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BONE DIGESTION AND INTESTINAL MORPHOLOGY OF THE BEARDED VULTURE

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ABSTRACT.—The diet of the bearded vulture (*Gypaetus barbatus*) consists largely of bone. Two experimental birds fed a diet of sheep ribs had a mean digestive efficiency of 50%, with most of the food being digested within 24 hr. The digestive tract of bearded vultures is not unusually long for a scavenging bird of its size, and does not contain a region for mechanical breakdown of the food. The stomach contains a high concentration of acid-secreting cells, and experiments with bone fragments in acid solutions suggested that this is the chief mechanism for decalcification. A bone diet may have a higher caloric content than an equivalent weight of soft tissues. The ecological consequences of this unusual diet are that this species is able to survive in areas with a very low availability of carcasses.

KEY WORDS: *bearded vulture; bone digestion;* Gypaetus barbatus; *intestinal morphology.*

Digestión de huesos y morfología intestinal de *Gypaetus barbatus*

RESUMEN.—La dieta de *Gypaetus barbatus* consiste esencialmente de huesos. Dos individuos experimentales se sometieron a una dieta de huesos de oveja, con un promedio de eficiencia digestiva del 50%, donde la mayoría del alimento llegó a digerirse en 24 h. El tracto digestivo de *G. barbatus* no es inusualmente largo para un carroñero de su tamaño y no contiene una región para la trituración mecánica del alimento. El estómago contiene una alta concentración de células secretoras de ácido, y experimentos con fragmentos en soluciones ácidas sugieren que este es el principal mecanismo para la descalsificación. Una dieta de huesos puede tener un mayor contenido calórico que un peso equivalente de tejidos blandos. Las consecuencias ecológicas de esta dieta inusual, serían que esta esta especie podría sobrevivir en áreas con muy baja disponibilidad de carroña.

[Traducción de Ivan Lazo]

The bearded vulture (*Gypaetus barbatus*) is a scavenger on the carcasses of large mammals in mountain regions in Africa, Asia, and Europe. It is unusual in that it eats bones. Small bones are swallowed whole and larger ones are dropped repeatedly onto rock slabs to break them into small enough fragments to be swallowed (Huxley and Nicholson 1963, Brown 1988). Several studies recently have shown that bone is not just an occasional food item, but the predominant food of the bearded vulture. Bone forms 70–90% of all food items (Hiraldo et al. 1979, Cramp and Simmons 1980, Brown and Plug 1990). Even owl pellets are eaten for their bone content (Heredia et al. 1990). Brown and Plug (1990) showed that if wild bearded vultures were presented with a choice of bone items and meat, they would select the bone, and old, dried bones significantly more frequently than fresh bones. Some mammalian carnivores, notably the spotted hyena (*Crocuta crocuta*), can also digest bone, but this forms only a small proportion of their normal diet (Kruuk 1972). The bearded vulture is the only vertebrate known to have a diet consisting largely of bone. We present here preliminary results from feeding trials to determine the digestive efficiency of bearded vultures on this unusual diet, and the time they required for digestion. We also carried out postmortem examinations to consider whether the

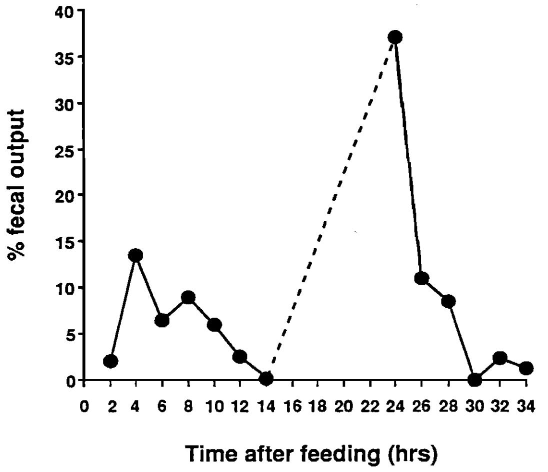

Figure 1. The time of fecal production from a pair of bearded vultures after ingestion of a bone meal.

intestine of the bearded vulture showed any specializations, and finally we speculate on the ecological implications of their diet.

METHODS

Feeding trials were carried out on two adult bearded vultures housed in the Research Zoo of Tel Aviv University, Israel in September 1992. It was not possible to separate the pair; all results presented here are mean values for the two. The cage floor was lined with sheeting to allow total fecal collection. A weighed quantity of 4-cm lengths of sheep rib bones was provided each afternoon and removed the following morning. A control sample of bone was also left outside the cage, to correct for dehydration of the bone samples left in the cage. All uneaten bone fragments were weighed and corrected for water loss to determine wet weight of bone eaten. A sample of the bone diet was dried at 70°C to constant weight to determine mean water content. This figure was used to calculate dry food intake. Bone samples were then ashed in a furnace at 535°C and ash weight used to determine mineral content of the diet. Organic content was derived from weight loss during ashing. All feces were collected daily, separated from uric acid material, and dried to constant weight at 70°C. Percent digestive efficiency was calculated as 1 − total dry weight feces/total dry weight bone eaten × 100. Four feeding trials were conducted over 13 d. Birds were deprived of food for 24 hr before the start of each trial.

The digestion time for food was recorded by starving the birds for 48 hr, providing them with food at 0630 H, and removing all uneaten food after they had finished feeding. The birds were then observed continuously and the time of all fecal production noted. Feces were collected and dried at 70°C. Birds were not fed again until 24 hr after the last appearance of fecal material. For security reasons, fecal collections could not be made at night.

The form in which calcium was present in the feces was investigated using X-ray diffraction analysis using Fe-filtered Co k radiation at scanning speed 2 θ min and range 4–64 2θ. The effects of pH and time on the rate of bone decalcification was investigated. Pieces of sheep rib bone from mature animals, as used in the feeding trials, were placed in hydrochloric acid solutions, buffered with N sodium acetate (Hale 1953), at pH 0.8, 1.1, and 1.5. The pHs used were within the range of acidity recorded from the stomachs of other raptor species (Herpol 1967, Duke et al. 1975). Solutions were maintained at 40°C in a water bath. The pH was checked every few hours and the solution replaced if necessary. The weighed bone pieces were each placed in individual vials and maintained there for 6, 12, 24, or 48 hr, after which time excess liquid was removed with paper towelling. Bone pieces were then reweighed, dried to constant weight at 70°C, and ashed in a furnace at 525°C for 24 hr Five bone samples were used for each of the experimental treatments. We also simulated the digestive effect of combined acid and pepsin, using commercial porcine pepsin solutions in the same range of pH conditions and the time periods outlined above.

The intestinal morphology of two bearded vultures was examined in postmortem examinations. The birds died in captivity, and had been part of the breeding program for the reintroduction of bearded vultures into the Alps (Frey and Walter 1989). Samples of alimentary tract were prepared for histological examination with Mallory, haematoxylin/eosin, and periodic acid-Schiff/alcean blue stains (Gurr 1962).

RESULTS

The rib bones used in the feeding trials and the decalcification study had a mean water content of 32% ± 1.8 (SE, $N = 12$), and dry bone weight was composed of 54% ± 1.7 (SE) mineral content and 46% ± 1.7 (SE) organic content. The mean digestive efficiency, as measured from total collection of fecal material, was 49.8% ± 1.3 (SE). The digestion time for food could, unfortunately, only be measured on one occasion, when the birds ate 146 g of bone. Most fecal production occurred within 24 hr after feeding (Fig. 1). Unfortunately, it was not possible to be with the birds overnight to record when the peak fecal production occurred. Virtually all fecal material was ejected within a few hours of dawn, because fecal material was not dehydrated when collected at 0600 H. Dehydration would have occurred in the dry air conditions in Tel Aviv if feces had been produced early in the night.

The dimensions of the digestive tract of the two birds were: esophagus lengths 25 and 21 cm; stomach lengths were both 17 cm, stomach widths 6 and 5 cm; small intestine lengths (including duodenum) 184 and 185 cm; wet weight of stomachs (empty) 80 and 75 g; and wet weights of small intestines (empty) 40 and 47 g.

The length of the small intestine of the bearded vulture is shown in Fig. 2 in relation to its body size and in comparison with a range of other raptor species (for method of scaling for body size see Barton and

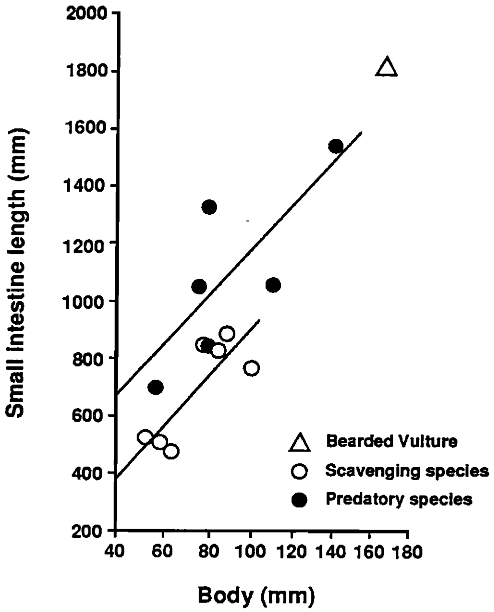

Figure 2. A comparison of the length of the small intestine of the bearded vulture in relation to an index of body size (sternum length × sternum diagonal)$^{1/2}$, with data from other birds of prey which have a scavenging diet and an active chase form of predation (from Barton and Houston 1994).

Houston 1994); the intestinal length is close to that predicted for a scavenging raptor.

The digestive tract showed some specialization. The esophagus was highly elastic and expandable to allow the passage of large food items, but no clearly defined crop (a diverticulum off the esophagus) was present. The bearded vulture is the only species of vulture to lack this large storage region in front of the stomach. Irregularly shaped fragments of bone would be difficult to store in a crop and then later retrieve for passage to the stomach. Bearded vultures must use the esophagus to store food; Brown (1988) recorded birds swallowing bones at least 250 mm long and 35 mm wide, which would be too large to contain in the stomach. Bearded vultures are also occasionally seen flying with the end of a bone still projecting from the mouth.

The esophagus had a mean wall thickness of 1.3 ± 0.1 mm (SE, $N = 20$), contained no mucus glands (as is typical of vertebrates), but did have a thickened epithelial layer from 23–126 μm thick with some keratinization underlaid by a connective tissue layer from 23–207 μm thick. These layers, together with the elasticity of the esophagus, must provide some protection from sharp bone pieces. The gastric stomach contained a very high density of acid secreting cells ($\bar{x} = 109 \pm 4$ (SE) cells per 10 000 μm^2, $N = 8$), with no pepsin-secreting cells visible in any of the sections we examined. Neither the gastric nor the pyloric stomach regions were highly muscular, the whole stomach wall having a mean thickness of only 2.3 ± 0.1 mm (SE, $N = 20$). There was no gizzard-like portion of the stomach which could act to mechanically grind food.

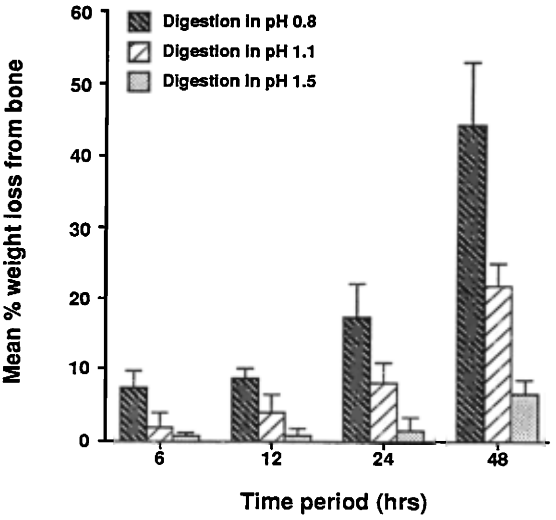

Figure 3. Weight loss of bone samples with time in solutions of different acidity.

Fig. 3 shows bone weight loss in acid solutions. Both the acidity and time influence weight loss (two-way ANOVA $F = 124.9$, df = 2,48 and $F = 124.5$, df = 3,48, $P < 0.01$; Fig. 3). There was a significant interaction between the effects of time and pH, so the rate of weight loss is dependent on the acidity of the solution ($F = 21.7$, df = 6,48, $P < 0.01$). Loss in weight was entirely caused by demineralization, and there was no significant loss in organic content of the bone (Fig. 4). Bone fragments placed in acid solutions containing porcine pepsin solutions to simulate stomach conditions failed to show any enhanced rate of weight loss over acid solutions alone.

Analysis of feces by X-ray diffraction showed a peak profile characteristic of calcium hydroxyapatite. No other calcium salt was represented except some calcite which, together with quartz, may have been ingested as soil particles.

DISCUSSION

The diet of the bearded vulture must be among the most unusual of all birds. It is remarkable that the

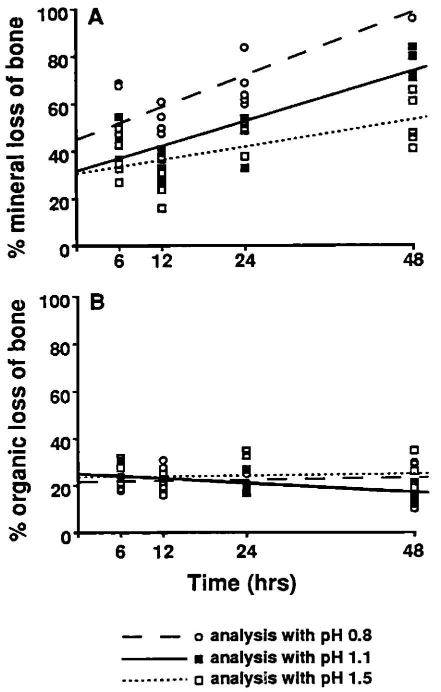

Figure 4. The effects of the level of acidity on the demineralization and loss of organic content of bone with time.

energy requirements can be derived largely from bone, but digestive efficiency on this diet is surprisingly high. Most predatory birds have digestive efficiencies between 75 and 80% (Duke et al. 1975, Barton and Houston 1993a). Bone is a complex, composite tissue with about two-thirds of the mass and one-half of its volume composed of inorganic salts. These are predominantly crystals of calcium phosphorus apatite [$Ca_3(PO_4)_{2n}CaCO_3$], present as tiny crystals about 40 nm long in an organic matrix which is composed of 90–96% collagen fibrils (Alexander 1983). There is also a variable amount of fat in the bone marrow. The rib bone diet used here had a mineral content of 54.2%, and the digestive efficiency of 50% is high. These figures imply that once the bone has been demineralized, the efficiency of absorption of the organic component must be almost complete. Efficiency of absorption may be assisted by the slow throughput time, for digestive efficiency increases with a reduced rate of food passage through the alimentary tract (Robbins 1983). The slow rate of digestion is almost certainly imposed by the time required to dimineralize the food. Barton and Houston (1993b) gave throughput times for seven species of birds of prey taking conventional meat diets. All seven had peak fecal output from 3–6 hr after ingestion. Bearded vultures also have some fecal production about 4 hr after feeding (Fig. 1), which may result from the small amounts of soft tissue adhering to the bones, but the bulk of fecal production is derived from bone tissue digestion and this occurs nearer to 24 hr after feeding.

Bone is such an unusual diet that the bearded vulture might be expected to have developed an unusually long digestive tract. Barton and Houston (1994) found considerable variation in small intestine length among species of predatory birds; these differences may be associated with predatory behavior. Species with active chasing methods of predation, such as falcons, seem to have comparatively short small intestines and digest their food comparatively poorly. Species which rely more on soaring flight and which do not require a high-speed chase to capture prey, such as scavengers and buzzards, have longer intestines and digest their food more efficiently (Barton and Houston 1993a). The reduced weight of a short digestive tract presumably enhances prey capture in active predators and this compensates for the reduced digestive efficiency of the smaller gut. However, Fig. 2 showed that the gut length in bearded vultures was not abnormal for a scavenging raptor.

The process by which bearded vultures break down bone tissue is not fully known. However, the esophagus and stomach show no specializations to suggest that mechanical breakdown is important. The results presented here confirm the findings of Duke et al. (1975) that the level of acidity is an important factor in the demineralization of bone. The pH levels in the bearded vulture stomach are unknown, but Houston and Cooper (1975) recorded a pH of 1 in an African white-backed vulture (*Gyps africanus*), and other raptors have been recorded with gastric pH as low as 0.7 (Herpol 1967). The stomach wall in the bearded vulture contains a high density of acid-secreting cells, and must be capable of producing a highly acidic environment. The feces of bearded vultures contained calcium hydroxyapatite, the same form of calcium as in bone. Therefore, the mineral salts seem to be leached from the bone tissue without chemical transformation. We only have one observation on the time taken for digestion, but this suggested that bearded vultures complete digestion within about 30 hr. An acid solution of pH 0.8 alone would not have completed demineralization within this time, but bone probably breaks down in the stomach much faster than in our acid solutions because of two factors. Firstly, there will be mechanical agitation from contractions of the stomach walls. Jackson et al. (1987) showed that even gentle movement of food samples resulted in significantly greater breakdown than stationary conditions. Bone fragments became comparatively soft after a period in strong acid, and gentle grinding together would have substantially increased their rate of breakdown. Secondly, the action of the acid will be augmented by pepsin activity to break down the collagen matrix. We were not able to obtain a commercial form of pepsin which remained active in our experimental conditions. Pepsins operate over very narrow pH ranges, which vary considerably between species (Withers 1992). Presumably bearded vultures have protein-splitting enzymes that have optimum activity in highly acidic solutions.

Very little is known of calcium metabolism in raptors, but bearded vultures are obviously adapted for a diet which has a highly unusual calcium/phosphorus ratio and exceptionally high calcium levels. Recommended feeds for domestic chickens should contain no more than 1.2% calcium (Scott et al. 1982) whereas bone contains 15–18% calcium.

Brown (1988) showed that mammal bones have a higher energy content than muscle tissue (6.7 and 5.8 KJ/g respectively) partly because of their high fat content. Brown and Plug (1990) calculated that a bearded vulture taking a diet of 70% bone, 25% muscle, and 5% skin (the best estimate available of natural diet) would ingest 674 KJ energy per 100 g, compared to 586 KJ energy for an equivalent weight of muscle. We have shown the digestive efficiency of bone to be 50%, and if we assume 75% efficiency for soft tissues, then for each 100 g of bone-dominated diet the bird would absorb 387 KJ compared to 440 KJ on a pure muscle diet. A bone-based diet is therefore energetically almost as valuable as a meat-based diet. A bone-based diet, however, has one major advantage in that it does not decompose. A skeleton left on a mountain hillside will rapidly dehydrate sufficiently to prevent bacterial breakdown of the mineralized tissues and the fatty marrow. Bearded vultures are known to return to skeletons after several months to continue feeding. All other scavenging birds which feed on soft tissues are faced with a race against time when they locate a carcass. If they do not consume the meat within a short period of time it will be destroyed by bacteria or insect larvae (Houston 1979). This has major implications for the availability of food for bone-eating and meat-eating scavengers. If, for example, bones remain in an edible condition for 10 times the length of time that soft tissues remain in an edible condition, this means that a bone-scavenger can survive with only one-tenth the number of carcasses within its foraging range compared to a meat scavenger. This is probably why bearded vultures are so successful in high mountain regions, such as Tibet and the Himalayas. Such areas have extremely low ungulate biomass and few carcasses become available. But when they do a bearded vulture can rely on them for a long period of time.

If bone is such a useful diet, why do other raptors not exploit it? Bone is a heavy food which takes a comparatively long time to digest. It is notable that even bearded vultures prefer to eat old bones rather than fresh (Brown and Plug 1990), probably because they will have lost about 30% of their weight. All vultures have extremely low energy flight costs because of their dependence on soaring. Other raptors which rely on powered flight, less efficient gliding, or species living in regions with less powerful soaring conditions, might expend too much energy when flying with a stomach full of heavy bone to warrant feeding on this diet. In addition, the slow time required for digestion of bone will preclude small species from using this diet, for their higher metabolic rates require a faster delivery of energy from the digestive tract. Perhaps only a very large, soaring bird living in a mountainous habitat with powerful upcurrents could afford to specialize in this way.

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