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Published in:
Polar Biology

DOI:
[10.1007/s00300-007-0332-9](https://doi.org/10.1007/s00300-007-0332-9)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2007

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Nicolaus, M., Le Bohec, C., Nolan, P. M., Gauthier-Clerc, M., Le Maho, Y., Komdeur, J., & Jouventin, P. (2007). Ornamental colors reveal age in the king penguin. *Polar Biology*, 31(1), 53-61.
<https://doi.org/10.1007/s00300-007-0332-9>

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Ornamental colors reveal age in the king penguin

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Received: 12 February 2007 / Revised: 22 June 2007 / Accepted: 25 June 2007 / Published online: 18 July 2007
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Abstract We investigated whether delayed plumage maturation occurred in king penguins (*Aptenodytes patagonicus*). Therefore we examined the relationships between age and sex on spectral properties and size of two colored plumage patches and a UV-reflective beak spot, using known-age cohorts. Unlike the colored patch on the breast, we found age differences in ear and beak coloration. These results suggest that head ornaments in king penguins could signal sexual maturity or social status. No sex differences were found in the intensity of colored ornaments, which can result from mutual mate choice or genetic correlation between sexes. Size of colored patches did not relate to age or sex.

Keywords Plumage maturation · UV · Ornamental size · Mutual ornamentation · *Aptenodytes patagonicus*

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Introduction

Many bird species perceive ultra-violet (UV) light and exhibit bright colors and extravagant ornaments including UV reflectance (Cuthill et al. 2000; Hart 2001; Hart and Hunt 2007), which are presumed to act in the process of sexual selection (Andersson 1994; Darwin 1871). Studies of some of these ornaments reveal that they are involved in species recognition and/or in mate choice (Jones and Hunter 1998, 1999). By examining the phenotype of a potential competitor or mate, one individual can assess the quality of another in terms of competitive ability or the direct or indirect benefits that would accrue from mating. Indeed, variation in ornamentation may reflect different indicators of fitness, such as immune system strength (Møller et al. 1998, 1999), life history traits (Roulin et al. 2003), parental investment (Saino et al. 2002), survival rate (Hörak et al. 2001), social dominance (Kraaijeveld et al. 2004) or breeding status (Jones et al. 2000). Therefore, secondary sexual characters are often honest signals, allowing males in good condition to express the most extravagant ornaments and therefore be more attractive to females and more dominant in intrasexual contests (Andersson 1994; Hamilton and Zuk 1982; Hill 1992). Colored ornaments are, however, not male-specific because in many species females can express the same phenotype as males. This suggests that sexual selection can also act on females (Hunt et al. 1999; Jones and Hunter 1998, 1999) or that sexes are genetically correlated (Rice 1984). Mutual sexual preferences and mutual ornamentation are also likely to be found in species in which each parents contribute significantly to rearing the offspring, especially if breeding is costly (Bennett and Owens 2002; Kokko and Johnstone 2002; Kraaijeveld et al. 2007).

In many bird species, a delay in the achievement of adult appearance is found. In numerous seabirds (e.g. Gibson 1967; Weimerskirch et al. 1989) and passerines (Komdeur et al. 2005; McDonald 1993), the transition from juvenile to adult status is indeed accompanied by a distinct change in the intensity and size of coloration, indicating that plumage characteristics may signal age. Several hypotheses that relate to the degree of competition for resources within species have been proposed to explain the adaptive significance of delayed plumage maturation (Beauchamp 2003). The “status signaling hypothesis” suggests that juveniles actively advertise their age and their subordinate status to initially profit longer from parental care and then to decrease the amount of aggressive interaction with older birds. This strategy should therefore provide a higher survival to the juveniles even though they are delayed in their reproductive attempts (Beauchamp 2003; Conover et al. 2000). Moreover, there is some evidence that the size and color of ornaments can also vary between adults seasonally (Ornborg et al. 2002; Tubaro et al. 2005), or with fecundity or pairing status (Badyaev and Duckworth 2003; Childress and Bennun 2002), suggesting that individual plasticity in ornamentation could, in some situations, indicate both age and reproductive status. In this study we investigated the potential relationships between age and sex on spectral properties and size of two colored plumage patches and a UV-reflective beak spot in the king penguin, *Aptenodytes patagonicus*.

Although many members of the penguin family are characterized by the presence of seemingly ornamental traits, little is known about their signal function (Jouventin 1982; Massaro et al. 2003). The king penguin is a suitable species to study the function of coloration because individuals have distinct and conspicuous yellow-orange feather patches on both sides of their heads (McGraw et al. 2004) and a conspicuous ultraviolet (UV) reflectance spot on their lower mandible (Dresp et al. 2005; Dresp and Langley 2006; Jouventin et al. 2005). These cephalic ornaments have been thought to play a role in species discrimination, as their position makes them visible during the long periods when birds are swimming at the ocean surface (Martinez 1992). Removal of colored feather patches in several species of penguins decreased the ability to mate in both sexes (Jouventin 1982), suggesting a potential role in sexual selection beyond simple species recognition. In king penguins, the experimental decrease of ear patch size has been found to increase time to pairing, which supports the hypothesis that their colored plumage is sexually selected (Jouventin et al. 2005). Moreover, like other penguin species, king penguins possess a complex visual courtship display where both partners exhibit their colored head ornaments (Jouventin 1982; Stonehouse 1960). For example, in the “ecstatic” display (flippers out, and beak pointed

straight up; Jouventin 1982), males and females prominently display their beak spot and head color to potential mates. Both sexes display apparent similar color pattern. King penguins usually breed biennially with different partners and the sexes contribute equally to incubation and raising the single chick (Descamps et al. 2002). The average age at first breeding is 5 years but a small proportion of birds try to breed at 3 and 4 years of age (Weimerskirch et al. 1992; Le Bohec et al., unpublished data). The occurrence of extra-pair paternity is poorly known in this species but it may occur, given that females have been observed copulating with several males during the courtship period and before having established a social pair bond (Olsson et al. 2001). The level of competition for mates may thus be high during the breeding season. King penguins might also conform to a pattern described by Kraaijeveld (2003), in which high levels of mutual ornamentation are related to high divorce rates in birds, which can lead to a high level of competition for mate or resources. In dense penguin colonies, the level of aggression between conspecifics is related to the reproductive status of the birds and the location of their territories inside the colony (Côté 2000).

Our main objectives here were twofold. First, we wanted to study whether color characteristics of king penguin ornaments vary with age. We predicted a difference between cohorts for two main reasons: in king penguins, old birds are more experienced and more successful in reproduction than young ones; therefore, if colored ornaments are honest signals, they are likely to carry information about individual quality including age. Following the idea of the “status signaling hypothesis”, selection may have favored a delay in plumage maturation as juveniles may gain direct advantages in signaling their subordinate status. By indicating to sexually mature birds that they are not a threat for resources acquisition (e.g. mate and nest site), juveniles may reduce the rate of aggression by conspecifics and consequently may increase their chance of survival. Second, we wanted to investigate whether size and color of ornamental patches, including their UV reflectance, varied with sex. We predicted that the sexes would be indistinguishable on the basis of their colored phenotype because king penguins’ mating system can favor the maintenance of mutual ornamentation.

Materials and methods

Study area and data collection

Our study was conducted during the breeding season in November 2003 in the king penguin colony “La Grande Manchotière”, comprising circa 16,000 breeding pairs (Delord et al. 2004), at Possession Island (46°25′S,

51°45'E) in the Crozet Archipelago. A sub-colony (0.8 ha) consisting of about 10,000 pairs has access to the sea by three pathways. Antennae allowing detection of electronic tags (Texas Instrument Recognition and Identification System (TIRIS)) are permanently buried in the ground on each pathway and connected to a computer for data collection. An electronic TIRIS transponder tag of 0.8 g has been implanted under the skin of 2,444 birds over the six study years, allowing us to recognize individuals as they enter or leave the sub-colony (Gendner et al. 2005). Because chicks and adults have been implanted with transponders in each of the years from 1998 onwards, we could assign the exact age to the birds marked as chicks. For this study we captured 49 implanted individuals after the antenna at the entrance to the sub-colony detected them and alerted us to their presence. We measured the color of these birds (described below) and divided them into four age groups: 1 (2 and 3 years old; $n = 19$), 2 (4 years old; $n = 12$), 3 (5 years old; $n = 9$) and 4 (6 years old; $n = 9$). These groups were composed of birds of exact known age. Birds of 2 ($n = 2$) and 3 ($n = 17$) years old have been pooled together in one age group to increase the power of the statistical analyses.

Of these birds, 20 were sexed using the molecular method of Griffiths et al. (1998). For those that were not blood sampled ($n = 22$), we determined sex on timing of arrival during the breeding season. The alternation and duration of the sojourns at sea and ashore of the implanted birds, allowed us to determine their sex. At the beginning of the breeding cycle, males are ashore for about 1 month to display and to provide the first long shift of incubation whereas females leave the colony just after courtship and laying (Stonehouse 1960; Weimerskirch et al. 1992). In the 20 cases where we had both blood samples and data on the birds' time of arrival, the sex as determined by molecular techniques always matched the sex as determined from arrival data, suggesting that the second method is reasonably reliable. Seven of the 49 birds studied could not be sexed because no blood samples were available and because they were too young to be sexed according to their reproductive cycle. In total, 15 females and 27 males were sexed.

Reflectance spectrometry

We measured reflectance characteristics from three body regions: the breast, the ear patch and the side of the beak (Fig. 1) using an S2000 spectrophotometer (Ocean Optics Inc., Dunedin, FL, USA). Measurements were taken perpendicular to the feather and to the beak horn surface at the same locations for all birds (Fig. 1). All reflectance measures were divided by the corresponding reflectance from a white Spectralon standard, a perfect reflector. The spectro-

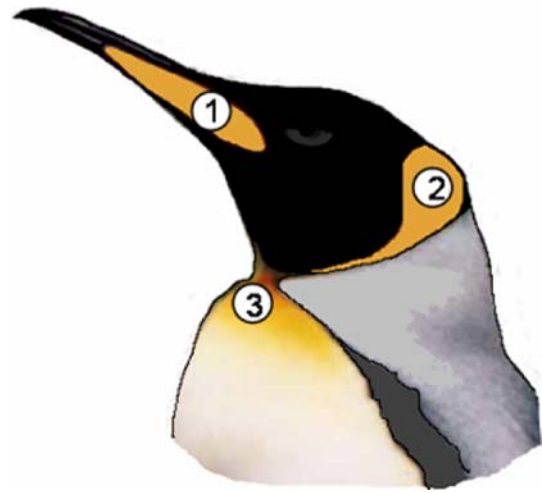


Fig. 1 Colored ornaments of the king penguin (*Aptenodytes patagonicus*) and representation of the three areas measured with the spectrophotometer 1. Beak spot. 2. Ear patch. 3. Breast patch

photometer was calibrated with the white standard at the beginning of each measuring session. A probe sheath was used to exclude ambient light and to standardize the distance between the probe and the feathers (about 3 mm). For each bird we took three measurements of each of the three regions by lifting and replacing the fiber-optic at the same place.

Color variables and color patches

We summarized our reflectance data by calculating derived measures of the spectral shape to approximate five dimensions of color: hue, UV-hue, chroma, UV-chroma and brightness (Endler 1990, Montgomerie 2006). Hue and UV-hue were, respectively, measured as the values of the wavelength at 600 nm and at the maximum reflectance within the UV wavelengths (320–400 nm). Chroma is a measure of saturation of a color and was calculated as the difference between the values of maximum and minimum reflectance (R), relative to the average reflectance across the curve ($(R_{\max} - R_{\min})/R_{\text{average } 320-700}$). We also calculated UV-chroma, the spectral saturation in the UV region (320–400 nm), as the sum of reflectance in the UV region relative to the sum of reflectance from 320 to 700 nm ($\text{Sum}(R_{320-400})/\text{Sum}(R_{320-700})$). Brightness, the spectral intensity, was estimated as the sum of reflectance from 320 to 700 nm ($\text{Sum}(R_{320-700})$).

We took high resolution pictures of all the birds we handled, using a SONY DSC-P9 4.2 megapixel digital camera. We quantified natural variation in the size of auricular and beak patches of all birds, by including in the picture a ruler next to the bird in the same plane as the feathers. All photographs were taken using the camera's flash inside a shelter, without zoom and at about 20 cm from the bird to create

standard conditions. We then analyzed the pictures using the public domain NIH Image J program (developed at the US National Institutes of Health and available for free download; <http://www.rsb.info.nih.gov/ij/>). For each patch, size was measured twice per individual and then averaged for the analysis. Breast patch was excluded from the analyses because of its diffuse and graded nature.

Data analyses

When the data were normally distributed, we compared the color parameters between the different age-classes using one-way ANOVA (Scherrer 1984). When application conditions for ANOVA were not met (even after transformation of the data), a Kruskal–Wallis test (Siegel and Castellan 1988) was used to compare more than two samples. Statistical analyses were performed with StatSoft, Inc. (2004) STATISTICA® (data analysis software system), version 7. Mean were expressed with standard deviation (SD) and with a coefficient of variation (CV). All statistical tests were two-tailed. Bonferroni adjustment was applied to correct for multiple testing (Rice 1989) resulting in significance level set at $P < 0.01$ (beak) and $P < 0.02$ (ear and breast).

Results

Relationship of age and sex to color intensity

We found that beak spectra exhibited a bimodal distribution with a high peak in the UV region and a second peak in the orange wavelengths (Fig. 2a), whereas the breast and ear patch spectra presented a simple distribution with maximum reflectance in the orange-red region (Fig. 2b, c). Beak spot reflectance increased with age, whereas this pattern was almost absent in the ear and breast regions (Fig. 2). Analyses of the color parameters showed that all the color and UV variables of the beak horn, apart from the UV chroma, and of the ear patch, apart from the hue, presented significant variation between age classes (Table 1; Fig. 3). None of the variables of the breast patch varied with age (Table 1). Color variables did not differ between males and females (Table 1). The mean (\pm SD) and the coefficients of variation of the color variables measured in the beak, ear and breast areas are presented in Table 2. Figure 3 represents the traits that showed significant variation with age; specifically, the color and UV variables of the beak horn and the chroma and brightness of the ear patch. Beak UV hue and beak brightness showed a linear increase with age (Fig. 3b, e) whereas for the other variables, values varied non-linearly with age and showed a difference mainly in the 6 years old age class (Fig. 3a, c, d, f).

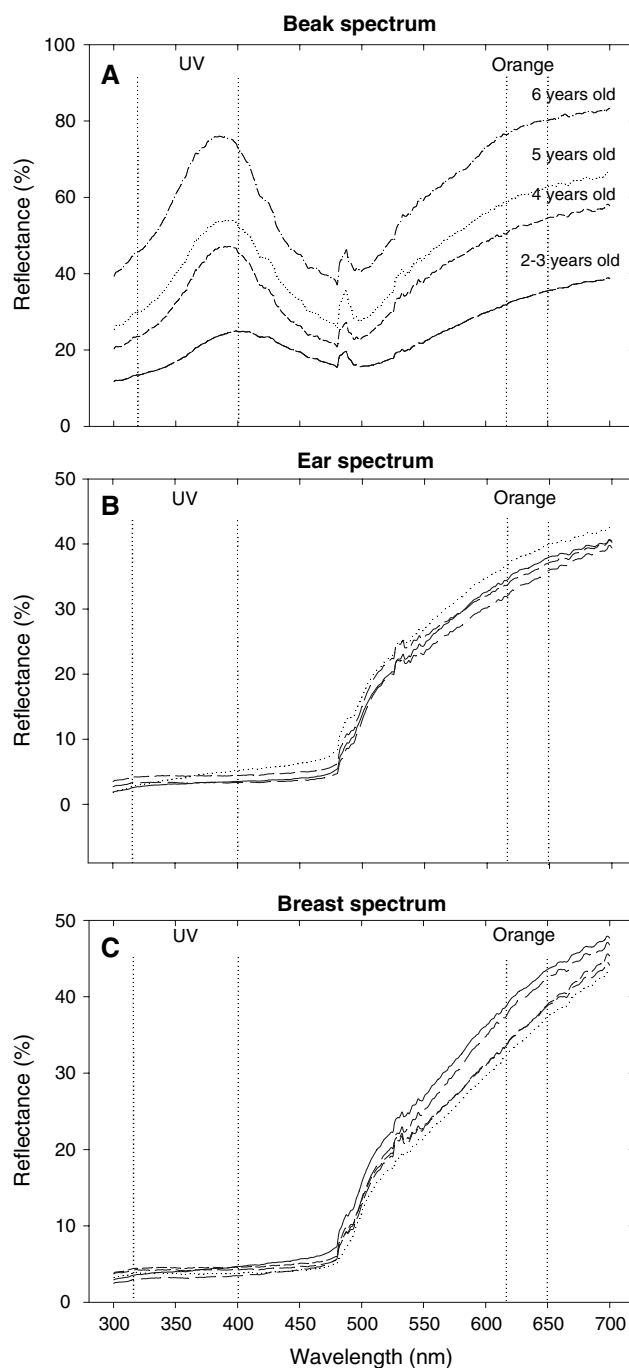


Fig. 2 Reflectance spectra of the beak horn (a), of plumage from the ear patch (b) and from the breast (c). Each spectrum is the average of individual values of one age class. The different age groups have been labeled on the beak spectrum a 2–3 years old ($n = 19$), 4 years old ($n = 12$), 5 years old ($n = 9$) and 6 years old ($n = 9$). Further details of the values used to generate these spectra are presented in Table 2

Relationship of sex and age to color patch size

Size of the colored patches varied between 8.2 and 21.1 cm² for the ear patches and between 4.1 and 9.6 cm²

Table 1 Influence of age and sex on the color parameters of the beak, the ear and the breast areas

	Age groups	<i>P</i>	Post hoc tests	Sex	<i>P</i>
Beak					
Chroma	$F_{3,49} = 8.10$	0.00	1 vs. 4, 2 vs. 4, 3 vs. 4	$F_{1,42} = 0.49$	0.48
Brightness	$F_{3,49} = 77.4$	0.00	1 vs. 2, 1 vs. 3, 1 vs. 4, 2 vs. 4, 3 vs. 4	$F_{1,42} = 0.16$	0.69
Hue	$H_{3,49} = 20.74$	0.00	1 vs. 4, 2 vs. 4, 3 vs. 4	$H_{1,42} = 0.30$	0.58
UV chroma	$F_{3,49} = 3.62$	0.02		$F_{1,42} = 0.02$	0.88
UV hue	$F_{3,49} = 83.35$	0.00	1 vs. 2, 1 vs. 3, 1 vs. 4, 2 vs. 4, 3 vs. 4	$F_{1,42} = 1.48$	0.23
Ear					
Chroma	$H_{3,49} = 35.46$	0.00	1 vs. 2, 1 vs. 3, 2 vs. 4, 3 vs. 4	$H_{1,42} = 0.05$	0.81
Brightness	$F_{3,49} = 38.25$	0.00	1 vs. 2, 1 vs. 3, 2 vs. 4, 3 vs. 4	$F_{1,42} = 0.21$	0.65
Hue	$H_{3,49} = 1.07$	0.78		$H_{1,42} = 4.96$	0.03
Breast					
Chroma	$F_{3,49} = 0.57$	0.64		$F_{1,42} = 0.27$	0.61
Brightness	$F_{3,49} = 0.46$	0.71		$F_{1,42} = 0.01$	0.93
Hue	$H_{3,49} = 2.62$	0.45		$H_{1,42} = 1.78$	0.19

Analysis of variance: one-way ANOVAs or Kruskal–Wallis tests

Significant values after a Bonferroni adjustment are denoted in bold

When color variables were related with age, significant post hoc tests between age groups are shown (Tukey post hoc test (parametric) or Dunn post hoc test (non-parametric))

Group1 2–3 years old ($n = 19$), group2 4 years old ($n = 12$), group3 5 years old ($n = 9$) and group4 6 years old ($n = 9$)

for the beak spots. The absolute patch size did not differ between sexes (ANOVA: ear patch $F_{1,42} = 0.47$, $P = 0.50$; beak patch $F_{1,42} = 0.00$, $P = 0.98$) nor between age classes (ANOVA: ear patches $F_{3,49} = 0.78$, $P = 0.51$; beak patch $F_{3,49} = 1.63$, $P = 0.19$).

Discussion

We found that age contributed significantly to inter-individual variance in color and UV characteristics of the beak horn and to some color variation of the ear patches. Breast coloration, however, did not vary with age. In addition, we found that the sexes were indistinguishable on the basis of their colored phenotypes. Sex and age did not explain any of the individual variation in ornament size.

Age, UV and coloration

As expected, we found age-related variation in many of the color characteristics of the beak horn and ear patches. Breast patch color variation, however, did not relate to age. It is already known that breast color is an honest signal for immune system strength in this species (Nolan et al. 2006). Therefore, the role of this colored patch seems to be related to bird quality but did not carry information about age or breeding status. Moreover, we found that all color and UV characteristics of the beak spot, apart from the UV chroma, varied with age, as did the chroma and brightness of the ear

patch. This suggests that beak horn, at least, is important in signaling age because its brightness and its UV hue exhibited a positive increase with age. The spectra of the different body areas support these results; beak spot reflectance increased with age whereas this pattern was almost absent in the ear and breast regions. In addition, the age effect on the other beak and ear color variables was not linear and was caused mainly by the oldest age class. Thus, our results suggest that delayed plumage maturation is occurring in king penguins. Observations of naturalists already reported that beak color turns brighter after several moults (Harrison 1993; Martinez 1992), and here we present evidence that this variation is related to age. Two non-exclusive hypotheses can be formulated in regards to these results: the beak and the ear color or UV characteristics might play a role in signaling breeding or social status or they might play a sexually selected role as honest signals of individual quality.

In the first case, immature birds might gain direct benefits in actively advertising their age and their subordinate status through some of their head color and UV characteristics if it reduces the rate of aggression by older birds and increases their subsequent survival. In king penguins that live in dense colonies, the competition for mates and nest sites during the courtship period is intense and associated with a high rate of agonistic encounters (Côté 2000). Birds that mate and start breeding early are indeed favored because they increase their chance of getting the best breeding locations in the colony that are less exposed to predation, which might give them a higher reproductive success

Fig. 3 Representation of the mean color and UV variables of the beak horn and the ear colored patch (\pm SE) that presented significant relation with age groups: Beak hue (a), beak UV hue (b), beak chroma (c), ear chroma (d), beak brightness (e), ear brightness (f); 2–3 years old ($n = 19$), 4 years old ($n = 12$), 5 years old ($n = 9$) and 6 years old ($n = 9$). * denoted significant difference between age groups

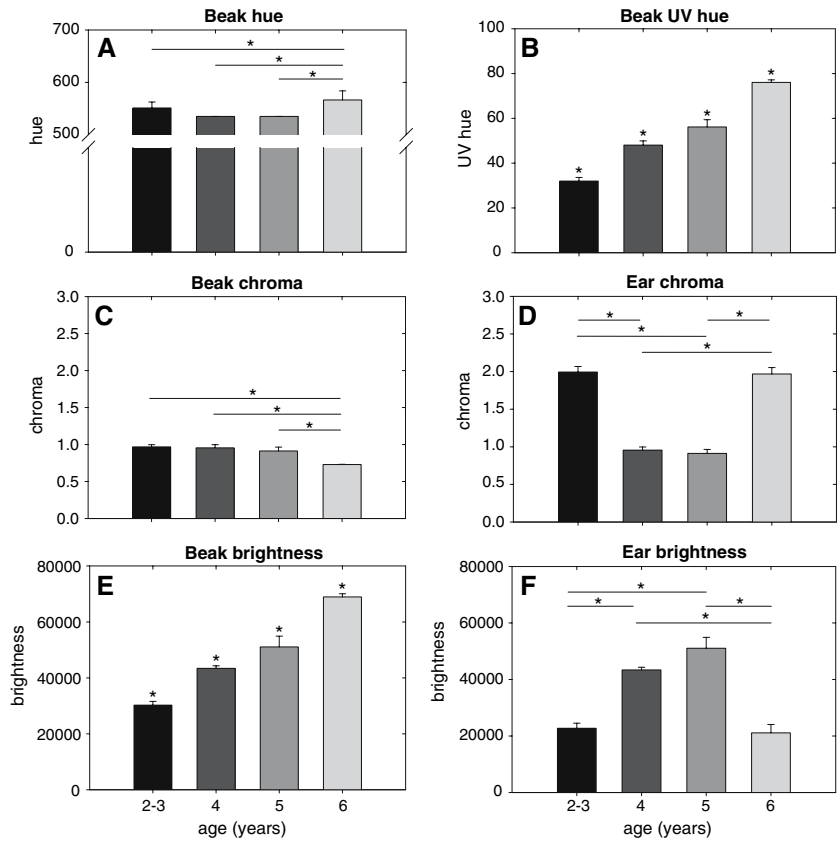


Table 2 Mean values (\pm SD) and coefficients of variation (CV) of the color parameters in the regions of the beak, the ear and the breast measured for each age groups

Age groups	Chroma			UV chroma			Brightness			Hue			UV hue		
	Mean	\pm SD	CV	Mean	\pm SD	CV	Mean	\pm SD	CV	Mean	\pm SD	CV	Mean	\pm SD	CV
Beak															
2–3	0.97	0.12	12.42	0.30	0.03	9.40	30,249.77	5,801.16	19.18	551.12	48.75	8.85	31.97	7.10	22.21
4	0.96	0.30	31.36	0.30	0.02	6.78	43,384.64	3,198.93	7.37	534.96	0.15	0.03	48.04	6.57	13.69
5	0.91	0.31	33.56	0.31	0.01	3.63	51,040.49	11,529.58	22.59	534.96	0.15	0.03	56.12	9.83	17.51
6	0.73	0.32	44.26	0.32	0.00	0.02	68,931.41	3,412.96	4.95	566.26	52.44	9.26	76.01	3.50	4.60
Total	0.89	0.26	30.40	0.31	0.01	4.96	48,401.58	5,985.66	13.52	546.83	25.37	4.54	53.03	6.75	14.50
Ear															
2–3		1.99	0.32	16.05			22,733.11	7,939.18	34.92	558.04	55.20	9.89			
4		0.96	0.15	15.64			43,384.64	3,198.93	7.37	534.96	0.15	0.03			
5		0.91	0.16	17.46			51,040.49	11,529.58	22.59	534.96	0.15	0.03			
6		1.97	0.26	12.97			21,131.92	8,846.66	41.86	550.17	45.77	8.32			
Total		1.46	0.22	15.53			34,572.54	7,878.59	26.69	544.53	25.32	4.57			
Breast															
2–3		2.14	0.25	11.50			23,473.08	7,644.84	32.57	543.01	35.56	6.55			
4		2.25	0.22	9.88			22,060.07	9,026.72	40.92	547.53	43.80	8.00			
5		2.19	0.20	9.31			20,352.50	5,502.10	27.03	534.81	0.17	0.03			
6		2.19	0.21	9.62			20,950.04	5,541.62	26.45	549.59	44.02	8.01			
Total		2.20	0.22	10.08			21,708.92	6,928.82	31.74	543.73	30.89	5.65			

2–3 years old ($n = 19$), 4 years old ($n = 12$), 5 years old ($n = 9$) and 6 years old ($n = 9$)

(Côté 2000). Moreover, king penguins are known to perform copulations with multiple males before definitive pairing, which suggests the possibility of extra-pair paternity in this species (Olsson et al. 2001). Birds thus have to vigorously defend their potential mate and their small territory. Consequently, selection might lead to age related maturation of breeding signals if, by advertising their age, young birds indicate that they are not a threat for mature birds in the competition for resources such as nest sites or mates.

In the second case, coloration and UV reflectance could be used by birds as a cue for mate choice. Life-history theory predicts that individual fitness should change positively with age, at least to a certain point, because reproductive performance increases with efficiency of learned foraging skills and breeding experience (Forslund and Part 1995; McGraw et al. 2001). In king penguins, recruitment rate into the breeding population increases with age as birds are on average sexually mature around 5 years old. Through assessing plumage and beak colors, king penguins may benefit by knowing the age of their potential mate as it reflects on that individual's "quality". Thus, head coloration might provide access to indirect information about individual age and could help to exclude juveniles from reproduction i.e., could help to discriminate between experienced and inexperienced breeders. The results of Jouventin et al. (2005) reporting that UV reflectance among paired king penguins was higher than among courting birds may support this hypothesis.

Structural color including UV reflectance from plumage and beak tissue appears to be an honest signal that can act in the process of mate choice, and could reflect the competitive ability of birds (Hunt et al. 2001; Pearn et al. 2003; Siitari et al. 2002, Siefferman and Hill 2005). We found here that beak spot spectra exhibited a significant peak in the UV region (320–400 nm; Fig. 2a), supporting previous studies that reported a strong UV reflectance from the beak spots of king and emperor penguins (*Aptenodytes forsteri*) (Jouventin et al. 2005). Moreover, because UV beak reflectance increases dramatically when king penguins reach breeding age, and because UV-reflective ornaments are typically found in body regions associated with active courtship displays (Hausmann et al. 2003), we suggest that UV reflectance may be associated with the birds' courtship behaviors and may play a role in mate choice for the most experienced breeders.

Sex and coloration

Males and females exhibited the same color characteristics, which could support the idea that plumage dimorphism is often significantly associated with sex differences in parental care such as brood provisioning or incubation (Bennett and Owens 2002; Kokko and Johnstone 2002). King

penguins are characterized by social monogamy during their breeding cycle and by shared reproductive investment between the sexes because males and females participate equally in incubation and raising the single chick. Therefore, penguin coloration patterns might have evolved similarly between males and females because in species with biparental care the choice of the partner is a crucial step to achieve reproduction. The fact that both sexes reflect UV from their beak and have similar color patterns suggests that males and females may use the same cue to select a partner. However, even though penguin ornaments may be under the pressure of mutual sexual selection the possibility of genetic correlation between the sexes cannot be discarded. Females might in fact develop a male-ornament not as the result of a selection process, but as a result of genes transmitted from fathers to daughters (see review in Kraaijeveld et al. 2007). Hence, in king penguins, resemblance between sexes could be either a by-product of genetic correlation between sexes or could be a result of mutual sexual selection acting via mutual mate choice and intra-sexual competition, or a combination of the two. We are currently examining this question in more detail and with a larger sample size in another study.

Size of colored ornaments

We know from previous work that colored ear patch size influences the probability of pairing in king penguins (Jouventin et al. 2005). In this study, absolute size of colored ornaments did not differ between sexes and between cohorts although it presented inter-individuals variation. Consequently, ornament sizes seem to have evolved similarly for both sexes, perhaps through mutual mate choice. Even though patch size seems to be under the influence of sexual selection, which could explain the maintenance of inter-individual variation, its signal content does not appear to include information about age. In a separate study of king penguins at the same site, ear patch size showed a role in mediating aggression among incubating birds, suggesting that individuals may bear a social cost for elaborating this signal (V. Viera, personal communication).

Our data suggest that delay in plumage maturation occurs in king penguins as has been shown for other species. Therefore, spectrophotometry can be used in king penguins as non-invasive method to identify individual age. Until now, only the orange color was thought to change with age in king penguins (Harrison 1993; Martinez 1992) but our results suggest that color communication among king penguins is more complex than was previously thought. Further investigations are needed to test if the expression of UV and other colorations are costly signals, and to tease apart the specific roles they play in sexual and natural selection.

Acknowledgments Logistical and financial supports for the observations in the field were provided by the Institut Polaire Paul Emile Victor (IPEV) and by the US National Science Foundation (OPP #0128913). Our field experiments were approved by the ethical committee of IPEV and the Institutional Animal Care and Use Committee of Auburn University, USA. We thank Marco van der Velde (University of Groningen, The Netherlands) for his help in sexing birds in the lab, as well as, Manuel Ballesteros for assistance in the field and all the numerous students who have participated in the different field seasons. We also thank F. Stephen Dobson (CEFE-CNRS Montpellier, France) for his useful comments on the manuscript.

References

- Andersson M (1994) Sexual selection. Princeton University Press, Princeton
- Badyaev AV, Duckworth RA (2003) Context-dependent sexual advertisement: plasticity in development of sexual ornamentation throughout the lifetime of a passerine bird. *J Evol Biol* 16:1065–1076
- Beauchamp G (2003) Delayed maturation in birds in relation to social foraging and breeding competition. *Evol Ecol Res* 5:589–596
- Bennet PM, Owens IPF (2002) Evolutionary ecology of birds. Life histories, mating systems and extinction. Oxford University Press, Oxford
- Childress RB, Bennun LA (2002) Sexual character intensity and its relationship to breeding timing, fecundity and mate choice in the great cormorant *Phalacrocorax carbo* lucidus. *J Avian Biol* 33:23–30
- Conover MR, Reese JG, Brown AD (2000) Costs and benefits of sub-adult plumage in mute swans: testing hypotheses for the evolution of delayed plumage maturation. *Am Nat* 156:193–200
- Côté SD (2000) Aggressiveness in king penguins in relation to reproductive status and territory location. *Anim Behav* 59:813–821
- Cuthill IC, Partridge JC, Bennett ATD, Church SC, Hart NS, Hunt S (2000) Ultraviolet vision in birds. *Adv Study Behav* 29:159–214
- Darwin C (1871) The descent of man and selection in relation to sex. Murray, London
- Delord K, Barbraud C, Weimerskirch H (2004) Long-term trends in the population size of king penguins at Crozet archipelago: environmental variability and density dependence? *Polar Biol* 27:793–800
- Descamps S, Gauthier-Clerc M, Gendner JP, Le Maho Y (2002) The annual breeding cycle of unbanded king penguin *Aptenodytes patagonicus* on Possession Island (Crozet). *Avian Sci* 2:87–98
- Dresp B, Langley K (2006) Fine structural dependence of ultraviolet reflections in the king penguin beak horn. *Anat Rec A Discov Mol Cell Evol Biol* 288A:213–222
- Dresp B, Jouventin P, Langley K (2005) Ultraviolet reflecting photonic microstructures in the king penguin beak. *Biol Lett* 1:310–313
- Endler JA (1990) On the measurement and classification of colour in studies of animal colour patterns. *Biol J Linn Soc* 41:315–352
- Forslund P, Part T (1995) Age and reproduction in birds—hypotheses and tests. *Trends Ecol Evol* 10:374–378
- Gendner JP, Gauthier-Clerc M, Le Bohec C, Descamps S, Le Maho Y (2005) A new application for transponders in studying penguins. *J Field Ornithol* 76:138–142
- Gibson JD (1967) The wandering albatross *Diomedea exulans*: result of banding and observations in New South Wales coastal waters and the Tasman sea. *Notornis* 14:47–57
- Griffiths R, Double MC, Orr K, Dawson RJG (1998) A DNA test to sex most birds. *Mol Ecol* 7(8):1071–1075
- Hamilton WD, Zuk M (1982) Heritable true fitness and bright birds: a role for parasites. *Science* 218:384–387
- Harrison P (1993) Seabirds, an identification guide. Christopher Helm, London
- Hart NS (2001) The visual ecology of avian photoreceptors. *Prog Retin Eye Res* 20:675–703
- Hart NS, Hunt DM (2007) Avian visual pigments: characteristics, spectral tuning, and evolution. *Am Nat* 169:S7–S26
- Hausmann F, Arnold KE, Marshall NJ, Owens IPF (2003) Ultraviolet signals in birds are special. *Proc Roy Soc Lond B* 270:61–67
- Hill GE (1992) Proximate basis of variation in carotenoid pigmentation in male house finches. *Auk* 109:U1–U12
- Hörak P, Ots I, Vellau H, Spottiswoode C, Moller AP (2001) Carotenoid-based plumage coloration reflects hemoparasite infection and local survival in breeding great tits. *Oecologia* 126:166–173
- Hunt S, Cuthill IC, Bennett ATD, Griffiths R (1999) Preferences for ultraviolet partners in the blue tit. *Anim Behav* 58:809–815
- Hunt S, Cuthill IC, Bennett ATD, Church SC, Partridge JC (2001) Is the ultraviolet waveband a special communication channel in avian mate choice? *J Exp Biol* 204:2499–2507
- Jones IL, Hunter FM (1998) Heterospecific mating preferences for a feather ornament in least auklets. *Behav Ecol* 9:187–192
- Jones IL, Hunter FM (1999) Experimental evidence for mutual inter- and intrasexual selection favouring a crested auklet ornament. *Anim Behav* 57:521–528
- Jones IL, Hunter FM, Fraser G (2000) Patterns of variation in ornaments of crested auklets *Aethia cristatella*. *J Avian Biol* 31:119–127
- Jouventin P (1982) Visual and vocal signals in penguins, their evolution and adaptive characters. Paul Bary, Berlin
- Jouventin P, Nolan PM, Dobson FS, and Nicolaus M (2005) Coloured patches influence pairing in king penguins. *Ibis* 147:XXX
- Jouventin P, Nolan PM, Ornborg J, Dobson FS (2005) Ultraviolet beak spots in king and emperor penguins. *Condor* 107:144–150
- Kokko H, Johnstone RA (2002) Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. *Phil Trans Roy Soc Lond B* 357:319–330
- Komdeur J, Oorebeek M, van Overveld TC, Cuthill IC (2005) Mutual ornamentation, age, and reproductive performance in the European starling. *Behav Ecol* 16:805–817
- Kraaijeveld K (2003) Degree of mutual ornamentation in birds is related to divorce rate. *Proc R Soc Lond B* 270:1785–1791
- Kraaijeveld K, Gregurke J, Hall C, Komdeur J, Mulder RA (2004) Mutual ornamentation, sexual selection, and social dominance in the black swan. *Behav Ecol* 15:380–389
- Kraaijeveld K, Kraaijeveld-Smit F, and Komdeur J (2007) The evolution of mutual ornamentation. *Anim Behav* (accepted)
- Martinez I (1992) Penguins in handbook of the birds of the world. Lynx, Barcelona
- Massaro M, Davis LS, Darby JT (2003) Carotenoid-derived ornaments reflect parental quality in male and female yellow-eyed penguins (*Megadyptes antipodes*). *Behav Ecol Sociobiol* 55:169–175
- McDonald DB (1993) Delayed plumage maturation and orderly queues for status—a manakin mannequin experiment. *Ethol* 94:31–45
- McGraw KJ, Nolan PM, Stoehr AM, Hill GE (2001) Intersexual differences in age-specific parental effort in the house finch (*Carpodacus mexicanus*). *Etologia* 9:35–41
- McGraw KJ, Wakamatsu K, Ito S, Nolan PM, Jouventin P, Dobson FS, Austic RE, Safran RJ, Siefferman LM, Hill GE, Parker R (2004) You can't judge a pigment by its color: carotenoid and melanin content of yellow and brown feathers in swallows, bluebirds, penguins, and domestic chickens. *Condor* 106:390–395
- Møller AP, Dufva R, Erritzoe J (1998) Host immune function and sexual selection in birds. *J Evol Biol* 11:703–719
- Møller AP, Christe P, Lux E (1999) Parasitism, host immune function, and sexual selection. *Quart Rev Biol* 74:3–20

- Montgomerie R (2006) Analyzing colors. In: Hill GE, McGraw KJ (eds) Bird coloration. Harvard University Press, Cambridge, pp 90–147
- Nolan PM, Dobson FS, Dresp B, Jouventin P (2006) Immunocompetence is signalled by ornamental colour in king penguins, *Aptenodytes patagonicus*. *Evol Ecol Res* 8:1325–1332
- Olsson O, Bonnedahl J, Anker-Nilssen P (2001) Mate switching and copulation behaviour in king penguins. *J Avian Biol* 32:139–145
- Ornborg J, Andersson S, Griffith SC, Sheldon BC (2002) Seasonal changes in a ultraviolet structural colour signal in blue tits, *Parus caeruleus*. *Biol J Linn Soc* 76:237–245
- Pearn SM, Bennett ATD, Cuthill IC (2003) The role of ultraviolet—reflectance and ultraviolet-A induced fluorescence in budgerigar mate choice. *Ethology* 109:961–970
- Rice WR (1984) Sex-chromosomes and the evolution of sexual dimorphism. *Evolution* 38:735–742
- Rice WR (1989) Analyzing tables of statistical tests. *Evol* 43:223–225
- Roulin A, Ducret B, Ravussin PA, Altwegg R (2003) Female colour polymorphism covaries with reproductive strategies in the tawny owl *Strix aluco*. *J Avian Biol* 34:393–401
- Saino N, Incagli M, Martinelli R, Moller AP (2002) Immune response of male barn swallows in relation to parental effort, corticosterone plasma levels, and sexual ornamentation. *Behav Ecol* 13:169–174
- Scherrer B (1984) Biostatistic. Gaetan Morin, Québec
- Siefferman L, Hill GE (2005) UV-blue structural coloration and competition for nestboxes in male eastern bluebirds. *Anim Behav* 69:67–72
- Siegel S, Castellan NJ (1998) Non-parametric statistics for the behavioural sciences. McGraw-Hill, New York
- Siitari H, Honkavaara J, Huhta E, Viitala J (2002) Ultraviolet reflection and female mate choice in the pied flycatcher, *Ficedula hypoleuca*. *Anim Behav* 63:97–102
- Stonehouse B (1960) The king penguin *Aptenodytes patagonica* of South Georgia island. Breeding behaviour and development. *Falkland Isl Depend Surv Sci Rep* 23:1–83
- Tubaro PL, Lutmaer DA, Loughheed SC (2005) Cryptic dichromatism and seasonal color variation in the diademed tanager. *Condor* 107:648–656
- Weimerskirch H, Lequette B, Jouventin P (1989) Development and maturation of plumage in the wandering albatross *Diomedea exulans*. *J Zool* 219:411–421
- Weimerskirch H, Stahl JC, Jouventin P (1992) The breeding biology and population dynamics of king penguins *Aptenodytes patagonica* on the Crozet Islands. *Ibis* 134:107–117