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PRESENCE OF BONE REMAINS IN THE OSSUARIES OF BEARDED VULTURES (*GYPAETUS BARBATUS*): STORAGE OR NUTRITIVE REJECTION?

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Abstract.—Ossuaries, or bone-breaking sites, are used by Bearded Vultures (*Gypaetus barbatus*) to prepare and store bone remains. The different nutritive values of different parts of the skeleton and bones and the fact that many remains stay in the ossuary for long periods without being consumed suggest that they may have another use besides storage. I tested whether the presence of bone remains in ossuaries may result from selection ("nutrient concentration" hypothesis) and rejection of bone remains on the basis of nutritive value. Of the remains found at the study sites, 84.9% belonged to medium-sized ungulates, 11.6% to large mammals, 2.5% to carnivores, and 1% to Suidae. Bone remains found were principally scapulas (14.9%), vertebrae (13.2%), skulls (12.5%), tibias (10.7%), mandibles (9.3%), ribs (8.3%), and humeri (7.2%). The larger proportion of less-nutritious skeletal parts (i.e., containing less oleic acid) and the significantly smaller proportion of distal epiphyses, which are more nutritious, support the nutrient concentration hypothesis. On the other hand, the scarce presence of remains of large mammals and Suidae and the high presence of scapulae, vertebrae, and skulls suggest that handling efficiency can also influence food selection. Bone selection based on nutritive value may allow Bearded Vultures to optimize parental foraging effort and maximize fitness. *Received 12 July 2007, accepted 31 October 2007.*

Key words: Bearded Vulture, bone-breaking sites, food preferences, foraging theory, *Gypaetus barbatus*, nutritive selection, ossuaries.

Presencia de Restos Óseos en Rompederos de *Gypaetus barbatus*: ¿Almacenaje o Rechazo Nutritivo?

Resumen.—Los rompederos son lugares utilizados por *Gypaetus barbatus* para romper, preparar o almacenar los restos óseos. El diferente valor nutritivo de las diferentes partes anatómicas del esqueleto y de los huesos, y el hecho de que los huesos puedan permanecer meses sin ser consumidos, sugieren la posibilidad de que exista una explicación alternativa al almacenaje. En este artículo evalúo si la presencia de restos óseos en los rompederos puede ser resultado de una selección previa (hipótesis de la concentración de nutrientes) y si el rechazo de algunos restos óseos podría ser consecuencia de su escaso valor nutritivo. El 84.9% de los restos encontrados pertenecieron a ungulados de tamaño medio, el 11.6% a mamíferos de gran tamaño, el 2.5% a carnívoros y el 1% a Suidae. Los restos óseos encontrados fueron principalmente escápulas (14.9%), vértebras (13.2%), cráneos (12.5%), tibias (10.7%), mandíbulas (9.3%), costillas (8.3%) y húmeros (7.2%). La asociación negativa entre una mayor proporción de partes esqueléticas con menor contenido nutritivo (i.e., menor contenido de ácido oleico), así como la menor proporción significativa de epífisis distales (más nutritivas), apoyan la hipótesis de la selección nutritiva. Por otro lado, la escasa presencia de restos de grandes mamíferos y Suidae y la gran presencia de escápulas, vértebras y cráneos sugieren que la eficiencia en la manipulación también puede influir la selección de los huesos. La selección nutritiva de los huesos puede permitir a *Gypaetus barbatus* optimizar el esfuerzo parental de forrajeo y maximizar su adecuación biológica.

In several species that catch and consume their food, prey processing has been considered an important behavior, in which the animal removes parts of the carcass that could hinder digestion or waste digestive energy or that, as a consequence of their morphology, could damage the digestive tract (Kaspari 1991). This behavior allows these species to optimize both the energy gained from food and the time spent foraging (Kaspari 1991, Ydenberg 1998).

The Bearded Vulture (*Gypaetus barbatus*) is a bone-eating species that inhabits mountainous regions of Europe and Africa (Hiraldo et al. 1979). Its diet is bone remains of medium-size ungulates (see Margalida et al. 2007); therefore, one of the characteristics of its behavioral ecology is the preparation of the remains in the ossuaries, or bone-breaking sites (Boudoint 1976, Margalida and Bertran 2001). These are rocky surfaces where Bearded Vultures deliberately drop bones, and entire animal carcasses, from a height while flying to break up the remains. This behavior allows the bird to fragmentize bones that, because of their length or width, cannot be swallowed, and to break up the different parts of a skeleton. Apart from the breaking or separation of bone remains, ossuaries are also used to store bone remains

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(Margalida and Bertran 2001). However, despite the apparent storage function, many remains are not used up and stay in the ossuary for as long as several months (A. Margalida pers. obs.) without being consumed. Bone remains that are left in ossuaries may be used principally by conspecifics or mammals (Margalida and Bertran 2003). Therefore, the costs involved in this food strategy may be reduced if the bird that dropped the bones selected certain parts to eat and others to reject on the basis of their nutritive value. The "nutrient concentration" hypothesis posits that removal of parts of prey maximizes the rate at which nutrients are concentrated in the remaining prey (Kaspari 1991). It is unknown whether bone remains present in the ossuaries after chick rearing have been rejected because of their low nutritive value.

Given that one function of the ossuary is to break up bone remains that are too large to swallow whole, if the nutrient concentration hypothesis is supported, then the remains that are found there should be those, such as ribs, skulls, and scapulas, of low nutritive value (i.e., low percentage of oleic acid). Of the long bones (e.g., femurs, humeri, tibias), parts of which are found in the ossuaries, the missing (selected) portion should be the distal parts and the remaining (rejected) portion the proximal parts, given that the former are more nutritious (Binford 1978). My objectives in the present study were to analyze the bone remains in ossuaries and discuss whether their typology supports the nutrient concentration hypothesis.

Methods

Study area.—The study was conducted in the Catalonian Pyrenees of northeastern Spain. During observations of nesting sites in studies of this species' breeding behavior between 1995 and 2000 (egg laying takes place in December–February and, after 52–54 days of incubation and an average of 120 days of chick rearing, the chicks abandon the nest in June–August; see Margalida and Bertran 2000, Margalida et al. 2003), I noted the ossuaries used by Bearded Vultures to prepare their food. Each pair used one or two ossuaries regularly, despite having various ossuaries available to them in the territory (Margalida and Bertran 2001). The average (± SD) elevation of the ossuaries was 1,497.0 ± 206.2 m ($n = 10$), with the average elevation by territory being 1,528.0 ± 222.1 (range: 1,280—1,850 m; $n = 5$). The mean altitude of nests was 1,497.0 ± 262.6 m (range: 1,283–1,940; $n = 5$). The average distance between an ossuary and the nearest nest of the pair was 1,304 ± 1,582 m (range: 70–4,300 m; $n = 10$).

Data collection.—The remains present in 10 ossuaries belonging to five territories were collected at the end of the breeding season (August of 1995 and 1997–2000). Bone splinters are difficult to identify and are occasionally ingested by Eurasian Griffon Vultures (*Gyps fulvus*) or other carnivores as a source of calcium (Bertran and Margalida 1997, A. Margalida unpubl. data). Therefore, to avoid biases, only bone remains >5 cm in length were considered.

Remains were identified with the help of reference collections (Muséum National d'Histoire Naturelle de Paris) and identification guides (Gállego 1987, Gállego et al. 1992). To avoid biases related to the overestimation of large bone remains, for each group of remains collected in the ossuaries, the minimum number of individuals present for each prey item was calculated (Poplin 1976).

The remains were grouped into four taxonomic categories: medium-sized ungulates, including domestic sheep (*Ovis aries*), Pyrenean Chamois (*Rupicapra pyrenaica*), and domestic goats (*Capra hircus*); large ungulates such as domestic cow (*Bos taurus*) and horse (*Equus caballus*); pigs (Suidae), including domestic pigs (*Sus scrofa* var. dom.) and Wild Boar (*Sus scrofa*); and carnivores, including Red Fox (*Vulpes vulpes*) and domestic dog (*Canis lupus familiaris*). For comparisons of the diversity of identified prey, only the four territories with the highest number of identified prey were considered.

Estimation of bones' nutrient content.—The bones (ribs) used in a study of bone digestion in Bearded Vultures had a mean water content of 32% and dry bone weight composed of 54% mineral content and 46% organic content (Houston and Copsey 1994). Brown (1988) showed that, because of their high fat content, mammal bones have higher energy content than muscle tissue (6.7 vs. 5.8 kJ g^{-1}, respectively). In addition, Houston and Copsey (1994) showed that for every 100 g of bone, Bearded Vultures absorbed 387 kJ, compared with 440 kJ on a purely meat-based diet, which suggests that a bone-based diet, because of its high fat content, is energetically almost as valuable as a meat-based diet. Because quantitative analyses of bone tissue from different anatomical parts of *O. aries* showed differences in the percentage of oleic acid (white bone grease content), I used this grease index value as a measurement of nutrient content of bones. "Bone grease" is the term used for the fat and grease contained in the bone tissue itself (Binford 1978). I used Binford's (1978) calculations for skeletal elements of a 90-month-old sheep; in that study, samples of tissue were extracted from the cancellous zone, a quantitative analysis was performed analyzing bone-marrow samples, and the results were reported as percentage of oleic acid in the total fat make-up of the sample. The grease indices for sheep and caribou calculated by Binford (1978) showed a linear and positive correlation ($r = 0.96$), which suggests that there is very little difference between species. Thus, we considered data obtained for sheep remains representative of all the species studied (principally wild and domestic ungulates). The proportion of oleic acid that each of the bones contain (Binford 1978) was used to compare with the proportion contained in the bone remains found in the ossuaries. In addition, the various anatomical parts found were grouped into three categories based on their oleic-acid content: <34% ($n = 9$ anatomical parts), 35–70% ($n = 9$), and >71% ($n = 7$) oleic acid. In assessing Bearded Vultures' selection of proximal or distal remains according to their relative nutritive contribution, only the parts belonging to long bones for which Binford (1978) provided data were considered (i.e., femur, humerus, tibia, ulna, radius, metacarpus–metatarsus).

For data analysis, the Spearman rank correlation was used to test the relationship between percentage of oleic acid and proportion of different bone remains found in ossuaries (Sokal and Rohlf 1995). One-way analysis of variance (ANOVA) was used to compare intergroup differences between the average percentage (log-transformed data) of bones found at ossuaries grouped by their percentage of oleic-acid content. Only the anatomical parts found in the ossuaries ($n = 25$ anatomical parts) were examined in this analysis. Chi-square tests with Yates correction were used to compare differences among territories and among anatomical parts of long bones.

Results

Of 205 bone remains gathered, 198 (96.6%) were identified to species. All remains were of mammals, 84.9% belonging to medium-sized ungulates (*O. aries, C. hircus, R. pyrenaica*), 11.6% to large mammals (*B. taurus, E. caballus*), 2.5% to carnivores (*C. l. familiaris, V. vulpes*, and Eurasian Badger [*Meles meles*]), and 1% to Suidae. After grouping the remains into the four taxonomic categories, no significant differences among territories were observed ($\chi^2 = 3.17$, df = 9, $P = 0.13$).

Of the identified bone remains (Fig. 1), 14.9% were scapulas, 13.2% vertebrae, 12.5% skulls, 10.7% tibias, 9.3% mandibles, 8.3% ribs, and 7.2% humeri. Other parts of the skeleton were each <5.4% of the total. A negative, significant correlation was found between the proportion of the anatomical parts and their oleic-acid content ($r_s = -0.59$, $n = 31$, $P < 0.001$; Fig. 1); that is, the remains at ossuaries had a lower nutritive value. When only the 25 anatomical parts found in the ossuaries were considered in the analysis, the results also showed significant differences ($r_s = -0.59$, $n = 25$, $P < 0.001$). The average percentages of these anatomical parts, grouped into the three categories, showed significant differences (ANOVA, $F = 6.19$, df = 2 and 24, $P = 0.0074$). The bone remains belonging to the category with less oleic-acid content (34%: 6.87 ± 1.07%) were the most abundant with respect to the second (35–70%: 3.12 ± 1.07%) and the third, most nutritive, category (>71%: 1.44 ± 1.21; Scheffé test, $P < 0.05$). With respect to the broken long bones, proximal epiphyses were found significantly more than expected, compared with distal epiphyses (75% vs. 25%, $\chi^2 = 8.00$, df = 1, $P = 0.0047$, $n = 60$).

Discussion

Bearded Vultures depend on food resources that appear in a spatially and temporally random manner. Their habitat is characterized by frequent adverse weather that makes finding bones difficult in terms of time and energy spent in foraging; for example, snow may cover the remains, making them especially hard to find. For a species with such restricted diets, storing food could be profitable and necessary for survival. Because bones remain edible 10× longer than soft tissues (Houston and Copsey 1994), Bearded Vultures are able to store bones at perches, nests, and ossuaries (Bertran and Margalida 1996, Margalida and Bertran 2003). Given that there is a risk of piracy by conspecifics or carnivores that visit these predictable sources of food, selection of the more nutritious remains would reduce the costs of food storage in ossuaries.

As central-place foragers, Bearded Vultures should benefit from processing a prey item before bringing it to their young, because this would reduce the energy required for carrying the food to the nest (Rands et al. 2000); for example, flight costs would be reduced by removal of parts that could increase drag (Pennycuick et al. 1988, Norberg 1995, Rands et al. 2000). The results of the present study suggest that bones of medium-size ungulates are selected (see also Brown and Plug 1990). Although bone size and species abundance may explain this selection, Bearded Vultures seem to avoid remains of large mammals because of their size and because they are likely more difficult to carry to the ossuaries for preparation and more difficult to swallow (Margalida and Bertran 1997). In addition, if the most nutritious parts are taken to the nest, and the preparation at the ossuaries allows for this selection,

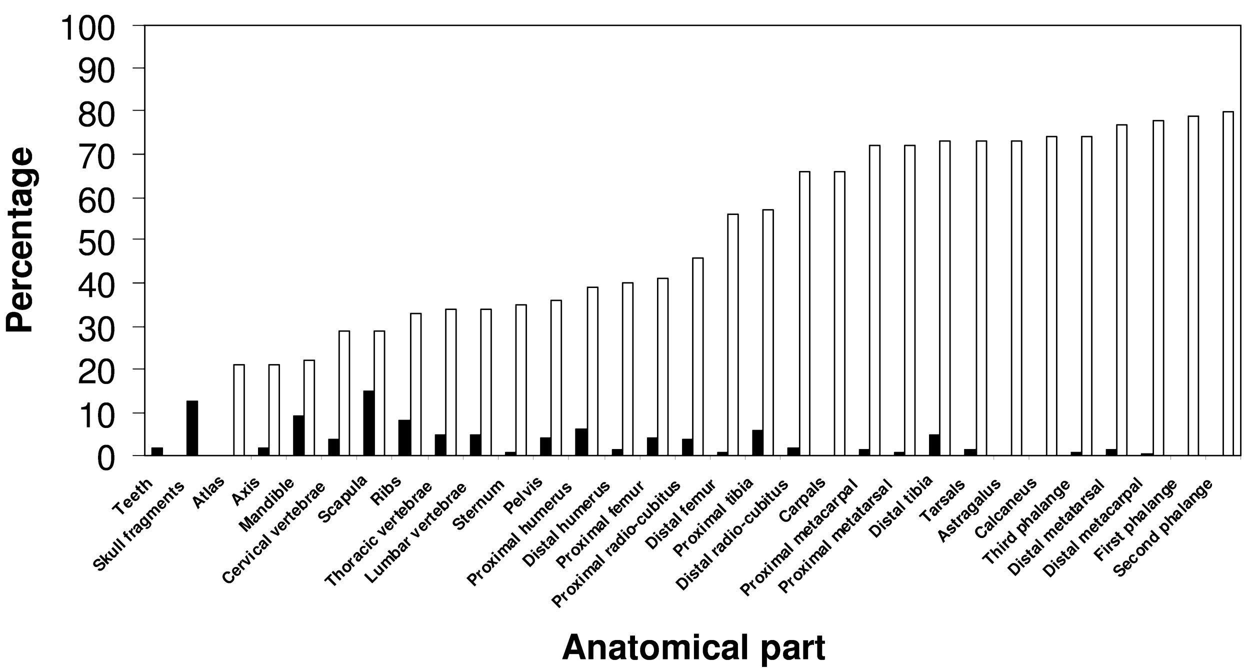

Fig. 1. Percentages of bone remains found in ossuaries (black columns) of Bearded Vultures in comparison with the percentages of oleic acid (white columns) extracted from the different anatomical parts (Binford 1978; for more details, see text).

this suggests that parental foraging effort is optimized and, thus, fitness is maximized (Schoener 1979, Stephens 1990).

North (1948) and Boudoint (1976), on the basis of anecdotal observations, reported finding more remains of proximal parts of bones than of distal parts at ossuaries. The negative association between the proportions of less-nutritious skeletal bone parts at the ossuaries and the significantly smaller proportion of distal epiphyses support the nutrient-concentration hypothesis. However, a possible explanation for this association could be the preparation cost and the decalcification process of proximal parts of long bones, which can take a lot of time and energy. For this reason, Bearded Vultures may prefer old and dried bones (that have lost ~30% of their weight) rather than fresh bones, because they are a heavy food that takes a long time to digest (Brown and Plug 1990, Houston and Copsey 1994). A comparison between bones taken to the nest and those found in ossuaries shows that the latter include significantly more scapulas, skull remains, and fragments of proximal portions of the long bones that are less nutritious (Margalida et al. 2007). Like insectivores and frugivores for which nutrient concentration is a common function of food preparation (Kaspari 1991), Bearded Vultures appear to select the most nutritious bones.

Despite such selection, the presence of bone remains of low nutritive value could also be related to the morphological characteristics of these bones and may have been stored because of the difficulty of ingesting them or the effort required to prepare them (i.e., handling efficiency). The adaptive behavioral and physiological differences with respect to other vulture species (Houston and Copsey 1994) suggest that the morphology, preparation, and ingestion of bones is not an important constraint for Bearded Vultures. Bearded Vultures ingest remains ≤25 cm long and ≤5 cm wide (Brown 1988, A. Margalida pers. obs.), but ingestion of scapulas, skulls, vertebrae, or ribs can also be complicated, apart from their meager nutrient content. Although Bearded Vultures apparently use the ossuaries to reduce the size of bone remains for ingestion and probably also to store food, the fact that many remains stay for long periods without being consumed suggests a possible rejection related to the time and energy that would have to be spent on their preparation. Although nutrient contents may explain bone selection, handling efficiency may also play a secondary role in food selection.

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