APPENDIX. Basal metabolic rate (BMR) and body mass (m_b) in herbivorous birds.

Species	m_b (g)	BMR (mL/O_2 /g h)	References
Anatidae			
Anas platyrhyncos	741	0.82	Daan et al. (1990)
Anas gibberifrons	391	0.77	McNab (1994)
Anas rhynchotis	480	0.80	McNab (1994)
Anas aucklandica chlorotis	529	0.79	McNab (1994)
Anas castaneas	944.1	0.78	Hinds et al. (1993)
Anser anser	3250	0.60	Kendeigh et al. (1977)
Aythya fuligula	611	0.86	Daan et al. (1990)
Anas penelope	723	0.70	Kendeigh et al. (1977)
Tadorna variegata	1199	0.61	McNab (1994)
Cygnus buccinator	8880	0.41	Benedict and Fox (1927)
Branta bernicla	1253	0.87	Daan et al. (1990)
Ralidae			
Crex crex	96	1.47	Kendeigh et al. (1977)
Fulica atra	412	0.89	Kendeigh et al. (1977)
Gallinula tenebrosa	519	0.87	McNab (1994)
Gallinula mortierii	944	0.66	McNab (1994)
Porphyrio porphyrio	973	0.71	McNab (1994)
Porphyrio mantelli	2764	0.44	McNab (1994)
Cuculidae			
Opisthocomus hoazin	598	0.48	Grajal A. (1991)
Tetraonidae			
Centrocerus urophasianus	2500	0.52	Vehrencamp et al. (1989)
Emberezidae			
Saltator coerulescens	47	1.49	Bosque et al. (1990)
Saltator orenocensis	32.7	1.72	Bosque et al. (1990)
Phytotomidae			
Phytotoma rara	41.6	2.47	this study

The Auk 118(3):785–789, 2001

Function and Temporal Variation in Use of Ossuaries by Bearded Vultures (*Gypaetus barbatus*) During the Nestling Period

ANTONI MARGALIDA[1] AND JOAN BERTRAN
Group of Study and Protection of the Bearded Vulture, Apdo. 43, E-25520 El Pont de Suert (Lleida), Spain

ABSTRACT.—We analyze the use and functionality of ossuaries by the Bearded Vulture (*Gypaetus barbatus*) in the Pyrenees during the nestling period. In 71% of cases, the ossuary was used to prepare food for chicks, in 11% for storing food, and only in 18% for preparing the adults' own food. Pairs used an average of two ossuaries at a mean distance from the nest of 789 m (SE ± 377). The average time dedicate to breaking bone was 5.3 min (SE ± 4.2) and 4.5 throws (SE ± 5.8) for each session in the ossuarie (n = 86). The temporal variation found in the use of the ossuaries, with maximum frequencies between 31–90 days of age of chicks, may be due to a possible qualitative variation in chicks' diets. Ossuaries are also used to store food, this being a differentiating and advantageous trait with respect to feeding behavior developed by other meat scavengers.

Bearded Vultures (*Gypaetus barbatus*) feed mainly on the carcasses of medium-sized domestic and wild ungulates (Hiraldo et al. 1979). Although most of the

[1] E-mail: margalida@gauss.entorno.es

TABLE 1. Use of bone breaking sites or ossuaries by Bearded Vultures in relation to the age of their chick Percentages appears in parentheses.

Food-handling sequence	1–30 days	31–60 days	61–90 days	91-fledging	Total
Searching-breaking-nest[a]	6 (46)[a]	14 (48)	8 (23)	2 (12)	30
Nest-breaking-nest	1 (8)	8 (27.5)	12 (34)	7 (41)	28
Ossuary-breaking-nest	2 (15)	4 (14)	3 (9)	0	9
Searching-breaking-consumption by adult	1 (8)	1 (3.5)	4 (11)	4 (23)	10
Nest-breaking-consumption by adult-abandoned food at ossuary	1 (8)	1 (3.5)	3 (9)	2 (12)	7
	2 (15)	1 (3.5)	5 (14)	2 (12)	10
Total	13	29	35	17	94

[a] See text for explanation.

skeleton of those species may be consumed, vultures preferentially select the longer bones. Adult individuals ingest bones up to 250 mm long and 35 mm wide without apparent difficulty (Brown 1988). They resolve the problem of ingesting larger bones by the use of bone-breaking sites, or *ossuaries.* Those sites are rocky surfaces where Bearded Vultures deliberately and repeatedly throw the remains from the air until they become fragmented or disjointed (Huxley and Nicholson 1963). Although some ossuaries may be used only occasionally, individuals typically have specific sites at their disposal, close to the nest, where bone breaking takes place regularly.

Although ossuaries are used year round by territorial adults, the importance of those sites is heightened during nestling (Heredia 1991). Studies of vulture activity at ossuaries include general descriptions of behavior (Boudoint 1976), the physical characteristics of the ossuaries (Brown 1988, Heredia 1991), the kinds of remains encountered (Heredia 1974, Brown and Plug 1990), and the intra- and interspecies interactions that occur there (Bertran and Margalida 1996, 1997).

Although it is generally assumed that 70 to 90% of Bearded Vultures' food is composed of bone remains (Brown and Plug 1990), 49% of the remains brought to one nest had a high proportion of meat (Margalida and Bertran 1997). Likewise, Brown and Plug (1990) observed that 12% of the remains brought to the nest were from meat (n = 65) and that 73% of those remains were brought during the first three weeks after hatching. Those authors also observed that 6% of remains collected by adults at feeding stations (n = 70) were from meat and that all of them were selected during the breeding season. Those results suggest existence of differences between diet during nestling period and the remainder of the year. However, information on diet of chicks is scarce (Brown and Plug 1990, Thibault et al. 1993, Margalida and Bertran 1997) and the study of activity at the ossuaries is one method for determining the possible temporal variation in the diet, on which no information exists.

Here we analyze the function of ossuaries and quantify their use in relation to the age of chicks.

Study area and methods.—This study was conducted in the central Pyrenees in northeast Spain, from 1992 to 1997. Data obtained during the study of the species' breeding behavior (Bertran and Margalida 1999, Margalida and Bertran 2000a, b) correspond to observations made on seven breeding pairs (265 ± SD = 157 h/pair, range 50 to 492 h). This area has one of the highest densities of Bearded Vultures in the Pyrenees (García et al. 1996), and apparently has sufficient food resources to cover the annual energetic needs of the breeding pairs (Margalida et al. 1997).

Bearded Vultures are solitary breeders that nests on large rocky outcrops (Hiraldo et al. 1979). Each pair generally has one to four ossuaries available within its territory (Heredia 1991).

Observations totalling 1,852 h were made using 20–60× field telescopes from vantage points dominating the nesting sites at 300 to 600 m from the cliff, from which both ossuaries and nests could be viewed simultaneously. Given the distance at which observations were made, it was not possible to identify the different types of remains dropped onto or gathered from the bone-breaking sites. The nestling period was considered as the time period from hatching (February to March) until fledging (June to July). In the studied pairs, the mean age of the chicks at fledging was 117.6 ± 3.2 days (range 113 to 122, n = 7).

To examine variation in use of ossuaries in relation to age of chicks, the nestling period was subdivided into four 30 day periods. The activities developed by the adults at the ossuaries were grouped as follows (Table 1): SBN: Return from food *searching* with food remains, *breaking* food, and bringing it to the *nest.* NBN: Leaving the *nest* with food remains, *breaking* food, and bringing it back to the *nest.* OBN: Collec-

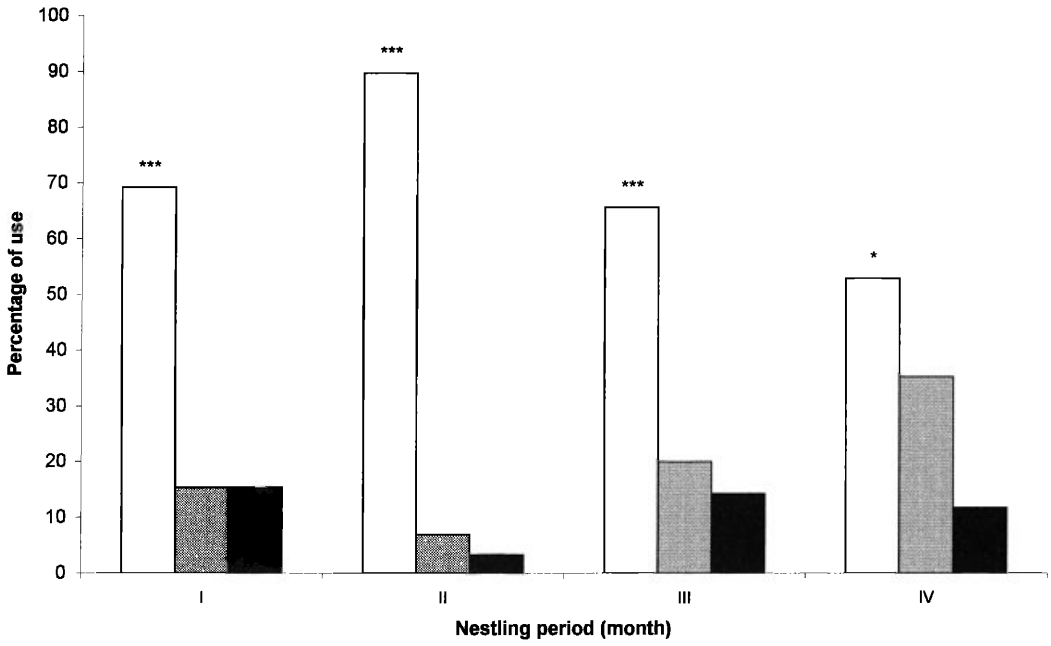

FIG. 1. Temporal variation in the use and functionality of the bone-breaking sites, or ossuaries, for preparing food. White columns: preparation of food for the chick; grey columns: preparation of food for the adult; black columns: storage of food. Chi-square test: *** $P < 0.01$; * $P < 0.05$.

tion of remains from the *ossuary, breaking* food, and bringing it to the *nest*; or collection of remains from the *ossuary* and bringing them to the *nest*. SBCA: Return from food *searching* with remains, *breaking* food, and *consumption* by the *adult*; or collection of remains from the ossuary, breaking them, and consumption by the adult; or collection of remains from the ossuary and consumption by the adult. NBCA: Leaving the *nest* with food remains, *breaking* food, and *consumption* by the *adult*. AO: *Abandoning* food remains at the *ossuary*, or breaking the remains and abandoning food at the ossuary. The remains abandoned could be recovered the same day or several days later and that behavior was considered food caching.

Observation times were standardized among pairs. For comparisons between periods, we determined a rate of daily use of the ossuary (number of bone-breaking sessions per hour) for each observation day and pair. For the statistical treatment of the data we used nonparametric tests (Sokal and Rohlf 1981).

Results.—We witnessed 94 visits to the ossuaries (Table 1), 71% of which were related to chick feeding, 18% of which were related to adult feeding, and 11% of which involved food storage (Fig. 1). Monitored pairs used an average of 2 ± 0.58 ossuaries (range 1 to 3, $n = 7$) at a mean distance from the nests of 789 ± 377 m (range 175 to 2,400, $n = 14$).

It took Bearded Vultures an average 5.3 ± 4.2 min (range 1 to 17, $n = 50$) to break bones. During those sessions, vultures dropped bones an average 4.5 ± 5.8 times (range 1 to 35, $n = 86$).

Bearded Vultures used ossuaries less in the first and fourth month of life of the chick (0.023 ± 0.059 and 0.027 ± 0.052 sessions h^{-1}/day, respectively) than during the second and third month (0.072 ± 0.123 and 0.073 ± 0.108 sessions h^{-1}/day, respectively) (Kruskall-Wallis $H = 8.35$, df = 3, $P = 0.04$). Comparison of the first and second half of nestling period (1 to 60 days vs. 61 days to fledging) showed significant inverse tendencies in the proportions of the SBN an NBN scenarios (Fisher's exact test, $P = 0.02$). Although the mean time at bone breaking sites dedicated to the preparation of food during the first half of the nestling period was lower than during the second half (<60 days: 4.48 ± 3.77 min, $n = 27$ vs. >61 days to fledging: 6.04 ± 4.54 min, $n = 23$), the difference was not statistically significant (Mann-Whitney *U*-test, $U = 231$, NS).

Discussion.—Our observations suggest that during the nestling period, ossuaries are used mainly for adapting the size of the food items to the needs of the chick and, to a lesser degree, for the preparation of the adults' own food.

The temporal variation in use of ossuaries may be due to a possible qualitative variation in chicks' diets. In captivity, chicks ingest small bone fragments combined with meat within a few hours after hatching (H. Frey pers. comm.). In the wild, meat as opposed to bone probably acquires special relevance

during the first month of life. Mammalian bone has a higher energetic content than muscle tissue (6.7 vs. 5.6 kJ/g, Brown 1988) so selection of meat as food probably is due to the chicks' limited ingestive capacity. Although prey predictability also would seem to condition the pattern of selection (Margalida and Bertran 1997) during the first few weeks after hatching, prey items delivered to the nest are generally food remains containing fresh meat. Those observations are consistent with published data (Brown and Plug 1990), which, together with the significantly lower frequency of visits to the ossuaries during the first month of chick rearing, suggest the presence of meat prey items in the diet. In that respect, feeding time invested by adults during the two weeks after hatching is significantly lower (Margalida and Bertran 2000a).

The fact that the use of the ossuaries decreases sharply in the fourth month of chick rearing might be related to two factors. (1) The capacity of the chick for ingesting bones is considerable at that time, which would allow the adults to reduce the preparation time at the ossuaries; or (2) during that phase, the seasonal movement of livestock to new pastures takes place, making it the period when the availability of food is highest (Margalida et al. 1997). The relative abundance of food and the consequent spatial and temporal predictability of searching for it, would permit vultures to select the most adequate types of remains, which might reduce time needed for their preparation at ossuaries.

The hypothesis of temporal variation in food quality also is supported by the differences observed in the behavior of the adults at ossuaries. Although during the first two months food is more frequently prepared before being carried to the nest (SBN), during the last two months it is usually prepared once the remains have been brought to the nest (NBN). Those differences could reflect the fact that during the first half of nestling period, limitations of the chick for ingesting bones force the adult to prepare the food prior to entering the nest. Meat remains and small bone fragments are consumed by the chick but generally it is the adult who ingests the bones (A. Margalida pers. obs.). The lower proportion of bones in the diet and use that the adults make of those, mean that they accumulate less in the nest and that the NBN scenario is observed less often. Nevertheless, during the second half of the nestling period, increase in bone remains in the diet leads to their accumulation in the nest. The greater capacity of the chick to ingest bone fragments makes the prior preparation of bones at the ossuaries unnecessary, and the increased frequency of observation of the NBN scenario would be related to the accumulation of remains at the nest and to the total use that the chick can make of those.

The nonsignificant increase in the use of ossuaries by adults to prepare their own food during the second half of the nestling period may be related to chicks' higher energetic needs and to the time invested in searching for food (Margalida and Bertran 2000a). The accumulation of food remains at the nest and in ossuaries makes the adults' feeding easier and allows them to maximize the time spent searching for food for the chick.

Bearded Vultures occasionally abandon food remains at ossuaries. Traditional ossuaries allow individuals to deposit and to recover remains when food is scarce or when adverse weather conditions (principally snowfall) limit flights in search of food. Thus, ossuaries would serve as predictable alternative food sources. That is possible due to the maintenance of that type of food in an edible condition, which has been estimated to be ten times longer than soft tissues (Houston and Copsey 1994). That represents an important advantage with regard to the feeding behavior of other meat scavengers. However, given the risk of piracy by conspecifics, storage of food in ossuaries is not very frequent and probably occurs at ossuaries close to the nest which would allow them to be surveyed and defended by the breeding pairs (see Bertran and Margalida 1996).

Our observations may allow better management of feeding stations, which are usually provisioned with bone remains. Although quantity of food available is not a limiting factor for breeding success (Margalida et al. 1997), food quality might be one. Provision of food to the feeding stations with a higher meat content during the first weeks after hatching may increase breeding success, given that most breeding failures in that species take place during that period (A. Margalida pers. obs.).

Acknowledgments.—We are grateful to J. Boudet, D. García, R. Heredia, and P. Romero for their assistance in the field, and to H. Frey for contributing his observations on and experience with captive birds. We are also grateful to K. Bildstein, A. Gamauf, J. J. Negro, K. G. Smith, and an anonymous reviewer for comments on the manuscript. S. Cahill, J. Cancalosi and S. Hardie translated the text into English. This study was supported by Departament d'Agricultura Ramaderia i Pesca of the Generalitat de Catalunya, Fundació Territori i Paisatge, Minuartia Estudis Ambientals and a Life Project of the European Union (94/E/A221/E/01126/ASJ).

Literature Cited

Bertran, J., and A. Margalida. 1996. Patrón anual de observaciones de Quebrantahuesos (*Gypaetus barbatus*) de diferentes grupos de edad en los sectores de nidificación. Alauda 64:171–178.

Bertran, J., and A. Margalida. 1997. Griffon Vultures (*Gyps fulvus*) ingesting bones at the ossuaries of Bearded Vultures (*Gypaetus barbatus*) Journal of Raptor Research 31:287–288.

BERTRAN, J., AND A. MARGALIDA. 1999. Copulatory behavior of the Bearded Vulture. Condor 101: 164–168.

BOUDOINT, Y. 1976. Techniques de vol et de cassage d'os chez le gypaète barbu (*Gypaetus barbatus*). Alauda 44:1–21.

BROWN, C. J. 1988. A study of the Bearded Vulture *Gypaetus barbatus* in southern Africa. Ph.D. dissertation, University of Natal, Pietermaritzburg, South Africa.

BROWN, C. J., AND I. PLUG. 1990. Food choice and diet of the Bearded Vulture *Gypaetus barbatus* in southern Africa. South African Journal of Zoology 25:169–177.

GARCÍA, D., A. MARGALIDA, X. PARELLADA, AND J. CANUT. 1996. Parámetros reproductores y evolución del Quebrantahuesos (*Gypaetus barbatus*) en Cataluña (NE España). Alauda 64:229–238.

HEREDIA, R. 1974. Nota sobre la alimentación del Quebrantahuesos (*Gypaetus barbatus*). Ardeola 19:345–346.

HEREDIA, R. 1991. Alimentación y recursos alimenticios. Pages 79–89 *in* El Quebrantahuesos (*Gypaetus barbatus*) en los Pirineos (R. Heredia and B. Heredia, Eds.). Instituto para la Conservación de la Naturaleza, Colección Técnica, Madrid.

HIRALDO, F., M. DELIBES, AND J. CALDERÓN. 1979. El Quebrantahuesos (L.). Monografías 22. Instituto para la Conservación de la Naturaleza, Madrid.

HOUSTON, D. C., AND J. A. COPSEY. 1994. Bone digestion and intestinal morphology of the Bearded Vulture. Journal of Raptor Research 28:73–78.

HUXLEY, J., AND E. M. NICHOLSON. 1963. Lammergeier *Gypaetus barbatus* breaking bones. Ibis 105: 106–107.

MARGALIDA, A., AND J. BERTRAN. 1997. Dieta y selección de alimento de una pareja de Quebrantahuesos (*Gypaetus barbatus*) en los Pirineos durante la crianza. Ardeola 44:191–197.

MARGALIDA, A., AND J. BERTRAN. 2000a. Breeding behaviour of the Bearded Vulture (*Gypaetus barbatus*): Minimal sexual differences in parental activities. Ibis 142:225–243.

MARGALIDA, A., AND J. BERTRAN. 2000b. Nest-building behaviour of the Bearded Vulture (*Gypaetus barbatus*). Ardea 88:259–264.

MARGALIDA, A., D. GARCÍA, AND R. HEREDIA. 1997. Estimación de la disponibilidad trófica para el Quebrantahuesos (*Gypaetus barbatus*) en Cataluña (NE España) e implicaciones sobre su conservación. Doñana Acta Vertebrata 24:235–243.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. W. H. Freeman and Co., San Francisco, California.

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.

Received 27 December 1999, accepted 20 January 2001. Associate Editor: K. Bildstein

---

The Auk 118(3):789–795, 2001

Individual and Seasonal Variation in External Genitalia of Male Tree Swallows

MICHAEL P. LOMBARDO[1]
Department of Biology, Grand Valley State University, Allendale, Michigan 49401, USA

ABSTRACT.—The cloacal protuberance (CP) of passerines functions primarily to store spermatozoa. When gently squeezed, the CP of male Tree Swallows (*Tachycineta bicolor*) everts to expose a small papilla from which semen can be expressed. From 1994 to 1999, I examined individual and seasonal variation in CP dimensions and papilla length of mated male Tree Swallows in western Michigan. Male CP volumes were greatest when their mates were laying eggs and declined to the nestling period. Papilla lengths did not vary over the course of the breeding season. Cloacal protuberance dimensions and papilla length were not associated with the age class of a male's mate, the date she started laying eggs, or number of eggs she laid. The decrease in CP size over the course of the breeding season is consistent with the steady decrease in reproductive opportunities for male swallows. Although it seems likely, whether or not the papilla of Tree Swallows functions as an intromittent organ awaits further study of the anatomical mechanics of copulation in these birds.

During the breeding season, the distal ends of the ductus deferens (seminal glomera) of male passerines fill with newly formed spermatozoa resulting in a swelling of the cloaca commonly referred to as the cloacal protuberance (CP) (King 1981). The CP can be considered as the external male genitalia. The di-

[1] E-mail: lombardm@gvsu.edu