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INTERACTIVE BEHAVIOUR BETWEEN BEARDED VULTURES *GYPAETUS BARBATUS* AND COMNON RAVENS *CORVUS CORAX* IN THE NESTING SITES: PREDATION RISK AND KLEPTOPARASITISM

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SUMMARY.—*Interactive behaviour between Bearded Vultures* Gypaetus barbatus *and Comnon Ravens* Corvus corax *in the nesting sites: predation risk and kleptoparasitism.*

Aims: Aggressive interactions between the Bearded Vulture *Gypaetus barbatus* and the Comnon Raven *Corvus corax* are frequent in the Pyrenean nesting sectors shared by both species. The Bearded Vulture's nesting sectors are vulnerable to kleptoparasitism (food is stored in a visible and predictable manner in nests, perching sites and ossuaries), and the Raven's parasitic-predatory abilities are well known. How both species interact was examined by studying their behaviour during the nestling period and analysing the factors that affect this behaviour.

Location: Central Pyrenees (Catalonia, NE Spain).

Methods: The aggressive interspecific encounters in 10 nesting sites (area = 3750 km^2) was quantified. The observations were carried out from locations where the nests, perching sites and ossuaries could be viewed simultaneously. The data were compared using non-parametric statistical tests.

Results: Most of the attacks on the Ravens occurred from nests and the highest percentage of defensive behaviour in the Bearded Vultures was observed when the chicks were only a few days old. The Ravens preferred to attack when the Bearded Vultures were near the nests, whether the latter were carrying food or not. The Ravens were only relatively effective in their kleptoparasitic attempts when they attacked in a group at times when the Bearded Vultures were manipulating the food in open areas.

Conclusions: The difference in size between both species, and the type of food affected the Ravens' parasitic efficiency. For the Bearded Vultures, the negative effects of coexisting with the Ravens are associated with the energetic costs derived from nest defence and the disturbance generated by the Ravens' kleptoparasitic attempts. Nevertheless, the Bearded Vultures' defensive behaviour suggests that risks of predation exist, mainly during the initial stages of the breeding period, which is when the chicks are likely to be more vulnerable.

Key words: Bearded Vulture, *Corvus corax*, *Gypaetus barbatus*, interespecific interactions, kleptoparasitism, nest defence, predation risk, Raven.

RESUMEN.—*Comportamiento interactivo entre Quebrantahuesos* Gypaetus barbatus *y Cuervos* Corvus corax *en los sectores de nidificación: riesgo de predación y cleptoparasitismo.*

Objetivos: Interacciones agresivas entre Quebrantahuesos *Gypaetus barbatus* y Cuervos *Corvus corax* son frecuentes en los sectores de nidificación pirenaicos compartidos por ambas especies. Los sectores de nidificación del Quebrantahuesos son vulnerables al cleptoparasitismo (el alimento se almacena de forma visible y predecible en nidos, posaderos y rompederos), mientras que es conocida la capacidad parásito-predadora de los Cuervos. Examinamos cómo ambas especies interaccionan temporal y comportamentalmente durante la crianza y analizamos los factores que afectan estas conductas.

Localidad: Pirineos Centrales (Cataluña, Noreste de España).

Métodos: Cuantificamos los encuentros agresivos interespecíficos en 10 sectores de nidificación (área = 3.750 km^2). Las observaciones se llevaron a cabo desde puntos donde los nidos, posaderos y rompederos eran visualizados simultáneamente. Los datos fueron comparados mediante pruebas estadísticas no-paramétricas.

Resultados: La mayoría de los ataques dirigidos hacia los Cuervos ocurrieron desde los nidos y la mayor intensidad defensiva de los Quebrantahuesos tuvo lugar cuando los pollos contaban con pocos días de vida. Los Cuervos dirigieron sus ataques preferentemente cuando los Quebrantahuesos se encontraban cerca de los nidos, independientemente de si éstos transportaban o no alimento. Los Cuervos sólo fueron relativamente eficaces en sus intentos de robo atacando en grupo cuando los Quebrantahuesos manipulaban el alimento en espacios abiertos.

Conclusiones: La diferencia de tamaño entre ambas especies y la naturaleza de alimento condiciona la eficacia parasitaria de los Cuervos. Para los Quebrantahuesos, los efectos negativos que implica la cohabitación

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con Cuervos estarían asociados a los costes energéticos derivados de la defensa de los nidos y a los estorbos en los intentos de piratería. No obstante, la conducta defensiva de los Quebrantahuesos sugiere la existencia de riesgos de predación, principalmente durante los primeros estadios de la crianza, período en el que los pollos pueden ser más vulnerables.

Palabras clave: Cleptoparasitismo, *Corvus corax*, Cuervo, defensa del nido, *Gypaetus barbatus*, interacciones interespecíficas, Quebrantahuesos, riesgo de predación.

INTRODUCTION

The Bearded Vulture *Gypaetus barbatus* is a solitary, osteophagous vulture which is considered as an endangered species in Europe (Tucker & Heath, 1994). The biggest European population of this species is that of the Pyrenees (Del Hoyo *et al*., 1994). Bearded Vulture diet is based mainly on the bones of the carcasses of medium-sized ungulates (Hiraldo *et al*., 1979). The characteristics of this food favour the accumulation of any prey that is not eaten immediately. As a result of this, nests, perching sites and ossuaries (rocky surfaces onto which the birds deliberately drop the bones in order to break them up into small pieces) often contain a considerable number of prey items (Hiraldo *et al*., 1979). In addition, the elaborate manipulation of this type of food generally takes place during the nestling period in the vicinity of the nesting areas (Heredia, 1991; Margalida & Bertran, 2001). The spatial predictability of the accumulated food and the conspicuous behaviour during the transportation and manipulation of the prey occasionally attract heterospecifics and conspecifics, which sometimes act as kleptoparasites (Bertran & Margalida, 1996, 1997; Margalida & Bertran, 2003).

The Bearded Vulture, like most raptors, is territorial and strongly defends its nesting space from potential competitors through aerial attacks (Margalida & Bertran, 2000; Bertran & Margalida, 2002). Aggressive interactions between Bearded Vultures and Common Ravens *Corvus corax* are relatively common; observations carried out on several pairs in the Pyrenees revealed that 26% of the territorial attacks were directed against Ravens (Margalida *et al*., 2001). In the western sector of the Catalan Pyrenees, there is a stable Raven population of over 200 pairs (ICO & J. Estrada, *unpubl. data*). Aggressive interactions between both species have been reported in the areas where the two coexist (Elosegi, 1989).

Territoriality frequently involves protecting offspring and food (Redondo, 1989). The Bearded Vulture's nesting areas present scenarios that make them vulnerable to kleptoparasitism: the food supply is predictable and the food visible (Brockman & Badnarz, 1979). The Raven is a great predator of eggs and chicks (*e.g*. Gaston & Elliot, 1996). Moreover, it is known that this species can combine its parasitic-predatory ability in raptor nests (Tella & Torre, 1990; Cramp & Perrins, 1994; Ratcliffe, 1997). In this respect, the Ravens predatory activities have been mentioned as one of the possible causes of breeding failure in the Bearded Vulture in the Pyrenees (see Margalida *et al*., 2003), but the potential effects of the kleptoparasitic and predatory behaviour have not yet been evaluated.

The aim of this paper is to examine how these species interact during the nestling period, and analyse the factors affecting this behaviour. We also examined the antipredatory behaviour of the Bearded Vulture in relation to the age of the chicks (predation vulnerability).

MATERIAL AND METHODS

The data were obtained between 1991 and 2001 in the course of a study on the breeding biology of Bearded Vultures in a 3750 km^2 area in the central Pyrenees, Catalonia, Northeastern Spain. The study area included 15 pairs of Bearded Vultures, that apparently had sufficient food resources to cover the annual energetic needs of all breeding pairs (Margalida *et al*., 1997) and 204-282 breeding pairs of Ravens (ICO and J. Estrada, *unpubl. data*). Ten different nesting areas of nine reproductive pairs of Bearded Vulture were studied, which coexist with the Raven. Nesting areas were monitored 76.5-503.7 h (mean ± SD = 178 ± 119.5) for a total of 1780 h. Observations were made using 20-60x telescopes from vantage points dominating the nesting areas at 300-500 m from the cliff, from which ossuaries, perching sites and nests could be viewed simultaneously.

Bearded Vulture and Raven attacks that took place within a radius of 500 m from the nests were quantified, considering that 200-500 m is the area defended by a Bearded Vulture pair (Hiraldo *et al*., 1979; Brown, 1990). The average distance between Bearded Vulture and Raven nests was 74.28 ± 33.31 m (range: 15-125 m; $n = 10$). Bearded Vulture attacks were defined as any behaviour consisting of an aerial chase until the intruder was expelled from the vicinity of a nesting area. For each territorial attack, the location where the aggressive interaction occurred was recorded. In order to examine the possible implication of each of the attacks initiated by Ravens with kleptoparasitic activity, it was recorded whether the potential host was carrying prey, the type of attack (aerial pursuit or harassment of a perched victim), and the location where the interaction took place and the number of Ravens involved. It was considered that an attempted theft had taken place when the Ravens managed to seize the Bearded Vulture's food, or part of it, by harassment.

In order to examine the temporal variation of interspecific interactions, the chick-rearing period was divided into six monthly intervals (February-July), which in the Pyrenees correspond phenologically from hatching (February-March) until fledging (June-July), (Margalida *et al*., 2003). For comparisons between months and nesting areas, a rate of daily interspecific interactions (number of aggressive interactions per hour) was determined for each observation day and nesting area. Significance was set at $P < 0.05$ and means were reported ± SD, and non-parametric statistics were used throughout.

RESULTS

In 10 nesting areas 158 instances of interspecific aggressive encounters were recorded, 75 of which (47.5%) were initiated by Bearded Vultures (0.04 ± 0.01 attacks/h) and 83 (52.5%) by Ravens (0.05 ± 0.03 attacks/h). Overall, the degree of defence by the Bearded Vulture pairs (attacks/h) did not correlate with the frequency of potentially kleptoparasitic attacks on them by the Ravens ($r_s = 0.46$, $P > 0.05$, $n = 10$).

Most territorial attacks by Bearded Vultures occurred from the nests (58.7%) and perching sites (33.3%). The rest of the territorial attacks (8%) took place from any part of the nesting area, with the attacking bird in flight. In all the observed cases, the Bearded Vulture attacks on Ravens concluded without physical contact.

Of the 83 aggressive encounters initiated by Ravens, 85.4% of the attacks took place when the potential host was carrying or manipulating prey. Of the total number of aggressive encounters initiated by Ravens, 59% took place when the Bearded Vulture was entering or leaving the nest (53% and 47% respectively, $n = 40$; Table 1). However, the successful klepto-

TABLE 1

Proportion and success of the potentially kleptoparasitic attacks carried out by Ravens in relation to the location of Bearded Vultures. Sample sizes are in parenthesis.
[Proporción y éxito de los ataques potencialmente cleptoparasitarios llevados a cabo por Cuervos en relación con la localización de los Quebrantahuesos. Los tamaños de muestra están entre paréntesis.]

Raven Attacks *[Ataques de Cuervos]*		
Host location *[Localización del huésped]*	Percentage of attacks *[Porcentaje de ataques]*	Percentage of successful attempts *[Porcentaje de ataques exitosos]*
Entering or leaving the nest *[Entrando o saliendo del nido]*	59.0 (49)	0
Flight *[Vuelo]*	15.7 (13)	0
Ossuaries *[Rompederos]*	12.0 (10)	20.0 (2)
Nest *[Nido]*	7.2 (6)	50.0 (3)
Perching sites *[Posaderos]*	6.0 (5)	40.0 (2)

parasitic attempts occurred at perching sites and ossuaries (40%, $n = 5$ and 20% $n = 10$, respectively; Table 1). In all these cases, the host was on the ground or perched and more than one Raven took part in all the attacks. In the attacks on potential hosts that were perched, more than one Raven tended to be involved (range: 2-4, mean = 2.13, 60% of 15 cases), whilst in the attacks on Bearded Vultures in flight, in general only one Raven was involved (77.9% of 68 cases) ($\chi^2 = 6.86$, df = 1, $P < 0.001$). Only 7.2% of the attacks by Raven occurred in nests (Table 1) and in three of the six cases they were driven out by the adults. On the remaining three occasions, the Ravens took advantage of the adult's absence to steal small pieces of food. On two occasions, the chick tried unsuccessfully to attack the invaders by beating its wings.

Bearded Vulture territorial defence differed between nestling stages. The attacks by Bearded Vultures tended to occur more frequently in the first stages of chick-rearing, with a significantly high peak occurring in March (Kruskal-Wallis $H = 13.27$, df = 5, $P = 0.021$) and to drop off suddenly after that (Fig. 1). Aggressive interactions initiated by Ravens occurred more frequently in April and May, but did not differ significantly during the six month study period (Kruskal-Wallis $H = 7.78$, df = 5, $P = 0.17$; Fig. 1).

DISCUSSION

The data suggest that the aggressive interactions between Bearded Vultures and Ravens are the result of the coexistence between one species whose feeding habits facilitate kleptoparasitism and another species that is highly opportunistic and constitutes a potential predator. Consequently, the aggressive behaviour of Bearded Vultures towards Ravens appears to be directly associated with the defence of the nests and its intensity is related to the age of the chicks. This is supported by the fact that most attacks (92%) were initiated from the nests or adjacent sites. Moreover, the significantly higher frequency in March is coincident with the hatching period and the first month of the chick's life when vulnerability to predation is higher. It was not found that pairs which received a higher frequency of attacks in their nesting areas displayed a higher defensive in-

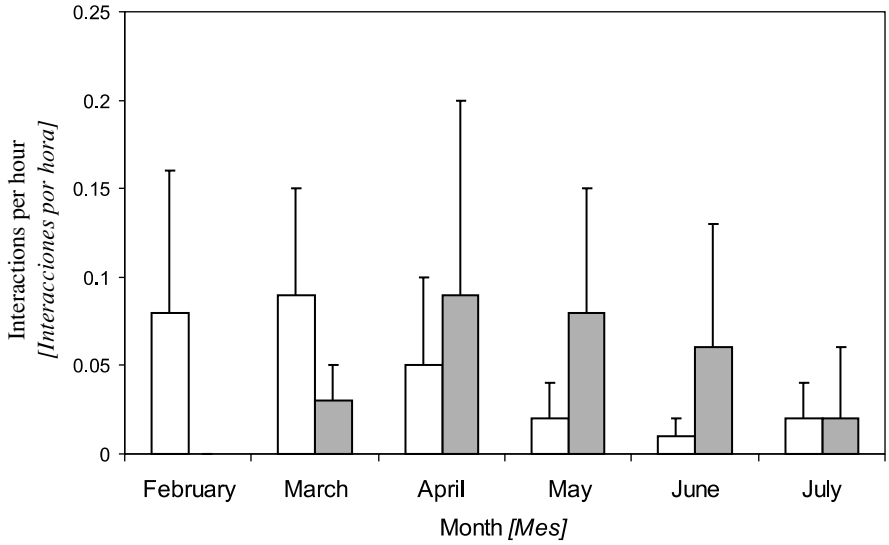

FIG. 1.—Temporal variation of the attacks h^{-1} initiated by Bearded Vultures and Ravens during the nestling period. White columns: Bearded Vultures; Grey columns: Ravens.
[Variación temporal de los ataques h^{-1} iniciados por Quebrantahuesos y Cuervos durante el período de crianza. Columnas blancas: Quebrantahuesos; columnas grises: Cuervos.]

tensity in the face of the Ravens. Nevertheless, the costs that these pairs nesting near to Ravens might have to pay can be the energy expenditure from this fighting and the potential risk that the eggs and/or young chicks may be exposed to predation during territorial interactions (Layna & Rico, 1991). Another risk of predation exposure for eggs and chicks can occur occasionally when certain factors lead the birds to temporarily abandon their nests (*e.g.* human disturbance, looking for and preparing food), as it has been observed in other large raptors (Real & Mañosa, 1986).

Aggressive encounters initiated by Ravens tended to be more frequent (but not significantly so) in the middle of the chick-rearing period. This coincides with the stage when the Bearded Vulture pairs are more active, moving around and preparing the remains in the ossuaries (Margalida & Bertran, 2001). The Raven is a species that exploits a great variety of food sources (Heinrich, 1989), which includes the soft parts attached to the bones of the carcasses (Hiraldo *et al*., 1991). Although Ravens are agile flyers with strong talons, in this case the difference in size between the two species does not favour robbing food in flight (Temeles, 1990). In spite of this, there was a high attack rate (75%) directed against Bearded Vultures in flight, more commonly when they entered or left their nests. Unlike other scavengers, the Bearded Vulture (depending on the size of the conspicuous shape) carries its prey in its talons or bill (Margalida & Bertran, 2000). In contrast, other species such as the Eurasian Griffon Vulture *Gyps fulvus*, which carries semi-digested food to the nest in its crop, have not been observed interacting with Ravens (*pers. obs.*). This appears to indicate that Ravens carry out routine attacks when they notice the presence of potential hosts in the vicinity of the nests. One possible advantage of this behaviour is that Ravens, through harassment, can force the Bearded Vulture to land on the ground. This behaviour was observed in other territories in the study area. In fact, the results show that Ravens can be relatively efficient at group pecking of small food remains, when the Bearded Vulture manipulates its prey in open spaces (perching sites and ossuaries). On the other hand, its success in stealing food from nests is determined by the absence of the adults. The low incidence of attempted nest robberies (7%) would suggest that this behaviour is not very profitable. Similar to that which has been reported for other species (Tella & Torre, 1990), in many cases Bearded Vulture chicks are capable of driving out intruding birds from the nest, including corvids and other raptors (*pers. obs.*).

Although the percentage of robberies by Ravens does not appear to be high (8% of the total interactions reported), it is possible that the success observed does not represent the total amount of food that they can obtain in the Bearded Vulture nesting areas. Similarly to what has been observed in Eurasian Griffon Vultures (Bertran & Margalida, 1997), Ravens occasionally search for places where food often accumulates (*pers. obs.*). This behaviour would suggest this could be a potential way of obtaining food, which in most cases would avoid aggressive interactions (Margalida & Bertran, 2003). In any case, the cost derived from the loss of food does not appear too high for the Bearded Vulture, due to the fact that the size of the prey it generally manipulates (extremities and other large bones) would make the stealing of whole prey items impossible.

In short, both the difference in the size of the two species and the type of food manipulated by the Bearded Vulture affect the Raven's parasitic efficiency. The negative effects of coexisting with the Common Raven for the Bearded Vulture appear to be more closely associated with the costs derived from nest defence and nesting space. However, although the frequency of intrusions by the Raven in the nests might be considered low, the Bearded Vulture's defensive behaviour suggests there are real predation risks during the initial phases of the breeding period when the chicks (due to their size) may be more vulnerable.

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