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ULTRAVIOLET BEAK SPOTS IN KING AND EMPEROR PENGUINS

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Abstract. In seabirds, colors of feathers and external tissues have only recently been studied, and ultraviolet (UV) color has not yet been detected. Using live individuals as well as museum skins, we found UV peaks of reflectance in two large *Aptenodytes* species, King (*A. patagonicus*) and Emperor (*A. forsteri*) Penguins. UV reflectance did not occur on the feathers, claws, or skin of these species, nor did we find UV reflectance in five other genera of penguins (11 species). UV peaks overlapped with spots of color on the lower beak that appeared orange for human observers, and beak spots differed slightly in location between the two species. Adults of both sexes possessed these UV markings, but they were lacking in juveniles, as was the orange color of the beak spot, and auricular patches used for selecting mates. Finally, measurements of free-ranging King Penguins showed that recently paired birds had higher UV reflectance than courting ones, suggesting possible roles of UV beak spots in pairing and as an indicator of sexual maturity.

Key words: Aptenodytes, *mate choice, ornament, penguin, ultraviolet reflectance.*

Manchas Ultravioleta en el Pico de los Pingüinos *Aptenodytes patagonicus* y *A. forsteri*

Resumen. En las aves marinas, los colores de las plumas y los tejidos externos sólo han sido estudiados recientemente, y el color ultravioleta (UV) todavía no se ha detectado. En individuos vivos así como en pieles de museo, nosotros encontramos picos de reflectancia UV en dos especies de pingüinos, *Aptenodytes patagonicus* y *A. forsteri*. El color UV no se encontró en las plumas, las garras o la piel de estas especies, ni encontramos color UV en otros cinco géneros de pin-

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güinos (11 especies). Los puntos UV se encontraban superpuestos con manchas de color ubicadas en la parte baja del pico que parecían anaranjadas para los observadores humanos. Las manchas del pico difirieron levemente en forma y localización entre las dos especies. Los adultos de ambos sexos presentaron las manchas UV, pero éstas no estaban presentes en los juveniles, al igual que el color anaranjado de la mancha del pico y los parches auriculares empleados en la selección de parejas. Medidas tomadas en individuos libres de la especie *A. patagonicus* demostraron que los que se habían apareado recientemente tenían presentaban reflectancias de UV mayores que las de aquellos que aún estaban cortejando, lo que sugiere un posible papel de las manchas UV del pico en el apareamiento y como indicadoras de la madurez sexual.

A substantial part of the visual color spectrum of birds is not visible to the human eye, specifically the ultraviolet region (UV, wavelengths of 320–400 nm; Bennett and Cuthill 1994, Cuthill et al. 2000b). Whereas mammals have three types of cone receptors to perceive colors, most birds have four types of cones, including one that is sensitive to ultraviolet light (Chen et al. 1984). Ultraviolet plumage reflectance has been found in a number of avian species (Eaton and Lanyon 2003). Although UV does not seem to be more important than other regions of the avian-visual spectrum (Hunt et al. 2001, Maddocks et al. 2001), together with other wavelengths, UV reflectance has been shown to play an important role in tasks such as mate choice (Hausmann et al. 2003), and prey detection and foraging (Johnsen et al. 1998, Sheldon et al. 1999, Cuthill et al. 2000a, Maddocks et al. 2002, Siitari and Huhta 2002) in several different bird species.

Color patterns of terrestrial birds have been well studied, but there is little research on seabird coloration (Jones and Hunter 1993, Cuthill et al. 2000a). A number of studies have identified UV reflectance from skin or scales in fish and lizards (Endler 2000), but there are only a few examples of birds having distinct UV reflectance from horned beak tissues (Hunt et al. 2003, Peters et al. 2004). Penguins, although poorly known, are ideal for a study of color because of their variation in color patterns; some species exhibit strikingly colored feathers and bill spots, while others do not. Because they are relatively unafraid of observers, penguins are easy to study, including taking measurements, and manipulating color patterns. One of the first studies to experimentally manipulate penguin plumage found striking results; the removal of colored feathers resulted in bachelor males having difficulty acquiring a mate (Jouventin 1982). Also, colored plumage of the Yellow-eyed Penguin (*Megadyptes antipodes*) has recently been found to be related to age, body condition, and breeding success (Massaro et al. 2003).

Plumage color is produced by either the deposition of pigments ingested in the diet, synthesized from dietary precursors, or on a precisely ordered nanostructure that reflects UV light (Shawkey et al. 2003). It is widely accepted that pigment-based coloration can signal body and breeding condition (Hill 1991, Veiga 1993) and recent evidence shows that structural colors are linked to diet quality (Keyser and Hill 1999, Sheldon et al. 1999, Doucet 2002). Thus, colored ornaments may indicate the quality (i.e., its future capacity to feed and rear young) of the signaling bird.

In the present study, we examined species-specific UV reflectance of plumage and horny tissues from museum skins of the penguin family (Spheniscidae). We tested birds of both sexes and all age classes for the presence of UV reflectance. We took the same measurements from a captive population of King Penguins and compared their UV reflectance with that of the museum skins. We focused on one genus (*Aptenodytes*) comprising two species, the King (*A. patagonicus*) and Emperor (*A. forsteri*) Penguins, that breed on sub-Antarctic islands and on the edge of the Antarctic continent, respectively. At ~1-m high and 10–40 kg, individuals of these species are the largest seabirds. Both species exhibit a beak spot on both sizes of the lower mandible that appears orange (with variations among individuals from yellow to red). We describe UV reflectance from these beak spots, and present field measurements that suggest a possible signal function of this UV reflectance. In a separate field study, we compared the beak spots of nonpaired (courting) and paired (mated) adult King Penguins, to investigate the possible signaling function of these UV-reflecting markings during mate choice.

METHODS

MEASUREMENTS OF MUSEUM SKINS AND CAPTIVE BIRDS

We used a spectrometer to examine reflectance from 45 skins (13 species from six genera, if we consider Southern and Northern Rockhopper Penguins as distinct species) in the National Museum of Natural History (Paris, France) on 19 September 2002 and 24 March 2003 (Table 1). Most birds were collected 30 years ago in the French Austral and Antarctic Territories. We measured spectral reflectance from feathers (white, black and colored) as well as horned skins (foot, claw, upper and lower mandible) for all species. For a more detailed investigation of coloration, we measured nine adult King Penguins, 10 adult Emperor Penguins, 10 juvenile King Penguins, and four juvenile Emperor Penguins. We also measured an additional seven live King penguins (six males, one female) on 23 March 2003 that were held in captivity at Océanopolis-Brest.

Reflectance measurements were made on penguins with a USB2000 spectrometer (Ocean Optics), equipped with a PX2 pulsed-xenon flash, and calibrated against a white standard (WS-2 Spectralon, Ocean Optics) with a resolution of 0.3 nm across the spectral range of 300–700 nm. We took measurements using a fiber-optic cable held at a 90° angle to the area of interest. We collected 3 to 5 measurements for each area, whether plumage or horny tissue, removing the probe between each measurement. We used nonparametric (Wilcoxon) tests to compare the spectral frequency at the point of highest reflectance in the UV range, and to compare proportional reflectance at the UV peak for museum specimens and live King Penguins, and for paired and unpaired King Penguins. Data are presented as mean ± SD.

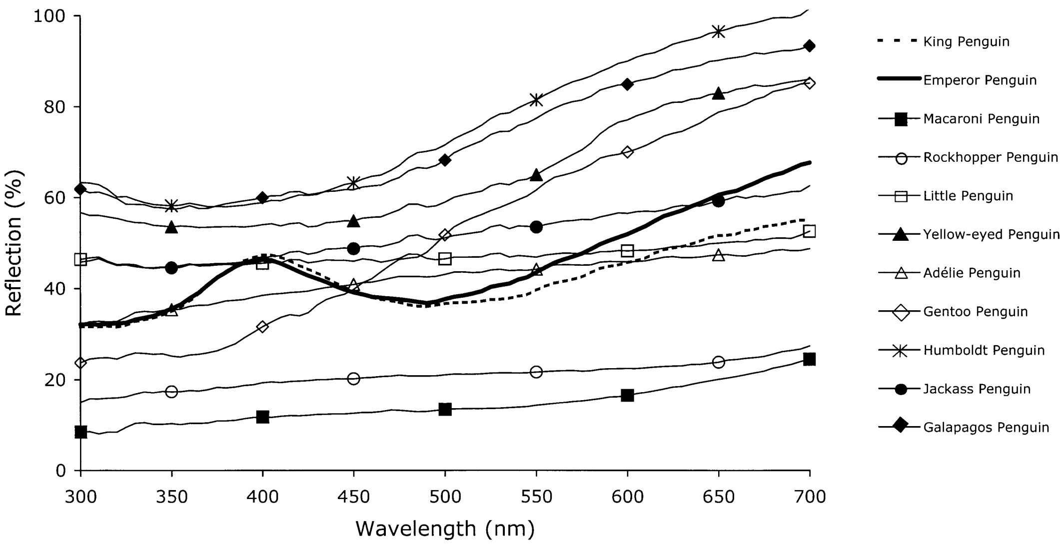

FIGURE 1. Spectral reflectance curves from the lower mandible of 11 penguin species; only the King (*Aptenodytes patagonicus*) and the Emperor (*A. forsteri*) showed distinct UV reflectance (320–400 nm).

FIELD MEASUREMENTS

We captured 57 adult King Penguins on Possession Island (46°25′S, 51°45′E) in the Crozet Archipelago (Indian Ocean), in a 2-week period in early January 2002. We identified adults by their orange auricular feathers and beak spots. "Nonpaired" birds (n = 23) were identified by their early nuptial displays (nuptial call), and by their association with a location on the beach where most mating occurs. "Paired" birds (n = 34) were identified by their late nuptial displays ("face-to-face", "bill clapping", "waddling gait", Jouventin 1982), and by their location in the brooding part of the colony. We captured an additional 134 individuals between mid-November 2001 and mid-January 2002 for which pairing status was unknown.

For all captured penguins, we took two measuments of the color of the beak spot at its widest point near the base of the beak using a Colortron (X-rite, Grandville, Michigan) portable reflectance spectrometer and averaged the measurements using Colorshop software (X-Rite, Grandville, Michigan). A Colortron spectrometer relies on twin tungsten light sources and daily calibrations against factory-supplied absolute black and absolute white standards to attain 10 nm resolution. The Colortron is sensitive across human-visible wavelengths and partially into the UV range of bird vision (390–700 nm); so we used percent reflectance at 400 nm as an index of peak UV reflectance of wild penguins. From King Penguins measured in captivity, the correlation between reflectance at 400 nm (Colortron) and peak UV reflectance (Spectrometer) was strong (r = 0.87, n = 7, P = 0.03). Thus, we are confident that this technique provided a reasonable and accurate measurement to compare courting and paired birds.

RESULTS

MUSEUM SPECIMENS AND CAPTIVE BIRDS

Of the 13 penguin species investigated (table 1), we show the reflectance curves for 11 of these species (Fig. 1). Some species such as the Gentoo Penguin (*Pygoscelis papua*) or all the crested Penguins (*Eudyptes* genus) show a colored beak, but only beak spots of the Emperor Penguin and King Penguin (*Aptenodytes* genus) exhibited a reflectance peak in the UV. Beak spots extended forward of the posterior end of the beak (Fig. 2). Beak spots of Emperor Penguins were closer to the top of the beak (where the two mandibles join) and were broader than those of King Penguins.

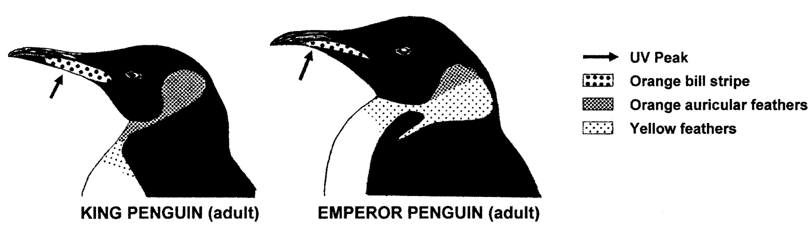

FIGURE 2. The precise location of UV reflectance on the lower orange part of the beak differs between Emperor and King Penguins. Colored auricular and breast feathers are also indicated.

Visual inspection of the reflectance graphs from the other 11 penguin species showed no distinct UV peak reflectance (Table 1). We found no distinct peak of UV reflection from any other color patch, including white feathers on the throat, black feathers on the back, colored feathers on the breast, stomach, throat, and auricular patches (orange-yellow in large penguins), black horny tissue of the beak, or on the claw or the black skin of the foot. Chicks and juveniles showed no UV reflectance on the beak (Fig. 3a), however, the superficial tissue on the lower mandible (the orange-colored beak spot) of adult large penguins was reflective in the UV (Fig. 3c). UV reflectance peaks were also absent in molting birds (Fig. 3d), but the sample size was too small ($n = 2$) to be conclusive.

From comparing King Penguin beak spots from museum skins with captive live birds (Fig. 3b), we found that peak UV reflectance was 13% greater in living birds (59% ± 4% in live birds and 46% ± 4% in museum skins; Wilcoxon test, $z = 3.3$, $P = 0.001$, $n = 7$, 9 live and museum birds, respectively). The wavelength of the UV peak (otherwise referred to as hue) varied within the same species, when comparing living birds and museum skins: live King Penguins reflected at 380 ± 1 nm, while museum specimens reflected at 401 ± 2 nm (Wilcoxon test, z = 3.3, $P = 0.001$, $n = 7$, 9 live and museum skins, respectively).

FIELD MEASUREMENTS

In our field measurements of beak UV reflectance, we compared courting birds ($n = 34$) to those individuals already mated ($n = 23$). Our index of UV reflectance (at 400 nm, see methods) was higher among paired King Penguins than among courting birds (means 63% ± 10%, and 54% ± 12%, respectively; Wilcoxon test, $z = 2.9$, $n = 34$, 23, $P < 0.01$). In addition, we found that males and females did not differ significantly in UV reflectance (means 65% ± 12% SD, and 61% ± 10%, respectively, Wilcoxon test, $z = 0.8$, $n = 17$, 17, $P = 0.41$).

DISCUSSION

We know that at least one penguin species (*Spheniscus humboldti*) is able to detect UV reflectance, as are most species of birds studied to date (Chen et al. 1984, Bowmaker and Martin 1985). Although UV reflectance has been found in a variety of species (Finger and Burkhardt 1994, Andersson 1996), only a few recent studies have shown UV reflectance from the horned parts such as the beak (Hunt et al. 2003, Peters 2004). Nonetheless, although it is likely that UV reflectance of beak spots is perceived by *Aptenodytes* penguins (see below), the function of this reflectance is unclear.

It is unlikely that these UV spots are adaptations to life at sea because UV light decreases rapidly below the surface of the water (Bradbury and Vehrencamp 1998). Depths of King Penguin dives are up to more than 300 m and Emperor Penguins dive deeper than 400 m (Kooyman et al. 1992, Kooyman and Kooyman 1995) where UV, as well most other wavelengths of light, may be virtually absent. On the water surface, it is possible that UV-reflecting beak spots may be used in species-specific identification. Beak spots might function in a similar manner as contact calls, used to find congeners at sea (Jouventin 1982), particularly when penguins hunt in single-species groups (Tremblay and Cherel 1999). For birds at sea, however, distinguishing species using beak spots would be difficult, and we have no specific evidence to support this function.

UV ornaments could play a role in pairing of breeding males and females, as an indicator of sexual maturity, or in mate choice (either intrasexual competition or intersexual selection). We measured only a small part of the UV range, thus our comparison between mated and nonmated penguins can only be considered a preliminary examination of the signaling function of UV beak reflectance during pairing. However, further study using a spectrometer recently confirmed the results of our Colortron measurements (Jouventin et al. in press), and supported our finding that UV reflectance of beak spots did not differ between male and female King Penguins, and did not appear until individuals mature sexually (Nicolaus, Nolan, and Jouventin, unpubl. data).

An increasing number of studies of birds indicate the importance of coloration (including UV) in intersexual signaling (Bennett et al. 1996, Johnsen et al. 1998), and this likely applies to penguins as well (Jouventin 1982, Massaro et al. 2003). In addition, auricular patches of orange feathers, as well as beak spots, are prominently exposed as the head and neck are used during behavioral displays associated with pairing in King and Emperor Penguins (Jouventin 1982). Nuptial displays have been described in several species of penguins, and King and Emperor Penguins share several similarities associated with these displays: colorful head feathers and beak of adults, but muted or lacking coloration in sub-adults, and the use of highly-ritualized postures that exhibit the head (''face-to-face'', Jouventin 1982). These similarities imply that colored feather patches as well as UV and orange colors of beak spots are good candidates for a role as optical signals.

The lower mandibles of King and Emperor Penguins are not only UV reflective, but also orange in color. The short-wave peak is close to the maximum sensitivity of the SWS1 visual pigment (VS cone) of penguins (ca. 405 nm, Bowmaker and Martin 1985, Wilkie et al. 2000, Ödeen and Håstad 2003). It is unclear if UV reflectance is a specific signal, or complementary to the orange coloration of lower mandibles. In addition, more than one color trait might influence pairing. For example, King Penguins have orange patches of auricular feathers that likely play a role in mate choice (Jouventin 1982, Jouventin et al., in press). A specific UV influence is not demonstrated by our association of UV reflectance of the beak spot and whether an individual was paired, because all wavelengths of light are present and perhaps visible to penguins. Consequently, additional measurements and sophisticated field experiments will be necessary to further investigate these UV peaks on the beak spots of penguins.

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TABLE 1. Results of spectrometer measurements from different body areas and plumage (black, white, and colored) from museum specimens of 13 different penguin species.

Species	Age class	Locality	Measurement locations	Presence of a UV peak	Sample size
King Penguin (*Aptenodytes patagonicus*)	adult	Kerguelen Is. (Indian Ocean)	white & black feathers, black skin (foot & claw), black part of beak, orange auricular feathers	No	9
	adult	Kerguelen Is. (Indian Ocean)	orange spot on lower mandibles	Yes	9
	juvenile & chick	Kerguelen Is. (Indian Ocean)	beak	No	10
Emperor Penguin (*Aptenodytes forsteri*)	adult	Terre Adélie (Antarctica)	white & black feathers, black skin (foot & claw), black part of beak, yellow auricular feathers	No	10
	adult	Terre Adélie (Antarctica)	orange spot on lower mandibles	Yes	10
	juvenile & chick	Terre Adélie (Antarctica)	beak	No	4
Adélie Penguin (*Pygoscelis adeliae*)	adult	Terre Adélie (Antarctica)	feathers, feet, beak	No	2
Gentoo Penguin (*Pygoscelis papua*)	adult	Crozet Is. (Indian Ocean)	feathers, feet, beak	No	2
Chinstrap Penguin (*Pygoscelis antarctica*)	adult	Terre Adélie (Antarctica)	feathers, feet, beak	No	2
Macaroni Penguin (*Eudyptes chrysolophus*)	adult	Crozet Is. (Indian Ocean)	feathers, feet, beak	No	2
Subantarctic Rockhopper (*Eudyptes chrysocome chrysocome*)	adult	Crozet Is. (Indian Ocean)	feathers, feet, beak	No	2
Subtropical Rockhopper (*Eudyptes chrysocome moseleyi*)	adult	St Paul Is. (Indian Ocean)	feathers, feet, beak	No	2
Erect-crested Penguin (*Eudyptes sclateri*)	adult	New Zealand	feathers, feet, beak	No	1
Little Penguin (*Eudyptula minor*)	adult	New Zealand	feathers, feet, beak	No	2
Galapagos Penguin (*Spheniscus mendiculus*)	adult	Galapagos Is. (Equator)	feathers, feet, beak	No	2
Jackass Penguin (*Spheniscus demersus*)	adult	Cape of Good Hope (South Africa)	feathers, feet, beak	No	2
Peruvian Penguin (*Spheniscus humboldti*)	adult	Chile (South America)	feathers, feet, beak	No	2
Yellow-eyed Penguin (*Megadyptes antipodes*)	adult	Campbell Is (New Zealand)	feathers, feet, beak	No	1

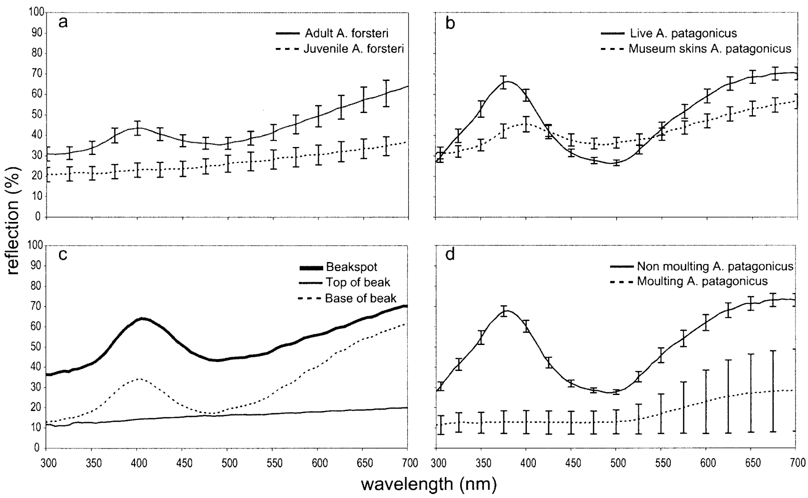

FIGURE 3. UV-reflectance peaks were: a) present in adults large penguins and absent in immature museum skins (shown here in Emperor Penguins), b) 13% higher in living King Penguins than in museum skins, c) variable according to the place on the lower mandible (high reflectance on the spot, medium near the posterior end of the beak, null at the top of the beak, and d) absent in molting birds. Curves depict an average reading from all measured individuals (see Table 1 and text). Error bars represent standard error of the mean.

ation and for assisting our measurements of captive birds. For their excellent assistance in the field, we thank Florence Hesters and Marion Nicolaus. We are particularly grateful to Marc Thery for preliminary measurements at MNHN. We thank two anonymous referees and Isabelle Coolen for their comments on versions of the manuscript. Logistical and financial support for observations in the field was provided by the Institut Polaire Français (IPEV) and by the U.S. National Science Foundation (Grant #OPP0128913 to PMN and FSD). Our field study was approved by the Ethical Committee of IPEV and the IACUC of Auburn University.

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