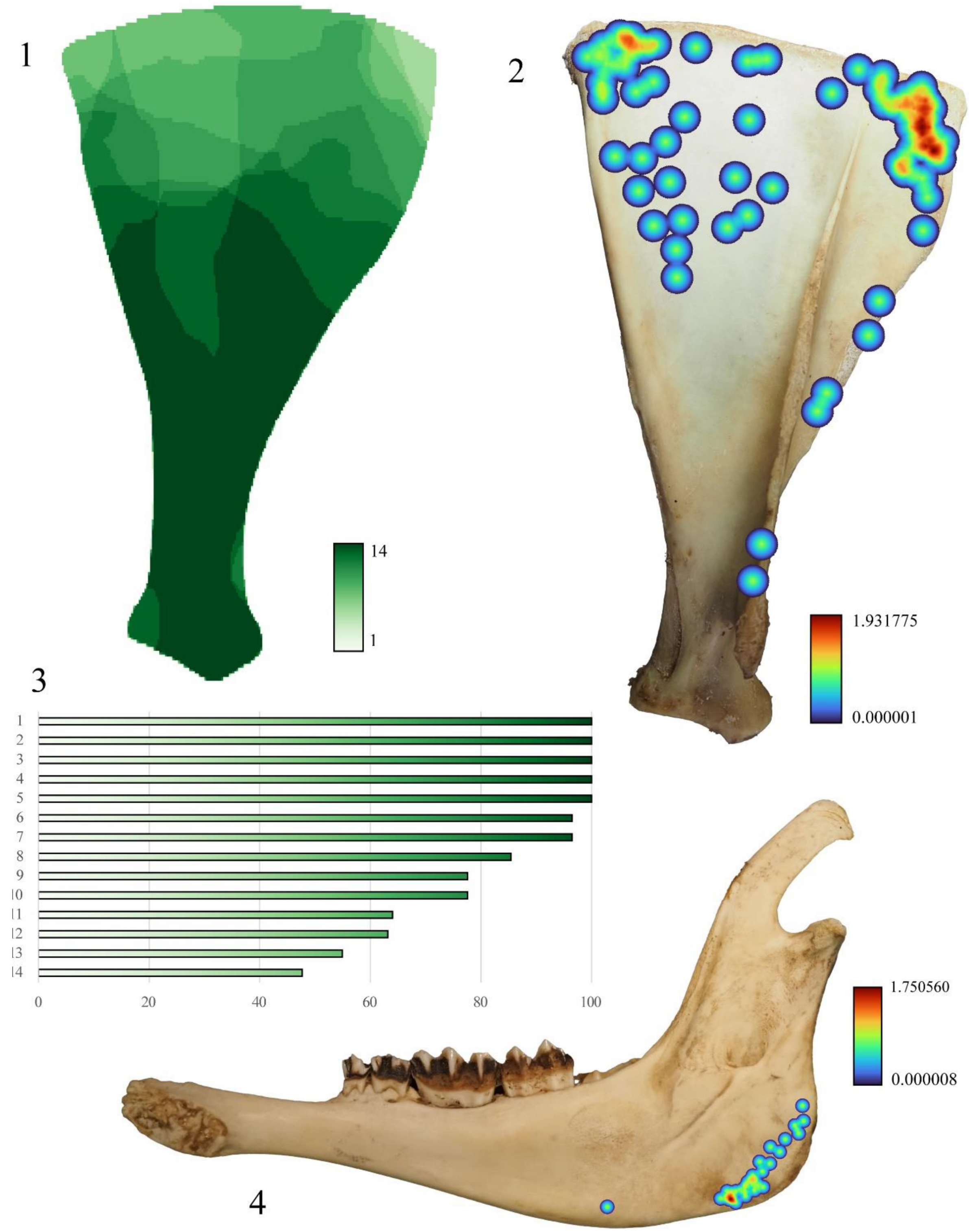

FIGURE 4 | (1) Bone survival composite of 14 small ungulate scapula elements presented on a single side. Bone preservation is indicated by green shades. (2 and 4) QGIS kernel density analysis of the distribution of pittings along the scapula (2) and mandible (4). (3) Percent survivorship of scapulae (#1 to #14). Photos and CAD J.D. [Colour figure can be viewed at wileyonlinelibrary.com]

punctures or notches in the proximal rim (Ballejo et al. 2016; Domínguez-Solera and Domínguez-Rodrigo 2011).

The damage caused by bearded vultures to mandibles typically begins at the outer corner of the bone. In contrast, mandibles modified by other vultures exhibit notches and punctures, which are associated with the removal of the masseter muscle and the disarticulation of the mandible from the cranium (Domínguez-Solera and Domínguez-Rodrigo 2011; Sanchis Serra et al. 2014). Among terrestrial carnivores, mandibles exhibit varying

FIGURE 5 | (1) Mandible bearing a notch on the basal corpus. (2) Mandible bearing longitudinal splitting along the basal corpus. (3) Mandible showing crenulated edge limited at the inferior angular process. Photos and CAD M. S. [Colour figure can be viewed at wileyonlinelibrary.com]

degrees of damage, ranging from limited impact on the vertical ramus to more extensive reduction, including the removal of the horizontal ramus, often accompanied by a greater number of pits and punctures, resulting in isolated teeth (Fourvel and Mwebib 2011; Sala et al. 2014; Stiner 1994).

6 | Conclusion

The pattern observed in scapulae and mandibles recovered from bearded vulture nests can be summarized as:

- Scapulae: The survival rate of ungulate scapulae, when considering the consumption of the element, is determined to be 83%, indicating a slight modification. In Corsican nests, the scapula angles (caudal and cranial) are often clipped and consumed (Robert and Vigne 2002b), being a taphonomic feature of bearded vultures. Moreover, the consumption is focused on the most brittle and thin areas, while avoiding the spine and edges that create a U-shape in some specimens. The distal end appears to be mostly undamaged, although there are a few instances of peeling and punctures on the spine and acromion that were observed during an advanced stage of consumption. In general, it is relevant the high presence of pits at the proximal portion.
- Mandibles: It seems that the consumption of ungulate mandibles by bearded vultures initiates at the outer corner of the mandible, as shown by the high rate of pits. Only one mandible is transversely broken, likely fractured within an ossuary, resulting in the separation of the base of the horizontal ramus; the latter was probably not transported to the nest.

The damage evidence is relevant to help in identifying the bearded vulture as a biological agent instead of others. It seems that scapulae could have been used as food for the nestlings (Attard Robert 2010), as such the cartilage on the proximal rim, which is more easily digested by the juveniles. Pits and punctures observed in the material may be attributed to the beaks of vultures; however, some of them could also be caused by the talons during bone handling.

Acknowledgments

This research benefited from financial support from the following agencies: Ramon y Cajal postdoctoral grant (RYC2021-032999-I, M.S.) with financial sponsorship from Ministerio de Ciencia e Innovación and the European Union NextGenerationEU; AGAUR Generalitat de Catalunya (SGR2021-00337); Ministerio de Ciencia e Innovación Government of Spain (PID2020-113960GB-100/AEI/10.13039/501100011033), CNRS-INEE International Research Network program (Grant No. IRN0871TaphEN). We are grateful for the invaluable assistance of the Fundación para la Conservación del Quebrantahuesos (FCQ) within the framework of the Bearded Vulture Recovery Plan in Aragon (Spain) and the project "Iberian Corridors Pro Bearded Vulture – Life pro BV" (LIFE 20 NAT/ES/001363). We would like to thank Óscar Díez and Carlos Sunyer (FCQ), as well as Àlex Llopis and Hans Frey (Vulture Conservation Foundation—LIFE GYPRESCUE), for their comments and assistance.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data generated during this study are included in this published article.

References

Attard Robert, I. 2010. "Evaluation de l'Impact du Gypaète (*Gypaetus barbatus*) et des Griffons dans la Constitution des Accumulations d'Ossements Animaux et Humains des Sites Anthropisés et Naturels Quaternaires." Thesis. Museum National d'Histoire Naturelle, Paris.

Ballejo, F., F. J. Fernández, and L. J. M. De Santis. 2012. "Tafonomía de Restos Óseos Provenientes de Egagrópilas de *Coragyps atratus* (Jote de Cabeza Negra) en el Noroeste de la Patagonia Argentina." *Revista del Museo de Antropología* 5: 213–222.

Ballejo, F., F. J. Fernández, C. I. Montalvo, and L. J. M. De Santis. 2016. "Taphonomy and Dispersion of Bones Scavenged by New World Vultures and Caracaras in Northwestern Patagonia: Implications for the Formation of Archaeological Sites." *Archaeological and Anthropological Sciences* 8: 305–315. https://doi.org/10.1007/s12520-015-0277-9.

Behrensmeyer, A. K., and A. P. Hill. 1988. *Fossils in the Making. Vertebrate Taphonomy and Paleoecology*. University of Chicago.

Binford, L. R. 1978. *Nunamiut: Ethnoarchaeology*. Academic Press.

Binford, L. R. 1981. *Bones: Ancient Men and Modern Myths*. Academic Press.

Bochenski, Z. M., T. Tomek, R. Tornberg, and K. Wertz. 2009. "Distinguishing Nonhuman Predation on Birds: Pattern of Damage Done by the White-Tailed Eagle *Haliaetus albicilla*, With Comments on the Punctures Made by the Golden Eagle *Aquila chrysaetos*." *Journal of Archaeological Science* 36: 122–129. https://doi.org/10.1016/j.jas.2008.07.018.

Brown, C. J., and I. Plug. 1990. "Food Choice and Diet of the Bearded Vulture *Gypaetus barbatus* in Southern Africa." *African Zoology* 25: 169–177.

Brugal, J.-P., P. Fosse, and J.-L. Guadelli. 1997. "Comparative Study of Bone Assemblages Made by Recent and Pleistocene Hyenids." In *Proceedings of the 1993 Bone Modification Conference*, edited by L. A. Hannus, L. Rossum, and R. P. Winham, 158–187.

Cano, A., and J. A. Valverde. 1959. "Notas Sobre el Quebrantahuesos *Gypaetus barbatus* en la Sierra de Cazorla." *Ardeola* V: 121–126.

Cruz-Uribe, K. 1991. "Distinguishing Hyena From Hominid Bone Accumulations." *Journal of Field Archaeology* 18: 467–486.

Davis, S. J. M., I. Robert, and J. Zilhão. 2007. "Caldeirão Cave (Central Portugal)—Whose Home? Hyaena, Man, Bearded Vulture." *Courier Forschungsinstitut Senckenberg* 259: 213–226.

Delaney-Rivera, C., T. W. Plummer, J. A. Hodgson, F. Forrest, F. Hertel, and J. S. Oliver. 2009. "Pits and Pitfalls: Taxonomic Variability and Patterning in Tooth Mark Dimensions." *Journal of Archaeological Science* 36: 2597–2608.

Domínguez-Rodrigo, M., and A. Piqueras. 2003. "The Use of Tooth Pits to Identify Carnivore Taxa in Tooth-Marked Archaeofaunas and Their Relevance to Reconstruct Hominid Carcass Processing Behaviours." *Journal of Archaeological Science* 30: 1385–1391.

Domínguez-Solera, S., and M. Domínguez-Rodrigo. 2011. "A Taphonomic Study of a Carcass Consumed by Griffon Vultures (*Gyps fulvus*) and Its Relevance for the Interpretation of Bone Surface Modifications." *Archaeological and Anthropological Sciences* 3: 385–392. https://doi.org/10.1007/s12520-011-0071-2.

Fernández-Jalvo, Y., and P. Andrews. 2016. *Atlas of Taphonomic Identifications*. Springer Netherlands. https://doi.org/10.1007/978-94-017-7432-1.

Fosse, P., A. Wajrak, J. B. Fourvel, et al. 2012. "Bone Modification by Modern Wolf (*Canis lupus*): A Taphonomic Study From Their Natural Feeding Places." *Journal of Taphonomy* 10: 197–217.

Fourvel, J.-B., and O. Mwebib. 2011. "Hyenas' Level of Dependence on Livestock in Pastoralist Areas in the Republic of Djibouti And Kenya: Relation Between Prey Availability and Bone Consumption Sequence." In *Prédateurs dans tous leurs états : évolution, biodiversité, interactions, mythes, symboles : actes des Rencontres internationales d'Archéologie et d'Histoire d'Antibes*, edited by J.-P. Brugal, A. Gardeisen, and A. Zucker, 351–370.

Frey, H., and W. Walter. 1986. "Zur Ernährung des Uhus, *Bubo bubo* (Linnaeus 1758), Aves, an Einem Alpinen Brutplatz in den Hohen Tauern (Salzburg, Österreich)." *Annalen des Naturhistorischen Museums Wien* 88, no. 89: 91–99.

Haynes, G. 1982. "Utilization and Skeletal Disturbances of North American Prey Carcasses." *Arctic* 35: 266–281. https://doi.org/10.2307/40509436.

Haynes, G. 1983. "A Guide for Differentiating Mammalian Carnivore Taxa Responsible for Gnaw Damage to Herbivore Limb Bones." *Paleobiology* 9: 164–172. https://doi.org/10.1017/S0094837300007545.

Laroulandie, V. 2005. "Anthropogenic Versus Non-Anthropogenic Bird Bone Assemblages: New Criteria for Their Distinction." In *Biosphere to Lithosphere, New Studies in Verterbrate Taphonomy, 9th ICAZ Conference*, edited by T. O'Connor, 25–30.

Laroulandie, V., J.-B. Mallye, R. Nadal, and T. David. 2024. "Le Gypaète Barbu (*Gypaetus barbatus*) Nichait-il Autrefois dans les Grands Causses?" *Ornithos* 31: 15–27.

Lloveras, L., J. Nadal, M. Moreno-Garcia, et al. 2014. "The Role of the Egyptian Vulture (*Neophron percnopterus*) as a Bone Accumulator in Cliff Rock Shelters: An Analysis of Modern Bone Nest Assemblages From North-Eastern Iberia." *Journal of Archaeological Science* 44: 76–90. https://doi.org/10.1016/j.jas.2014.01.018.

Lyman, R. L. 1994. *Vertebrate Taphonomy*. Cambridge University Press. https://doi.org/10.1017/CBO9781139878302.

Marean, C. W., Y. Abe, P. J. Nilssen, and E. C. Stone. 2001. "Estimating the Minimum Number of Skeletal Elements (MNE) in Zooarchaeology: A Review and a New Image-Analysis GIS Approach." *American Antiquity* 66: 333–348. https://doi.org/10.2307/2694612.

Margalida, A. 2008a. "Bearded Vultures (*Gypaetus barbatus*) Prefer Fatty Bones." *Behavioral Ecology and Sociobiology* 63: 187–193. https://doi.org/10.1007/s00265-008-0649-6.

Margalida, A. 2008b. "Presence of Bone Remains in the Ossuaries of Bearded Vultures (*Gypaetus barbatus*): Storage or Nutritive Rejection?" *Auk* 125: 560–564. https://doi.org/10.1525/auk.2008.07124.

Margalida, A., and J. Bertran. 2000. "Breeding Behaviour of the Bearded Vulture *Gypaetus barbatus*: Minimal Sexual Differences in Parental Activities." *Ibis* 142: 225–234. https://doi.org/10.1111/j.1474-919x.2000.tb04862.x.

Marín Arroyo, A. B., P. Fosse, and J.-D. Vigne. 2009. "Probable Evidences of Bone Accumulation by Pleistocene Bearded Vulture at the Archaeological Site of El Mirón Cave (Spain)." *Journal of Archaeological Science* 36: 284–296. https://doi.org/10.1016/j.jas.2008.09.007.

Marín-Arroyo, A. B., and A. Margalida. 2012. "Distinguishing Bearded Vulture Activities Within Archaeological Contexts: Identification Guidelines." *International Journal of Osteoarchaeology* 22: 563–576. https://doi.org/10.1002/oa.1279.

Milchev, B., N. Spassov, and V. Popov. 2012. "Diet of the Egyptian Vulture (*Neophron percnopterus*) After Livestock Reduction in Eastern Bulgaria." *North-Western Journal of Zoology* 8: 315–323.

Ogada, D. L., M. E. Torchin, M. F. Kinnaird, and V. O. Ezenwa. 2012. "Effects of Vulture Declines on Facultative Scavengers and Potential Implications for Mammalian Disease Transmission." *Conservation Biology* 26: 453–460. https://doi.org/10.1111/j.1523-1739.2012.01827.x.

Parkinson, J. A., T. W. Plummer, and R. Bose. 2014. "A GIS-Based Approach to Documenting Large Canid Damage to Bones." *Palaeogeography, Palaeoclimatology, Palaeoecology* 409: 57–71. https://doi.org/10.1016/j.palaeo.2014.04.019.

Pokines, J. T., S. E. Baker, and C. Pollock. 2021. "Avian Taphonomy." In *Manual of Forensic Taphonomy*, 581–604. CRC Press. https://doi.org/10.4324/9781003171492-16.

Robert, I., and J. W. F. Reumer. 2009. "Taphonomic Reinterpretation of a Bone Sample of Endemic Pleistocene Deer From Crete (Greece): Osteoporosis Versus Regurgitation." *Palaeodiversity* 2: 379–385.

Robert, I., and J.-D. Vigne. 2002a. "Bearded Vulture *Gypaetus barbatus* Contributions to the Constitution of Two Different Bone Assemblages: Modern Reference Data and an Archaeological Example in Corsica." *Acta Zoologica Cracoviensia* 45: 319–329.

Robert, I., and J.-D. Vigne. 2002b. "The Bearded Vulture (*Gypaetus barbatus*) as an Accumulator of Archaeological Bones. Late Glacial Assemblages and Present-Day Reference Data in Corsica (Western Mediterranean)." *Journal of Archaeological Science* 29: 763–777.

Sala, N., and J. L. Arsuaga. 2013. "Taphonomic Studies With Wild Brown Bears (*Ursus arctos*) in the Mountains of Northern Spain." *Journal of Archaeological Science* 40: 1389–1396. https://doi.org/10.1016/j.jas.2012.10.018.

Sala, N., J. L. Arsuaga, and G. Haynes. 2014. "Taphonomic Comparison of Bone Modifications Caused by Wild and Captive Wolves (*Canis lupus*)." *Quaternary International* 330: 126–135. https://doi.org/10.1016/j.quaint.2013.08.017.

Sanchis Serra, A., C. Real Margalef, J. V. Morales Pérez, et al. 2014. "Towards the Identification of a New Taphonomic Agent: An Analysis of Bone Accumulations Obtained From Modern Egyptian Vulture (*Neophron percnopterus*) Nests." *Quaternary International* 330: 136–149. https://doi.org/10.1016/j.quaint.2013.10.047.

Sanz, M., and J. Daura. 2023. "Estudios Actualísticos de Quebrantahuesos en el Parque Nacional de Ordesa y Monte Perdido y su Aplicación a la Arqueología." In *VIII Jornada de investigación del Parque Nacional de Ordesa y Monte Perdido*, 104–112.

Sanz, M., J. Daura, A. M. Costa, and A. C. Araújo. 2023. "The Characterization of Bearded Vulture (*Gypaetus barbatus*) Coprolites in the Archaeological Record." *Scientific Reports* 13: 57. https://doi.org/10.1038/s41598-022-25288-x.

Schoville, B. J., and E. Otárola-Castillo. 2014. "A Model of Hunter-Gatherer Skeletal Element Transport: The Effect of Prey Body Size, Carriers, and Distance." *Journal of Human Evolution* 73: 1–14. https://doi.org/10.1016/j.jhevol.2014.06.004.

Seguin, J., J. Torre, and V. Bretagnolle. 2010. "Distribution, Population Size and Breeding Parameters in the Insular Population of Bearded Vultures *Gypaetus barbatus* of Corsica Over 28 Years." *Bird Study* 57: 361–368. https://doi.org/10.1080/00063651003716754.

Stavrova, T., A. Borel, C. Daujeard, and D. Vettese. 2019. "A GIS Based Approach to Long Bone Breakage Patterns Derived From Marrow Extraction." *PLoS ONE* 14: e0216733. https://doi.org/10.1371/journal.pone.0216733.

Stiner, M. C. 1994. *Honor Among Thieves: A Zooarchaeological Study of Neandertal Ecology*. Princeton University Press.

Stiner, M. C., N. D. Munro, and M. Sanz. 2012. "Carcass Damage and Digested Bone From Mountain Lions (*Felis concolor*): Implications for Carcass Persistence on Landscapes as a Function of Prey Age." *Journal of Archaeological Science* 39: 896–907. https://doi.org/10.1016/j.jas.2011.10.020.

Thibault, J.-C., J.-D. Vigne, and J. Torre. 1993. "The Diet of Young Lammergeiers *Gypaetus barbatus* in Corsica: Its Dependence on Extensive Grazing." *Ibis* 135: 42–48. https://doi.org/10.1111/j.1474-919X.1993.tb02808.x.

Valensi, P., E. Crégut-Bonnoure, X. Margarit, and A. Defleur. 2011. "Découverte Exceptionnelle d'Un nid de Gypaète Barbu (*Gypaetus barbatus*) en Provence: Cas de l'Abri Protohistorique de la Baume du Houx (Plan d'Aups, Var, France)." *Comptes Rendus Palevol* 10: 49–59. https://doi.org/10.1016/j.crpv.2010.12.001.

Vigne, J. D.. 1988. "Les Mammifères Post-Glaciaires de Corse. Étude Archéozoologique." *Gallia Préhistoire*. Suppléments 26.

Vigne, J.-D. 1995. "Critères de Détermination des Onglons d'Artiodactyles de Corse. Pour Une Contribution à la Connaissance du Régime Alimentaire du Gypaète." *Revue Ecologie* 50: 85–92.

White, T. E. 1952. "Observations on the Butchering Technique of Some Aboriginal Peoples: I." *American Antiquity* 17: 337–338. https://doi.org/10.2307/276520.

Yravedra, J., S. De Los Terreros, M. Andrés, P. Fosse, and J. P. Besson. 2014. "Taphonomic Analysis of Small Ungulates Modified by Fox (*Vulpes vulpes*) in Southwestern Europe." *Journal of Taphonomy* 12: 37–67.