The importance of visual cues for nocturnal species: eagle owls signal by badge brightness

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Nocturnal species may communicate by visual signals more frequently than previously thought. In fact, such species are habitually active around sunset and sunrise, when light conditions are still suitable for visual communication. We investigated the communication function of a visual cue in the eagle owl *Bubo bubo*, a nocturnal predator. In this species, territorial and courtship displays peak during the sunset and sunrise periods and involve the display of a white badge located on the throat whose reflectance properties are sex and period dependent. Experimental intrusions were conducted at 30 eagle owl territories in order to understand the function of the white badge during contests. We analyzed the reactions of both male and female owners toward a taxidermic mount with a normal brightness and a brightness-reduced white badge, with both male and female territorial calls. Our results indicate that the white badge of eagle owls plays an important role in visual communication during contests. Males displayed more frequently toward male low-brightness mounts, which were also approached more closely or attacked. Female behavior did not differ between experimental groups. Furthermore, a positive relationship between male badge brightness and breeding output suggested a potential role of the white badge as an honest signal of male quality. The need to convey information by visual communication in a nocturnal species may have promoted the evolution of visual signals employed at crepuscule. *Key words:* achromatic color, animal communication, brightness, *Bubo bubo*, eagle owl, white badge. *[Behav Ecol 18:143–147 (2007)]*

In daylight, there are many different ways that animals can convey information using color signals to intruders, neighbors, mates, siblings, and offspring. Bird plumage represents one of the best examples in the evolution of color signals (Baker and Parker 1979; Butcher and Rohwer 1989). However, at sunset, colors become progressively indistinguishable, creating a need for more effective modes of signaling. Because vocalizations have always been considered the primary way by which nocturnal bird species communicate "in the dead of night," signaling by visual phenotypic traits has been rarely investigated. But visual behavioral displays during specific conditions of ambient light (e.g., crepuscular light) could act as additional cues for social communication by nocturnal species.

Most nocturnal species are active around sunset and sunrise (Martin 1990). In these periods of the day, specific conditions of ambient light interfere with and affect animal communication (Bradbury and Vehrencamp 1998). Empirical evidence has shown that ambient light plays a role in the evolution of color patterns and signals (Endler and Théry 1996; McNaught and Owens 2002; Gomez and Théry 2004). Therefore, any visual signal used around dawn and dusk should optimize the use of the scarce light available. In this context, achromatic plumage patches (i.e., pigment-free white feathers) are the best candidates for crepuscular signaling, when contrast is more important than color (Aragonés et al. 1999). Variability in the total amount of light reflected by a white patch may be exploited as a high-contrast signal against dark backgrounds (Endler 1993; Endler and Théry 1996).

To make inferences about the signaling function of a phenotypic trait, experimental approaches should be based on in-depth background knowledge of the main properties of the signal and biological model. Our recent works on a wild population of eagle owls *Bubo bubo* makes this crepuscular and nocturnal species an excellent model to investigate the functions of achromatic ornaments in the context of visual signaling in crepuscular conditions. In particular, based on previous work on the species, we know that 1) eagle owls have a white badge on the throat that is especially visible during vocal displays, when the throat is repeatedly inflated and deflated (Penteriani et al. 2006); 2) this badge has similar dimensions in both sexes, but its total reflectance (i.e., brightness) is sex and period dependent (Penteriani et al. 2006); 3) the period in which the badge brightness is highest coincides with the time when territorial and courtship displays are at their peak (Penteriani 2002; Delgado and Penteriani forthcoming); 4) such displays are mainly performed by males, but females also show a peak in display rate during the prelaying period (Penteriani 2002, 2003); and 5) display activity peaks at sunset and sunrise (Penteriani 2002).

The main objective of our study was to investigate the possibility that eagle owls communicate by a visual signal, that is, the white badge. To do this, we evaluated the function of the eagle owl's white badge during contests by simulating territorial intrusions. We analyzed the reactions of territory owners toward a taxidermic mount with a control badge (i.e., normal-brightness treatment) or a brightness-reduced badge, with both male and female territorial calls. We predicted that, if the brightness of the owl badge is a status-signaling trait reflecting individual quality and fighting ability (status-signaling hypothesis; Rohwer 1975; Lyon and Montgomerie 1986), allowing opponents to assess the relative likelihood of winning a contest (e.g., owner vs. intruder asymmetries in fight abilities; Maynard Smith and Parker 1973, 1976), different responses to the mount would be expected during different trials. Under that

scenario, contests should range from ritualized displays of different duration without physical contact (e.g., call displays) to direct attacks, reflecting the highest intensity of aggression (Riechert 1998). Above all, different reactions to different badge treatments would indicate the importance of visual cues in owl conspecific communication.

METHODS

We conducted experiments at 30 eagle owl territories in the Sierra Norte of Seville (37°30′N, 06°03′W, SW Spain; details in Penteriani et al. 2005), between November 2002 and January 2003 (prelaying period). We analyzed the response of both territorial males and females (easy to distinguish because of their different call, Penteriani 1996) to a single taxidermic mount, positioned in a very visible location and close to the nest (at a distance of ca. 100–200 m), for which 2 different types of throat badges were prepared: normal-brightness and brightness-reduced badges.

Total reflectance (hereafter also defined as "brightness") was measured as the sum of the reflectance data (%) in the range 360–700 nm using a Minolta CM-2600d portable spectrophotometer (Minolta Co., Ltd., Osaka, Japan) with UV (xenon flashlight source) and visible light (standard illuminant D65). Brightness reduction of the badges applied to the decoy was carried out by smearing the plumage with 2 different amounts of a 40/60% (w/w) mixture of duck preen gland fat and UV-absorbing chemicals (50/50 w/w blend of Parsol 1789 and MCX, Roche, Basel, Switzerland). We used this UV filter because part of the reflectance spectrum of the badge belongs to the UV range (320–400 nm; Penteriani et al. 2006). The badge of the control mount was only smeared by duck preen gland fat (see Alonso-Alvarez et al. 2004). To avoid that the continuous use of the decoy in the field could alter the brightness of our badges, after each trial we controlled for the reflectance and, if necessary, we washed and reapplied both the preen gland fat and UV-blocking substances. At the term of each new treatment, we even verified that the new process of washing and reapplying these oily substances did not cause substantial feather changes in reflectance. In fact, we always controlled that the manipulations produced badges whose total reflectance was comprised between the lowest and the highest value (450 and 2286, respectively) recorded in our population ($n = 8$ owls, previously captured for radio tracking studies, always in the prelaying period to avoid possible difference in the reflectance properties of the badge brightness; see Figure 1).

A single decoy was employed to ensure that it was badge reflectance and not some other correlated phenotypic trait that was responsible for any differences in the behavioral responses. Moreover, because eagle owls are slightly sexually dimorphic, we chose as a decoy a stuffed individual with a body size intermediate between the average size of locally captured males and females (Delgado and Penteriani 2004). Recently, several papers addressed the risks of pseudoreplication in playback experiments when the same stimulus is presented (e.g., McGregor 2000; Kroodsma et al. 2001). The design of our experiment avoided such a problem because the stimulus that we tested was not related to the body characteristics (i.e., decoy features) but to the features of the badge brightness. This latter, due to the above-cited successive manipulations and our scheme of decoy presentation, represented a multiple stimuli randomly presented to the individuals of our population.

At each territory, we presented the mount (always placed on the ground) 4 times: 1) with a normal-brightness badge and an associated male playback call, 2) with a brightness-reduced badge and an associated male playback call, 3) with a normal-brightness badge and an associated female playback call, and 4) with a brightness-reduced badge and an associated female
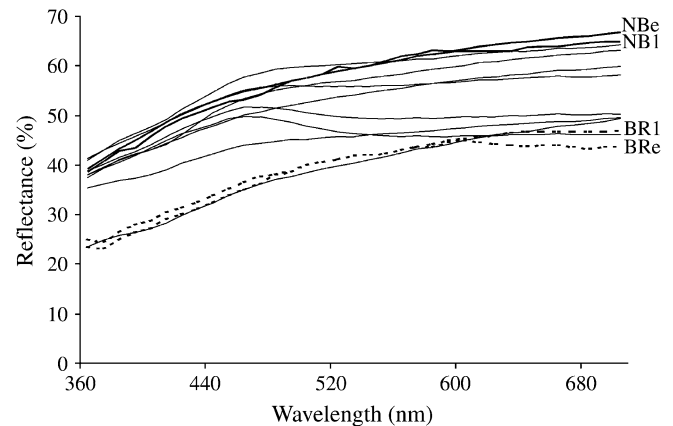

Figure 1
Reflectance spectra of the brightness-reduced badge (dotted line), the normal-brightness badge (bold line), and 8 eagle owls (solid lines) for which information was available (eagle owls belonged to the same study area in which we carried out the experiment). For both the brightness-reduced (BR) and the normal-brightness (NB) badges, we showed the reflectance curves from early (e) and late (l) in the experiment. Manipulations produced badges whose total reflectance was comprised between the lowest and the highest values recorded in our owl population (see text for additional information on treatments).

playback call. Trials were performed with a 24-h interval between tests, and presentation order was randomized to avoid a training effect (Alonso-Alvarez et al. 2004).

Each trial ($n = 120$) started 1 h before sunset, coinciding with one of the 2 peaks of eagle owl calling activity (Penteriani 2002, 2003) and lasted 30 min. Playback calls were broadcasted by means of a loudspeaker (SONY CDF-S100, 4.6 W) placed within 1 m of the decoy. To avoid the possibility that some uncontrolled aspects of call features could be responsible for the observed behavioral responses, in all trials we used the same playback calls, of one male and one female not belonging to the study population (to avoid possible interference due to neighbor habituation).

To measure the behavioral response of the territorial occupants to the simulated intrusion, during each trial we recorded 1) the minimum distance between the territory owner and the mount (scored as 0 = physical contact, 1 = 0–10 m, 2 = 11–50 m, 3 = 51–100 m, and 4 = >100 m), 2) the presence or absence of a vocal response, 3) the total duration of vocal displays, 4) the latency between the beginning of the trial and the owner's first call, 5) the owner's position compared with the mount (scored as 1 = owl lower than the mount, 2 = owl and mount at the same level, and 3 = owl in a dominant position), 6) the frequency of movements among different perches, and 7) the distance between mates (1 = 0–10 m, 2 = 11–50 m, 3 = 51–100 m, and 4 = >100 m), recorded after each movement.

Except when analyzing differences in the minimum distance between the owner and the mount, comparisons between treatments were only performed for those territories where physical contact did not occur (20 out of 30 territories). This was because in most cases the attack interrupted the trial so early that not all variables could be recorded.

Finally, because the fecundity (i.e., mean number of nestlings) of the above-cited 8 radio-tagged owls was available for the 2003 and 2004 breeding seasons, their breeding output was correlated with the total reflectance of the badge.

Statistical analyses

Generalized linear models (McCullagh and Nelder 1989) were used to test the effect of the white badge on the responses of

both territorial males and females. The statistical analyses were performed with SAS Macro program GLIMMIX and PROC GENMOD (version SAS 8.2, SAS Institute 2001). This allowed to select appropriate distribution and link functions. Two random factors (territory and trial order) were always included in the tests, although their effect was never significant ($P > 0.05$). We fitted to the models as explanatory variables 2 different 2-level factors (badge treatment and sex of the playback call) and their interaction. Models were built through a stepwise backward procedure, following Alonso-Alvarez et al. (2004).

RESULTS

Male behavior during contests

Behavioral responses to the simulated intrusion varied widely among individuals, ranging from absence of contest engagement to overt physical aggression (some individuals attacked not more than 4 min after the beginning of the trial). In the latter case, attacks were always initiated from behind the mount's back, striking the back of the head with the claws and throwing down the mount, sometimes to a considerable distance from its original position. We consider that such aggression would have caused significant injuries or, in many cases, death to the intruder.

When analyzing male aggressiveness toward male intruders, owners approached the brightness-reduced male-like mount more closely (estimate of badge treatment ± standard error (SE): -1.86 ± 0.66, $F_{1,40} = 8.74$, $P = 0.003$). In fact, attacks were exclusively performed on the brightness-reduced male-like mount ($n = 10$; mean time elapsed between the first call of the owner and the attack: 10.4 ± 6.2 min, range $= 4$–20 min). The males that attacked the mount started calling before the males that only performed vocal displays ($\chi^2 = 344.90$, degrees of freedom [df] $= 51$, $P < 0.0001$). The probability of being engaged in vocal displays was higher (explained deviance in the null model: 62.27%) toward male (estimate of playbacked call ± SE: 3.055 ± 0.650, $F_{1,78} = 22.07$, $P < 0.0001$) and brightness-reduced (estimate of badge treatment ± SE $= 2.019 \pm 0.649$, $F_{1,78} = 9.68$, $P = 0.003$) mounts. The normal-brightness male-like mount completely inhibited the response of 8 males (40%; Figure 2). However, there were not significant differences between normal-brightness and brightness-reduced mounts in the rest of the behavioral parameters during the male-male trials (all $P > 0.40$).

Female behavior during contests

Females were engaged in only 15 contests out of 80 (excluding those where males attacked the mount; Figure 2). If we assume that the absence of vocal activity did not imply female absence from the experiment area (as supported by radio tracking information; Delgado MM and Penteriani V, unpublished results), we may conclude that the sex or the brightness of the mount did not affect the probability of being engaged in vocal activity ($P > 0.05$; Figure 2). Only 5 times (6.3%) females called alone (4 toward the female-like mount). The rest of the behavioral variables did not show significant differences between treatments (all $P > 0.05$). When in a duet, females always started calling after males (x $= 406.7 \pm 455.7$ s) and, usually, at a distance of 50–100 m to the mate.

Badge brightness and male quality

The analysis of the relationship between the percentage of reflectance and fecundity of the 8 radio-tagged territorial males showed that breeding output was positively correlated with the
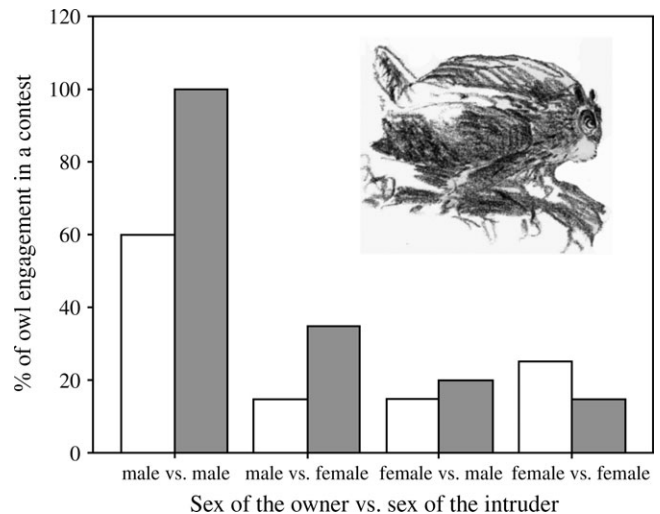

Figure 2
Frequencies of eagle owl vocal engagement in contests, depending on the badge (white bar, normal-brightness badge; gray bar, brightness-reduced badge) and call (male or female) characteristics of the mount, as well as on the sex of the territory owner (male or female). Male normal-brightness mount inhibited call display of 40% of territorial males, whereas females showed lower aggressiveness than males.

total reflectance of the male badge ($r = 0.71$, $P = 0.047$; Figure 3).

DISCUSSION

Our results indicate that the white badge of eagle owls plays an important role in visual communication during contests. This is the first time, to our knowledge, that it is possible to establish an active role of visual signaling in a nocturnal species.

Male responses could be summarized as follows: 1) brightness-reduced male-like mounts were approached more closely and were the only group to be directly attacked, 2) vocal displays were frequently performed toward low-brightness
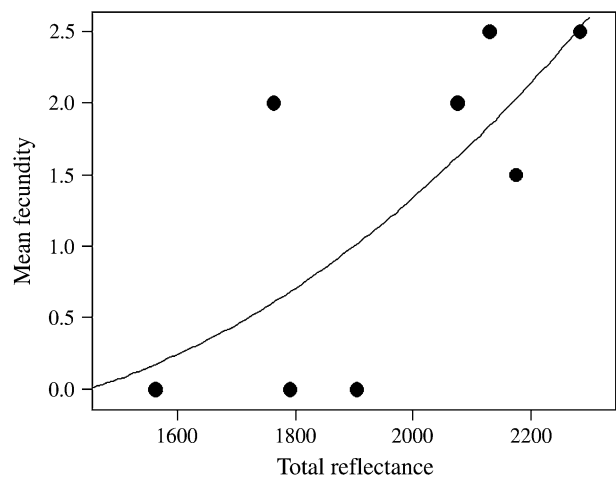

Figure 3
Relationship between the total reflectance of the badge of territorial males and mean fecundity (calculated as the mean of 2 consecutive breeding seasons). Males showing the highest brightness were the best breeders in terms of number of fledged young.

intruders, whereas some birds remained silent when confronted with a normal-brightness intruder, and 3) there was less vocal behavior and activity when the intruder was a female. Meanwhile, females did not show differences between treatments, displaying less frequently than males and mainly supporting their mate (e.g., territorial duets) or responding to the intrusion only when males refrained from contests.

The dynamics of the contests were consistent with the idea that the brightness of the white badge was used as a status-signaling trait. The response indeed ranged from ritualized calls to direct attacks. Consequently, the eagle owl white badge might be considered a phenotypic signal that reliably informs opponents about their asymmetries in fighting skills, minimizing the risk of wasteful and potentially injuring fights. Evaluating the chances of winning against an opponent before deciding whether to retreat from, approach, or physically attack an intruder could be considered as an "assessor" strategy (Maynard Smith 1982). Such a strategy should minimize the costs of unfavorable contests (i.e., when asymmetries are favorable to the opponent). Under this scenario, and in agreement with expectations from theoretical game models (Maynard Smith 1982), high-quality individuals may decide to respond to a high-quality intruder because of their similar badge properties (i.e., small asymmetries in fighting abilities). Thus, direct attacks should be more probable as the signaling status of the opponents becomes more similar ("likes-will-fight prediction" in status-signaling hypothesis; Rohwer 1975). The high frequency of like-versus-like contests as a demonstration of status signaling comes from the fact that subordinate individuals tend to avoid dominant ones (Bradbury and Vehrencamp 1998; Senar and Camerino 1998). Immobile mounts cannot escape, and therefore, a model resembling a subordinate should receive higher aggression rates. Our results showing high level of aggression to low-brightness mount would agree with such scenario. At least 2 experimental studies manipulating phenotypic traits on stuffed decoys showed such pattern (Jarvis and Bakken 1984; Jones and Hunter 1999; but see Alonso-Alvarez et al. 2004). Similarly, Mateos and Carranza (1997) found that live male pheasants in enclosures and modified for less bright plumages by means of make-up powders received more aggressions than controls.

Animals may adopt submissive or neutral behaviors when their chance of winning a fight (or the benefit/cost ratio) is low (Bradbury and Vehrencamp 1998; Hurd and Enquist 2001). This may explain why the high-brightness badge inhibited the vocal response of 40% of the males. These males could be lower quality individuals and, possibly, also owners of poor-quality territories. In fact, the value of the defended resource may also affect the willingness to accept contest escalation and its consequences (Riechert 1998).

Our results of owl badge characteristics as a signal of individual quality fit well with the remarks of Johnstone and Norris (1993) that badges that serve to settle conflicts should also constitute honest indicators of individual condition. As far as we know, there is no evidence about the direct physiological cost of producing achromatic traits. However, honest signaling may be also preserved by honesty-maintaining mechanisms (i.e., costs induced by social interactions), which would prevent cheating because only high-quality dominant individuals would stand the cost of aggression (Rohwer 1975; Møller 1987). In the case of the eagle owl, the high cost associated to injuries during direct attacks should avoid the spread of cheaters in the population. Only those birds able to sustain the escalade would exhibit high-brightness badges.

The function of the badge in intrasexual competition was supported by the patterns of responses during contests, especially, for males. Possibly, the inconsistent or weak responses of females to the intrusions may be associated with a strategy of defense conditional to the presence and effectiveness of the male response (Penteriani V and Delgado MM, unpublished data). In fact, females could mainly cooperate with their mates during territorial defense because territorial duets are a more effective deterrent than displays by single individuals (cooperative territoriality hypothesis; Langmore 1998; Hall 2000).

Because cues involved in territorial defense may share some design rules with mate-attraction signals, both intra- and intersexual functions of this trait are possible. If a secondary trait contains information on phenotypic quality, that trait may have a dual role for territoriality and mating, which are usually difficult to separate (Berglund et al. 1996; Veiga 1996). In this way, the "ornament–armament model" (Berglund et al. 1996) proposes that intrasexual competition would usually be the initiating selective process of many secondary sexual traits, mate choice acting later as a reinforcing factor. The relationship between badge brightness and male fecundity suggests that this trait effectively holds information on individual quality that could have a role in mate choice. Similarly, recent study of Doucet et al. (2005) has shown that achromatic plumage reflectance can significantly predict male reproductive success in black-capped chickadees (*Poecile atricapillus*).

To conclude, the badge-dependent different reactions of owner males suggest that visual signaling could represent a widely overlooked element in nocturnal animals' communication. The peak in vocal displays at crepuscule in our study species (Delgado and Penteriani forthcoming) suggests that visual signals used by traditionally defined nocturnal species may be more widely employed than was previously thought (see also Aragonés et al. 1999). Moreover, approximately more than 70% of owls in the world are not strictly nocturnal: a number of species that are at least partially diurnal (like the eagle owl) starts their activity during daylight or twilight and cease it after sunrise (Martin 1990). In this context, it is interesting that white patches (see Hansen and Rohwer 1986) and flash marks associated with crepuscular displays are common features of many different nocturnal or crepuscular, cryptic bird species such as *Burhinus* spp. (Martin 1990), great snipe (*Gallinago media*, Höglund et al. 1992), little bustard (*Tetrax tetrax*, Jiguet and Bretagnolle 2001), and nightjars (Aragonés et al. 1999). The need to convey information to conspecifics by visual communication in nocturnal species may have determined convergent evolution toward white visual signaling at crepuscule in distantly related groups of nocturnal species.

SUPPLEMENTARY MATERIAL

Supplementary Material S1 can be found at http://www.beheco.oxforjournals.org/.

(Comunidades Autónomas de Andalucía).We trapped and marked owls under the Junta de Andalucía—Consejería de Medio Ambiente permits No. SCFFS-AFR/GGG RS-260/02 and SCFFS-AFR/CMM RS-1904/02. Experiments comply with the current Spanish laws.

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