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INTERSPECIFIC AND INTRASPECIFIC KLEPTOPARASITIC INTERACTIONS OF THE BEARDED VULTURE (*GYPÆTUS BARBATUS*) AT NESTING AREAS

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Kleptoparasitism is the stealing of previously procured food from heterospecifics or conspecifics (Brockmann and Barnard 1979). This behavior is quite widespread among birds, especially among seabirds (Furness 1987). Although kleptoparasitic interactions in vultures have been reported in the literature (Brockmann and Barnard 1979, Pascual and Santiago 1991, Bertran and Margalida 1996, Margalida and Heredia 2002) information on this behavior at nesting areas is scarce. This may be due to the fact that vulture species generally interact around the carcass (Álvarez et al. 1976, König 1983, Blanco et al. 1997, Mundy et al. 1992) and that they deliver food, which they carry in their crop to the nest, making theft of this food by other birds difficult.

The Bearded Vulture (*Gypaetus barbatus*) is a solitary and territorial osteophagous vulture that inhabits mountain areas of the southern Palearctic and the Afrotropical region (del Hoyo et al. 1994). In contrast to the ecology of other vultures, this species presents some features that may favor kleptoparasitism: (1) the carrying of large bones or bone fragments that are visible to other species, (2) the repeated breaking actions that take place in the ossuaries, and (3) the predictability of food sources where prey items accumulate (ossuaries, perches, and nests). Nevertheless, kleptoparasitic events involving the Bearded Vulture have only been reported occasionally (Elosegi 1989).

In the eastern Pyrenees, the Bearded Vulture population occurs in a high population density (Margalida et al. 2003) and with an abundant food supply (Margalida et al. 1997). These factors suggest a low frequency of kleptoparasitism events because this feeding strategy is favored when food is less abundant (Stillman et al. 1997). On the other hand, a low frequency of interspecific interactions would be expected as consequence of low benefits that could be obtained by heterospecifics from stealing a specialized food such as bone remains.

In this note, we document some interspecific and intraspecific kleptoparasitic interactions of the Bearded Vulture at nesting areas and we analyze the factors affecting this behavior.

MATERIAL AND METHODS

Fieldwork was undertaken between 1991–97 in the central Pyrenees (Catalonia, northeast Spain) during a larger study of the breeding biology of this species (Margalida and Bertran 2000). Eight focal pairs were studied and we recorded incidental observations of another seven pairs during the pre-laying, incubation, and chick-rearing periods (September–July).

Bearded Vulture nests are situated on rocky cliffs at altitudes between 650 m and 2100 m. Among the species which coexist with the Bearded Vulture and which often interact with it are the Golden Eagle (*Aquila chrysaetos*) (10 territories), the Egyptian Vulture (*Neophron percnopterus*) (four territories), the Common Raven (*Corvus corax*) (14 territories), and the Eurasian Griffon (*Gyps fulvus*) (nine territories). At the same time, there are also intraspecific interactions with individuals of various age classes (immatures, <3 yr; subadults 4–5 yr; adults >6 yr) that often visit the nesting areas.

Observations were made using 20–60× telescopes from vantage points that allowed a good view of nesting sites

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Table 1. Inter- and intraspecific kleptoparasitic actions of Bearded Vultures observed in nesting areas in Spain.

KLEPTOPARASITE	HOST	
	BEARDED VULTURE (ADULT)	GOLDEN EAGLE
Bearded Vulture (immature)	19	0
Bearded Vulture (subadult)	2	0
Bearded Vulture (adult)	1	1
Golden Eagle	2	0
Griffon Vulture	13	0
Common Raven	16	0

(300–600 m). Notes were made of all interactions in which food was stolen, the species involved, and the situation in which they occurred (in flight, on the nest, at an ossuary, or on a perch). In all intraspecific interactions observed, we recorded the individual's age, which was determined following Bertran and Margalida (1996).

RESULTS

We observed 54 interactions consisting of food theft, 26 of which took place at ossuaries, 24 at the nest, 3 in flight, and 1 on a perch. Twenty-two of all interactions were intraspecific, while the remaining 32 were interspecific. No significant difference was observed among the situations where the two types of interactions took place ($\chi^2_2 = 1.5$, $P = 0.47$). In 96.3% of all interactions Bearded Vulture adults acted as hosts and only in two did they act as kleptoparasite (Table 1).

Intraspecific Interactions. Thirteen of all intraspecific thefts took place at the ossuaries, eight at the nest, and only one in flight. The frequency of thefts observed was higher than expected in places where prey remains accumulated, such as nests or ossuaries. Direct kleptoparasitic actions in flight were avoided ($\chi^2_1 = 9.28$, $P < 0.001$). Twenty-one actions (95.5%) were carried out by non-breeding individuals. Birds that were less than 3 yr old took part in 19 of all actions and this age group used this feeding strategy more often than expected ($\chi^2_2 = 13.01$, $P < 0.001$). The only kleptoparasitic action in flight took place between two adult birds in a territory held by a polyandrous quartet. The parasitic individual followed insistently a bird that was carrying the bone remains, flapping its wings vigorously. After an aerial chase of 15 min, the adult bird that was carrying the remains dropped its prey, which the other adult bird collected on the ground.

Interspecific Interactions. Of 32 interspecific interactions observed in which food was stolen, in only one case was the Bearded Vulture the kleptoparasitic species: the vulture robbed a Golden Eagle of the prey it was holding in its talons while perched in the vicinity of its nest. Once in flight, the eagle chased the vulture and tried to recov-

er the prey, which fell into a wooded area from which it could not be recovered. In the remaining 31 interactions, the Bearded Vulture acted as host. In flight it was kleptoparasitised only twice, both by Golden Eagles which chased and took from the vultures' talons the prey they were carrying. On one of these occasions, the prey was dropped and the eagle retrieved it before it touched the ground. Of the other 29 occasions, the Bearded Vulture suffered 16 of the thefts at the nest by ravens and 13 of the thefts at ossuaries by Eurasian Griffons. As occurred with intraspecific interactions, interspecific events of kleptoparasitism mostly occurred in those places where food was accumulated/gathered, with kleptoparasitic chases in flight being significantly infrequent ($\chi^2_1 = 12.44$, $P < 0.001$).

DISCUSSION

Our results suggest that the non-breeding population of Bearded Vultures, perhaps due to limited foraging efficiency (Brown 1988, Bertran and Margalida 1996), as has been suggested with other species (Fisher 1985, Caldwell et al. 1999), are making use of the spatial and temporal predictability of food resources by becoming kleptoparasites. All thefts suffered at the nest by breeding pairs of Bearded Vulture took place during chick-rearing, a period when prey items often accumulate at the nest sites. Theft at ossuaries or in flight occurred during winter (pre-laying and incubation periods), a time when food availability is reduced and weather may greatly limit the activities of foraging and locating food. For those age groups (principally <3 yr) that are more dependent on predictable food sources such as feeding stations (Heredia 1991), this might be a foraging strategy used much more regularly. These results are in agreement with the idea that immature or inexperienced birds may compensate for their less-effective foraging abilities by kleptoparasitism (Wunderle 1991). To the contrary, kleptoparasitism by adults could be an opportunistic foraging behavior. Nevertheless, our observations were mainly done close to the nest and do not include observations during foraging. This accounts for the fact that breeding adults were the host bird in 96% of all observed events. Nevertheless, the abundant food available and the relatively infrequent number of stolen prey, suggest that kleptoparasitism amounts to a small cost for the breeding pairs, without any measurable impact on breeding success (see Margalida et al. 2003).

As a result of the cost/benefit rate, two factors would determine that the species that attempted stealing would resort to this indirect strategy: the territorial behavior of the Bearded Vulture (Margalida and Bertran 2000, Bertran and Margalida 2002) and the accumulation of prey remains in nesting areas. Dominance of adults over immatures is a well documented phenomenon in raptors (Newton 1979), but a reverse-dominance pattern also has been observed (Rodríguez-Estrella and Rivera-Rodríguez 1992). In the case of conspecifics, plumage coloration of

Bearded Vulture adults could act as status signal (Negro et al. 1999). This signal could be used by territorial adults to displace other immature Bearded Vultures not by attacking them, but simply by signalling their status while approaching them (Bautista et al. 1998). On the other hand, the Bearded Vulture's low wing loading and its large wingspan give this species great dominance in flight (Donázar 1993) and make it difficult for an opponent to steal food successfully. In the case of conspecifics, the fact that younger birds are less skillful in flight would mean that they would be less successful in actions of direct piracy, so that the energetic cost of those attempts might be greater than the likely benefits obtained from those actions (Fisher 1985).

Concerning the interspecific interactions, the prey remains consumed by Bearded Vultures mostly consisting of bone remains, would be energetically inadequate for many raptor species (e.g., Golden Eagles). In the case of Eurasian Griffons, they would be occasionally more interested in obtaining bone remains at ossuaries (Bertran and Margalida 1997) in order to compensate for a possible lack of calcium in their diet (Mundy and Ledger 1976). The dominance of the Eurasian Griffon on the ground, given its larger size and the accumulation of bone fragments and splinters at ossuaries, would favor the strategy of obtaining calcium at these sites (Bertran and Margalida 1997). Furthermore, the Bearded Vulture's attacks of intruders in the vicinity of the nest throughout the breeding season (Brown 1988, Margalida and Bertran 2000) would act as deterrent and would make food storages near the nest the least convenient for stealing. The success in aggressive encounters appears determined by the body size and condition, and the previous possession of the disputed resource (Bautista et al. 1998). In contrast, those species with higher aerial maneuverability but with smaller size, such as ravens, would have to focus their actions at the nest, where prey remains also accumulate. Obtaining prey remains there may be less costly for those birds because: (1) adults are gradually less often present at the nest as the breeding season progresses (Brown 1990, Margalida and Bertran 2000) and (2) prey items present in the nest have a higher meat content as consequence of differential requirements in nutrients for the chick (Margalida and Bertran 1997, Margalida and Bertran 2001).

Finally, kleptoparasitism could be a strategy of demonstrating dominance or competence (Bautista et al. 1998). The fact that in our study area the Bearded Vulture density is high (Margalida et al. 2003), heterospecifics compete by the same nest sites (Margalida and García 1999), and food supply is abundant, suggest that kleptoparasitic actions could be determined by other resources than food. For example, demonstrating dominance or competence by nest sites or in breeding territories may result in social benefits (Caldow et al. 1999, Yates et al. 2000).

RESUMEN.—Documentamos interacciones interespecíficas e intraspecíficas de cleptoparasitismo en el quebrantahuesos en los sectores de nidificación. De un total de 54 interacciones, 26 tuvieron lugar en rompederos, 24 en el nido, tres en vuelo y uno en posaderos. Veintidós de las interacciones fueron intraspecíficas y las 32 restantes interespecíficas con cuervos (*Corvus corax*), buitres leonados (*Gyps fulvus*) y águilas reales (*Aquila chrysaetos*). La mayoría de las interacciones tuvieron lugar en zonas donde el alimento se acumulaba (nidos y rompederos) evitando las acciones directas en vuelo. En el caso de los adultos, este comportamiento podría ser una acción oportunista pero para las aves de <3 años sí podría tratarse de una estrategia alimenticia. Puesto que la disponibilidad trófica es suficiente, la población reproductora está incrementándose y las especies heterospecíficas compiten por los mismos sectores de nidificación, el cleptoparasitismo podría estar relacionado con otros factores no relacionados con la obtención de alimento.

[Traducción de los autores]

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