BRIGHTNESS FEATURES OF VISUAL SIGNALING TRAITS IN YOUNG AND ADULT EURASIAN EAGLE-OWLS

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ABSTRACT.—Recent research has demonstrated the important role of visual communication in nocturnal birds. Achromatic plumage patches (i.e., pigment-free white feathers) with high levels of contrast against dark backgrounds are excellent candidates for visual signaling in the dark or at twilight, when differences in color may be less effective. In this study, with the goal of investigating the signaling role of certain achromatic plumage patches, we examined the characteristics and patterns of the brightness (i.e., total reflectance) of Eurasian Eagle-Owl (*Bubo bubo*) white feather patches for both young birds and adult individuals. Our results showed that (1) the total reflectance of young birds' white feathers differed significantly from that of adult owls' white feathers; (2) the brightness differed between the sexes in adults only, with females showing a significantly higher reflectance than males; (3) the total reflectance of the white patch around a young bird's mouth was positively correlated with brood size; (4) the total reflectance of the white badge on the throat of adults was positively correlated with their hematocrit values; (5) an assortative mating scenario based on the brightness of an individual's white badge was deemed possible; and (6) we did not detect any significant relationship in the levels of reflectance for related individuals: the young and their parents were not found to be distinguishable based on the brightness of their white feather patches.

KEY WORDS: *Eurasian Eagle-Owl*; Bubo bubo; *plumage brightness*; *visual signaling*; *white feathers*.

CARACTERÍSTICAS DEL BRILLO DE LAS SEÑALES VISUALES EN JÓVENES Y ADULTOS DE *BUBO BUBO*

RESUMEN.—Trabajos recientes han demostrado la importancia del papel que las señales visuales desempeñan en la comunicación de las aves nocturnas. Los plumajes acromáticos (es decir, aquellos libres de pigmentos) con altos niveles de contraste contra un fondo oscuro son los mejores candidatos para enviar señales visuales en la noche o en horas crepusculares, cuando las diferencias de color pueden ser menos efectivas. Con el objetivo de investigar el papel en la señalización de ciertos parches de plumas acromáticas, estudiamos las características y los patrones de brillo (es decir, la reflectancia total) de la mancha blanca presente en polluelos y en adultos de *Bubo bubo*. Los resultados mostraron que (1) la reflectancia total de la mancha blanca de los polluelos difirió significativamente de la de los adultos; (2) en adultos existen

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diferencias en el brillo de la mancha blanca en función del sexo, siendo las hembras las que tienen valores más altos de reflectancia; (3) la reflectancia total de la mancha blanca de los polluelos está positivamente relacionada con el tamaño de nidada; (4) en el caso de los adultos, existe una relación entre la mancha blanca en la garganta y el valor de hematocrito de los individuos; (5) es posible que la mancha blanca de los búhos adultos actúe como una señal en un posible escenario de emparejamiento selectivo; y (6) no detectamos ninguna diferencia en el brillo de la mancha dentro de los núcleos familiares, es decir, los individuos de cada familia no parecen diferenciarse en función de los rasgos de la mancha blanca.

[Traducción de los autores editada]

Plumage coloration is one of the most common ways birds convey information, including an individual's quality and social status, to conspecifics. Both males and females may also use plumage characteristics in mate choice (Hill and McGraw 2006a, 2006b). Additionally, several studies have confirmed the role of coloration in parent-offspring communication, with parents responding to nestlings' skin, plumage, mouth color, and markings (e.g., Jourdie et al. 2004, Kilner 2006, Wiebe and Slagsvold 2009, Ligon and Hill 2010, Parejo et al. 2010). In diurnal birds, this type of information is generally conveyed through a wide range of carotenoid- and melanin-based colors, as well as structural colors (e.g., blue, violet, ultraviolet, and white patches; Hill and McGraw 2006a, 2006b). Males normally have more colorful and conspicuous plumage than females, with females typically the selective sex. Similar to males, however, females also may display plumage patches and conspicuous ornamentation that may serve a selective signaling function (e.g., Roulin 1999, Amundsen and Pärn 2006, Roulin and Altwegg 2007, Legagneux et al. 2010, Parejo et al. 2011).

Thus far, most studies on the use of plumage coloration in signaling among animals have focused on diurnal species, because communication in nocturnal birds was traditionally thought to rely solely on vocalization (Hill and McGraw 2006a, 2006b). However, a growing body of literature has recently demonstrated the role of visual communication in nocturnal birds (Aragonés et al. 1999, Penteriani et al. 2006, 2007a, 2007b, Penteriani and Delgado 2009, Parejo et al. 2010, Bortolotti et al. 2011), particularly through achromatic patches (i.e., pigment-free white feathers). Because visual signals used in the dark or at twilight are communicated in low light conditions, achromatic plumage patches with high levels of contrast against dark backgrounds are excellent candidates for signaling when differences in color may be less effective. White feathers result from the scattering of light in all directions by un-pigmented feather keratin (Prum et al. 1999).

The Eurasian Eagle-Owl (*Bubo bubo*) has two different, age-dependent patches of white feathers. The first patch forms as a large white border tracing the edge of nestlings' and fledglings' (hereafter referred to as "young") mouths (Fig. 1A). This patch begins to become clearly visible at approximately 30–35 d of age and gradually disappears in full-grown individuals (i.e., before the start of natal dispersal). These white patches appear to play a role in parent-offspring communication and may serve to signal the quality of the young, to assist parents in feeding, or to increase a fledgling's visibility in the dark. Feeding parents appear to be able to discriminate among young based on the brightness of their mouth feathers, which may result in the young with higher brightness being fed more or with better food (Penteriani et al. 2007b).

Full-grown individuals develop a second white badge visible on the throat only during call displays (Penteriani et al. 2006; Fig. 1B). These displays are mainly performed at dawn, dusk, or in the moonlight, when visual contrast is higher (Penteriani and Delgado 2009, Penteriani et al. 2010). Both males and females display this badge, and its brightness appears related to an individual's physical state (Penteriani et al. 2006) and/or fecundity, with males showing the highest brightness producing more young (Penteriani et al. 2007a).

In this study, we examined the characteristics and patterns of the brightness of eagle-owl white feather patches. First, we focused on identifying potential relationships between the brightness of the eagle-owl's two white feather patches and several internal (e.g., an individual's physical condition) and external (e.g., availability of main prey) factors with the potential to affect the properties of reflectance. Second, we examined possible brightness differences between the white feathers of the young and breeders. Because the white plumage of the young birds and breeders serves different functions, we hypothesized that the reflectance properties of their plumage also might differ and, for example, show different patterns of variation between the sexes. Thirdly, we

Figure 1. The difference between the white patch around the mouth of a Eurasian Eagle-Owl young bird (A) and the white badge on the throat of a full-grown individual (B).

investigated whether breeding pairs mated assortatively based on plumage characteristics. Although assortative pairing can occur for many reasons other than mate choice, assortative mating by plumage color may occur when mate choice is directly related to phenotype (Bortolotti et al. 2008). Finally, we tested whether plumage brightness could be used to identify siblings and their parents by comparing the feather brightness of owls within family groups.

METHODS

Trapping and Collecting Blood from Young Birds and Breeders. From 2003 to 2010, we measured feather brightness in a sample of 89 owls from 25 nesting sites in Sierra Morena in southwestern Spain. The sample consisted of 30 breeders (21 males and 9 females) and 59 young (31 males and 28 females). We captured most of the breeding males using a taxidermic mount and playback of a male call to simulate a territorial intrusion. A dho gaza net positioned behind the mount caught any males responding to the calls. We trapped females and several other males using bownets placed in

nests when young were 20–35 d old. At this age, young birds are capable of thermoregulation and night temperatures are consistently warm in the study area (approximately 20°C). We placed nestlings in a box covered by a metal grid to ensure they were visible to their parents, which we then captured when they returned to the nest. A maximum of three trapping nights per breeding season occurred at any given nest. We measured the body mass of trapped breeders and young (30–35 d old) to the nearest 10 g using a 1-kg Pesola scale. We used forearm length and mass to calculate body condition indices (BCI, Table 1; Green 2001) and collected 2 ml of blood from the brachial vein. Blood samples were stored in tubes with heparin at 4°C for transport to the laboratory, where we centrifuged each sample for 10 min at 4000 rpm to obtain hematocrit (HT) values (i.e., the volume percentage of red blood cells; Table 1). We used HT as an indicator of nutritional status (Delgado et al. 2010, Campioni et al. in press); nutritional deficiencies result in anemia due to a shortage of essential amino acids (Costa and Macedo 2006).

Table 1.   Health status, nest-site quality, and brood sizes of Eurasian Eagle-Owl young ($n = 59$) and breeders ($n = 30$) included in this study.

VARIABLES	YOUNG			BREEDERS		
	MEAN	SD	RANGE	MEAN	SD	RANGE
Hematocrit	43.9	8.49	29.1–70.2	50.7	6.94	41.7–66.7
Body condition index	0.00	0.05	−0.09–0.08	0.00	0.04	−0.05–0.08
Rabbit biomass in diet (%)	58	6.2	42–79	58	10.8	42–93
Rabbit latrines per km of transect	23.1	9.93	7.7–36.3	21.2	11.57	7.7–46
Brood size	2.7	0.74	1–4	2.3	0.99	0–4

Despite HT variability (e.g., due to sex, age, season, and nutritional status; Fair et al. 2007), HT may be considered an accurate indicator of physical condition when used in conjunction with other parameters, such as body mass (Fair et al. 2007). We aged the young birds according to Penteriani et al. (2004) and sexed them using DNA extracted from the blood samples (Delgado et al. 2010, Campioni et al. in press).

Measurement of White Plumage Brightness. We assessed the total reflectance of the white feathers of young birds and breeders using a Minolta CM-2600d portable spectrophotometer (Minolta Co., Ltd., Osaka, Japan) with UV (xenon flashlight source) and visible light (standard illuminant D65). For each owl, we superimposed four layers of three feathers (12 total) on a dark velvet surface with 0% reflectance (Quesada and Senar 2006, Penteriani et al. 2006). We estimated brightness as the percentage of total reflectance data in the interval 360–700 nm. Feathers were plucked from the birds and analyzed in the laboratory for all individuals, with the exception of 17 young birds; for these 17 birds, white feathers were assessed during a field experiment rather than in the laboratory (Penteriani et al. 2007b).

Diet Analysis and Main Prey Availability. Previous diet analyses showed that rabbits (*Oryctolagus cuniculus*) are the main prey of our study population (Campioni et al. in press). Therefore, we considered the abundance of nearby rabbits and the amount of rabbit biomass in an individual's diet (Table 1) as potentially additive factors affecting an individual's physical state and, consequently, the brightness of its white plumage. We collected prey remains and pellets during visits to nests, roosting perches, and feeding perches in the breeding territories, and used them to assess the diet of eagle-owls. We identified prey species using bone identification keys and by comparing with a reference

collection at the Laboratory of Archaeo-sciences at IGESPAR (Instituto de Gestão do Património Arquitectónico e Arqueológico) in Portugal. Using these data, we determined the minimum number of prey individuals consumed. We calculated rabbit biomass percentages using the mean mass estimates obtained from previous studies or bone measurements to estimate the mass of each individual (Lourenço 2006). We used rabbit fecal pellet counts, performed from March to May 2009, to estimate the relative abundance of rabbits at the 25 nesting sites used in this study (latrine counts; Palomares 2001a, 2001b). To obtain comparable indices of prey abundance (i.e., number of latrines per km of transect, Table 1), we drew a circular plot around each nest. The area of the circular plot was equal to the mean eagle-owl home-range size in our study population (218.9 ± 30.8 ha), as calculated by the minimum convex polygon method (Campioni et al. in press). Within these plots, we walked 2.2-km transects and recorded the number of latrines (n_{tot} = 3440 latrines) found within 4 m of each side of the transects (Campioni et al. in press). In our study area, rabbit density remains relatively stable over time within eagle-owl breeding sites, because frequent releases of rabbits inside the study area create a favorable and steady prey source.

Statistical Analyses. We first used a *t*-test to compare the total reflectance of the white feather patches of young birds and breeders. Because the total reflectance differed between the two groups (see Results), we built two separate models for young and breeders. We used linear mixed models (Zuur et al. 2009) because we had repeated information for some nests between and within years. Therefore, we included year and nest site as first- and second-level random effects, respectively. When random factors did not improve the model's likelihood value, as was the case for breeders, the final model was a less complex linear model. We used the two age-specific
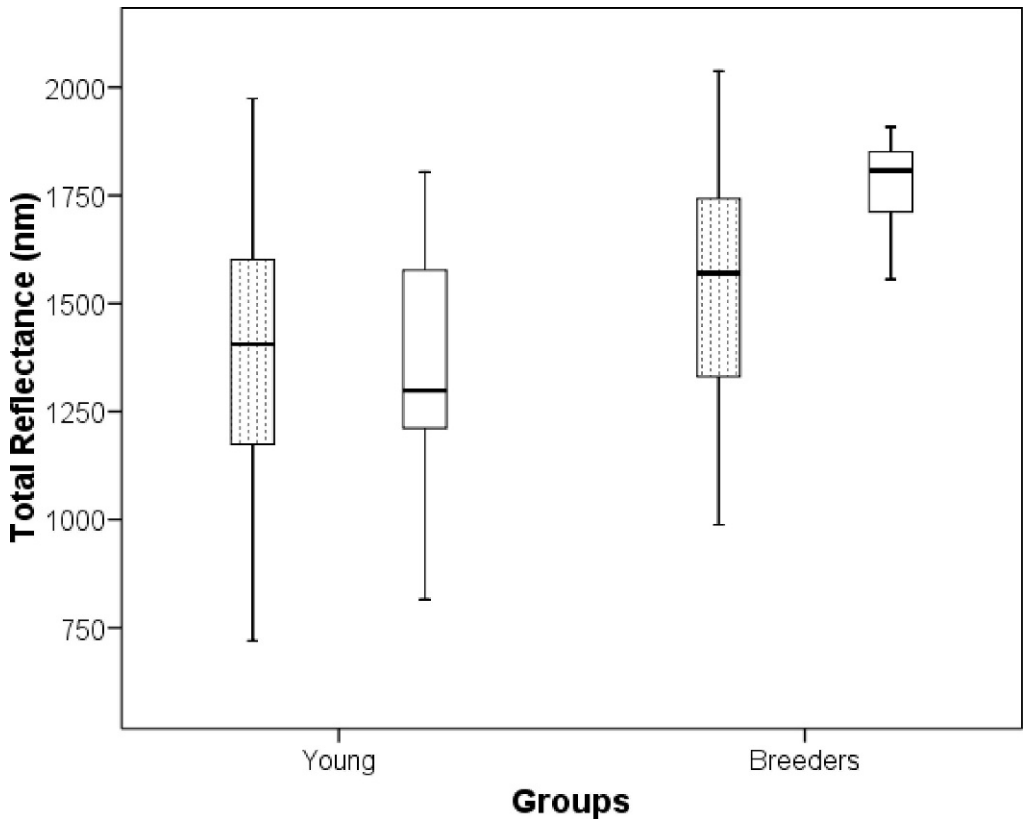
Figure 2.   Sex-specific variation (males = stippled bar; females = open bar) in the total reflectance of white feather patches in Eurasian Eagle-Owl young birds and adult breeders.

models to explore relationships between the total reflectance of eagle-owls' white patches and the following variables (i.e., fixed factors): (1) individual traits, including sex, age, hatching order (only for young birds), and the two indicators of an individual's health status (i.e., HT and BCI); (2) nest-site quality, expressed as the percentage of rabbit biomass in the diet of a family in a given territory and as the availability of rabbits in the vicinity of the nest site; and (3) brood size (Table 1). For young birds, we also included a binomial variable representing whether brightness was measured in the laboratory or in the field to eliminate any possible effects of the physical location in which we used the spectrophotometer to analyze characteristics of the feathers.

We performed all statistical analyses using the R 2.10.1 statistical software (R Development Core Team 2009) with the nlme package (Pinheiro et al. 2009). We first explored the data to ensure

that the assumptions of normality, homogeneous variance, and independence of observations were met, and found that the residuals of the dependent variables were all homogeneous, independent, and normally distributed. We derived simplified models using backward selection of variables from the full model, and compared candidate models using likelihood ratio tests. For each analysis, we used a specific subsample of individuals for which we had data on all variables included within the specified model.

We tested the possibility of assortative mating based on badge brightness using an ANOVA to compare brightness variability among and within breeding pairs. We used a linear mixed model to test for family ($n = 12$ owl families, corresponding to 73 individuals) resemblance in brightness (i.e., similar values of reflectance among siblings and their parents).

All tests were two-tailed and statistical significance was set at $\alpha < 0.05$.

Table 2.   Final models showing relationships between the total reflectance of Eurasian Eagle-Owl white feather patches and individual traits, nest-site quality, and brood size.

BIRD AGE	VARIABLE	ESTIMATE	SE	t	P
Adult breeders[a]	Intercept	620.1	389.3		
	Hematocrit	14.0	7.0	2.0	0.050
	Sex	213.7	100.7	2.1	0.045
Young[b]	Intercept	1122.3	133.9		
	Brood size	111.9	49.2	2.3	0.032

[a] Total reflectance of white throat badge evaluated with linear model fit by maximum likelihood.
[b] Total reflectance of white patch around mouth evaluated with linear mixed (including nested random effects of Year and Nest Site) model fit by maximum likelihood.

RESULTS

Brightness of White Feather Patches: General Patterns. The total reflectance of white feather patches averaged significantly lower in young (mean ± SD = 1371 ± 293.4 nm, n = 59) than in adults (1625 ± 282.4 nm, n = 30; t_{87} = −3.90, P = 0.0001; Fig. 2). The only significant relationship revealed by the linear mixed model developed for young birds was that the total reflectance of white feather patches varied significantly among brood sizes (Table 2, Fig. 2, Fig. 3). The only significant relationships revealed by the linear model developed for breeders were that the total reflectance of the white feather badges was positively correlated with HT values (Table 2, Fig. 4), and females (1785 ± 162.5 nm, n = 9) showed higher brightness levels than males (1556 ± 297.4 nm, n = 21; Table 2, Fig. 2, Fig. 5).

Assortative Mating by Badge Brightness. Although the available sample was small (n = 6 pairs), variability in the total reflectance of white feather badges was higher among breeding pairs than within pairs ($F_{5,6}$ = 5.4, P = 0.032; Fig. 5).

Variation in Badge Brightness Within and Among Families. We did not detect any significant variation in feather brightness between young and their parents or siblings, and differences in feather brightness among families were not enough to identify individual families of owls ($F_{10,62}$ = 1.4, P = 0.22).

DISCUSSION

Our results were consistent with experimental evidence from previous studies on the eagle-owl, indicating that white plumage in both young and breeders plays an important role in animal communication among crepuscular and nocturnal species (Penteriani et al. 2007a, 2007b, 2009, 2010).

In breeders, the brightness of the white throat badge was positively correlated with hematocrit values. Hematocrit may be considered an indicator of phenotypic condition, with high hematocrit values associated with a better nutritional state and lower levels of infection (Costa and Macedo 2006, Fair et al. 2007). Males with the highest levels of brightness fledge more young, an indication of their quality as mates (Penteriani et al. 2007a). Signals may be reliable indicators of individual quality if they are costly (Zahavi 1975, Grafen 1990, Iwasa et al. 1991). Following Kose and Møller (1999), we can suggest at least two potential costs associated with using white plumage for signaling. First, melanization strengthens feathers; non-melanized feathers are more likely to break due to their higher levels of structural weakness (Burtt 1986, Bonser 1995, Kose and Møller 1999). Second, if feathers without melanin are particularly susceptible to breakage, it is also possible that feather parasites may display a preference for the melanin-free parts of feathers (Kose and Møller 1999). Diet quality also may affect white plumage patterns in birds (McGlothlin et al. 2007). Although the costs associated with the brightness of white feathers is a topic in need of further research (Hill 2006, Prum 2006), our results suggest a definite relationship between bright, white plumage and an individual's physical state. This relationship is a prerequisite for the use of white markings as a signal for the quality of an individual, supporting previous evidence from Gustafsson et al. (1995) and McGlothlin et al. (2007).

Because the white badges of eagle-owls play a role in determining the intensity of territorial responses to intruders (Penteriani et al. 2007a), our results supporting evidence that the badge may be a signal of individual quality are in agreement with the assertion of Johnstone and Norris (1993), who stated that badges used to settle conflicts should also be accurate indicators of an individual's condition. The costs imposed by social interactions may ensure
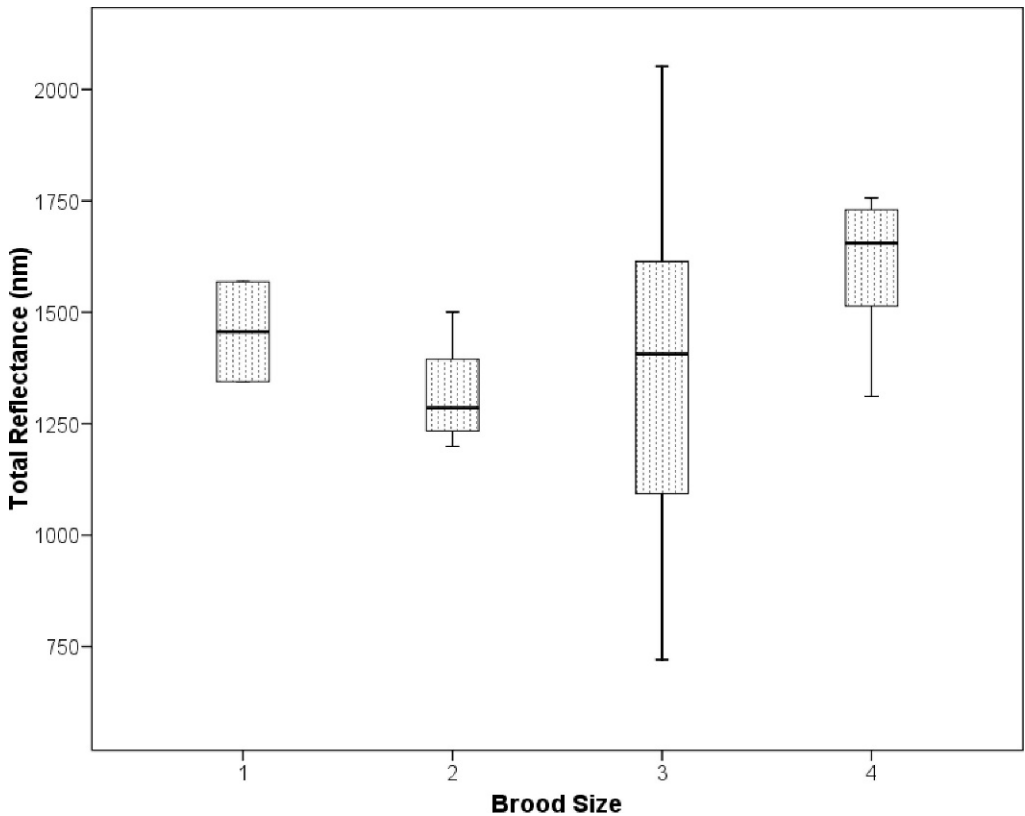
Figure 3. Illustration of the significant relationship between the total reflectance of the white feather patch around young eagle-owls' mouths and brood size.

honesty in signaling; only high-quality, dominant individuals would be capable of withstanding the costs of aggression, minimizing the benefits of cheating (e.g., Møller 1987).

Previous analyses of museum specimens showed higher levels of throat-patch brightness in females than in males (Penteriani et al. 2006). This finding may have some importance during mate choice (Amundsen and Pärn 2006 and references therein), given that in some monogamous species with biparental care, males appear to choose their mates in the same way as females (e.g., males may rely on a female's white feathers to assess her quality; Hanssen et al. 2009, Parejo et al. 2011). In several species of birds, both sexes have a level of parental investment; therefore, both males and females should be selective when it comes to partners (Trivers 1972). It is now clear that female coloring has a number of functions, including the communication of a variety of individual qualities (e.g., Amundsen and Pärn 2006, Roulin et al. 2001, 2003, Roulin and Altwegg

2007, Roulin 2009). An alternate and not mutually exclusive explanation is that plumage coloration plays a role in female-female competition for both mates and territories, although female owls generally show low levels of intrasexual aggression toward intruding females (Penteriani et al. 2007a).

Although the available sample was small, the potential assortative mating pattern found in this study also may support the role of white feathers as a signal of individual quality. Assortative mating, which may occur through a variety of behavioral mechanisms (Bitton et al. 2008, Bortolotti et al. 2008), has been observed in both structurally colored species (Andersson et al. 1998, Komdeur et al. 2005, Bitton et al. 2008) and species showing white marks (Bortolotti et al. 2008). For example, assortative mating may be determined by individuals' mutual preference for similar phenotypes (e.g., Burley 1983, Johnstone et al. 1996) and/or by intrasexual competition for nest sites. This competition may result in high-quality individuals gaining access to
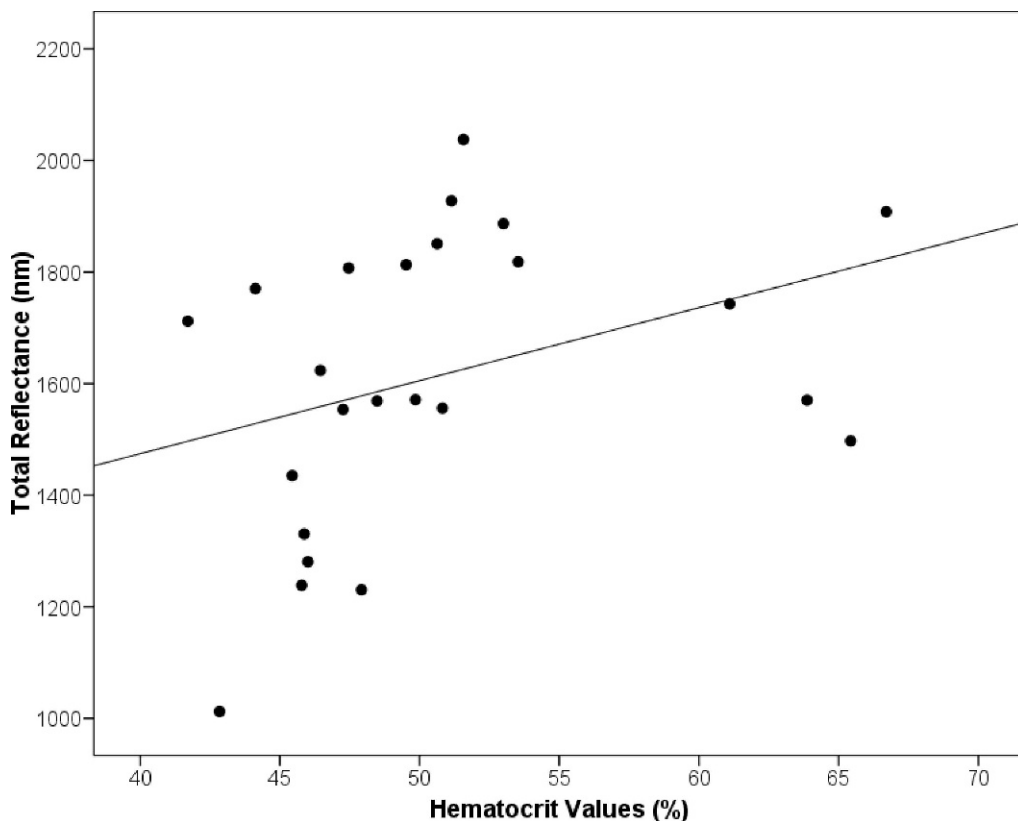
Figure 4. Illustration of the significant relationship between the total reflectance of the white feather badges on breeding Eurasian Eagle-Owls and their hematocrit values.

the best territories and pairing with high-quality mates (Creighton 2001, Ferrer and Penteriani 2003).

The fact that there were no differences in the brightness of white feathers between male and female young is noteworthy, especially when considering that, in some owl species, young brothers and sisters differ in color (e.g., Gasparini et al. 2009, Roulin et al. 2012). Possibly, differences in the brightness of the white signal may only appear in full-grown birds, because it is only after dispersal that these individuals need to signal their state to conspecifics (e.g., during territorial confrontation or mating). Because we found no sex differences in feather brightness of the young, our results suggest that parents do not discriminate between the sexes of their offspring using the brightness of white plumage. To our knowledge, there is only one reported case in which nestling males differ from nestling females in mouth coloration (Barn Swallow,

Hirundo rustica; Saino et al. 2008). Even with the difference in mouth coloration, there was no direct evidence of sex discrimination by Barn Swallow parents. In a previous experimental study, Penteriani et al. (2007b) hypothesized that, within the same brood, parental care is apportioned based on the brightness of the owlets' white markings around the mouth. In a subsequent study, Parejo et al. (2010) demonstrated the role of visual communication between parents and offspring for a nocturnal species, the Common Scops-Owl (*Otus scops*). In feeding behavior, parents favored lighter young that showed lower ultraviolet reflectance of the cere. Cumulatively, this evidence supports the possibility that a nestling's white feathers could be a signal of offspring state, thereby determining the amount of parental care given to each young. That is, parents may decide to feed their young in a way that maximizes their own reproductive success (Godfray 1995, Mock and Parker 1997).
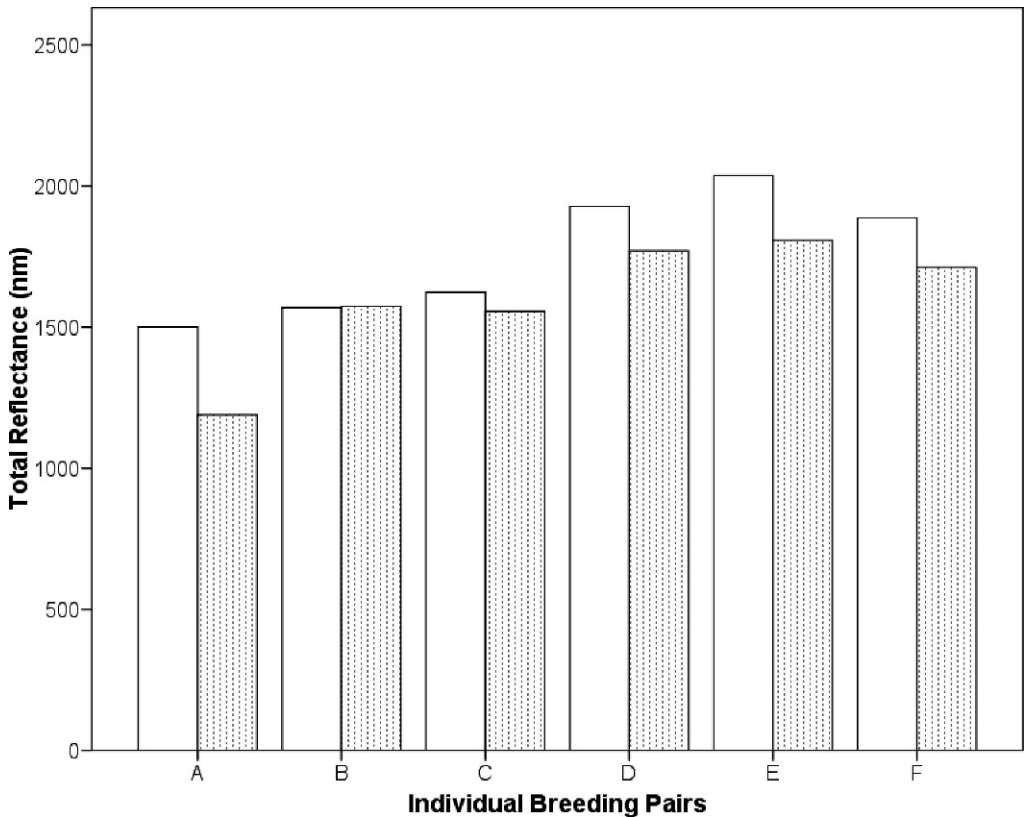
Figure 5. Variation in the total reflectance of the white feather badges within (males = stippled bar; females = open bar) and among breeding pairs of eagle-owls, illustrating greater variation among pairs than within pairs, thereby suggesting possible assortative mating based on feather brightness.

In this study, we found new evidence supporting the possibility that the brightness of a young bird's white feathers signals its quality. We detected a positive correlation between brightness and brood size, which may indicate that because larger broods are associated with better nesting sites (e.g., sites rich in high-quality food sources) and/or better parents, feather brightness may also be a consequence of the quality of the nest's surrounding environment and/or physical characteristics of the parents. However, we did not find any correlation between plumage coloration and the amount of rabbit biomass in the parents' diet or rabbit availability in the breeders' home ranges.

This study contributes new information to the growing field of visual communication in nocturnal animals. Evidence has clearly shown that visual communication is critical to diurnal birds and that, for decades, we have overlooked more sophisticated strategies of animal communication. Birds may not be the only group of species in which nocturnal animals communicate through visual signals. Research on crepuscular and nocturnal species with achromatic patches and patterns on their fur or skin may reveal previously unsuspected ways to send information in the dark of night.

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