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Bearded Vultures (Gypaetus barbatus) Prefer Fatty Bones
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ORIGINAL PAPER

Bearded vultures (*Gypaetus barbatus*) prefer fatty bones

Antoni Margalida

Abstract In animal species, prey processing and the provisioning of nutrients are subject to several constraints related with finding, ingesting and processing food. In most bird species, these constraints are obvious as a consequence of food morphology. In the case of the bearded vulture (*Gypaetus barbatus*), in comparison with other species, its behavioural and physiological adaptations apparently allow this vulture to ingest bone remains irrespective of their morphology. Here, by comparing bones delivered to the nest to be consumed (selected) and remains found at an experimental feeding station and at bone-breaking sites or ossuaries (rejected), I tested whether bearded vultures are capable of choosing from among the various anatomical parts of an animal carcass in relation to their fatty acid content (nutrient concentration hypothesis), their size (width-reduction hypothesis) or both. The results suggest that bearded vultures prefer the fatty anatomical parts (with a high percentage of oleic acid) of an animal carcass regardless of bone length, although bone morphology as a consequence of handling efficiency or the ingestion process may also play a secondary role in food selection. The close association between the bones selected and their high fat value implies an optimisation of foraging time and of the increased energy gained from the food. This is in line with selective foraging to redress specific nutritional imbalances (nutrient concentration hypothesis) and, secondarily, the width-reduction hypothesis.

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Introduction

In the optimal foraging theory, the energy nutrient intake has been used as a surrogate for fitness, although several studies have found little support for such a relationship when fitness and energy intake maximisation are subject to constraint (Illius et al. 2002).

Although vertebrate carnivores optimise the rate of prey capture rather than the nutritional balance of their prey (Stephens and Krebs 1986), herbivores and omnivores adjust their food selection behaviour to regulate the intake of multiple nutrients (Raubenheimer and Simpson 1997; Berthound and Seely 2000). Invertebrate predators can also forage selectively for potential lipids in order to redress specific nutritional imbalances (Mayntz et al. 2005). In bird species, the costs and benefits of foraging behaviour differ when an individual ingests all the acquired food or when the resources are delivered to a mate, catch-site or to offspring (Ydenberg 1988). The costs associated with feeding are activities of food acquisition and the maintenance of the energy reserve once secured (Cuthill and Houston 1998). Prey processing allows to prepare food in ingestible portions, and to remove inedible parts that could hinder digestion, waste energy or affect the forager through toxicity or mechanical damage to the digestive tract to be removed (Davies 1977; Kaspari 1991). In central-place foragers obliged to transport a prey item rather than consume it at the place of capture, another benefit is the removal of excess mass, reducing the costs involved in carrying the prey (Ydenberg 1988).

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Prey handling and the provisioning of nutrients are subject to several constraints associated with the finding, ingesting and processing of food (Schoener 1971; Kaspari 1991). However, for bearded vultures (*Gypaetus barbatus*; Accipitridae), the use of bone-breaking sites or ossuaries to prepare their specialised food (Margalida and Bertran 2001), and the high concentration of acid-secreting cells in their stomach allow them to ingest and digest bones repeatedly within a 24-h period (Houston and Copsey 1994). Unlike other vultures, this species carries prey remains to the nest in its feet and bill and does not feed its young by regurgitation (Brown and Plug 1990; Margalida and Bertran 2000a). The adaptive behavioural and physiological differences with respect to other species suggest that the morphology, preparation and ingestion of bones cannot be considered as important constraints for bearded vultures. Recently, the study of remains found in ossuaries suggested an alternative explanation to bone storage, related to a possible rejection of some bone remains as a consequence of their low nutritive value (Margalida 2008). Nevertheless, in this study, it was suggested that the time and energy spent on their preparation (handling efficiency) may also play a secondary role in food selection. Two hypotheses that are not mutually exclusive may explain the selection of bone remains in the bearded vulture. According to the *width-reduction hypothesis*, prey preparation increases the ability to swallow prey. In addition, the *nutrient concentration hypothesis* posits that the removal of parts of prey maximises the rate at which nutrients are concentrated in the remaining food (Kaspari 1991). I hypothesise that if a nutritive selection of bones exists (bone-nutritive selection) in the bearded vulture, remains present in ossuaries and feeding stations should be the bones with the lowest fat content. On the contrary, bones selected to be delivered (and consumed) to the nest should be those with highest fat content. On the other hand, according to the width-reduction hypothesis, if anatomical parts are selected according to their size (bone-morphology hypothesis), remains present in ossuaries and feeding stations (not selected) should be the largest. On the contrary, bones selected to be consumed (i.e. delivered to the nest) should be small.

Here, by comparing bones (i.e. anatomical parts selected) delivered to the nest to be consumed of a medium-sized ungulate (sheep *Ovis aries*, considered the ideal prey item) and remains found in an experimental feeding station and ossuaries (i.e. anatomical parts rejected), I test whether bone selection among the various anatomical parts of an animal carcass may be explained by their fat content (nutritive value), their size (morphological selection) or both.

Materials and methods

The study species

The bearded vulture is a long-lived territorial vulture with a wingspan of 255–270 cm and a weight of 4–6 kg (Hiraldo et al. 1979; personal observation). This species nests on rocky cliffs and territorial adults' have main foraging areas of 250–700 km^2 (Brown 1988, Margalida, unpublished data) although home ranges may reach 7,468 km^2 (Brown 1988).

Clutch size is usually two eggs, but only one chick survives as a consequence of sibling aggression (Margalida et al. 2004). In monogamous pairs, both sexes invest equally in rearing the offspring, although males take a more active part in nest building and territorial defence, while tending the nest is more pronounced in females (Margalida and Bertran 2000a,b; Margalida and Bertran 2005). This species is the only vertebrate with a bone-dominated diet that can ingests bones up to 280 mm long and 40 mm wide without difficulty. The bearded vulture resolves the problem of ingesting large bones by the use of bone-breaking sites or ossuaries. These sites are rocky surfaces where the birds throw the remains from the air until they become sufficiently fragmented or disjointed to be swallowed (Boudoint 1976; Margalida and Bertran 2001). Unlike other vultures, this species carries prey remains to the nest in its feet and bill and does not feed its young by regurgitation (Brown and Plug 1990; Margalida and Bertran 2000a). Its diet is based on mammals (93%), birds (6%) and reptiles (1%; Margalida et al. 2009). Medium-sized mammals constitute 61% of their diet. The bearded vulture's diet seems to be based mainly on the bones of wild and domestic ungulates (Margalida et al. 2007, 2009). The bones have a mean water content of 32% and dry bone weight was made up of 54% mineral content and 46% organic content (Houston and Copsey 1994). Due to their high fat content, mammal bones have a higher energy content than muscle tissue (6.7 vs 5.8 kJ/g respectively, Brown 1988).

Study area, data collection and observation methods

The study was carried out in the Pyrenees (NE Spain). Between October 2003 and May 2004, I placed 39 sheep carcasses in an experimental feeding station. I observed the abandoned bone remains consumed by other scavenger species such as Eurasian griffon vultures (*Gyps fulvus*), Egyptian vultures (*Neophron percnopterus*) and common ravens (*Corvus corax*). Because bones can remain untouched for several months and bearded vultures may select old bones as a consequence of the low water content and of how easy they are to digest (Brown and Plug 1990), I

collected bones 30 months after their consumption by vultures in October 2006. Carrion consumed by Eurasian griffon vultures and other scavenger species allows the bearded vulture (breeding and non-breeding population) to take different anatomical parts without apparent difficulty (and sometimes the entire carcass is brought to the ossuaries where the bones are selected afterwards). I estimated the proportion of bones found in relation to the expected number (e.g., two scapulas and one skull is expected from each sheep) in order to standardise the data. As a second source of bone selection, I considered that the bones present in the ossuaries were those rejected by bearded vultures. Between 1994 and 2000, samples from ten bone-breaking sites ($n=5$ pairs) were collected after breeding. Each pair uses one or two ossuaries regularly despite having various ossuaries available to them in the territory (Margalida and Bertran 2001). As bone splinters were difficult to identify and occasionally ingested by Eurasian griffon vultures as a source of calcium (Bertran and Margalida 1997) or by other species such as carnivores (personal observation), only bone remains >5 cm were taken into consideration (see Margalida 2008). To avoid biases related with the overestimation of large bones remains, the minimum number of individuals present for each prey item was calculated (Poplin 1976). After determining bone characteristics at the feeding station and bone-breaking sites between 2000 and 2006, we video-monitored 12 breeding attempts (although data were available for six different pairs due to breeding failures or image interruption, Margalida et al. 2006) to document the diet of bearded vultures as a measure of selected bone-types.

Data obtained in bone-breaking sites (1994–2000) and prey items delivered to the nest observed (2000–2006) were not paired, because the pairs studied were different. Thus, the two sample sources analysed are independent, avoiding the possibility that remains present in the ossuaries were also brought to the nest.

To test whether bearded vultures choose the most nutritive/fatty bones, I compared the percentage of oleic acid that each bone contains (see white columns of Fig. 1) with the proportion of sheep bones available at a feeding station, at ten bone-breaking sites and brought to six nests. As quantitative analyses of bone tissue from different anatomical parts of sheep showed differences in the percentage of oleic acid (white bone grease content), I used this grease index value as a measurement of its nutritive content (see Binford 1978). Bone grease is the term used for the fat and grease contained in the bone tissue itself (Binford 1978). To do this, the Binford (1978) calculations were used for skeletal elements of a 90-month-old sheep in which samples of tissue were extracted from the cancellous zone and a quantitative analysis was

performed also analysing bone-marrow samples. The analysis was reported as the percentage of oleic acid in the sample's total fat content. In the Pyrenees, sheep may constitute >50% of their diet. I selected the 12 most representative bones that form the sheep's skeleton and those that were observed in their diet, to compare bone selection with the proportion of oleic acid the bones contain. Because there are differences between the fat content in distal and proximal parts of long bones, I calculated the average of each large bone summing two proportions of the distal part and the proximal divided by three. For example, the grease value of a proximal humerus is 39% and for a distal humerus 40% (Binford 1978), thus I used 39.7% as the average value. In the case of the vertebral column, I had to also calculate an average value due to the differences in oleic acid contents. For this item, because it was considered as a unit and values are similar (34% for lumbar, 29% for cervical and 34% for thoracic vertebrae) the average of the three values (32.33%) was considered as the total value. In the case of bones delivered to the nest, because bearded vultures may select specific items among the different remains, each bone item was considered as an independent sample. Thus, a posterior extremity delivered to the nest was considered as two independent items: the average of the three phalanges (77.67% of oleic acid because the first phalange contains 79%, the second 80% and the third 74%) and one tarsal (73%).

On the other hand, I measured the maximum length and width of each anatomical part hypothesising that if size is an important factor for bone selection (bone-morphology hypothesis), larger bones (with respect to their length and width) should be present in ossuaries and feeding stations and, on the contrary, small bones should be selected and delivered to the nests. As length and width measures were strongly correlated ($r_s=0.77$, $P=0.0017$, $n=12$), and yielded qualitatively similar results in the analyses, only length results are presented. The lengths of bone remains found in the feeding station were measured and, in addition, biometric data were obtained in the literature (Gállego et al. 1992).

Statistical analyses

The means of means for bone remains found and observed at each bone-breaking site and nest, respectively, from each territory were used as a sample unit to avoid pseudoreplication problems. The Spearman rank correlation coefficient was used to test the relationship between the proportion of rejected bone-types (i.e. found at ossuaries and at the feeding station) or of selected bone-types (i.e. delivered to nests) and their oleic acid content. Partial correlation values taking into account bone length were calculated in
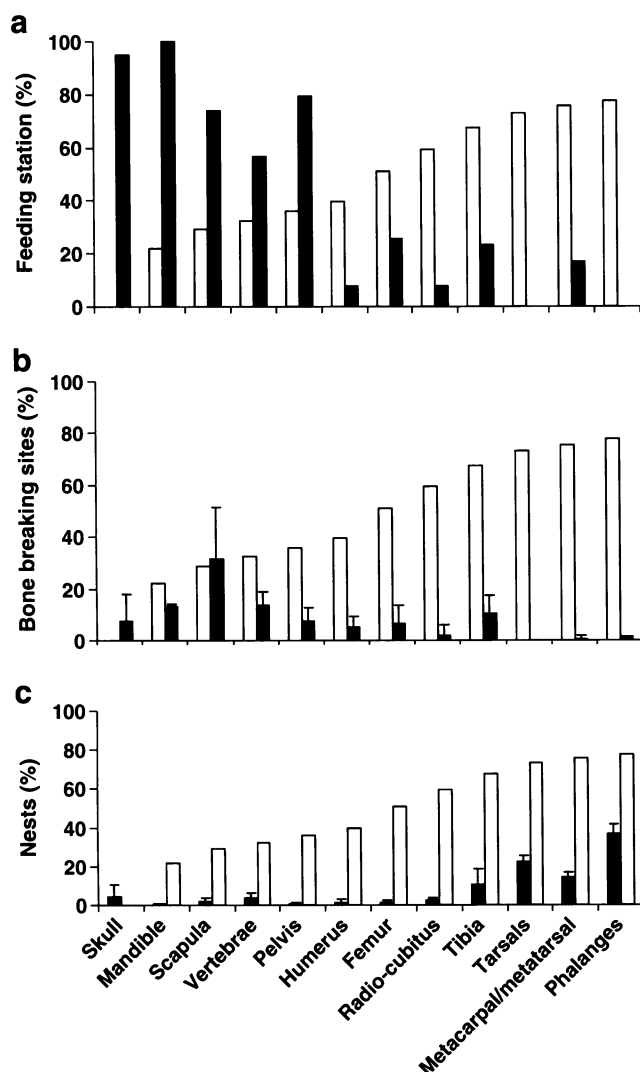
Fig. 1 **a** Proportion of the anatomical parts found in the feeding station with respect to the number of bones remaining as a percentage of those initially available. **b** Percentage (±1 s.d.) of bone remains found in bone-breaking sites. **c** Percentage (±1 s.d.) of bone remains brought to the nest. White bars show the percentage of oleic acid that each fresh bone contains (Binford 1978)

accordance with Sokal and Rohlf (1995) to discard the effect of bone morphology in the selection of different anatomical parts. Afterwards, observed frequencies of the four main categories selected (tibia, tarsal, metacarpal/metatarsal and phalanges) or avoided (skull, mandible, scapula and vertebrae) were compared with Chi-square contingency tables (Sokal and Rohlf 1995). To implement this test avoiding pseudoreplication problems, before, I tested whether interterritorial differences among the four categories existed (each collection of bones obtained in ossuaries and prey items delivered to the nest from a territory was considered as a sample unit). Because no significant differences were found among samples obtained

from the nests and from the ossuaries (chi-square $P>0.05$ for all of the samples considered), data was pooled.

Results

Between October 2003 and May 2004, I placed 39 sheep carcasses at the feeding station and collected the bones that were not consumed 2.5 years later. The proportion of skeletal parts found ($n=189$) and hence not selected by bearded vultures was significantly and negatively correlated with the oleic acid content ($r_s=-0.86$, $P=0.00016$, $n=12$; Fig. 1a). Partial correlation between the skeletal parts found and the percentage of oleic acid content, while controlling for the length of the bones was also significant ($r_s=-0.76$, $P=0.002$, $n=12$). However, there was a negative relationship between bone size and oleic acid content ($r_s=-0.67$, $P=0.0085$, $n=12$), suggesting that small (length) bones have more fatty acid content.

As some bones may be removed from the feeding station by other species such as mammals, the second source of evidence to demonstrate that bearded vultures choose the most nutritive bones was provided by the remains ($n=95$) found in bone-breaking sites ($n=10$). These sites are rocky surfaces where bearded vultures deliberately and repeatedly drop remains from the air until they become fragmented or disjointed. The negative and significant relationship ($r_s=-0.75$, $P=0.0025$, $n=12$) of bone remains found with the percentage of oleic acid, suggests again a reluctance by the bearded vulture to eat bones with low fat content (Fig. 1b). Partial correlation between skeletal parts found and the percentage of oleic acid content, while controlling for the length of the bones, was also statistically significant ($r_s=-0.53$, $P=0.05$, $n=12$).

I confirmed fatty bone selection by bearded vultures by installing micro-cameras in nests. Of the bone remains ($n=544$) delivered to nests ($n=6$), bearded vultures positively and significantly selected the bones with the highest fat content ($r_s=0.64$, $P=0.012$, $n=12$; Fig. 1c). Partial correlation between skeletal parts observed delivered to the nest and the percentage of oleic acid content, while controlling for the length of the bones was also significant ($r_s=0.66$, $P=0.0097$, $n=12$).

The four most abundant bones found at bone-breaking sites (skull, mandible, scapula and vertebrae), which accounted for 65.9% of the sample, were less nutritious and differed significantly from the proportion of the same bones brought to the nest ($\chi^2=13.73$, $df=3$, $P=0.003$). On the contrary, the four most abundant bones brought to the nest (tibia, tarsal, metacarpal/metatarsal and phalanges), which accounted for 86.8% of the sample, were the most nutritious and differed significantly from the proportion of

the same bones found at bone-breaking sites (χ^2=53.95, df=3, P<0.0001).

Discussion

This is the first examination of the bearded vulture's preferred feeding habits which takes into account the anatomical part selection of remains of a medium-sized ungulate (sheep), which is considered to be the most suitable prey to be swallowed by this species (Margalida et al. 2007, 2009). The results reveal a close association between selected bone-types and their nutritive value (fat content) regardless of bone size, although handling efficiency may also play a secondary role in this selection. In this respect, bearded vultures positively select bone remains of medium-sized ungulates (Brown and Plug 1990; Margalida et al. 2009). Skeletal parts of larger species (e.g., *Bos taurus*, *Equus caballus*) are probably discarded as a consequence of the costs of transporting (to the nest or ossuaries) and handling efficiency. In addition, temporal variation in food quality during the chick-rearing period seems to occur (Margalida and Bertran 2001) and this is related to the chick's limited ingestive capacity during the first month. Thus, among the bone remains selected to be delivered to the nest, meat content (for example in the skulls) may also influence this selection.

Although ossuaries are also used to store food, being a differentiating and advantageous trait with respect to feeding behaviour developed by other meat scavengers (Margalida and Bertran 2001), the results suggest a negative relationship between bone remains present and their nutritive content regardless of bone morphology. These results coincide with the analyses carried out at ossuaries considering all mammal remains and 31 different anatomical parts studied, suggesting that the presence of bones in ossuaries may be explained by a nutritive rejection rather than storage function (Margalida 2008).

The bearded vulture is a central-place forager that inhabits mountainous regions with low temperatures, which increases basal metabolic expenditure. Their diet, based on spatio-temporally unpredictable bone remains, implies costs associated with the time and effort involved in searching for food with apparently negligible nutritional content. Nevertheless, for every 100 g of bone, this species would absorb 387 kJ compared to 440 kJ on a purely meat-based diet, suggesting that a bone-based diet (due to its high fat content) is energetically almost as valuable as a meat-based diet (Houston and Copsey 1994). Thus, processing and selecting a food item before bringing it to the nest optimises foraging time and increases the amount of energy gained from the food. So, as has been suggested in other species

(Mayntz et al. 2005), bearded vultures forage to gain a balanced nutrient intake, rather than maximising the energy intake subject to constraints (Simpson and Raubenheimer 2001; Simpson et al. 1994). In this respect, the diversity of prey items delivered to the nest in this species (e.g., small mammals, micromammals, birds, reptiles, see Thibault et al. 1993, Margalida et al. 2009) supports this prediction. In addition, given that there is a risk of kleptoparasitism by conspecifics and heterospecifics that visit feeding stations and ossuaries (Margalida and Bertran 2003), prey preparation and the selection of the more fatty remains would influence the transport costs and decisions of central-place foragers (Cuthill and Kacelnik 1990; Rands et al. 2000), reducing the costs that this food strategy implies.

This is in line with the idea of selective foraging aimed at redressing specific nutritional imbalances through extraction of specific nutrients from a single prey item (Manytz et al. 2005). It also supports the nutrient concentration hypothesis, which posits that partial prey removal maximises the rate at which nutrients are concentrated in the remaining prey (Sherry and McDade 1982; Kaspari 1991). However, the existence of a negative relationship between bone size and fatty acid content make it hard to interpret the relations between these variables and the selection. In this sense, although bone morphology may also explain feeding preferences, the adaptive behavioural (use of ossuaries) and physiological characteristics of this species suggest that the ingestion of bones cannot be considered as important constraints. Thus, the width-reduction hypothesis probably plays a secondary role in food selection.

Finally, it seems necessary to point out that the results are conservative and the selection of nutritious bones is probably much stronger than the results obtained. This is due to two factors: firstly, if carnivorous or other birds take bones from the feeding place it is reasonable to assume that

Fig. 2 Bearded vulture choice a leg of sheep in a feeding station of the Spanish Pyrenees (© Antoni Margalida)

these bones will be the most nutritive. For this reason, the availability of fatty bones for the bearded vulture would be less than is supposed. Secondly, some of the nutritive bones found in ossuaries may be consumed by bearded vultures after the visits to collect samples.

These results have interesting conservation applications for the management of wild and captive populations of this threatened species, showing the significance of behavioural ecology for conservation biology (Caro 1998). The establishment of supplementary feeding points (Fig. 2) for the management of bearded vulture populations has been used in the Pyrenees (Heredia 1991) and Southern Africa (Brown 1990). However, these conservation measures have been undertaken without any previous analysis regarding the potential differences in the nutritive quality of the food. Because the conservation efforts for the population dynamics of bearded vultures should facilitate the geographic expansion (Margalida et al. 2008), the management of feeding stations could facilitate the dispersion of non-breeding individuals increasing the value of demographic parameters (Carrete et al. 2006) and favouring the maintenance of a metapopulation structure. In the future, supplementary feeding programmes to increase breeding success and facilitate geographic expansion could be optimised, with the most nutritive bones being delivered. In this respect, anatomical parts as tibias, tarsals, and extremities seem to be the most appropriate for the species.

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