

Possible functions of alternative nests in raptors: the case of Bonelli's Eagle

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Abstract Four non-exclusive hypotheses have been proposed to explain the alternative nest-building behaviour of raptors: (1) nests as an advertising signal in territories, (2) frustration nests, (3) competition avoidance by nest-site and (4) reduction of nest ectoparasites. We report here data collected during an observational study of a population of Bonelli's Eagle *Hieraetus fasciatus* in southeastern Spain. Our data does not support the first two hypotheses based on the closeness of nests within territories, the lack of correlation between the number of nests and the distance to neighbours and the construction of secondary nests at similar frequencies after breeding failures as after successes. In contrast, the construction of alternative nests to avoid competition with other cliff-nesting raptor species breeding nearby was clearly important since 30% of the pairs obtained some direct benefit from the existence of alternative nests within their territories. We also found abundant Coleoptera (*Dermestidae*) and Diptera (*Carnidae*, *Calliphoridae* and *Phoridae*) as ectoparasites in nests, and the alternative use of nests, synergetically with the presence of greenery as mechanisms for avoiding ectoparasites, was an important factor for the breeding success of the eagle. Our data suggest that competition avoidance and, in particular, the reduction of nest ectoparasite hypotheses are the more plausible explanations for the maintenance of alternative nests in raptors.

Keywords Bonelli's Eagle · Competition · Ectoparasites · Nest re-use · Nest composition

Introduction

Nest building requires a considerable expenditure of energy, and it is common for many birds to make a thousand or more trips to gather the necessary materials (Collias and Collias 1984). This effort is even greater in raptors, since each pair “maintains” or “builds” several nests and uses different nests in different years (Newton 1979)—up to ten nests per pair in some cases (Beecham and Kochert 1975; Ontiveros 1999). It is to be expected that raptors derive some evolutionary advantage by this behaviour since natural selection would be expected to favour anything that tends to economise on effort. Several non-exclusive hypotheses have been put forward to explain this behaviour in raptors.

In the “signal-function” hypothesis, nests have come to serve as an advertising signal of the territory to others of their species almost as effectively as the owners themselves could do (Newton 1979). In this way, some raptor species situate their nests in the open crown of trees, at the very top of trees or in exposed cliffs. These nests are conspicuous from the air and may help the occupants to avoid intra- and also interspecific conflicts for territories. According to this hypothesis, a group of nests located in the same territory should be conspicuous and widely dispersed within the same territory.

In the “frustration-nest” hypothesis, following a reproductive failure, the pair may build a frustration nest, which may be used in future years (Postupalsky 1974; Brown 1976). Reproductive failure is frequent in raptors, and the lack of reproductive duties after failure enables the

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breeding pair to construct a completely new nest during the rest of the season (Newton 1979).

In the “nest-competition hypothesis, by maintaining alternative nests, a pair has the opportunity to shift at the last moment if they are disturbed or if the nest is taken over by another species (Newton 1979). Nest-site competition is well known in several species (Krüger 2002), and cases of nests being occupied by other raptor species have been cited for Bonelli’s Eagle *Hieraetus fasciatus* in particular (Fernández and Insausti 1990; Carrete et al. 2005) and in raptors in general (Newton 1979; Ewins et al. 1994; Hansell 2000). The existence of alternative nests could improve or maintain breeding success under these circumstances.

In the “ectoparasite-avoidance” hypothesis, the use of alternative nests is a mechanism to avoid ectoparasites, many of which remain in the nest in sequential years causing nestling mortality (Wimberger 1984). According to Hansell (2000), the most significant arthropod ectoparasites present in bird nests are mites and ticks (Acarina) and insects of the orders Hemiptera (bugs), Siphonoptera (fleas) and Diptera (flies). However, aromatic compounds present in plants, primarily monoterpenes and isoprenes, often function as insect repellents (Levin 1971; Rasmusen 1972), and many bird species take advantage of this property and use green plants in the construction of their nests (Rodgers et al. 1988; Clark 1991; Lambrechts and Dos Santos 2000). According to this hypothesis, reused nests should have lower productivity than nests that are not reused, and greenery aromatic compounds in nests should increase reproductive success.

Raptors are more likely than passerines to reuse nests and use green vegetation in nest construction (Wimberger 1984). However, most studies of these aspects of avian reproductive ecology have evaluated passerine species (Richner et al. 1993; Gwinner et al. 2000; Lambrechts and Dos Santos 2000; Stanback and Dervan 2001), and little data are available on raptors (but see Wimberger 1984; Fernández and Azkona 1993). The four hypotheses cited above were put forward to explain the construction of multiple nests by raptors many years ago, but, to date, they have not been tested empirically. We did not consider a fifth hypothesis, the “sexual selection hypothesis” in this paper, since in Bonelli’s Eagle (and in most raptors) the eagles mate for years, and both males and females contribute to nest construction and nestling care (Newton 1979).

We report data on a population of Bonelli’s Eagle studied for 11 consecutive years. We analysed breeding success, nest-site availability, number of nests, spatial distribution of nests within and among pairs, nest orientation, nest reuse, nest greenery, parasites in nests, and interspecific nest usurpation, in the context of the four above mentioned hypotheses.

Materials and methods

Our study population consisted of 20 Bonelli’s Eagle pairs in eastern Andalusia (southern Spain) during the 1994–2004 period. All nests included in this study were located in cliffs. The study area is largely mountainous, and the climate is Mediterranean, with mean minimum temperatures ranging from 0.5° to 6.5°C in the winter (January), mean maximum temperatures ranging from 28.0° to 34.5°C in the summer (July) and a mean annual rainfall of 375–850 mm (30-year standard meteorological averages; CMA 1997). The vegetation consists of *Quercus ilex*, scrubland and various species of pine (*Pinus* spp.), interspersed with cultivated cropfields and tree plantations in the foothills, plains and valleys.

This population is suitable for evaluating the four hypotheses on the function of alternative nests for a number of reasons: (1) pairs have high nest-site availability within their territories and always have alternative nests (Ontiveros 1999); (2) breeding success and the density of pairs have not been affected by human interference (Ontiveros and Pleguezuelos 2000), (3) the population has the highest breeding success for the species in Western Europe, indicating a healthy status, (Ontiveros and Pleguezuelos 2003b); (4) other cliff-nesting raptor species (possible competitors for nests) are present in the study area.

Several predictions follow from each of the four hypotheses on the function of alternative nests in raptors.

Signal-function hypothesis

If nests have a signal function in raptor territories, they should be numerous and/or widely dispersed within territories, thereby increasing the probability that potential competitors might encounter them. This should be especially true within our study area, where the rough terrain makes the observation existing nests more difficult, even for birds that circle high in the sky, such as diurnal raptors.

We located all of the nests in each pair’s territory, checking cliffs where Bonelli’s Eagles habitually nest. We calculated the nest area of each eagle pair by circumscribing all nests of a given pair within a minimum convex polygon (MCP), a simple and commonly used method in ecological studies (Samuel and Fuller 1994). We then measured the area of resulting polygons using a 1:10,000 geographic information system (GIS) database, with a 1-m resolution prepared by the regional government of Andalusia, and ARCVIEW GIS 3.2. Finally, we compared this area with the average territory maintained by pairs of this species in this region (7677 ha; Ontiveros 1999; Mínguez et al. 2005). We also measured the breeding density, which we took as the distance of the closest neighbour between

pairs of Bonelli's Eagle (distance between the central distribution of the nests).

If the number and distribution of nests within a territory functions as a signal to possible competitors, we would expect a wide MCP and/or more nests when territories are aggregated than when they are isolated in the territories (a negative relationship between the number of nests and the breeding density).

Frustration-nest hypothesis

If this hypothesis is correct, nest construction after reproductive failures should be more frequent than nest construction after reproductive success. We therefore observed the bird population for this behaviour.

Nest-competition hypothesis

Larger birds of prey, such as the Golden Eagle *Aquila chrysaetos* and the Eagle Owl *Bubo bubo*, may prey on incubating female and nestling Bonelli's Eagles (Real and Mañosa 1990), take over Bonelli's Eagle nests (in the case of Golden Eagles; Fernández and Insausti 1990; Carrete et al. 2005) and induce nest-site change within or between seasons. Based on the nest competition hypothesis, pairs suffering more nest predation and/or usurpation should exhibit a higher rate of nest-change and/or reproductive failure.

There are a number of healthy raptor populations in the study area, including cliff-nesting species, such as the Golden Eagle, the Eagle Owl and the peregrine falcon *Falco peregrinus*, that are potential nest competitors/predators of the Bonelli's Eagle. We estimated populations of at least 16, 25 and 30 pairs, respectively in the study area. We therefore analysed possible cases in which these species took over nests of Bonelli's Eagle and possible effects on breeding success.

Ectoparasite-avoidance hypothesis

Two predictions arise from the hypothesis that the use of alternative nests and fresh greenery in nest construction evolved to inhibit infestations of ectoparasites: (1) pairs with higher rates of nest-change should have higher increased breeding success compared to pairs that reuse nests; (2) nests containing more green material with aromatic compounds should have fewer ectoparasites than nests lacking such material.

To assess the first prediction, we correlated the breeding success of pairs and inter-annual nest-change rate.

Breeding success was defined as the average number of fledglings raised per year, and nest-change rate was defined as the number of pairs of consecutive years characterized by a nest-change/total number of consecutive pairs of years traced.

To assess the second prediction, we selected a subsample of ten nests (due to the difficult access to some nests). In each nest, we descended the cliff and removed up to 1.5 kg of material from the central part of the nest (Gwiazdowicz et al. 2005). Bonelli's Eagle nests average 120 × 80 cm on the top surface and weigh dozens of kilograms (Cramp 1998; unpublished data of authors). Consequently, the removal of 1.5 kg of nest material does not significantly affect nest structure. The nest material was taken a few days after the nestlings had left each nest (2–7 days for all the pairs) in order to avoid interfering with the breeding process. We noted the percentage of plants in the nests and the total number of larvae found in the nest material, since these are better indicators of a nest-parasite population than the adult ectoparasite (Richner and Tripet 1999) due to fluctuating levels of the adult parasites (Bize et al. 2003).

The breeding success of Bonelli's Eagle in south-eastern (SE) Spain is positively correlated with a SE (120.6°) nest-site orientation (Ontiveros and Pleguezuelos 2003a). Thus, we considered nests located within a semicircle centered at 120.6° to have a preferred nest orientation and those in the opposite semicircle not to have a preferred nest orientation (see Fig. 1 in Ontiveros and Pleguezuelos 2003a).

Results

The percentage of Bonelli's Eagle pairs raising at least one nestling ranged from 70.6 to 93.3% according to year, and averaged $82.8 \pm 7.4\%$ over the 11-year study period (199 breeding events). Average productivity was 1.39 ± 0.22 ($n = 20$) and there was no difference in this parameter among years (Kruskal–Wallis test: $H_{10, 199} = 11.77$, $P = 0.30$).

Signal-function hypothesis

We found 84 nests in territories of Bonelli's Eagle pairs (mean 4.2 ± 3.8 , $n = 20$), 60 of which (71.4%) were occupied during at least one season of the study period. Each pair occupied an average of 2.9 ± 1.2 nests ($n = 20$), and the number of nests in a territory was unrelated to cliff availability ($r_s = -0.036$, $P = 0.87$, $n = 20$) and to breeding density ($r_s = -0.3$, $P = 0.19$, $n = 20$).

Nests were located near other nests, with the mean distance between the most distant nests of a territory

being 487.8 ± 451.7 m ($n = 20$). Seventy percent of all territories had at least two nests situated within 10 m of each other, and 15% of territories had at least two nests located only 1 m apart. The average distance among central points of all MCP (breeding density) was 9.1 ± 2.9 km ($n = 20$). Minimum convex polygons calculated from nest locations had an average area of 5.37 ± 6.69 ha, which is only 0.068% of the territory occupied by a pair (see Materials and methods). Thus, the potential area occupied by nests was negligible with respect to the territory used by eagles.

Frustration-nest hypothesis

Of the 34 cases of breeding failure detected, only one was followed by nest-construction behaviour (2.9%), and of 165 cases of successful breeding, four were followed by nest construction (2.4%). This difference in nest-construction behaviour was not significant ($\chi^2 = 0.03$, 1, *df*, $P = 0.86$). There was no relationship between reproductive failure rate (number of years without breeding success/total number or tracing years) and the total number of nests in a territory ($r_s = -0.008$, $P = 0.97$).

Nest-competition hypothesis

Of the 20 Bonelli's Eagle pairs observed, three suffered from a peregrine falcon taking over their nests. After this usurpation, the eagles did not return to these nests, which were periodically occupied by falcons. However, the evicted pairs did breed in alternate nests within their territories, and breeding success was not affected by these occurrences (Wilcoxon test = 0.53, $P = 0.59$, $n = 3$). In contrast, we detected two territories with nests used by Bonelli's Eagle or Golden Eagle in different years, with both species carrying out nest-change in these cases. During the study period, one eagle clutch was eaten by a mammalian predator. This accessible nest has not been reused by eagles since that time (10 years ago) which bred in alternative nests. In all, six of the 20 Bonelli's Eagle pairs (30%) obtained some direct benefit from the use of alternative nests.

Ectoparasite-avoidance hypothesis

The average rate of nest-change in consecutive years was 0.56 ± 0.22 ($n = 20$). We found no significant relationship between the number of nests within territories and nest-change rate ($r = 0.30$, $P = 0.19$, $n = 20$), but pairs with a higher rate of nest-change enjoyed increased breeding success ($r = 0.49$, $P = 0.02$, $n = 20$).

The breeding success of pairs was negatively correlated with the total number of Diptera in nests ($r_s = -0.67$; $P < 0.00001$). Arthropods and plants associated with nests are shown in Table 1. A correlation matrix between the number of different arthropods and the percentage of plant taxa in nests (*Pinus* sp., *Quercus ilex*, *Prunus amigdalus*, *Rosmarinus officinalis*, *Hedera helix*, *Olea europaea*, *Salix* sp., *Stippa tenacissima*) showed no significant relationship ($P > 0.2$ in all comparisons). However, when we accounted for the effect of nest orientation (see Materials and methods), we found a significant and negative relationship between the total number of Diptera and the percentage of pine in the preferred (sunny) orientation ($r_s = -0.948$, $P = 0.013$, $n = 5$), but there was no significance in nests with non-preferred (shade) orientations ($r_s = -0.441$, $P = 0.38$, $n = 5$). Hence, nests with sunnier orientations and higher percentages of pine greenery had lower frequencies of Diptera larvae.

Discussion

The four major hypotheses that have been put forwarded as possible explanations for raptor pairs having alternative nests have never been tested. Despite the important consequences of multiple nest use on the ecology and conservation status of some raptor species, this topic has been unexplored during recent years, probably due to ethical issues involved with the experimental manipulation of nests or eagles. Although the results presented here are derived from an observational study, we are able to provide evidence that the existence of multiple nests helps maintain the coexistence of different raptor species and that the use of multiple nests and of pine greenery are effective in reducing nest ectoparasites. However, our data do not support the signal-function hypothesis or the frustration-nest hypothesis in the study area.

Raptors are among the few groups of birds in which population size and breeding success are clearly limited by the availability of nesting sites (Newton 1979). Andalusia, however, has the largest population of Bonelli's Eagles in Europe (270–309 pairs; Arroyo et al. 1995). Despite potential intraspecific competition within this dense population, Bonelli's Eagle nests within territories were situated together, located on the most suitable nesting cliffs (Oñativeros 1999), and there was no relationship between proximity to potential competitors and the number or dispersion of nests. This high grouping of nests within territories does not support the signal-function hypothesis.

In contrast with predictions derived from the frustration-nest hypothesis, nest construction was independent of breeding success, with similar percentages of new nests built after reproductive failures and successes. Cases of

Table 1 Breeding data, nest ectoparasites and nest plant composition for *Hieraaetus fasciatus* within the study area (eastern Andalusia) in the 1994–2004 period

Pair	Breeding success	Breeding data ^a						Ectoparasites ^b (frequency)					Plants in nests (%)		
		NN	NNU	MND	NCR	RFR	CA	Ant	Att	Cal	Car	Pho	Pinus	Quercus ilex	Other
1	1.10	3	3	215	0.50	0.28	4	2	101	20	3	0	0	18.8	81.2
2	1.00	4	3	1502	0.57	0.25	8	0	0	0	4	3	87.1	11.4	1.4
3 ^c	1.00	4	3	924	0.33	0.40	8	0	83	0	0	0	96	2	2
4 ^c	1.40	4	3	335	0.43	0.10	8	23	336	0	0	0	60.3	34.3	5.4
5 ^c	1.25	2	2	784	0.25	0.12	9	57	0	1	3	1	0	99.7	0.3
6 ^c	1.80	5	4	495	0.67	0	11	184	5	0	1	0	79.3	18.6	2.1
7	1.11	4	3	1458	0.25	0.33	4	426	2	1	0	1	0	35.7	64.3
8 ^c	1.80	4	2	601	1	0	11	0	214	0	0	0	83.5	13.7	2.8
9	1.27	3	3	282	0.50	0.18	3	0	49	0	0	0	72.5	16.5	8.3
10	1.30	2	2	12	0.50	0.10	3	186	62	0	0	0	86.8	11.9	1.3
11	1.73	18	6	390	0.70	0									
12	1.18	11	5	260	0.75	0.36									
13	1.40	4	3	443	0.29	0.10									
14	1.18	3	3	5	0.71	0.27									
15	1.50	2	2	58	0.75	0.09									
16	1.73	2	2	12	0.67	0.18									
17	1.50	4	2	633	0.40	0.10									
18	1.18	3	2	1013	0.33	0.10									
19	1.40	7	5	25	1	0.27									
20	1.34	3	2	15	0.67	0.33									

^a NN, Number of nests within territories; NNU, number of nests used; MND, maximum distance (m) between nests within a territory; NCR, nest-change rate; RFR, reproductive failure rate; CA, cliff availability (km²)

^b Ant, *Anthrenus*; Att, *Attagenus*; Cal, *Calliphoridae*; Car, *Carnidae*; Pho, *Phoridae*

^c Pairs with the nest located to preferred orientation (more information on variables in the section Materials and methods)

nest construction by raptors after reproductive failure cited in the literature are scarce and isolated. To the best of our knowledge, frustration nests have only been described from Ospreys and Golden Eagles (Brown 1976; Postupalsky 1974). Over a long study period (11 years), Fernández and Azkona (1993) detected no relationship between breeding failure and the number of nests in Golden Eagle territories. These authors also rejected the frustration-nest hypothesis and suggested that the use of multiple nests could serve to avoid ectoparasites. A possible alternative to this hypothesis is that birds may add to existing nests rather than build new nests after reproductive failures. However, we never observed eagles rebuilding existing nests after breeding failures (34 cases) in the 11 years of monitoring this population.

However, we do believe that the nest-competition hypothesis is plausible. Cases of raptor nests being usurped are frequent in the literature (Fernández and Insausti 1990; Ewins et al. 1994; Hansell 2000), and three primarily cliff-nesting raptors—in addition to the Bonelli's Eagle—occur within the study area. Despite the potential for interspecific

nest-site competition, the breeding success of Bonelli's Eagle pairs was not affected by nest competition, due to the existence of multiple nests. Similarly, although 40% of bearded vulture *Gypaetus barbatus* nests in the Pyrenees (a rugged area of northern Spain with high nest-site availability) were usurped by other species, this did not influence the breeding success of this cliff-nesting raptor (Margalida and García 1999).

Our data also support the ectoparasite-avoidance hypothesis as an explanation of the function of alternate nests and the existence of multiple nests located within a few meters of each other. The presence of ectoparasites in nests has resulted in behavioural, physiological and immunological strategies by birds to reduce the effect of parasites (Møller and Erritzoe 1996; Hart 1997; Heeb et al. 1996), even by avoiding the reuse of nests (Oppliger et al. 1994; Merino and Potti 1995). We found a clear relationship among pines, flies and breeding success; the higher the percentage of pine used in the construction of the nest, the lower the percentage of flies and the higher the breeding success.

The antiparasite hypothesis is also considered to be the most feasible explanation for why some birds bring green material to nests (Wimberger 1984; Lambrechts and Dos Santos 2000). Wimberger (1984) found that greenery use was significantly correlated with nest reuse in North American and European Falconiformes. Our results are in agreement with those of Wimberger (1984): the nest greenery identified in our study was mainly derived from trees and shrubs, although highly aromatic herbs do occur in the area. The presence of pine material in the nest correlated negatively with the number of flies in the nest. *Pinus* species have high levels of aromatic compounds (Guenther et al. 1995), which often function as insect repellents (Levin 1971)—for example, by inhibiting their moult (Clark and Mason 1988).

Blow fly larvae found in Bonelli's Eagle nests (Calliphoridae) are ectoparasites of young birds (Harold and Telford 1947; Marshall 1981; Sabrosky et al. 1989) and have an important negative impact on the breeding success of some birds (Puchala 2004). Adults are free-living flies that lay their eggs in the nest material after the bird eggs have hatched (Gold and Dahlsen 1989). The fly larvae live in the nest material and feed intermittently on chicks by sucking their blood, thereby causing nestling mortality and decreasing the breeding success of hosts (Richner et al. 1993). The relationship between dermestid beetles and raptors may approach mutualism when beetles are scarce, but it is parasitic when beetles are numerous (Phillips and Dindal 1977), since larval dermestid beetles can cause severe external lesions in the hosts (Snyder et al. 1984). In agreement with our results, other authors have failed to detect any effect of resin-rich plants (such as pines) on dermestid larvae (Rodgers et al. 1988; Fauth et al. 1991). Greenery in nests seem to be a limiting factor for ectoparasites (Levin 1971), and a sunny orientation of nests also decreases the harmful effects of nest arthropods (Olendorff and Stoddart 1974; Heeb et al. 2000). In fact, a high nest-moisture level is associated with the harmful effects of parasites, and birds in dry regions (such as the study area) have fewer ectoparasites than do birds in wet regions (Moyer et al. 2002).

Hypotheses to explain the function of alternate nests in raptors were first proposed a long time ago; however, little evidence has been put forward to support or reject these hypotheses, perhaps due to the inconvenience of experimental studies in raptors. Additional studies are needed to clarify this important aspect of raptor ecology. However, at the moment, we propose that the “nest-competition” hypothesis and, in particular, the “ectoparasite-avoidance” hypothesis are the only hypotheses supported by data.

Zusammenfassung

Mögliche Funktionen alternativer Nester bei Greifvögeln: der Fall des Habichtsadlers

Wir zeigen Daten aus einer Population des Habichtsadlers *Hieraaetus fasciatus* in Südostspanien, die für vier Hypothesen zur Funktion alternativer Nester in Greifvögeln relevant sind: (1) Nester als Werbesignal in Territorien, (2) “Frustrationsnester”, (3) Vermeidung von Nistplatzkonkurrenz und (4) Verminderung von Ektoparasiten im Nest. Der kurze Abstand der Nester innerhalb von Territorien, das Fehlen einer Korrelation zwischen der Anzahl Nester und der Entfernung zu den Nachbarn und die Konstruktion eines ähnlichen Anteils sekundärer Nester nach dem Scheitern wie nach dem Erfolg einer Brut stehen nicht im Einklang mit den beiden ersten Hypothesen. Auf der anderen Seite war die Konstruktion alternativer Nester zur Vermeidung von Konkurrenz mit anderen klippenbrütenden Greifvogelarten, die in der Nachbarschaft nisteten, offensichtlich wichtig, da 30% der Paare einen direkten Vorteil aus der Existenz alternativer Nester in ihrem Territorium zogen. Schließlich fanden wir reichlich Käfer (Dermestidae) und Zweiflügler (Carnidae, Calliphoridae and Phoridae) als Ektoparasiten in den Nestern, und die Benutzung alternativer Nestern war gemeinsam mit dem Vorhandensein grüner Zweige als Mechanismen zur Vermeidung von Ektoparasiten ein wichtiger Faktor für den Bruterfolg des Adlers. Unsere Daten lassen darauf schließen, dass die Hypothesen zur Vermeidung von Konkurrenz und insbesondere zur Verminderung von Ektoparasiten im Nest die plausibleren Erklärungen für das Vorkommen alternativer Nester bei Greifvögeln liefern.

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