Night Visions

Even after sundown, Eurasian eagle owls rely on sight for social communication.

By Vincenzo Penteriani and María del Mar Delgado

Photographs by Vincenzo Penteriani

On an October afternoon more than ten years ago, one of us (Penteriani) was searching for a breeding pair of Eurasian eagle owls in the hills of Provence, in southeastern France. The owls were nesting somewhere in a small cluster of white, calcareous cliffs, and the male could be counted on to begin his vocal display at dusk. As sunset approached, the first shadows covered the cypresses and oaks that dot the landscape. On cue a male eagle owl started to call, his distinctive *oohu-oohu* issuing from thickets of dense brush on the cliffs. A methodical scan with binoculars failed to reveal his location, however, and with the Sun down and the light dimming rapidly, it seemed time to give up and head home.

Suddenly, through the binoculars, a white flash appeared within the dark vegetation, and the male owl came into focus. Once, twice, each time he called, he inflated a white patch of feathers on his throat. For someone who had already spent a decade studying the species, that was a surprising sight—undocumented in the scientific literature. Yet there it was, a signal in the dusk hinting that the nocturnal birds might broadcast their presence visually as well as vocally.

In daylight, animals show an extreme diversity of communication strategies, visual signaling being one of the most obvious and widely used. Variability in coloration is a particularly common signal, and bird plumage is one of the best examples. At sunset, however, colors become progressively more indistinguishable, and thus useless for signaling. Scientists have long assumed that owls and other crepuscular and nocturnal birds forgo such visual signals and rely solely on sound.

The Eurasian eagle owl, however, seemed to show otherwise. Indeed, its unpigmented throat feathers are ideal for signaling at twilight, when contrast is more important than color. Moreover, while owls have famously acute night vision, some evidence suggests that their perception of color is limited at best—so white feathers would seem a fitting way for them to communicate by night. That insight in Provence inspired our subsequent research into the eagle owl's evening displays.

The two of us began working together in 2002 at the Spanish National Research Council's Doñana Biological Station in Seville. There we founded the Night Ecology Group to identify and study overlooked behavioral strategies of nocturnal species. With the eagle owl as our model, we sought to learn whether and how nocturnal birds communicate by visual signals—as far as we know the first scientific attempt to probe that question. At the time we were not at all sure we would obtain any significant results, but since then a few other teams have also found it a promising area for investigation. We conducted our fieldwork north of Seville in the Sierra Morena, and southwest of Seville in and around Doñana National Park. The terrain in those locations conveniently enabled us to proceed with minimal disturbance to the birds. Eagle owls prefer to nest on difficult-to-access cliffs, but in the Sierra Morena—and to a lesser extent in forested Doñana—they tend to nest on the ground or among low rocks.

First, some background on the owl itself. The Eurasian eagle owl (*Bubo bubo*) has a huge range throughout Europe and Asia, excepting only the extreme north; it occupies a wide variety of habitats, from boreal forests to Mediterranean scrubland, steppes, and deserts. With a wingspan of about six feet, it is tied for the title of world's largest owl with its relative, the rare Blakiston's fish owl (*B. blakistoni*) of Russia, China, and Japan. Although female eagle owls are slightly larger than males and their calls are distinct, the two sexes look nearly alike, with identical brown-and-white-speckled sable plumage. Both possess white throat feathers, we found, which only emerge from the dark outer plumage during call displays. Pairs usually mate monogamously for life (though they sometimes divorce or engage in bigamy), and occupy a stable territory of perhaps a square mile in area. Both sexes, but particularly males, fiercely defend their territories against interlopers—usually unmated males looking to oust the resident patriarch. Call displays are the first line of defense, and most of the time they're sufficient. Territorial fights are rare, but they can get nasty, and often result in the death of one combatant.

The owls become active in the early evening, displaying vocally at dusk, and then moving off into the night to hunt and feed any owlets. Birds, insects, and small mammals—occasionally even foxes and other carnivores—are their prey. They display

At sunset a juvenile Eurasian eagle owl alights on a rocky outcrop in Spain's Sierra Morena.

Adult male eagle owl puffs out its white throat badge as it calls, near dusk. Badges are readily visible in the low-lit hours when owls are active. With such displays, owls of both sexes claim their territories and communicate with their mates.

again at dawn before retiring to roost on a crag or in a tree for the day. The owls inflate and deflate their throat with each call, exposing the badge. The posture they assume when calling—body bowing forward, head held erect—enhances its visibility. Both males and females use such displays to announce their territorial ownership, as well as to communicate with their mates.

We began our studies with a detailed analysis of the variability in the badge's size and brightness. Our first goal was to explore potential patterns related to sex and season, to better understand the badge's function. With the help of several members of our research team, we made spectrometric measurements of white throat feathers we collected from thirty-nine eagle owl specimens preserved in the two largest bird collections in Spain: those of the Doñana Biological Station and of the National Museum of Natural Science in Madrid. To compare the sizes of the white badges, we measured their surface area on each specimen.

We found that white badges have similar dimensions in both sexes, but their reflectance varies by sex and season. Females generally sport brighter badges than males, and both sexes' badges were brighter in specimens collected just before the early-winter egg-laying period, when territorial and courtship displays peak, than they were in specimens collected at other times of the year. Moreover, bigger females—which may make the most reproductively fit mates—tended to have brighter badges than smaller females. Those results supported our hypothesis that eagle owls use their white badges as a visual signal, and suggested that the badges may serve as a sexual indicator of mate quality. To obtain stronger evidence, however, we needed experimental studies and direct behavioral observations.

In our first field experiment, we evaluated the function of the eagle owl's white badge during contests by simulating territorial intrusions. We visited thirty owl territories with a single taxidermied eagle owl mount whose badge we prepared so as to display either reduced brightness or normal coloration. To prepare the reduced-brightness badge, we applied a chemical that reduced the feathers' ultraviolet reflectance—mixed into duck preen-gland fat for easy spreading. The normal

Adult male tends to his owlets after feeding them. Eagle owls don't build nests, but rather lay their eggs on rocky ledges, in cave mouths, or on the ground near a rock or the base of a tree or bush. Occasionally, they take over a nest abandoned by another bird.

Fledgling eagle owl, about forty days old, displays characteristic white feathers around its beak. Even after owlets leave the nest, they depend on their parents for food. Their white facial feathers all but disappear once they become fully independent, at around five months.

badge (our control) got just a coating of the fat. We presented the mount to the owners of each territory on four separate nights, testing the effect of both badge preparations, while playing a recording of either a male or a female eagle owl's territorial call.

We were impressed that the territory owners showed very different responses to the mount depending on the brightness of its badge and its putative gender (as signaled by the recorded call). Males were far more aggressive toward the mount than females, and particularly so toward the "male" intruder with a brightness-reduced badge. Overall, the responses ranged from ritualized call displays without physical contact, when the intruder had a normal-brightness badge, to direct attacks when the intruder had a brightness-reduced badge. The different reactions to the two badge treatments confirmed that the visual cue is indeed important in eagle owl communication. But what does badge brightness communicate?

As part of the same study, we also used data we'd collected from eight radio-tagged territorial males. We measured their breeding success over two seasons, along with the brightness of their badges. Males with brighter badges were more fecund. Taken together, the results suggest that badge brightness may represent an honest signal of male fitness and fighting ability; opponents may use it to assess their odds of winning a contest, and it may ultimately help owls avoid high-stakes, potentially fatal territorial battles.

Most avian taxa, including owls, vocalize most at sunrise and sunset—a phenomenon known as the "dawn and dusk chorus." Despite ornithologists' great interest in the dawn and dusk chorus, until our work it had been studied exclusively in diurnal songbirds. At least twelve hypotheses as to its purpose are in circulation, among them that singing is the best use of a bird's time when it is too dark to forage effectively, and that dawn and dusk correspond to daily hormonal cycles. But we thought the explanation might be quite different for nocturnal birds.

We conducted a second field experiment to quantify the contrast of the white throat badge against eagle owls' bodies and the background habitat in the ambient light of dusk, when the owls' calls peak. We prepared a taxidermied eagle owl with its badge exposed as if it were calling, and placed it within the territories of twenty-five eagle owl pairs. We took a picture of the decoy every five minutes, from an hour before sunset until fifteen minutes after the male territory owner's last evening call. (There's no guarantee of getting a good line of sight to the resident owl itself, which is why we used the mount.)

Back at the laboratory, we studied the photographs, measuring the contrast of the white badge against the mount's body and the background habitat throughout each of the twenty-five pairs' call-display periods. We found that eagle owls perform their dusk displays just when the ambient light gives their white badges the greatest contrast with the surrounding feathers and habitat. It seems that Eurasian eagle owls call more at dusk than during the night because that's when their visual signals are the most conspicuous. And the same may well hold for the owls' dawn displays, too. Eagle owls' white plumage patches and the timing of their displays may have coevolved to maximize the effectiveness of their social communication.

Owls' acute visual sensitivity permits some image detection under most naturally occurring nighttime con-

Juvenile male eagle owl, about seventy days old, sets out for the night at sunset. At that age, owlets foray up to several hundred yards away from their natal nest at night, but return to its vicinity at sunrise.

Eagle owl prepares to consume a mongoose. Visible on the rock below are white feces, which the owls deploy—along with white or bright prey feathers—as territorial markers.

ditions, though moonlight certainly enhances visibility. Consequently, we thought it likely that eagle owls call more during full Moons than they do on darker nights, as has been reported of other owl species. In 2003, we had begun capturing eagle owls of both sexes and outfitting them with radio transmitters mounted on backpack-like harnesses. Our team spends three nights each week tracking down the owls and recording their social and hunting behavior, movements, and habitat use from sunset to sunrise. To date we've outfitted 30 breeding adults in this way (including the 8 we observed as part of the intruder study) and 150 juveniles. We can follow each of them for about two years—the life of the transmitter's battery. An owl will not condescend to be captured a second time, so it is stuck with the backpack for life, but none have shown any ill effects so far.

By 2008, we had accumulated a detailed behavioral database. We analyzed the eagle owls' call patterns on nights throughout the lunar cycle and verified that moonlight strongly affects eagle owl vocal displays. The owls call more, and therefore display their white throat feathers more, on moonlit nights than on dark nights—apparently to take advantage of the enhanced conspicuousness of their white throat feathers.

We also investigated the role of visual signals in communication between eagle owl parents and their offspring. Baby birds beg before, and while, their parents feed them—one of the most widely investigated aspects of avian parental care. Early studies assumed that offspring employ a single signal—begging calls—and so most research was devoted to the vocalizations of the young. Later research showed that parent-offspring relationships can involve several distinct signals, including such visual cues as mouth color, which provide parents with additional information about their offspring's condition. A combination of vocal and visual cues can increase parental response, with avian parents tending to bestow the most and best resources on their fittest offspring.

Baby Eurasian eagle owls fledge about 40 days after hatching. As they grow stronger, they venture farther and farther from the nest, even as far as nearly a mile. Yet they continue to depend upon their parents for food until they leave home for good, about 170 days after hatching. (We've shown in a separate line of research that the direction in which juvenile eagle owls disperse is largely influenced by the dominant winds. Essentially, owls are dispersed like seeds!) We noticed that just before owlets fledge, a strip of white feathers appears around their beaks. The white feathers become considerably less apparent once the owlets disperse. We suspected that parent eagle owls might use them to judge the relative fitness of their young during their critical fledgling stage, and then allocate food to the fittest.

We devised an experiment to test that hypothesis, predicting that experimentally reducing the brightness of owlets' mouth feathers should lead to less parental investment, and thus to poorer physical condition. With our team members, we visited seven different nests, housing a total of nineteen owlets, every seven days during a period of three weeks. On the first visit, owlets from each nest were randomly assigned to one of two experimental groups: the brightness-reduced group or the control group. We brushed the owlets' white beak feathers with either the darkening mixture we'd used in our territorial intrusion experiment, or, for the controls, just the duck preen-gland fat. During our three weekly visits we took blood samples and morphometric measurements—the length of the forearm and body mass.

As we'd predicted, after three weeks the control owlets were in better physical condition and somewhat bigger than owlets with brightness-reduced beak feathers, suggesting that parents may actively discriminate among their young at feeding time. As in territorial interactions, white feathers seem to play an important role in parent-offspring communication.

We wondered whether Eurasian eagle owls might communicate using other visual cues besides their own white feathers. We noticed that abundant and extremely visible white feces and prey feathers appear near eagle owl nests during the breeding season. During the off-season, by contrast, the owls seemed to defecate and pluck their avian prey in less conspicuous locales. Perhaps the eagle owls were marking their territories.

To test that hypothesis we recorded the spatial and temporal distribution of fecal marks and prey-plucking sites in twenty eagle owl pairs' territories throughout one entire year. We characterized the visibility of plucking sites and fecal marks, their position relative to the home nest and to neighboring eagle owl territories, and their placement and prominence in the area's main valley. We found that the owls left only the white or bright feathers of certain bird prey—but never dark feathers, nor the dull fur of their most common prey, rabbits—on the most prominent available plucking sites close to their nests.

We also recorded the color of the surfaces the owls defecated on. Our analysis showed that eagle owls preferred to leave their white feces on the most conspicuous surfaces: prominently positioned dark rocks with vertical sides were ideal. When we spray painted over the feces on a number of the posts, the eagle owls would usually re-mark them within a night or two. It seems they regularly patrol and maintain their territorial signage. [*See "Samplings," November 2008.*]

Contrary to common wisdom, our research shows that Eurasian eagle owls use a surprisingly large repertoire of visual signals to communicate in a variety of contexts, even in the dark. There's every reason to suspect that visual signaling is more widely employed by nocturnal animals, including some birds, mammals, and frogs, than previously thought. Like eagle owls, a number of other nocturnal bird species bear patches of white feathers and make twilight displays, including the great horned owl, the great gray owl, the little owl, the great snipe, and various species of bustards and nightjars. Whether they, too, communicate by means of visual signals remains to be studied. Our findings might also be relevant to diurnal songbirds with contrasting white plumage badges that breed in dark forest habitats, such as certain flycatchers. And they might apply to species with contrasting color bars that live in open habitats, such as some plovers.

In any case, the general rule seems to be that avian conversations—whether between early birds or night owls—involve visual, as well as vocal, dialogue. We human eavesdroppers must listen *and* watch.

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