

Green plant material versus ectoparasites in nests of Bonelli's eagle

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Abstract

The greenery and arthropod nest composition has been studied in a population of Bonelli's eagle *Hieraetus fasciatus* in south-east Spain, relating them to the plant availability within territories and breeding success of pairs. Greenery was invariably from trees and shrubs, with pine and oak species accounting for 78% of the nest composition in weight. All eagle pairs with *Pinus pinaster* availability in territories actively selected it for nest greenery. This pine species is characterized by a high level of aromatic compounds, particularly β -pinene, highly repellent for insects. The amount of pine greenery in the nest was correlated with a lower presence of ectoparasites in that nest (blow fly larvae, *Protocalliphora*), and higher breeding success of pairs. We discuss whether a coevolutionary process between parasites and their hosts has guided a particular nesting strategy of the eagles to improve their breeding success.

Introduction

In the evolutionary process, different breeding strategies have emerged to increase breeding success through different nest types (Collias & Collias, 1984). In this way, different bird species nest on the ground, in holes or in aerial sites, and some of them place green plant material in their nests. Sometimes, this greenery is not a proper part of the nest structure, but is placed haphazardly around the edges or inside the nest (Hansell, 2000).

Raptorial birds are more likely than passerines to use green vegetation in nest construction (Wimberger, 1984). However, most of the studies on the functional significance of greenery in nests have been performed in passerines, due to easy access to their nests and the threatened conservation status of most raptors, which prevents experimental studies. When passerine species use greenery in their nests, the plants are mainly aromatic herbs (Clark, 1991; Gwinner, 1997; Lambrechts & Dos Santos, 2000); however, greenery identified in raptor species nests was invariably from trees and shrubs, never from herbaceous species (Wimberger, 1984). Several non-exclusive hypotheses have been put forward to explain the presence of green material in bird nests:

(1) The courtship hypotheses suggest that males use green plants to attract females (Fauth, Krementz & Hines, 1991). Males carry herbs and tree leaves into their nest and also ornament them with flowers, lichens, bark, large feathers or artefacts such as ribbon, pieces of metal or plastic foil (Collias & Collias, 1984; Gwinner, 1997).

(2) Compounds in green nest material control nest-dwelling ectoparasites, because herbs can delay the development of mites, for instance by inhibiting their moult (fumigation hypothesis; Clark & Mason, 1988). These compounds are hydrocarbons, mainly monoterpenes and isoprenes (Rasmussen, 1972). A finding consistent with this hypothesis is that birds breeding in holes, in which parasites are assumed to accumulate with repeated nest use, use green nest material more frequently than open-nesters, which use their nests only once (Clark & Mason, 1988).

(3) Herbs improve the condition of the nestling, perhaps by stimulating elements of the immune system that help them to cope better with ectoparasites (medication hypothesis; Gwinner et al., 2000).

Parasites can impair the growth and survival of nestlings and the parents have evolved several strategies to reduce the cost of parasitism. One strategy is to incorporate green plant material into the nest, which can mitigate the nest-based parasite load. Thus, in nests with a large amount of green material, the fumigation hypothesis predicts that there are less nest-based parasites, and the medication hypothesis that nestlings improve their healthy condition; in both predictions, pairs increasing breeding success.

Bonelli's eagle *Hieraetus fasciatus* is an endangered European raptor (Rocamora, 1994) that, in southern Spain, nevertheless has a good conservation status and nests mainly in cliffs, within rugged landscapes (Arroyo, Ferreiro & Garza, 1995). In this paper, we present data from a Bonelli's eagle population located in the south-eastern

Iberian Peninsula, and analyse the productivity of the pairs, arthropods and green material in nests, and relate them to the availability of vegetation species within the territories. For several reasons, this population is appropriate to test hypotheses on the function of green plant material in nest: (1) territories differ in landscape, particularly in vegetation composition; (2) pairs have high nesting-site availability in their territories (Ontiveros, 1999); (3) within each territory, there are several nests used alternatively among years; (4) adults carry large amounts of green material before and during the breeding season; (5) breeding success and breeding density are weakly affected by human interference in the study area (Ontiveros & Pleguezuelos, 2003a); and (6) the population has the highest breeding success for this species in Western Europe, indicating a healthy status (Ontiveros & Pleguezuelos, 2003a,b).

Material and methods

A clumped population of Bonelli's eagle pairs was studied in eastern Andalusia (southern Spain) during the period 1994–2006. All nests included in this study were located in cliffs, because this eagle is a cliff-nesting raptor that rarely nests in trees in Spain (Arroyo *et al.*, 1995). The study area is largely mountainous, and the climate is typically Mediterranean, with the mean minimum temperatures ranging from 0.5 to 6.5 °C in winter (January), the mean maximum temperatures ranging from 28.0 to 34.5 °C in summer (July) and the mean annual rainfall ranging from 375 to 850 mm (30-year standard meteorological averages; CMA, 1997). The vegetation consists of evergreen oak *Quercus ilex*, scrubs and some species of pines *Pinus* spp., mixed with cultivated areas of cereals and orchards in the foothills, plains and valleys.

Initially, the sample was of 84 nests belonging to 20 Bonelli's eagle pairs. However, we rejected 26 nests because they were unoccupied during the study period (13 years), 19 nests because they were occupied for only 1 year (thus unsuitable for gaining an average picture for productivity of the pairs) and 28 nests because of the presence of different circumstances that prevented their inclusion in the analysis, such as nesting-cliff inaccessibility for greenery analysis, predation and human disturbance. Thus, we tracked a subsample of 11 pairs from which we recorded 45 unequivocal breeding attempts, in order to analyse nest-greenery selection and nest-greenery effects on breeding trade-offs of the eagles.

To examine each nest, we rappelled the nesting-cliff and removed plant material in a radius of 40 cm from the central point of nest, taking up to 1.5 kg of material. Bonelli's eagle nest measures on average 120 × 80 cm on the top surface and weighs dozens of kilograms (Cramp, 1998; D. Ontiveros, J. Caro, J. M. Pleguezuelos, unpubl. data). Therefore, removing up to 1.5 kg of nest material does not significantly affect the nest structure. The nest material was collected in 2002, a few days after the nestlings left each nest (2–7 days for all the pairs), avoiding interference with the breeding process. Owing to the low adult mortality of the species in

the study area (Real & Mañosa, 1997; pers. obs.) and the maintenance of vegetal composition in territories, we assumed that the nest-greenery composition for the year 2002 was representative of the remaining years of the study period. We analysed the weight of plant species used in the nest, and the total number of ectoparasites found in the nest material.

Here, we do not test the courtship hypothesis (see 'Introduction') to explain the presence of nest greenery in bird nests, but it seems inconsistent for a raptor species such as Bonelli's eagle because (1) pairs remain stable over their lifetime; (2) both (male and female) contribute to nest building and maintenance (Newton, 1997); (3) if this hypothesis was meaningful, the courtship could be performed with dry twigs and branches, not with green material. We test the greenery effects on breeding success, which implies the confirmation of nest-greenery selection and their beneficial effects, according to the following evidences: firstly, birds collect green plant materials preferentially from species that contain compounds toxic to arthropods and secondly, that these materials in fact increase breeding success, reducing the parasite numbers in the nest by fumigation effects, or directly affecting nestlings. We tested the two conjectures as follows:

Greenery selection

Greenery material selection was tested by means of the Savage electivity index, $W_i = U_i/D_i$ (Manly, McDonald & Thomas, 1993), where $U_i = u_i/u_+$; u_i is the observed weight of the plant species in the nest i and u_+ is the total weight of nest sample, and $D_i = d_i/d_+$; and d_i is the total percentage surface occupied by the plant species in territories with respect to the total surface area of the territories (d_+). The Bonelli eagle territory in the study area, calculated from half the average distance between the central distribution of the nests of neighbouring pairs in a clumped population, has a radius of 5.0 ± 1.2 km (mean \pm SD; $n = 32$; Ontiveros, 1999). Nevertheless, all observations of eagles carrying material to nest during the study period were recorded close to the nesting cliffs; therefore, in a parsimonious way, we chose a circular surface area defined by half of the radius of the potential eagle territory as a feasible area for eagles to collect plants. To measure the vegetation surface area in this zone, the geographic information system was used on landscape maps (1:10 000) prepared by the regional government of Andalusia (Spain), executed with the ARCVIEW GIS 3.2 software. The Savage index ranges from 0 to infinite; values approach 0 for increasing avoidance, and to infinite for increasing preference. The index assumes the value 1 when use is proportional to availability. We tested the statistical significance of this index by comparing the statistic $(W_i - 1)^2/se(W_i)^2$ with the corresponding critical value of a χ^2 distribution with one degree of freedom (Manly *et al.*, 1993), and the standard error of the index $[se(w_i)]$ by $\sqrt{\{(1 - D_i)/(u_+ \times D_i)\}}$ considering the null hypotheses that the eagle are selecting the nest greenery in proportion to availability u_i .

Ectoparasite effects

For the ectoparasite analyses, we carefully checked the nest material, collecting all stages of arthropods. For parasites, we searched for larval and pupal stages, because these are better indicators of the nest-parasite population than are adult individuals (Richner & Tripet, 1999), due to fluctuating levels in adult-parasite infestation (Bize *et al.*, 2003). To evaluate the importance of greenery in repelling ectoparasites, we related the percentage of plant species present in nest with the number of ectoparasite larvae, and eagle-pair breeding success. Breeding success was defined as the average productivity for each pair in each nest (the average number of fledglings raised per year). We also considered the nest-change rate (number of possible nest-changes/number of nest-changes), an index of alternative nest function within territories better than simply nest number, and the cliff availability (UTM $1 \times 1 \text{ km}^2$ with suitable nesting-cliffs within territories; Ontiveros, 1999).

Because of the different amount of nest materials obtained and the wide range of nest occupancy in the sample, we performed partial correlation tests, controlled by the weight of sample material of nest as a covariate, and accomplished with a weighting option for years of nest occupancy. The weight option allowed us to adjust the contribution of individual cases to the outcome of an analysis (Sokal & Rohlf, 1998).

Results

During this study, the laying period of the Bonelli's eagle ranged between 28 January and 24 February, and fledglings left the nest between 12 May and 10 June. The mean breeding success was 1.28 fledglings per pair ($SD = 0.33$), and each nest was occupied a mean of 4.27 years ($SD = 2.32$), these results being derived from 45 breeding attempts during the 13 years of the study.

The greenery identified in nests was invariably from trees and shrubs, pine and oak species grouping 78% of nest composition, with a minor presence of other plants (Table 1). Pines (*Pinus halepensis* and *Pinus pinaster*) were the main aromatic plants found in the nests, and we calculated the Savage index only for these species. Three out of the 11 territories were devoid of pine species, and we found seven with a significant positive selection of pine material for nests and one with a significant negative selection (Table 2). The territories with pines were occupied by *P. pinaster*, except territory 10, which harboured only *P. halepensis*, and was just in this territory where we found a negative selection for

pine material in nest. The percentage of *P. pinaster* in nests was correlated with the breeding success of pairs ($r_{\text{partial}} = 0.82$; $P = 0.004$), i.e. more pine greenery in nests and more fledglings per nest.

Diptera were the only ectoparasites found in Bonelli's eagle nests (Table 2), specifically blow fly larvae (family Calliphoridae, genus *Protocalliphora*), other arthropods being Coleoptera and Miriapoda. There was a highly significant and negative relationship between the percentage of *P. pinaster* material and the number of blow fly larvae in nests ($r = -0.78$; $P < 0.008$), and between the number of blow fly larvae and the breeding success of the nests ($r_{\text{partial}} = -0.73$; $P = 0.017$).

We failed to find any relationship between the percentage of *P. pinaster* surface and number of nests in territories ($r = 0.48$; $P = 0.12$), or the nest-change rate ($r = 0.39$; $P = 0.22$), both variables transformed. When partial correlations were performed in order to control for the factor cliff availability within territories, we neither found a relationship between percentage of *P. pinaster* and number of nests, nor nest-change rate ($r_{\text{partial}} > 0.48$; $P > 0.15$ in both comparisons).

Discussion

The nest greenery identified in the present study was invariably from trees and shrubs, never from herbaceous species, as in passerine nests. This finding coincides with the results of Wimberger (1984), who found that, in North American and European Falconiformes, greenery use varies geographically within a species in relation to the availability of suitable plant species, but at the moment, the greenery selection was not assessed, as we did for pine greenery in the present study. Furthermore, we found a clear relationship among pines, flies and breeding success: the higher the percentage of pine in nests, the lower the amount of parasite flies, and the higher the breeding success of eagle pairs.

It has been demonstrated that some passerines species collect green plant materials preferentially from species that contain compounds toxic to arthropods, (Sengupta, 1981; Clark & Mason, 1988; Lambrechts & Dos Santos, 2000). The wood stork *Micrateria americana* stocks its nest with green plants such as cypress, red cedar, wax myrtle or pines. These preferred plants are rich in resins, and are, therefore, expected to repel ectoparasites (Rodgers, Wenner & Schwirker, 1988). In this way, we also found greenery from pines as the most abundant plant in nests of Bonelli's eagle.

The groups of ectoparasites most responsible for host mortality in nestling birds are Diptera, fleas, ticks and mites

Table 1 Average weight (in percentage) and standard deviation (SD) of green plant species within Bonelli's eagle *Hieraaetus fasciatus* nests

	<i>Pinus pinaster</i>	<i>Pinus halepensis</i>	<i>Quercus ilex</i>	<i>Salix</i> sp.	<i>Olea europaea</i>	<i>Prunus dulcis</i>	<i>Rosmarinus officinalis</i>	<i>Stipa tenacissima</i>	<i>Hedera</i> sp.	Unidentified
Mean	50.8	0.27	27.1	0.09	0.0009	3.2	1.43	0.03	0.01	12.2
SD	44	0.9	26.4	0.2	0.0003	9.2	4.6	0.12	0.04	24.6
n	7	1	11	2	1	2	2	1	1	3

n, number of nests with presence of any of the identified species for 11 territories of Bonelli's eagle in the south-eastern Iberian Peninsula.

Table 2 Percentage of plant species in nests (U_i), percentage of plant species availability in territories (D_i), Savage index (W_i) for *Pinus pinaster* except in pair 10 (for *Pinus halepensis*), productivity of Bonelli's eagle pairs (b.s), breeding attempts (n), and total number of Diptera in each nest-greenery sample for 11 territories of Bonelli's eagle *Hieraaetus fasciatus* in the south-eastern Iberian Peninsula

Pair	Plant in nests (U_i)				Plant species availability (D_i)				W_i	χ^2	P	b. s. (n)	Diptera
	<i>P. halepensis</i>	<i>P. pinaster</i>	<i>Q. uercus ilex</i>	Other	<i>P. halepensis</i>	<i>P. pinaster</i>	<i>Q. ilex</i>	Other					
1	0	0	18.8	81.2	0	0	0.6	99.4	0	–	–	1 (2)	23
2	0	87.1	11.4	1.4	0	63.8	2.4	33.8	1.85	7.22	0.007	1.33 (3)	7
3	0	60.3	34.3	5.4	0	11.5	0.11	88.4	5.24	189	<0.00001	1.5 (4)	1
4	0	96	2	2	0	63.8	2.4	33.8	2.04	11.15	0.0008	1.5 (2)	1
5	0	0	99.7	0.3	0	0	21.4	77	0	–	–	1.28 (7)	5
6	0	79.3	18.6	2.1	0	35.2	8.4	56.4	2.26	16.2	0.0005	1.7 (5)	1
7	0	0	35.7	64.3	0	0	0.6	99.4	0	–	–	1 (3)	2
8	0	83.5	13.7	2.8	0	35.2	8.4	56.4	2.37	17.1	0.00003	1.66 (3)	0
9	0	75.5	16.5	8.3	0	18.5	19.4	62.1	4.06	97.5	<0.00001	1.33 (3)	0
10	2.7	0	35.7	61.6	30.4	0	6.25	63.4	–0.009	65.3	<0.00001	1 (3)	9
11	0	86.8	11.9	0	1.3	18.5	19.4	62.1	4.69	142	<0.00001	1.5 (10)	0

(Herman, 1955). Particularly, the *Protocalliphora* fly larvae that we found in nest overwinter and emerge about the time the eggs hatch (Tirrell, 1978; Marshall, 1981). Ectoparasites can have negative effects on the fitness of their host, reducing the growth and survival of nestlings (Richner & Heeb, 1993; Oppliger, Richner & Christe, 1994; Merino & Potti, 1995; Fitze, Tschirren & Richner, 2004), causing anaemia (Clark & Mason, 1988; Fauth *et al.*, 1991), increasing the metabolic rate (Møller *et al.*, 1994), affecting dispersal (Brown & Brown, 1992) and contributing to the mortality of some raptors (Philips & Dindal, 1977; Delannoy & Cruz, 1991). Moreover, parasites may not directly affect the mortality of nestlings or adults; rather, in a more subtle way, they may affect morbidity (Clark, 1991), thereby inflicting greater impact on birds than simply nest mortality.

Blow fly larvae found in Bonelli's eagle nests (*Protocalliphora*) are ectoparasites of birds (Harold & Telford, 1947; Marshall, 1981; Sabrosky, Bennett & Hitworth, 1989) and other authors have demonstrated the important negative impact on the breeding success of some birds (Hurtz-boussès *et al.*, 1998; Bize *et al.*, 2004; Puchala, 2004) and the increase of parental effort in parasited nests (Hurtz-boussès *et al.*, 1998). Adults are free-living flies that lay their eggs in the nest material, after the host eggs hatch (Gold & Dahlsten, 1989). The fly larvae live in the nest material and feed intermittently on birds by sucking their blood, causing nestling mortality and decreasing the breeding success of hosts (Richner, Oppliger & Christe, 1993).

The antiparasite hypothesis is considered to be the most feasible explanation for why some birds use alternative nests, and bring green material to the nest (Wimberger, 1984; Lambrechts & Dos Santos, 2000). In fact, given a choice between used and unused nests, some bird species chose the unused and parasite-free nests significantly more often (Stanback & Dervan, 2001). In response to parasitism, birds have evolved behavioural, physiological and immunological strategies to reduce the effect of parasites (Heeb *et al.*, 1996; Møller & Erritzoe, 1996; Hart, 1997). When

detecting the presence of ectoparasites in their nests, the host can avoid parasite contact by changing nest sites and/or carrying aromatic plants to nests (Oppliger *et al.*, 1994; Christe, Richner & Oppliger, 1996a; Lambrechts & Dos Santos, 2000). The host can also counteract these detrimental effects with increased preening and nest sanitation, and by actively removing ectoparasites from the nestlings (Fraga, 1984; Christe *et al.*, 1996a) and/or increasing the feeding rate (Christe, Richner & Oppliger, 1996b). However, ultimately, parents may pay the cost of ectoparasitism by a reduction in future reproductive success, which may be mediated by the increase in current parental effort (Richner & Tripet, 1999).

The aromatic compounds of plants are hydrocarbons, mainly monoterpenes and isoprenes (Rasmussen, 1972). Pine species have high levels of aromatic compounds (Guenther *et al.*, 1995), which often function as insect repellents (Levin, 1971), for instance, by inhibiting the insect moult (Clark & Mason, 1988). Moreover, the maximum concentration of terpenes is produced by Mediterranean species in the coldest season of the year (Llusià *et al.*, 2006) and under wet conditions (Llusià & Peñuelas, 1998), periods that in the Mediterranean habitats of the study area coincide with the nest occupancy by Bonelli's eagles (Arroyo *et al.*, 1995). *Pinus halepensis* can be characterized on the basis of its significant α -pinene content, and *P. pinaster* on the basis of its β -pinene content (Gomes da Silva *et al.*, 2001), and it has been demonstrated that the former is attractive and the latter highly repellent for insects (Heikkinen & Hrutfiord, 1965). Thus, the only pair that negatively selected pine material for nests (pair 10; Table 2) had no availability of *P. pinaster* in the territory.

Finally, we could think that territories with a low abundance of *P. pinaster* must have a larger number of nests, but this prediction is not suitable for a cliff-nesting raptor as Bonelli's eagle. In this raptor, the number of nests within territories depends primarily on cliff availability, which differs among territories (Ontiveros, 1999), preventing more nests actually in some of them.

The knowledge of the interaction between parasites and their hosts is necessary to understand the factors influencing the breeding success of raptors, and possible coevolutionary mechanisms with their specific parasites. In this study, we demonstrate that a raptor species actively selects a pine species as greenery for their nests, the amount of this pine in the nest being negatively correlated with the number of ectoparasites and positively with the breeding success of pairs. Our results agree with data published previously (Wimberger, 1984; Merino & Potti, 1995; Hurtrez-Boussès *et al.*, 1997) but add several new contributions, such as the active selection of insect-repellent plant species for greenery, and the confirmation of the fumigation hypothesis in a species that do not bring herbaceous species to nest. In this way, the significance of the nest ectoparasite burden of birds reusing their nests must be a determining factor for their breeding success. More evidence supporting this idea includes the frequent use of alternative nests and the positive correlation with breeding success of the eagles (Ontiveros & Pleguezuelos, 2003a), and the selection of sunny orientation of nests in Bonelli's eagle (Ontiveros, 1999), which may reduce the burden of the nests (Olendorff & Stoddart, 1974), as strategies in the war against ectoparasites.

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References

- Arroyo, B., Ferreiro, E. & Garza, V. (1995). *El Águila perdicera (Hieraaetus fasciatus) en España. Censo, reproducción y conservación*. ICONA. Madrid: Serie Técnica.
- Bize, P., Roulin, A., Pfluger, D. & Richner, H. (2003). Parasitism and developmental plasticity in Alpine swift nestlings. *J. Anim. Ecol.* **72**, 633–639.
- Bize, P., Roulin, A., Tella, J.L., Bersier, L. & Richner, H. (2004). Additive effects of ectoparasites over reproductive attempts in the long-lived alpine swift. *J. Anim. Ecol.* **73**, 1080–1088.
- Brown, C.R. & Brown, M.B. (1992). Ectoparasitism as a cause of natal dispersal in cliff swallows. *Ecology* **73**, 1718–1723.
- Christe, P., Richner, H. & Oppliger, A. (1996a). Great tits and fleas: sleep baby sleep. *Anim. Behav.* **52**, 1087–1092.
- Christe, P., Richner, H. & Oppliger, A. (1996b). Begging, food provisioning and nestling competition in great tit broods infested with ectoparasites. *Behav. Ecol.* **72**, 127–131.
- Clark, L. (1991). The nest protection hypothesis: the adaptive use of plant secondary compounds by European starlings. In *Bird–parasite interactions*: 205–221. Loye, J.E. & Zuk, M. (Eds). Oxford: Oxford University Press.
- Clark, L. & Mason, J.R. (1988). Effect of biologically active plants used as nest material and the derived benefit to starling nestling. *Oecologia* **95**, 234–240.
- CMA (1997). *La información ambiental de Andalucía*. CMA: Junta de Andalucía.
- Collias, N.E. & Collias, E.C. (1984). *Nest building and bird behaviour*. New Jersey: Princeton University Press.
- Cramp, S. (1998). *The complete birds of the Western Palaearctic. Software optimedia*. Oxford: Oxford University Press.
- Delannoy, C.A. & Cruz, A. (1991). Philornis parasitism and nestling survival of the Puerto Rican sharp-shinned hawk. In *Bird–parasite interactions*: 93–103. Loye, J.E. & Zuk, M. (Eds). Oxford: Oxford University Press.
- Fauth, P.T., Krementz, D.G. & Hines, J.E. (1991). Ectoparasitism and the role of green nestling material in the European starlings. *Oecologia* **88**, 22–29.
- Fitze, P.S., Tschirren, B. & Richner, H. (2004). Life history and fitness consequences of ectoparasites. *J. Anim. Ecol.* **73**, 216–226.
- Fraga, R.M. (1984). Bay-winged cowbirds *Molothrus badius* remove ectoparasites from their brood parasites the screaming cowbirds *Molothrus rufoaxillaris*. *Biotropica* **16**, 223–226.
- Gold, C.S. & Dahlsten, D.L. (1989). Prevalence, habitat selection and biology of Protocalliphora (Diptera: Calliphoridae) found in nests of mountain and chestnut-backed chickadees in California. *Higardia* **57**, 1–19.
- Gomes da Silva, M.D.R., Mateus, E.P., Munhá, J., Drazyk, A., Farrall, M.H., Paiva, M.R., Chaves das Neves, H.J. & Mosandl, A. (2001). Differentiation of then pine species from Central Portugal by monoterpene enantiomer-selective composition analysis using multidimensional gas chromatography. *Chromatog.* **53** (Suppl.), 412–416.
- Guenther, A., Hewitt, C.N., Erickson, D., Fall, R. & Geron, C. (1995). A global model of natural volatile organic emissions. *J. Geophys. Res.* **100**, 8873–8892.
- Gwinner, H. (1997). The function of green plants in nest of European starlings *Sturnus vulgaris*. *Behaviour* **134**, 337–351.
- Gwinner, H., Oltrogge, M., Trost L., & Nienaber, U. (2000). Green plants in starling nest: effects on nestlings. *Anim. Behav.* **59**, 301–309.
- Hansell, M. (2000). *Bird nests and construction behaviour*. Cambridge: Cambridge University Press.
- Harold, M.H. & Telford, H.W. (1947). Protocalliphora larvae infesting nestling birds of prey. *Condor* **49**, 74–75.
- Hart, B.L. (1997). Behavioural defence. In *Host–parasite evolution*: 59–77. Clayton, D.H. & Moore, J. (Eds). Oxford: Oxford University Press.
- Heeb, P., Werner, I., Richner, H. & Kölliker, M. (1996). Horizontal transmission and reproductive rates of hen fleas in Great Tit nest. *J. Anim. Ecol.* **65**, 474–484.
- Heikkinen, H.J. & Hrutfiord, B.F. (1965). *Dendroctonus pseudotsugae*: a hypothesis regarding its primary attractant. *Science* **150**, 1457–1459.

- Herman, C.M. (1955). Diseases of birds. In *Recent studies in avian biology*: 450–467. Wolfson, A. (Ed.). Urbana, IL: University Illinois Press.
- Hurtrez-Boussès, S., Blondel, J., Perret, P., Fabrequettes, J. & Renaud, F. (1998). Chick parasitism by blowflies affects feeding rates in a Mediterranean population of blue tits. *Ecol. Lett.* **1**, 17–20.
- Hurtrez-Boussès, S., Perret, P.J., Renaud, F. & Blondel, J. (1997). High blowfly parasitic loads affect breeding success in a Mediterranean population of blue tits. *Oecologia* **112**, 514–517.
- Lambrechts, M.M. & Dos Santos, A. (2000). Aromatic herbs in Corsican blue tit nests: the Potpourri hypothesis. *Acta Oecol.* **21**, 175–178.
- Levin, D.A. (1971). Plant phenolics: an ecological perspective. *Am. Nat.* **105**, 157–181.
- Llusià, J. & Peñuelas, J. (1998). Changes in terpene content and emission in potted Mediterranean woody plants under severe drought. *Can. J. Bot.* **76**, 1366–1373.
- Llusià, J., Peñuelas, J., Alessio, G.A. & Estiarte, M. (2006). Seasonal contrasting changes of foliar concentrations of terpenes and other volatile organic compound in four dominant species of Mediterranean shrubland submitted to a field experimental drought and warming. *Physiol. Plant.* **127**, 632–649.
- Manly, B.F., McDonald, L.L. & Thomas, D. (1993). *Resource selection by animals. Statistical design and analysis for field studies*. London: Chapman and Hall.
- Marshall, A.G. (1981). *The ecology of ectoparasitic insects*. London: Academic Press.
- Merino, S. & Potti, J. (1995). Mites and blowflies decrease growth and survival in nestlings pied flycatchers. *Oikos* **73**, 95–103.
- Møller, A.P., De Lope, F., Moreno, J., González, G. & Perez, J.J. (1994). Ectoparasites and host energetics: house martin bugs and house martin nestlings. *Oecologia* **98**, 263–268.
- Møller, A.P. & Erritzoe, J. (1996). Parasite virulence and host immune defence: host immune response is related to nest reuse in birds. *Evolution* **50**, 2066–2072.
- Newton, I. (1997). *Population ecology of raptors*. Berkhamsted: T. and A.D. Poyser.
- Olendorff, R.R. & Stoddart, J.W. (1974). Management of raptors. In *The potential for management of raptor populations in western Grasslands, Raptor Research Report No. 2*: 47–88. Hamerstrom, F.N., Harrell, B.E. & Olendorff, R.R. (Eds). Raptor Research Foundation: Vermillion, SD, USA.
- Ontiveros, D. (1999). Selection of nest cliff by Bonelli's eagle (*Hieraetus fasciatus*) in southeastern Spain. *J. Raptor Res.* **33**, 110–116.
- Ontiveros, D. & Pleguezuelos, J.M. (2003a). Physical, environmental and human factors influencing breeding success of Bonelli's eagle *Hieraetus fasciatus* in Granada (SE Spain). *Biodivers. Conserv.* **12**, 1193–1203.
- Ontiveros, D. & Pleguezuelos, J.M. (2003b). Influence of climate on Bonelli's eagle (*Hieraetus fasciatus* V.) breeding success through the Western Mediterranean. *J. Biogeogr.* **30**, 755–760.
- Oppliger, A., Richner, H. & Christe, P. (1994). Effect of an ectoparasites on lay date, nest-site choice, desertion, and hatching success in the great tit (*Parus major*). *Behav. Ecol.* **5**, 130–134.
- Philips, J.R. & Dindal, D.L. (1977). Raptor nests as a habitat for invertebrates: a review. *J. Raptor Res.* **11**, 87–96.
- Puchala, P. (2004). Detrimental effects of larval blow flies (*Protocalliphora azurea*) on nestlings and breeding success of Tree Sparrows (*Passer montanus*). *Can. J. Zool.* **82**, 1285–1290.
- Rasmusen, R.A. (1972). What do the hydrocarbons from trees contribute to air pollution? *J. Air Pollut. Assoc.* **22**, 537–543.
- Real, J. & Mañosa, S. (1997). Demography and conservation of Western European Bonelli's Eagle (*Hieraetus fasciatus*) populations. *Biol. Conserv.* **79**, 59–66.
- Richner, H. & Heeb, P. (1993). Effect of an ectoparasite on reproduction in great tits. *J. Anim. Ecol.* **62**, 703–710.
- Richner, H., Oppliger, A. & Christe, R. (1993). Effect of an ectoparasites on reproduction in great tits. *J. Anim. Ecol.* **62**, 703–710.
- Richner, H. & Tripet, F. (1999). Ectoparasitism and the trade-off between current and future reproduction. *Oikos* **86**, 535–538.
- Rocamora, G. (1994). Bonelli's eagle *Hieraetus fasciatus*. In *Birds in Europe, their conservation status. Birdlife Conservation, Series 3*: 184–185. Tucker, G.M. & Heath, M.F. (Eds). Cambridge, UK: Birdlife International.
- Rodgers, J.A. Jr., Wenner, A.S. & Schwikerst, S.T. (1988). The use and function of green nest material by wood storks. *Wilson Bull.* **100**, 411–423.
- Sabrosky, C.W., Bennett, G.E. & Hitworth, T.L. (1989). *Bird blow flies (Protocalliphora) in North America (Diptera: Calliphoridae) with notes on the Palaearctic species*. Washington, DC: Smithsonian Institution Press.
- Sengupta, S. (1981). Adaptive significance of the use of Margosa leaves in nests of house sparrows *Passer domesticus*. *Emu* **81**, 114–115.
- Sokal, R.R. & Rohlf, F.J. (1998). *Biometry*. 3rd edn. New York: Freeman.
- Stanback, M. & Dervan, A.A. (2001). Within-season nest-site fidelity in Eastern Bluebirds: disentangling effects of nest success and parasite avoidance. *Auk* **118**, 743–745.
- Tirrell, P.B. (1978). Protocalliphora avium (Diptera) myiasis in great horned owls, red-tailed hawks, and Swainson's hawks in North Dakota. *J. Raptor Res.* **12**, 21–27.
- Wimberger, P.H. (1984). The use of green plant material in bird nest to avoid ectoparasites. *Auk* **101**, 615–618.