

## Attack success in Bonelli's Eagle *Aquila fasciata*

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This paper presents the first study of foraging behaviour and hunting success in Bonelli's Eagle. Attack success was modelled as a function of biological and environmental variables using observations made during a long-term monitoring. The overall attack success was 28.2%, based on 110 attack observations recorded between 1985 and 2008 in south-eastern Spain. Group size of prey was the most explicative independent variable, indicating that the probability of attack success declined with increasing prey group size. Surprise was the main and most successful attack mode, mainly on preys foraging on the ground. The probability of success in surprise and non-surprise attacks probably declined with prey group size due to the effects of vigilance and confusion, respectively. The best model for attack success also suggested that attacks were more likely to be successful when directed at prey in areas with low bush canopy cover. This finding highlights the importance of open habitat types which provide foraging opportunities for the Bonelli's Eagle. Management measures for increasing open habitats in territories may create a habitat structure more favourable for prey detection by Bonelli's Eagles.



### 1. Introduction

Many prey-related factors may affect hunting success, such as species, behaviour and vulnerability (Quinn & Cresswell 2004, Cresswell *et al.* 2010), sex and age (Kenward 2006) and group size (Kenward 1978, Lindström 1989, Funston *et al.* 2001, Roth & Lima 2003, Cresswell & Quinn 2010). Al-

ternatively, from the predator point of view, hunting success may be related to the type of predator, sex and age or experience (Desrochers 1992, Rutz *et al.* 2006, Daunt *et al.* 2007), but also by the individual characteristics of the predator (Sand *et al.* 2006). Finally, environmental factors such as season, habitat type (Redpath *et al.* 2002, Blumstein *et al.* 2004, Ebensperger & Hurtado 2005, Katzner

*et al.* 2006) and weather conditions (McGowan *et al.* 2002) will also influence the outcome. Two important components in the kill rates of large predators are the variation in attack success between solitary prey and groups of prey (Sand *et al.* 2006) and the degree of structural complexity of the physical environment (Andruskiw *et al.* 2008). Here we explore these two important components in the Bonelli's Eagle.

First, several studies have shown declines in attack success rate with increasing group size in a wide number of taxa, including raptors (Kenward 1978, Krause *et al.* 1998, Funston *et al.* 2001, Roth & Lima 2003, Cresswell & Quinn 2004). Similarly, there are studies that describe how the frequency of attacks depends on group size because groups tend to be more conspicuous than solitary animals (Vine 1973) and are therefore more prone to being attacked (Lindström 1989, Botham *et al.* 2005, Carere *et al.* 2009, Zuberogoitia *et al.* 2012). The selective benefits of group living may increase with the group size, although this will depend on the predator species and hunting mode, with group size providing benefits through both detection and confusion for predators that catch prey by surprise and that escape by flying away in groups (Cresswell & Quinn 2010). Being in a group decreases the probability of an individual being attacked and increases predator confusion during an attack (Lima 1995, Bednekoff & Lima 2005, Ale & Brown 2007). Another benefit is that individuals in large groups can diminish the amount of time they spend on vigilance, while maintaining the probability of a predator being detected, thus potentially increasing foraging time and the amount of food that can be consumed (Sansom *et al.* 2008).

Second, in semi-arid Mediterranean landscapes, crops provide the main food for prey species that form part the bulk of the Bonelli's Eagle diet (Cramp & Simmons 1980, Moreno *et al.* 1996, Calvete *et al.* 2004, Vargas *et al.* 2006, Tapia & Domínguez 2007). Habitat structure can affect the ability to detect and to access prey and may favour the characteristic hunting behaviour of a predator species (Arlettaz *et al.* 2010). A high degree of vegetation cover may hinder hunting manoeuvrability and favour the prey species (Ontiveros *et al.* 2005). However, Bonelli's Eagles may make use of the terrain to launch surprise attacks

with dense vegetation cover enabling it to get near its potential prey without being observed (Real 1982). Alternatively, a low degree of vegetation cover might facilitate exposure to the bird of prey, although the abundance of potential prey on the ground in given situations may not *per se* be a good indicator of food accessibility (Thirgood *et al.* 2003, Ontiveros *et al.* 2005), because it may then be more difficult for an eagle to get close without being detected.

The Bonelli's Eagle *Aquila fasciata*, is a large raptor considered endangered in Europe, where it has a population estimated at 920–1,100 pairs (BirdLife International 2004). Currently there is no information available on biological and environmental factors that could be determinant in its selection of foraging habitat and hunting success. Bonelli's Eagles prefer open areas for nesting and hunting potential prey (Carrete *et al.* 2002, Ontiveros *et al.* 2005, López-López *et al.* 2006, Carrascal & Seoane 2009). They preferentially attack prey by surprise on or near the ground, although they can also harass and hunt prey in short pursuits (Cramp & Simmons 1980, Real 1982, Ferguson-Lees & Christie 2004). Both modes of hunting can be carried out by individuals alone or in a pair (Cramp & Simmons 1980). Recent studies on the diet of this species indicate the preferential capture of European Rabbits *Oryctolagus cuniculus* when they are relatively abundant, with other prey being selected only when rabbits are scarce, normally Red-legged Partridges *Alectoris rufa* and Pigeons *Columba* spp. (Gil-Sánchez *et al.* 2004, Palma *et al.* 2006, Moleón *et al.* 2007). All these prey species tend to live in groups (Cramp & Simmons 1980, Monclús & Rödel 2008).

In this paper, we test three hypotheses to explain possible variation in the attack success of Bonelli's Eagle. We predict that attack success will (1) decrease with prey group size, (2) increase with low vegetation cover that may facilitate accessibility to prey and (3) decrease with increasing prey group size for both surprise and non-surprise attacks.

## 2. Methods

The study area covers 31 breeding territories and 1 dispersal area where every year an indeterminate number of non-breeding individuals gather (Bal-

Table 1. Variables used in models to analyse attack success for Bonelli's Eagles in south-eastern Spain.

Acronym	Definition
SEX-AGE	Sex and age related to the mode of hunting. Categorical variable with four classes: female solo-hunt (FEMALE) vs. male solo-hunt (MALE) vs. pairs-hunt (TANDEM) vs. undetermined sex (UNDET; i. e., non-adult individuals).
AGE	Age of the individual. Categorical variable with two classes: adults (ADULT) vs. non-adult individuals (NON ADULT; i. e., juveniles, immature and sub-adults).
ATTACK	Eagle location at the beginning of the attack. Categorical variable with two classes: PERCHED vs. FLIGHT.
MODE	Attack mode. Categorical variable with two classes: SURPRISE vs. NON-SURPRISE.
PREY-LOCATION	Prey location at the beginning of the attack. Categorical variable with two classes: AIR vs. SOIL.
GROUP	Prey group size. Discrete quantitative variable (range 1–50).
PREY-TYPE	Prey type which corresponds to each type of habitat utilization (PT1: species which breed on the ground and feed on the ground; PT2: species which do not breed on the ground and forage on the ground; PT3: other species).
HABITAT	Habitat type. Categorical variable with two classes: open shrubs (OPEN) vs. closed shrubs (CLOSED).

bontín 2005), all lying within the provinces of Murcia and Almería, SE Spain (for more details on the distribution of species, see Martínez *et al.* 2010a). This is a mountainous area largely covered by scrubland and small extensions of forests surrounded by a heterogeneous landscape of dryland and irrigated crops interspersed with urban areas (Martínez *et al.* 2008b).

All hunting attacks were recorded during monitoring of nesting territories (minimum number of visits per season was 6) and by counting dispersing individuals from fixed census stations and vehicles in order to estimate the number of individuals between September and December (1985–2008) in the dispersal area (Mañosa *et al.* 1998). Although observations were made by different observers, the attacks and captures were unambiguous and were recorded in the same way by all observers (Redpath *et al.* 2002). Between January 1985 and December 2008, 110 Bonelli's Eagle attacks were recorded by direct observation: 90 by adult territorial birds and 20 by non-adults. An attack was defined as direct rapid flight towards a clearly identifiable prey (Cresswell 1994), and a capture was an attack that resulted in the raptor catching hold of the prey (Cresswell & Quinn 2004). In this way, every attack was classified as success or failure. Observations were made from points with good visibility, which consisted in

making scans noting the predator, the prey and/or the groups of prey within a radius of 400–500 m around the observer (Altmann 1974, Kitowski 2003). All capture attempts with undetermined outcomes were excluded from analysis (Collopy 1983). Overall, 14 of 124 (11.30%) attempts by eagles were of unknown capture success due to distance from observer and/or local topography.

Eight variables were recorded for each attack (Table 1). The age of the individuals was classified as ADULT or NON-ADULT (juveniles, immature and sub-adults, up to 4 calendar years) in agreement with plumages described by Parellada (1984) and Forsman (1999). In adult territorial individuals, sex was determined by direct observation based on the sexual dimorphism exhibited by the species – males in general having a smaller wingspan and paler plumage than females, which tended to be larger, darker and showing a greater contrast between ventral and dorsal feathers (Parellada 1984, Forsman 1999). Attacks on the part of individuals whose sex could not be determined in breeding and dispersal areas were excluded from analysis (Collopy 1983). It was also noted whether the eagles attacked alone or in pairs. The type of attack was defined by the position of the eagle at the beginning of the attack (from a perch or in flight). The attack mode was classified into two types: surprise and non-surprise (Cress-

well 1996). The position of the prey at the outset of the attack was classified as on the ground (SOIL) or in flight (AIR). In order to evaluate the effect of group size, the number of individuals attacked was established as a discrete quantitative variable (1–50). The groups of prey attacked were composed of different species of birds (Pigeons, Red-legged Partridges, etc). In contrast, solitary prey attacked by eagles were mammals (predominantly European Rabbits) or reptiles (Ocellated Lizards).

The type of prey attacked was classified as a function of its habitat use according to the classification of Delibes *et al.* (1975): class 1, species that breed and forage on or from the ground; class 2, species that do not breed on the ground but forage on or from the ground; class 3, other species (those that breed in a variety of places and forage in the air and those that breed and forage in water or in wetlands). The mean weights attributed to the prey species attacked by Bonelli's Eagle were taken from Snow and Perrins (1998a, b), and Martínez and Calvo (2005). Finally, we recorded the habitat type of surroundings where the prey was at the beginning of the attack. This was classified as open (such as grasslands and open scrublands), characterised by low vegetation cover or closed, characterised by high vegetation cover (such as dense scrublands and trees). The habitat type were classified as open when the vegetation cover in a 20 m radius of the prey was 1–69% and closed when the vegetation cover was more than 70%.

Following the methodological approach outlined by Burnham and Anderson (2002), we used the set of variables shown in Table 1 to develop 8 a priori hypothesized models to explain attack success (Table 2). The strategy of selecting a reduced set of candidate models guards against the risk of overfitting and finding spurious relationships (Johnson & Omland 2004). We used generalized linear mixed models (GLMMs) to examine the effects of the selected variables on attack success. GLMMs are an extension of generalized linear models to accommodate dependence among observations within groups (territories in our case), considering both fixed and random effects. We considered territory as a random effect (Franklin *et al.* 2000, Martínez *et al.* 2008a), and the rest of the variables as fixed effects. As attack success was modelled as a binary variable (1 = success, 0 = failure), we used a logit link function (with binomial

Table 2. *A priori* hypothesized mixed models used to relate the effects of biological and environmental factors with attack success in the Bonelli's Eagle. Acronyms are described in Table 1.

Hypothesized model	Model structure	Expected results
$\theta_{\text{SEX-AGE}}$	$\beta_0 + t_i + \beta_1 \text{ FEMALE} + \beta_2 \text{ MALE} + \beta_3 \text{ TANDEM}$	$\beta_3 > \beta_2 > \beta_1 > 0$
$\theta_{\text{AGE}}$	$\beta_0 + t_i + \beta_1 \text{ ADULT}$	$\beta_1 > 0$
$\theta_{\text{ATTACK}}$	$\beta_0 + t_i + \beta_1 \text{ FLIGHT}$	$\beta_1 < 0$
$\theta_{\text{MODE}}$	$\beta_0 + t_i + \beta_1 \text{ SURPRISE}$	$\beta_1 > 0$
$\theta_{\text{PREY-LOCATION}}$	$\beta_0 + t_i + \beta_1 \text{ AIR}$	$\beta_1 < 0$
$\theta_{\text{GROUP}}$	$\beta_0 + t_i + \beta_1 \text{ GROUP}$	$\beta_1 < 0$
$\theta_{\text{PREY-TYPE}}$	$t_i + \beta_1 \text{ PT1} + \beta_2 \text{ PT2}$	$\beta_1 > \beta_2 > 0$
$\theta_{\text{HABITAT}}$	$\beta_0 + t_i + \beta_1 \text{ OPEN}$	$\beta_1 > 0$

error distribution) for attack success models. Analyses were performed with the R statistical package (R Core Team 2013), using the “glmmML” package (Broström & Holmberg 2011).

We followed an information-theoretic approach in the analysis of our data (Burnham & Anderson 2002). Model comparisons were based on the bias-corrected version of Akaike's information criterion (AICc), and were ranked using AICc differences ( $\Delta_i$ ) and Akaike weights ( $w_i$ ). We initially tested and compared the base models in Table 2. Then, using the best a priori models as starting points (Franklin *et al.* 2000), we examined nine additional models that included interactions and combinations of the predictor variables and the quadratic model for the quantitative variable GROUP.

### 3. Results

The overall success rate of attacks was 28.2% (79 failures and 31 prey captures were observed,  $n = 110$ ). Of the 110 attacks recorded, those launched from a perch (tall cliffs) were the most frequent (55.5%,  $n = 61$ ). The rest (44.5%,  $n = 49$ ) were launched in flight.

The most frequently attacked prey species were Pigeons (51.8%) followed by Rabbits (14.5%) and Red-legged Partridges (12.7%). The mean weight of the prey attacked by males was  $416 \pm 65$  g ( $n = 32$ ), by females  $459 \pm 78$  g ( $n = 20$ ) and by a pair,  $360 \pm 60$  g ( $n = 34$ ). There were no statistical differences in the body mass of the prey

Table 3. Ranking, based on AICc, of *a priori* hypothesized models used to explain attack success in the Bonelli's Eagle. *K*: number of parameters estimated;  $\Delta_i$ : AICc differences;  $w_i$ : Akaike weights.

Hypothesized model	<i>K</i>	AICc	$\Delta_i$	$w_i$	Coefficients (SE)
$\theta_{\text{GROUP}}$	3	122.4	0.0	0.81	$\beta_1 = -0.170$ (0.065)
$\theta_{\text{HABITAT}}$	3	126.5	4.1	0.10	$\beta_1 = 2.449$ (1.047)
$\theta_{\text{PREY-LOCATION}}$	3	127.5	5.0	0.06	$\beta_1 = -1.452$ (0.507)
$\theta_{\text{MODE}}$	3	130.7	8.2	0.01	$\beta_1 = 1.132$ (0.468)
$\theta_{\text{PREY-TYPE}}$	4	130.8	8.3	0.01	$\beta_1 = 1.222$ (1.174) $\beta_2 = -0.091$ (1.184)
$\theta_{\text{AGE}}$	3	135.1	12.7	0.00	$\beta_1 = 0.863$ (0.669)
$\theta_{\text{ATTACK}}$	3	135.3	12.8	0.00	$\beta_1 = -0.572$ (0.437)
$\theta_{\text{SEX-AGE}}$	5	137.7	15.9	0.00	$\beta_1 = -0.636$ (0.784) $\beta_2 = 0.160$ (0.614) $\beta_3 = 0.619$ (0.589)

attacked by each sex (non-parametric Kruskal-Wallis test:  $H = 0.02$ ,  $P = 0.88$ ).

The ranking of *a priori* hypothesized models to explain attack success (Table 3) showed that the best approximating model was  $\theta_{\text{GROUP}}$ , which indicates that attack success is mainly influenced by prey group size. This relationship is negative, so that eagles are likely to fail when attacking larger groups of prey (Fig. 1a). Based on AICc differences and Akaike weights, no alternative univariate models merit consideration (Table 3). Of the nine additional models examined (Table 4), we selected a model including the additive effect of four variables: prey group size, habitat type, prey location at the beginning of the attack and attack mode (Table 5). This final model substantially decreased the AICc of the best *a priori* hypothesized model, which indicated that the last three variables can provide additional explanation of the data.

More specifically, this model reveals that the probability of attack success also increases when the attack event occurs in open habitats (Fig. 1b), when the prey is located on the ground (Fig. 1c) and when the eagle carries out a surprise attack (Fig. 1d). The variance component attributed to random effects in the final model was low (0.237), indicating negligible differences among territories ( $P = 0.55$ ). The final model reduced the deviance of the null model by 35%.

## 4. Discussion

### 4.1. Foraging behaviour and hunting success

Bonelli's Eagle has been described as a generalist bird of prey that usually carries out surprise attacks from perches on both solitary prey and on groups,

Table 4. Ranking, based on AICc, of the nine additional models used to explain attack success in the Bonelli's Eagle. Asterisks denote models with interaction terms. *K*: number of parameters estimated;  $\Delta_i$ : AICc differences;  $w_i$ : Akaike weights.

Model	<i>K</i>	AICc	$\Delta_i$	$w_i$
$\theta_{\text{GROUP} + \text{HABITAT} + \text{PREY-LOCATION} + \text{MODE}}$	6	98.2	0.0	0.71
$\theta_{\text{GROUP} + \text{HABITAT} + \text{PREY-LOCATION}}$	5	100.3	2.1	0.25
$\theta_{\text{GROUP} + \text{HABITAT} + \text{MODE}}$	5	103.9	5.7	0.04
$\theta_{\text{GROUP} + \text{HABITAT}}$	4	108.2	10.0	0.00
$\theta_{\text{GROUP} * \text{HABITAT}}$	5	110.0	11.7	0.00
$\theta_{\text{GROUP} + \text{MODE}}$	4	117.2	19.0	0.00
$\theta_{\text{GROUP} * \text{MODE}}$	5	118.2	20.0	0.00
$\theta_{\text{GROUP} + \text{PREY-LOCATION}}$	4	118.9	20.7	0.00
$\theta_{\text{GROUP} * \text{PREY-LOCATION}}$	5	120.5	22.3	0.00

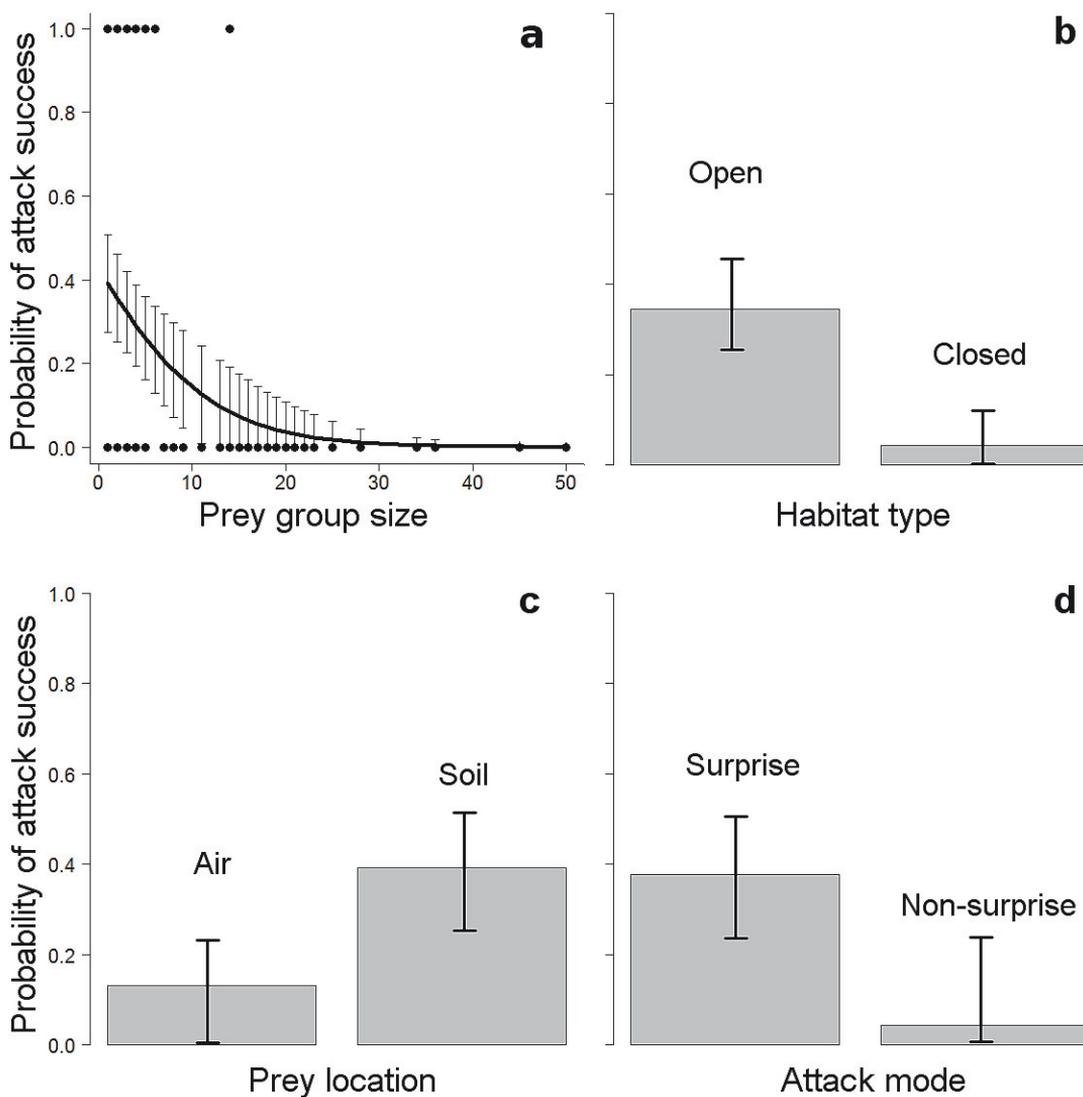


Fig. 1. Relationship between probability of attack success and the main explanatory variables: (a) prey group size, (b) habitat type, (c) prey location at the beginning of the attack and (d) attack mode. Each panel shows the results of the individual models presented in Table 3. Vertical lines represent 95% confidence intervals. Dots in panel (a) represent the raw data (attack success and failures).

whether on the ground or in the air (Cramp & Simmons 1980, Real 1982). Our results lend weight to this assertion since it was seen to attack mainly from perches and contrast with the results obtained for other large Mediterranean soaring eagles, the Spanish Imperial Eagle *Aquila adalberti* and the Golden Eagle *Aquila chrysaetos* which hunt primarily from the air (Ferrer 2001, Watson 1997) or the specialist Short-toed Snake Eagle *Circaetus gallicus*, whose hunting behav-

our is also predominantly aerial (Bakaloudis 2010).

The attack success of Bonelli's Eagle was 28%. Closely related species, such as Golden Eagle and Lesser Spotted Eagle *Aquila pomarina* have been shown to have slightly lower success rates: 20% and 24%, respectively (Collopy 1983, Mirski 2010), while the success of the Greater Spotted Eagle *Aquila clanga* may be higher at 34% (Graszynski *et al.* 2002).

Table 5. Summary of the best additional model for attack success in the Bonelli's Eagle. Variable acronyms are defined in Table 1.

Variable	Coefficient	95% CI
Model {0 <sub>GROUP + HABITAT + PREY-LOCATION + MODE</sub> }		
GROUP	-0.231	(-0.398, -0.063)
HABITAT (= OPEN)	3.754	(1.398, 6.110)
PREY-LOCATION (= AIR)	-1.706	(-2.973, -0.439)
MODE (=SURPRISE)	1.241	(0.044, 2.438)
AICc = 98.2		

#### 4.2. What factors determine attack success?

Most studies directed at evaluating age-related differences in hunting success have found adults to be better than non-adults (Toland 1986, Redpath *et al.* 2002, Kitowski 2003) both in terms of capture and manipulation and as regards the selection of hunting areas (Desrochers 1992, Rutz *et al.* 2006, Daunt *et al.* 2007). This would imply that non-adults need to expend more energy than adults and probably spend more time hunting, which would give them fewer options for the successful capture of prey. In contrast and reflecting the results obtained in other raptor species (Collopy 1983, Buchanan 1996, Sarasola & Negro 2005), our analyses do not suggest the existence of such differences between adults and non-adults, although the relatively few observations of non-adults hunting may imply a certain bias.

In raptors, sex-related differences have been observed in hunting behaviour, particularly with regard to the selection of microhabitats (Newton 1979, Marquiss & Newton 1982). In this study, no such differences in hunting success by sex were detected, perhaps due to the small sample size. Hence, our models show that sex is not a good predictor of hunting success in Bonelli's Eagle, which is similar to the results obtained in other studies of cliff-nesting raptors: Golden Eagles (Collopy 1983) and Peregrines *Falco peregrinus* (Jenkins 2000, Zuberogoitia *et al.* 2002). Similarly, one of the characteristic features of the Bonelli's Eagle is that they usually hunt in pairs. This hunting mode consists of different strategies, coordinated between both sexes, which allow them to obtain a greater efficiency in the capture of prey (Equip de Biologia de la Conservació Àliga Perdiguera 2012). However, our models suggest that there is

no an improvement in attack success when the eagles hunt in pairs. Several studies have shown that the hunting strategies, prey type and prey vulnerability might be also factors determining in the hunting success of predators (Cresswell & Quinn 2004, Kenward 2006, Cresswell *et al.* 2010). However, these factors were not good explanatory variables of attack success in Bonelli's Eagle either.

In contrast, prey group size constituted the most significant factor in the best model because attack success decreased significantly with increasing the group size of the potential prey. Several studies have singled out this factor to explain attack success in a wide range of taxa, including raptors (Kenward 1978, 2006, Krause *et al.* 1998, Roth & Lima 2003, Cresswell & Quinn 2010). Our results, therefore, lend weight to hypothesis 1.

Different habitat features can influence the detectability of prey by raptors, such as the ground-level vegetation and the abundance of potential perching sites (Janes 1985). The openness of the habitat was a determining factor when explaining hunting success for prey on the ground. It was probably advantageous for Bonelli's Eagles to attack solitary individuals or small groups in areas of low vegetation cover (Fig. 1), which may be regarded as a compromise between prey conspicuousness and accessibility, and reducing predator detectability (Bakaloudis 2009, Martínez *et al.* 2010b, Arlettaz *et al.* 2010). In contrast, terrain with a high degree of vegetation cover (mainly dense scrubland) while offering an abundance of prey (Ontiveros *et al.* 2005), may hinder the hunting activity of Bonelli's Eagle (e.g. Palma *et al.* 2006). Detectability or accessibility may therefore play a crucial role in the foraging habitat of Bonelli's Eagle, as has been seen in other raptor

species and owls (Bechard 1982, Aschwanden *et al.* 2005, Jacob & Hempel 2003, Ontiveros *et al.* 2005, Bakaloudis 2009, Arlettaz *et al.* 2010). These findings support hypothesis 2.

Numerous studies have concluded that one of the most important factors contributing to the attack success of birds of prey is surprise (see Cresswell 1996). Our results support this assertion because surprise was a key factor in attacks launched against prey on the ground. This may permit the eagles to utilize terrain and cover to conceal their approach (see Real 1982, Kenward 2006). Our observations agree with findings from other raptor species such as Sparrowhawks *Accipiter nisus* and Merlins *Falco columbarius*, which are more successful hunters when they attack by surprise than from the open (Cresswell 1996, Cresswell *et al.* 2003). Carrying out surprise attacks followed by long periods of inactivity may be a strategy for conserving energy and minimizing the risk involved in hunting (Cresswell 1996, Jenkins 2000). This situation may well fit the hunting strategy attributed to Bonelli's Eagle, in which individuals have been seen to spend long periods perched on cliffs, interspersed with brief hunting sorties (Bosch *et al.* 2010).

The selective advantages of prey species living in groups seems to increase with the group size, although this may depend on raptor species and its mode of hunting (Cresswell & Quinn 2010). However, our results do not include any interaction between attack mode and prey group size. Figure 1 shows that there was a similar decline in attack success with increasing prey group size for both surprise and non-surprise attacks. Thus, Bonelli's Eagle is likely to be affected by the confusion effect because non-surprise attacks were less successful for large groups when detectability benefits should not be apparent (Cresswell & Quinn 2010). Consequently, Bonelli's Eagles should be more likely to attack smaller group size in order to minimize confusion (Cresswell & Quinn 2010). Therefore, our results support hypothesis 3.

### 4.3. Management implications

Our best additional model points to the important role played by open areas, which facilitate hunting opportunities for Bonelli's Eagle and other Medi-

terranean raptor species (Franco & Sutherland 2004, Ontiveros *et al.* 2005, Carrete & Donázar 2005, Moreno-Rueda & Pizarro 2007). This has important implications for landscape management if the accessibility and availability of prey species is to be favoured for the benefit of large Mediterranean eagles (Bakaloudis 2009). Indeed, the main recommendation to be derived from our model would be the promotion and maintenance of open landscapes to improve the hunting opportunities of Bonelli's Eagle (Ontiveros *et al.* 2005). Grazing (by goats and sheep) has significantly decreased in recent decades as a consequence of abandonment of the land and the intensification of agriculture (with a consequent increase in scrubland). Such alterations in the landscape may remove the foraging habitat of Bonelli's Eagle and other Mediterranean raptors (Ontiveros *et al.* 2005, Bakaloudis 2009). As Bakaloudis (2009) maintains, encouraging ungulates as part of human hunting activity (e.g. Spanish Ibex *Capra pyrenaica*) may be a cheap way of managing mountainous terrain with a dense shrub cover and for creating open spaces. Such a policy, if well planned and scientifically managed, could prove an added socio-economic value in some rural areas of SE Spain (Casas *et al.* 2009). The best strategy for conserving the foraging habitat of Bonelli's Eagle would therefore seem to be to maintain Mediterranean agro-systems, thereby favouring low vegetation cover, promoting the availability of open areas and a mosaic-type landscape, while avoiding extensive reforestation (Ontiveros *et al.* 2004, 2005).

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### Saalistusmenestykseen vaikuttavat tekijät vuorikotkalla (*Aquila fasciata*)

Tutkimuksessa selvitettiin vuorikotkan saalistuskäyttäytymistä- ja menestystä Espanjassa käyttäen hyväksi pitkäaikaista havaintoaineistoa vuosilta 1985–2008. Havaittua saalistusmenestystä selitettiin sekä saaliin että saalistajan käyttäytymisellä ja

ympäristötekijöillä. Havaituista 110 saalistusyrityksestä 28,2 % onnistuivat. Tärkein onnistumiseen vaikuttava tekijä oli saaliin ryhmäkoko, jonka kasvaessa vuorikotkan saalistusmenestys pieneni. Saalistusmenetelmistä suosituin, ja myös tehokkain, oli yllätyshyökkäys. Vuorikotkan saalistusmenestys parani myös ympäristön avoimuuden kasvaessa. Tutkimuksen tulokset korostavat avoimien elinympäristöjen tärkeyttä vuorikotkan saalistusmenestyksessä, joka pitäisi myös ottaa huomioon lajin hoitosuunnitelmissa.

## References

- Ale, S.B. & Brown, J.S. 2007: The contingencies of group size and vigilance. — *Evolutionary Ecology Research* 9: 1263–1276.
- Altmann, J. 1974: Observational study of behavior sampling methods. — *Behaviour* 49: 227–267.
- Andruskiw, M., Fryxell, J.M., Thompson, I.D. & Baker, J.A. 2008: Habitat-mediated variation in predation risk by the American marten. — *Ecology* 89: 2273–2280.
- Arlettaz, R., Krähenbühl, M., Almasi, B., Roulin, A. & Schaub, M. 2010: Wildflower areas within revitalized agricultural matrices boost small mammal populations but not breeding Barn Owls. — *Journal of Ornithology* 151: 553–564.
- Aschwanden, J., Birrer, S. & Jenni, L. 2005: Are ecological compensation areas attractive hunting sites for common kestrels (*Falco tinnunculus*) and long-eared owls (*Asio otus*)? — *Journal of Ornithology* 146: 279–286.
- Bakaloudis, D.E. 2009: Implications for conservation of foraging sites selected by Short-toed eagles (*Circaetus gallicus*) in Greece. — *Ornis Fennica* 86: 89–96.
- Bakaloudis, D.E. 2010: Hunting strategies and foraging performance of the short-toed eagle in the Dadia-Lefkimi-Soufli National Park, north-east Greece. — *Journal of Zoology* 281: 168–174.
- Balbontín, J. 2005: Identifying suitable habitat for dispersal in Bonelli's eagle: An important issue in halting its decline in Europe. — *Biological Conservation* 126: 74–83.
- Bechard, M.J. 1982: Effect of vegetative cover on foraging site selection by Swainson's Hawk. — *Condor* 84: 153–159.
- Bednekoff, P.A. & Lima, S.L. 2005: Testing for peripheral vigilance: do birds value what they see when not overtly vigilant? — *Animal Behaviour* 69: 1165–1171.
- BirdLife International 2004: Birds in Europe: population estimates, trends and conservation. — Cambridge, UK: BirdLife International. BirdLife Conservation. (BirdLife Conservation Series N° 12).
- Blumstein, D.T., Runyan, A., Seymour, M., Nicodemus, A., Ozgul, A., Ransler, F., Im, S., Stark, T., Zugmeyer, C. & Daniel, J.C. 2004: Locomotor ability and wariness in yellow-bellied marmots. — *Ethology* 110: 615–634.
- Bosch, R., Real, J., Tintó, A., Zozaya, E.L. & Castell, C. 2010: Home-ranges and patterns of spatial use in territorial Bonelli's Eagles *Aquila fasciata*. — *Ibis* 152: 105–117.
- Botham, M.S., Kerfoot, C.J., Louca, V. & Krause, J. 2005: Predator choice in the field: grouping guppies, *Poecilia reticulata*, receive more attacks. — *Behavioral Ecology and Sociobiology* 59: 181–184.
- Broström, G. & Holmberg, H. 2011: glmmML: Generalized linear models with clustering. — R package version 0.82-1. <http://CRAN.R-project.org/package=glmmML>
- Buchanan, J.B. 1996: A comparison of behaviour and success rates of merlins and peregrine falcons when hunting dunlins in two coastal habitats. — *Journal of Raptor Research* 30: 93–98.
- Burnham, K.P. & Anderson, D.R. 2002: Model Selection and Multimodel Inference. A Practical Information-Theoretic Approach. — 2nd Edn. New York: Springer.
- Calvete, C., Estrada, R., Angulo, E. & Cabezas-Ruiz, S. 2004: Habitat factors related to wild rabbit conservation in an agricultural landscape. — *Landscape Ecology* 19: 531–542.
- Carere, C., Montanino, S., Moreschini, F., Zoratto, F., Chiarotti, F., Santucci, D. & Alleva, E. 2009: Aerial flocking patterns of wintering starlings, *Sturnus vulgaris*, under different predation risk. — *Animal Behaviour* 77: 101–107.
- Carrascal, L.M. & Seoane, J. 2009: Factors affecting large-scale distribution of the Bonelli's eagle *Aquila fasciata* in Spain. — *Ecological Research* 24: 565–573.
- Carrete, M., Sánchez-Zapata, J.A., Martínez, J.E., Sánchez, M.A. & Calvo J.F. 2002: Factors influencing the decline of a Bonelli's eagle *Hieraetus fasciatus* population in Southeastern Spain: demography, habitat or competition? — *Biodiversity and Conservation* 11: 975–985.
- Carrete, M. & Donazar, J.A. 2005: Application of central-place foraging theory shows the importance of Mediterranean dehesas for the conservation of the cinereous vulture, *Aegypius monachus*. — *Biological Conservation* 126: 582–590.
- Casas, F., Mougeot, F., Viñuela, J. & Bretagnolle, V. 2009: Effects of hunting on the behaviour and spatial distribution of farmland birds: importance of hunting-free refuges in agricultural areas. — *Animal Conservation* 12: 346–354.
- Collopy, M.W. 1983: Foraging behavior and success of Golden eagles. — *Auk* 100: 747–749.
- Cramp, S. & Simmons, K.E.L. (eds.) 1980: The Birds of the Western Palearctic. Volume II. — Oxford University Press. Oxford.

- Cresswell, W. 1994: Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. — *Animal Behaviour* 47: 433–442.
- Cresswell, W. 1996: Surprise as a winter strategy in Sparrowhawks *Accipiter nisus*, Peregrines *Falco peregrinus* and Merlins *F. columbarius*. — *Ibis* 138: 684–692.
- Cresswell, W., Lind, J., Kaby, U., Quinn, J.L. & Jakobsen, S. 2003: Does an opportunistic predator preferentially attack non vigilant prey? — *Animal Behaviour* 66: 643–648.
- Cresswell, W. & Quinn, J.L. 2004: Faced with a choice, sparrowhawks more attack the more vulnerable prey group. — *Oikos* 104: 71–76.
- Cresswell, W. & Quinn, J.L. 2010: Attack frequency, attack success and choice of prey group size for two predators with contrasting hunting strategies. — *Animal Behaviour* 80: 643–648.
- Cresswell, W., Lind, J. & Quinn, J.L. 2010: Predator-hunting success and prey vulnerability: quantifying the spatial scale over which lethal and non-lethal effects of predation occur. — *Journal of Animal Ecology* 79: 556–562.
- Daunt, F., Wanless, S., Harris, M., Money, L. & Monaghan, P. 2007: Older and wiser: improvements in breeding success are linked to better foraging performance in European shags. — *Functional Ecology* 21: 561–567.
- Delibes, M., Calderón, J. & Hiraldo, F. 1975: Selección de presa y alimentación en España del Águila Real (*Aquila chrysaetos*). — *Ardeola* 21: 285–303. (In Spanish with English summary).
- Desrochers, A. 1992: Age and foraging success in European blackbirds: variation between and within individuals. — *Animal Behaviour* 43: 885–894.
- Ebensperger, L.A. & Hurtado, M.J. 2005: On the relationship between herbaceous cover and vigilance activity of degus (*Octodon degus*). — *Ethology* 111: 593–608.
- Equip de Biologia de la Conservació Àliga Perdiguera. 2012: — Department of Animal Biology, Vertebrates Unit, University of Barcelona. Spain. <http://www.ub.edu/aligaperdiguera/EEAPcas/indexcas.htm>.
- Ferguson-Lees, J. & Christie, D.A. 2004: *Rapaces del Mundo*. — Editorial Omega, Barcelona. España. (In Spanish).
- Ferrer, M. 2001: The Spanish imperial eagle. — *Lynx Editions*. Barcelona. Spain.
- Forsman, D. 1999: The raptors of Europe and The Middle East. A Handbook of Field Identification. — T & AD Poyser, London, UK.
- Franco, A.M.A. & Sutherland, W.J. 2004: Modelling the foraging habitat selection of lesser kestrels: conservation implications of European Agricultural Policies. — *Biological Conservation* 120: 63–74.
- Franklin, A.B., Anderson, D.R., Gutiérrez, R.J. & Burnham, K.P. 2000: Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. — *Ecological Monographs* 70: 539–590.
- Funston, P.J., Mills, M.G.L. & Biggs, H.C. 2001: Factors affecting the hunting success of male and female lions in the Kruger National Park. — *Journal of Zoology* 253: 419–431.
- Gil-Sánchez, J.M., Moleón, M., Otero, M. & Bautista, J. 2004: A nine-year study of successful breeding in a Bonelli's eagle population in southeast Spain: a basis for conservation. — *Biological Conservation* 118: 685–694.
- Graszynski, K., Kornischke, B. & Meyburg, B.U. 2002: On the biology of the Greater Spotted Eagle (*Aquila clanga* Pallas 1811). — In *Raptors in the New Millennium* (ed. Yosef, R., Miller, M.L. & Pepler, D.): 62–75. International Birdwatching & Research Center Eilat.
- Jacob, J. & Hempel, N. 2003: Effects of farming practices on spatial behaviour of common voles. — *Journal of Ethology* 21: 45–50.
- Janes, S.W. 1985: Habitat selection in raptorial birds. — In *Habitat selection in birds* (ed. Cody, M.L.): 159–188. Academic Press, London.
- Jenkins, A.R. 2000: Hunting mode and success of African Peregrines *Falco peregrinus minor*: does nesting habitat quality affect foraging efficiency? — *Ibis* 142: 235–246.
- Johnson, J.B. & Omland, K.S. 2004: Model selection in ecology and evolution. — *Trends in Ecology and Evolution* 19: 101–108.
- Katzner, T.E., Bragin, E.A., Knick, S.T. & Smith, A.T. 2006: Spatial structure in the diet of imperial eagles *Aquila heliaca* in Kazakhstan. — *Journal of Avian Biology* 37: 594–600.
- Kenward, R.E. 1978: Hawks and doves: factors affecting success and selection in goshawk attacks on wood-pigeons. — *Journal of Animal Ecology* 47: 449–460.
- Kenward, R.E. 2006: *The Goshawk*. — T & AD Poyser. London.
- Kitowski, I. 2003: Age-related differences in foraging behaviour of Montagu's harrier *Circus pygargus* males in south-east Poland. — *Acta Ethologica* 6: 35–38.
- Krause, J., Ruxton, G.D. & Rubenstein D. 1998: Is there always an influence of shoal size on predator hunting success? — *Journal of Fish Biology* 52: 494–501.
- Lima, S.L. 1995: Back to the basics of anti-predator vigilance: the group-size effect. — *Animal Behaviour* 49: 11–20.
- Lindström, I. 1989: Finch flock size and risk of hawk predation at a migratory stopover site. — *Auk* 106: 225–232.
- López-López, P., García-Ripollés, C., Aguilar, J.M., García-López, F. & Verdejo, J. 2006: Modelling breeding habitat preference of Bonelli's eagle (*Hieraetus fasciatus*) in relation to topography, disturbance, climate and land use at different spatial scales. — *Journal of Ornithology* 147: 97–106.
- Mañosa, S., Real, J. & Codina, J. 1998: Selection of settlement areas by juvenile Bonelli's eagle in Catalonia. — *Journal of Raptor Research* 32: 208–214.
- Marquiss, M. & Newton, I. 1982: Habitat preference in

- male and female sparrowhawks *Accipiter nisus*. — *Ibis* 124: 324–328.
- Martínez, J.A., Calvo, J.F., Martínez, J.E., Zuberogoitia, I., Zabala, J. & Redpath, S.M. 2008a: Breeding performance, age effects and territory occupancy in a Bonelli's eagle (*Hieraetus fasciatus*) population. — *Ibis* 150: 223–233.
- Martínez, J.E., Martínez, J.A., Zuberogoitia, I., Zabala, J., Redpath, S.M. & Calvo, J.F. 2008b: The effect of intra- and interspecific interactions in the large-scale distribution of cliff-nesting raptors. — *Ornis Fennica* 85: 13–21.
- Martínez, J.E. & Calvo, J.F. 2005: Prey partitioning between mates in breeding Booted Eagles (*Hieraetus pennatus*). — *Journal of Raptor Research* 39: 159–163.
- Martínez, J.E., Calvo, J.F., Martínez, J.A., Zuberogoitia, I., Cerezo, E., Manrique, J., Gómez, G.J., Nevado, J.C., Sánchez, M., Sánchez, R., Bayo, J., Pallarés, A., González, C., Gómez, J.M., Pérez, P. & Motos, J. 2010a: Potential impact of wind farms on territories of large eagles in southeastern Spain. — *Biodiversity and Conservation* 19: 3757–3767.
- Martínez, N., Jenni, L., Wyss, E. & Zbinden, N. 2010b: Habitat structure versus food abundance: the importance of sparse vegetation for the common redstart *Phoenicurus phoenicurus*. — *Journal of Ornithology* 151: 297–307.
- McGowan, A., Cresswell, W. & Ruxton, G.D. 2002: The effects of daily weather variation on foraging and responsiveness to disturbance in overwintering red knot *Calidris canutus*. — *Ardea* 90: 229–237.
- Mirski, P. 2010: Effect of selected environmental factors on hunting methods and hunting success in the Lesser Spotted Eagle *Aquila pomarina* in North-Eastern Poland. — *Russian Journal of Ecology* 41: 197–200.
- Moleón, M., Gil-Sánchez, J.M., Real, J., Sánchez-Zapata, J.A., Bautista, J. & Sánchez-Clemt, J.F. 2007: Non-breeding feeding ecology of territorial Bonelli's Eagles *Hieraetus fasciatus* in the Iberian Peninsula. — *Ardeola* 54: 135–143.
- Monclús, R. & Rödel, H.G. 2008: Different forms of vigilance in response to the presence of predators and conspecifics in a group-living mammal, the European rabbit. — *Ethology* 114: 287–297.
- Moreno-Rueda, G. & Pizarro, M. 2007: Snake species richness and shrubland correlate with the short-toed eagle (*Circaetus gallicus*) distribution in southeastern Spain. — *Annales Zoologici Fennici* 44: 314–320.
- Moreno, S., Villafuerte, R. & Delibes, M. 1996: Cover is safe during the day dangerous at night: the use of vegetation by European wild rabbits. — *Canadian Journal of Zoology* 74: 1656–1660.
- Newton, I. 1979: Population ecology of raptors. — T & AD Poyser. Calton.
- Ontiveros, D., Real, J., Balbontín, J., Carrete, M., Ferreira, E., Ferrer, M., Mañosa, S., Pleguezuelos, J.M. & Sánchez-Zapata, J.A. 2004: Biología de la conservación del Águila perdicera *Hieraetus fasciatus* en España: investigación científica y gestión. — *Ardeola* 51: 461–470. (In Spanish with English summary).
- Ontiveros, D., Pleguezuelos, J.M. & Caro, J. 2005: Prey density, prey detectability and food habits: the case of Bonelli's eagle and the conservation measures. — *Biological Conservation* 123: 19–25.
- Palma, L., Beja, P., Miguel, P. & Da Fonseca, L.C. 2006: Why do raptors take domestic prey? The case of Bonelli's eagles and pigeons. — *Journal of Applied Ecology* 43: 1075–1086.
- Parellada, X. 1984: Variació del plomatge i identificació de l'àliga cuabarrada (*Hieraetus fasciatus fasciatus*). — *Rapinyaires Mediterranis* II: 70–79. (In Catalan).
- Quinn, J.L. & Cresswell, W. 2004: Predator hunting behaviour and prey vulnerability. — *Journal of Animal Ecology* 73: 143–154.
- R Core Team 2013: R: A language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Real, J. 1982: Contribució al coneixement de la biologia i distribució de l'àliga cuabarrada *Hieraetus fasciatus* (Vieillot, 1822) a la Serralada Pre-litoral catalana (Falconiformes, Accipitridae). — *Tesina de llicenciatura*. Universitat Autònoma de Barcelona. Barcelona. (In Catalan).
- Redpath, S., Amar, A., Madders, M., Leckie, F. & Thirgood, S. 2002: Hen harrier foraging success in relation to land use in Scotland. — *Animal Conservation* 5: 113–118.
- Roth, T.C. & Lima, S.L. 2003: Hunting behavior and diet of Cooper's hawks: an urban view of the small-bird-in-winter paradigm. — *Condor* 105: 474–483.
- Rutz, C., Whittingham, M.J. & Newton, I. 2006: Age-dependent diet choice in an avian top predator. — *Proceedings of the Royal Society B* 273: 579–586.
- Sand, H., Wikenros, C., Wabakken, P. & Liberg, O. 2006: Effects of hunting group size, snow depth and age on the success of wolves hunting moose. — *Animal Behaviour* 72: 781–789.
- Sansom, A., Cresswell, W., Minderman, J. & Lind, J. 2008: Vigilance benefits and competition costs in groups: do individual redshanks gain an overall foraging benefit? — *Animal Behaviour* 75: 1869–1875.
- Sarasola, J.H. & Negro, J.J. 2005: Hunting success of wintering Swainson's hawks: environmental effects on timing and choice of foraging method. — *Canadian Journal of Zoology* 83: 1353–1359.
- Snow, D.W. & Perrins, C.M. 1998a: The birds of the Western Palearctic. Concise Edition, Vol. I, Non-Passerines. — Oxford University Press, Oxford, UK.
- Snow, D.W. & Perrins, C.M. 1998b: The birds of the Western Palearctic. Concise Edition, Vol. II, Passerines. — Oxford University Press, Oxford, UK.
- Tapia, L. & Domínguez, J. 2007: Broad-scale habitat use by red-legged partridge (*Alectoris rufa*) in a low-den-

- sity area in northwestern Spain. — *European Journal of Wildlife Research* 53: 178–182.
- Thirgood, S.J., Redpath, S.M. & Graham, I.M. 2003: What determines the foraging distribution of raptors on heather moorland?. — *Oikos* 100: 15–24.
- Toland, B. 1986: Hunting success of some Missouri raptors. — *Wilson Bulletin* 98: 116–125.
- Vargas, J.M., Guerrero, J.C., Farfán, M.A., Barbosa, A.M. & Real, A. 2006: Land use and environmental factors affecting red-legged partridge (*Alectoris rufa*) hunting yields in southern Spain. — *European Journal of Wildlife Research* 52: 188–195.
- Vine, I. 1973: Detection of prey flocks by predators. — *Journal of Theoretical Biology* 40: 207–210.
- Watson, J. 1997: *The Golden Eagle*. — T & AD Poyser, London, U.K.
- Zuberogoitia, I., Ruiz Moneo, F. & Torres, J.J. (eds.) 2002: *El Halcón Peregrino*. — Servicio de Publicaciones de la Diputación Foral de Bizkaia, Bilbao, Spain. (In Spanish).
- Zuberogoitia, I., Martínez, J.E., Zabala, J., Belamendia, G. & Calvo, J.F. 2012: Solitary hunters sharing an abundant trophic resource. The case of a brambling wintering roost and simultaneous hunting by raptors. — *Journal of Raptor Research* 46: 318–322.