Dietary habits in the endangered Bearded Vulture *Gypaetus barbatus* from Upper Pleistocene to modern times in Spain: a paleobiological conservation perspective

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Summary

Although most Old World vulture species are declining or threatened in Asia and Africa, in Europe healthy vulture populations still exist. However, recent application of sanitary legislation that has greatly reduced the availability of animal carcasses is now a concern for conservationists. Until now, no studies have been undertaken to determine long-term dietary shifts in these species in Europe, but such studies are essential to optimising the resources invested in conservation and to anticipating the ecological needs of the target species. Here, we present a first attempt to examine the dietary variation in the Bearded Vulture *Gypaetus barbatus* from the late Pleistocene to the present day. Medium-size wild ungulates such as southern chamois *Rupicapra pyrenaica*, Spanish ibex *Capra pyrenaica*, red deer *Cervus elaphus* and roe deer *Capreolus capreolus* dominate the diet during the Pleistocene supporting the hypothesis that Bearded Vulture distribution was largely determined by the presence of such species. On the contrary, domestic species, such as sheep *Ovis aries* and goat *Capra hircus*, are the most common taxa in the diet in modern and historic periods. The actual dependence of the species on livestock, along with a restrictive sanitary legislation, threaten the conservation of this and other endangered avian scavengers in Europe. This new paleobiological conservation perspective confirms that efforts to establish a self-sustaining Bearded Vulture population should be enhanced by the widespread availability of medium-sized wild ungulates and by the presence of extensive and traditional grazing practices.

Introduction

Despite the great effort of conservation projects, several Old World vultures are still endangered, mainly due to previously unexpected threats, such as the ingestion of veterinary drugs (Green *et al.* 2006, Naidoo *et al.* 2009), the appearance of illegal poisoning practices (Hernández and Margalida 2008, 2009, Virani *et al.* 2011, Margalida 2012) and the restrictions on animal disposal put in place by sanitary authorities such as those imposed by the European Union with the appearance of bovine spongiform encephalopathy (Donázar *et al.* 2009, Margalida *et al.* 2010, 2012). Given this scenario, a detailed characterisation of the trophic ecology and long-term dietary shifts of these species must be an important tool for conservation projects based on the management of food resources (Newsome *et al.* 2010). In addition, this information can be especially important in understanding extinction risks (Dietl and Flessa 2011) and can provide relevant insights on the ability of the species to adapt to changing environmental conditions, allowing us to infer their possible future trends.

Although geo-historical data are essential to optimisation and application of successful conservation strategies, the majority of conservation-related research to date is based on short timescales

(Willis and Birks 2006, Froyd and Willis 2008, Dietl and Flesa 2011). To our knowledge, accurate, long-term studies on dietary shifts are only available for the New World California Condor *Gymnogyps californianus* (Chamberlain *et al.* 2005) and Bald Eagle *Haliaeetus leucocephalus* (Newsome *et al.* 2010). Here, we present the first attempt to reconstruct the long-term diet for the Bearded Vulture *Gypaetus barbatus* in Spain, a highly threatened bird of prey which is now the subject of great conservation efforts. The diachronic evolution of its diet from the late Pleistocene to the present day is characterised by means of the anatomical and taxonomical identification of faunal assemblages, as a result of the study of the bone remains recovered from a prehistoric nesting site, three historic nests (occupied between 1940–1950 located in Asturias, Murcia and Andalusia) and three modern sites (located in Catalonia).

The prehistoric distribution of the Bearded Vulture was probably similar to that of the 19th century (Arribas 2004) before massive human overpopulation at the end of the second half of the twentieth century. Unfortunately the current population of the Bearded Vulture has changed since then, with increasingly reduced distribution and population size due to direct persecution, mainly through poisoning and shooting (Hiraldo *et al.* 1979, Margalida 2010). Because this species delivers food directly to the nest, bone remains accumulated there are a direct reflection of its diet, allowing us to make comparisons between periods without apparent bias. The ultimate aim of the data presented here is to provide a new tool for the development of future management strategies and the optimisation of resources in vulture conservation policies.

Material and Methods

The study species

The Bearded Vulture is the only vertebrate with a bone-dominated diet. For each 100 g of bone, this species absorbs 387 KJ compared to the 440 KJ of a purely meat-based diet, suggesting that, due to its high fat content, this diet is energetically feasible (Houston and Copsey 2004). The European Bearded Vulture population is currently limited to the Pyrenees (France and Spain), Corsica, Crete and the Alps, with breeding populations estimated at only 170 territories in 2011 (A. M. unpubl. data).

Bone collection

Bones were gathered from modern and historical nests in Spain as well as from a Pleistocene cave where evidence of nesting Bearded Vultures has been identified (Figure 1). Although the study is based on different geographical regions, data obtained seems representative of the diet of the species in the Iberian Peninsula according to the literature (Hiraldo *et al.* 1979, Marín-Arroyo *et al.* 2009, Margalida 2010). El Mirón Cave (northern Spain; Marín-Arroyo *et al.* 2009), is located on a vertical cliff of limestone at Monte Pando (eastern Cantabria) and its entrance is a cornice along its walls overlooking the central vestibule at a considerable height. This is a suitable place for nests and could explain the eventual accumulation of bones below due to falling bones and nest decomposition. Additionally, historical bones were obtained from three ancient nests occupied by Bearded Vultures in southern (H1 and H2) and northern (H3) Spain during 1940–1950 (Margalida *et al.* 2009b). Finally, bones from three modern nests were collected during visits by one of the authors (A. M.), to three current sites in the Pyrenees during the summer of 2008 (M1, M2 and M3).

Regarding chronology, ungulate bone remains recovered at El Mirón Cave belong to a late Upper Pleistocene deposit dated between 14,000–10,000 BP (Marín-Arroyo *et al.* 2009). Only bones with digestive traces, similar to those observed in current experimental taphonomic studies with wild and captive Bearded Vultures were attributed to this species at this site (Marín-Arroyo and Margalida 2012). They were the result of long bone regurgitation together with hair and hooves, from which keratin cannot be easily digested, and the foot remains (metapodials plus
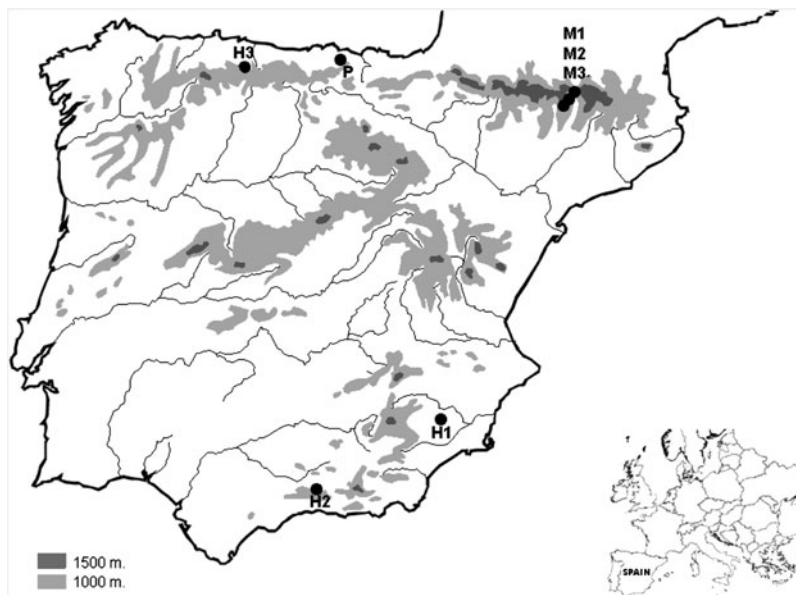
Figure 1. Study area showing the locality of the nest-sites in which bone remains were collected. Prehistoric (P), Historic (H1, H2 and H3) and Modern sites (M1, M2 and M3).

phalanges) attached to them. After a detailed taphonomic analysis, none of these regurgitated bones were identified as originating from carnivore activity as no gnawing marks were identified. In addition, they do not display any cut marks that could link them to human consumption (Marín-Arroyo 2010). It is likely, however, that the site may hold more fossils brought by Bearded Vultures but without distinctive features. As the cave was also alternately used by human groups in the past, in order to avoid any bias due to incorrect attribution, only the remains clearly identified as the product of Bearded Vulture activities have been used here.

Taxonomic identification

The prey remains collected from Pleistocene, historic and modern nests were identified with the help of osteological reference collections (Sociedad de Ciencias Aranzadi, San Sebastián, Spain and our own collections). Distinctive morphological features together with bone surface aspect and cortical thickness were used. Because mammals constitute 93% of the Bearded Vulture diet (birds 6% and reptiles 1%) and ungulates comprised 71% of the mammals identified ($n = 636$ prey items identified through direct observations; Margalida *et al.* 2009a), only ungulate bones were used in this analysis in order to avoid the probable underestimation of small prey items (e.g. birds, lagomorphs, carnivores and rodents) due to conservation bias as a consequence of the fragility of their bones (Margalida *et al.* 2007). Concerning the possible biases related to the differential taphonomic preservation of anatomical parts, we previously tested whether the differences in bone density could influence their conservation over time. No relationship between each anatomical element and its bone density value (Lam *et al.* 2003) was found in any of the periods and nests considered (Mann-Kendall test $P > 0.05$ for all samples). Bone remains have been grouped into four taxonomic categories according their size: 1) cow *Bos* spp. (*primigenius/ taurus*) and horse *Equus caballus*; 2) red deer *Cervus elaphus* and wild boar *Sus scrofa* and pig *Sus scrofa* var. dom. 3) Spanish ibex *Capra pyrenaica*, southern chamois *Rupicapra pyrenaica*, roe deer *Capreolus capreolus*, 4) sheep *Ovis aries* and goat *Capra hircus*.

Anatomical classification

To analyse temporal variations in the presence of the anatomical parts represented within the diet, bones were also placed into six anatomical categories: head (including skull, mandible, atlas and axis), ribcage (ribs, sternum and scapula), vertebral column (cervical, thoracic and lumbar vertebrae plus pelvis and sacrum), forelimb (humerus, radius/ulna, carpals and metacarpal), hind limb (femur, tibia, tarsals and metatarsals) and phalanges. This classification takes into account not only the typical anatomical connection but also similar dietary utility in terms of amount of bone grease (Emerson 1990), its percentage of oleic acid (Binford 1978) and the length of the element; see Marín-Arroyo and Margalida (2012) for Bearded Vulture Bone Utility Index.

Statistical analyses

Chi-squared test were used to discern differences among taxonomic and anatomical preferences over time. Frequencies were compared through contingency tables and values are presented as means ± SD.

Results

Taxonomic variation in the diet

We found significant differences in dietary composition between modern nests ($\chi^2_8 = 24.28$, $P = 0.002$) and historic nests ($\chi^2_8 = 21.58$, $P = 0.006$). To avoid pseudo-replication problems, we tested individual nest differences (modern and historic nests) with respect to prehistoric times and in all cases we found significant differences in the diet composition ($P < 0.0001$ in all cases). Domestic species, such as *Ovis/Capra*, were the most common taxa in the diet in modern ($71.47 \pm 2.75\%$, $n = 377$ remains) and historic periods ($74.43 \pm 15.52\%$, $n = 56$), whereas in the prehistoric period ($n = 270$) the diet was based principally on medium-sized wild ungulates such as southern chamois/roe deer/Spanish ibex (65.2%) and red deer (34.8%) (Figure 2a). In spite of these differences in taxonomic representation between periods, which are obviously due to the absence of domestic species during Pleistocene, the medium mammal size is common to all periods.

Anatomical variation of the skeletal parts selected

The anatomical composition of the diet (Figure 2b) showed differences between the skeletal parts found in modern nests ($\chi^2_{10} = 150.36$, $P < 0.0001$) and in historic ones ($\chi^2_{10} = 38.48$, $P < 0.0001$). To avoid pseudo-replication problems, we tested individual nest differences with respect to prehistoric times and in all cases (individual data of modern M1, M2 and M3 vs prehistoric and individual data of historic H1, H2 and H3 vs prehistoric) we found significant differences in anatomical composition ($P < 0.0001$ in all cases) showing an important trend towards metapodials + phalanx remains in prehistoric times, whereas in historic and modern nests the skeletal profiles are more heterogeneous (Figure 2b).

Discussion

Based on their dietary habits, our results suggest that the distribution of European Bearded Vultures from the Pleistocene to the present day is still linked to areas with high availability of medium-sized ungulate carcasses. The dietary shift from wild to domestic species found in historical and modern times is a direct consequence of the reduction of the former in the ecosystem when they were replaced by the latter (Zeder 2008). During prehistoric times, depending on the topographic environment, red deer, Spanish ibex and southern chamois were the most representative species in the diet of Bearded Vultures in Spain. The animal remains found in numerous European prehistoric sites, either with an anthropogenic or paleontological origin, show
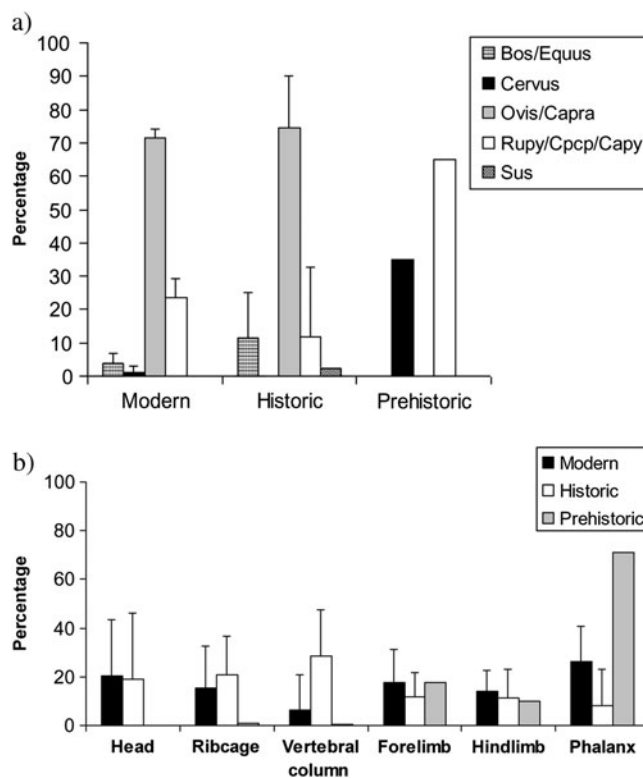
Figure 2. Percentage (± SD) of the different taxonomic (a) and anatomical (b) remains identified in nest sites occupied by bearded vultures according to the three study periods. Bos/Equus: *Bos taurus* and *Equus caballus*; Ovis/Capra: *Ovis aries* and *Capra hircus*; Rupy/Cpcp/Capy: *Rupicapra pyrenaica*, *Capreolus capreolus* and *Capra pyrenaica*.

that these medium-sized mammals were very abundant in the paleoenvironment and profusely consumed both by hunter-gatherer groups and carnivores, thus providing a constant source for Bearded Vulture scavenging (Marín-Arroyo 2009a). The diet of this scavenger would then have been mainly influenced by the availability of animal resources within its territory, for example red deer and Spanish ibex in the case of El Mirón, a cave located in a rocky environment but also close to broad alluvial plains in the Asón Valley, eastern Cantabria (Marín-Arroyo 2009c). Conversely, in historic and modern nests, sheep and goats were the predominant species. The switch to domestic ungulate consumption observed in historical and modern times reflects the reduction of wild ungulate populations due to hunting and the simultaneous expansion of livestock herding throughout Europe around 10,000–9,000 years BP. The direct persecution of predators (i.e. wolf *Canis lupus*, brown bear *Ursus arctos*; Martínez-Abraín *et al.* 2009) probably also reduced carcass availability of wild ungulates. Thus, the increase in domestic ungulate populations during the last century would have offered Bearded Vultures an abundant new source of medium-sized carcasses that would have allowed them to expand their habitat beyond northern and more mountainous refugia. However, despite the availability of large-sized mammal carcasses in historic and modern times, these were rarely consumed, which could be related to the bone weight and input obtained. Nevertheless, this fact also led them to depend on livestock.

   Taking into account the importance of medium-sized ungulates in the diet of Bearded Vultures (Margalida *et al.* 2009a, 2010), our data also suggest that medium-sized wild ungulates probably dominated the diet of Bearded Vultures during the Upper-Pleistocene (62.6% of the bone

remains identified), a fact that has important implications for understanding the past geographical range of this species, as it supports the hypothesis that their abundance in certain mountainous areas was largely controlled by the presence of wild ungulates (Hiraldo *et al.* 1979, Hirzel *et al.* 2004, Margalida 2010). However, while our study is based on large and medium-sized ungulates (the main species in the diet of Bearded Vultures; Brown and Plug 1990, Thibault *et al.* 1993, Margalida *et al.* 2009a,b), small mammals can also be important to the species, principally during the breeding season (i.e. meat content to feed the chick, Margalida *et al.* 2005, 2009a). These results suggest that the Bearded Vulture is therefore quite specialised and thus highly sensitive to changes in the availability of the resources on which it relies.

Concerning the anatomical preferences, a significant trend towards the consumption of foot limb bones (extremity) remains has been observed. These skeletal parts are easier to transport, swallow and digest and have a higher oleic acid content (Morin 2007, Marín-Arroyo and Margalida, 2012), a fact that again agrees with a positive selection by Bearded Vultures in order to maximise energy balance (Margalida 2008, Margalida *et al.* 2009a). In prehistoric times this preference is even more intense, probably due to the greater availability of these skeletal elements as a result of human or carnivore discards after hunting, as feet are not very nutritional for them (Marín-Arroyo 2009c).

Apart from the topographic location where the nests were located, it should not be ignored that the inter-nest differences are probably also related to the extraction of remains by other vertebrate scavengers (e.g. corvids) that may profit from them (Margalida and Bertran 2003) and with subsequent taphonomic processes. Nevertheless, a more complete study with a large data set including other Pleistocene and historic nests situated in similar environments should be conducted.

Long-term dietary shifts have important implications for understanding the past distribution of the species and to optimise the development of conservation strategies (Chamberlain *et al.* 2005). Given the results obtained, conservation concerns related to the application of sanitary legislation that significantly reduces food availability provided by domestic carcasses, as have been discussed recently (Donázar *et al.* 2009, Margalida *et al.* 2010, 2011b, 2012), are well-founded. Regions with a limited availability of carcasses of medium-sized wild ungulates and the application of restrictive sanitary legislations that may reduce the number of domestic carcasses, can limit the presence of these species (Donázar *et al.* 2009, Margalida *et al.* 2010). Although the specialised diet of the species makes them less sensitive than other vultures that are more meat-dependent (Margalida *et al.* 2011a, Margalida and Colomer 2012), efforts to establish a self-sustaining Bearded Vulture population may be enhanced by the widespread availability of wild ungulates as an additional food source, and by the presence of extensive and traditional grazing practices (Thibault *et al.* 1993, Margalida *et al.* 2009a,b, 2011a).

Acknowledgements

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