RESEARCH PAPER

Mutual Mate Choice for Colorful Traits in King Penguins

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Abstract

While studies of mate choice based on male color pattern are ubiquitous, studies of mate choice based on ornamental color traits in sexually monomorphic species are less common. We conducted manipulative field experiments on two color ornaments of king penguins (*Aptenodytes patagonicus*), the size of auricular patches of orange feathers and degree of UV reflectance from beak spots, to determine how the degree of ornamentation influenced pairing rate. In a reduction of auricular patch size, females paired significantly more quickly than males in both control and experimental samples. When this bias was taken into account statistically, pairing of individuals with reduced auricular patches was significantly delayed. We also reduced, but did not eliminate, UV reflectance from beak spots by applying a UV filter; no sex difference in pairing rate was evident in this experiment. Treated birds paired significantly more slowly than untreated control individuals, taking more than a week longer to pair on average than their unmanipulated counterparts, a result that was significant for males and approached significance for females. Our results may indicate mutual mate choice via UV reflectance of the beak spot. Given that this is a species where breeding is extremely slow and considerable investment by both males and females is required for successful reproduction, our results support the hypothesis that in such species, sexual selection might act on the same ornament in both sexes.

Introduction

Abundant evidence from recent years has supported what Darwin (1871) suspected, that male animals use a wide variety of ornaments during their courtship of females (Andersson 1994). Behavioral traits such as songs (Catchpole & Slater 1995; Searcy & Yasukawa 1996) or dances (McDonald 1989), and morphological traits such as tail length (Møller 1988) or body size (Clutton-Brock et al. 1982) help males of various species attract potential mates. Ornamental colors of the skin or feathers have been particularly well studied (e.g. Hill & McGraw 2006a; b). Even a quick sampling of the literature on signaling via ornaments suggests that these colors can convey information about an individual's age (Nicolaus et al. 2007; penguins), condition (Scheuber et al. 2003; damselflies), immunocompetence (Grether et al. 2004; guppies) or other aspects of quality (Thompson & Moore 1991; lizards). Thus, there is

compelling evidence for female mate choice based on ornamental traits and particularly for choice based on a male's colorful ornaments.

Females of many species also display colorful ornaments and in some cases are indistinguishable in appearance from males, at least to the human eye (Amundsen 2000). Bright female colors were historically explained as the result of a correlation with male color patterns (Darwin 1871) or as selectively neutral byproducts of the individual's physiology (Wallace 1889, 1891). Although there has been support more recently for the hypothesis that drab female colors result from predation on nesting females (Irwin 1994; Omland 1997), there is also a growing consensus that in certain cases selection should favor males that exercise mate choice and favor females that compete for the best males as mates. For example, mutual mate choice and competition are predicted when there is substantial biparental care of the offspring (Johnstone et al. 1996; Amundsen 2000), or in species with reduced clutch- or litter-size and extended periods of parental care, as in many seabirds (Bried & Jouventin 2001a).

Seabirds are exceptionally slow breeders, with parents often raising only one chick every 2 yr (Jouventin & Dobson 2002). Males and females are sexually monomorphic in most seabird species, and studies of sexual selection in this group are few (but see below). Thus, for most of the species, we do not know whether sexual selection acts on either sex – or both – during pairing, nor do we know the ornaments that might be used to mediate mate choice or intrasexual competition. Some species, however, have brightly colored patches of feathers or integument in both sexes that seem obvious candidates as sexual ornaments (e.g. bright yellow 'eyebrow' feathers of macaroni, *Eudyptes chrysolophus*, and rock-hopper penguins, *E. chrysocome*; Jouventin 1982). King penguins (*Aptenodytes patagonicus*) and emperor penguins (*A. forsteri*) have brightly colored orange-yellow feathers on the breast, on the auricular regions of the head, and a large orange-colored spot on the hard tissue of the lower mandible which might act as signals to other individuals (Dresp et al. 2005; Jouventin et al. 2005).

Under the best of circumstances, king penguins produce only two offspring every 3 or 4 yr because of the lengthy periods required for molt, courtship, and care of the young (Jouventin & Lagarde 1995). Thus, both males and females should choose and compete for the best available mate, since successful reproduction requires at least 14 mo of cooperation by the pair (Jouventin & Mauget 1996). Because

annual divorce rates are high in this species (approx. 80% according to Olsson 1998), individuals are likely to undergo pair formation numerous times during their lives.

Earlier experiments on king penguins by Stonehouse (1960) and Jouventin (1982) tested the role of auricular plumage patch size in pairing by painting over the entire patch; manipulated animals were unable to find a mate until the paint wore off, significantly delaying or ending their ability to reproduce that year. However, those studies removed the whole signal, manipulating it outside the natural range of variation and thereby making it difficult to interpret the biological significance of their results. To build upon these pioneering studies, we previously conducted a similar experiment (Jouventin et al. 2008) in which we reduced male auricular patch size within the natural range of variation, and found a significant reduction in pairing speed. Those data are newly analyzed here to allow direct comparison with our new data on reduced female auricular patch size (reported here) and to allow application of survival analysis (see below).

Female king penguins display the same ornaments as males and, as discussed above, males should also be selected to choose carefully among potential mates, just as females do (Jouventin et al. 2008; Pincemy et al. 2009). In other words, the possibility exists that patch size plays a role in female pairing as well. Therefore, we conducted a similar experiment on females.

We found previously that early pairing king penguin males had higher levels of UV beak reflectance than females or late-pairing males (Jouventin et al. 2005; Dobson et al. 2008). Skin- or tissue-based UV color is correlated with measures of quality (Mougeot et al. 2005; Mougeot & Arroyo 2006) and reproductive investment (Velando et al. 2006) in other bird species and there is experimental evidence that it can play an important role in mate choice (Hunt et al. 2001; Torres & Velando 2005). However, most previous experiments studying the role of UV color in mate choice have removed the UV signal entirely by placing a UV filter between the test subjects (but see Ballentine & Hill 2003), so the manipulation moved the signal outside its natural range of variation.

The objective of the present study was to test the hypothesis that colored integumentary patches found on the auricular regions and beak of king penguins play a significant role in pair formation in both sexes. Specifically, we predicted that reduced expression of these traits would reduce an

individual's probability of finding a mate. We conducted a field experiment in which we reduced UV reflectance from the beak within natural bounds and tested the effect of lowered UV reflectance on an individual's probability of pairing. We determined daily probabilities of pairing using statistical techniques more commonly used for estimating survival rates (i.e. where pairing and remaining unpaired is analogous to death and survival in a survival analysis). This application of survival analysis is not frequently used in this manner (but see Pincemy et al. 2009), and may prove useful in other behavioral studies.

Methods

Study Species and Study Site

Among the penguins with conspicuous integumentary ornaments, the king penguin is an excellent model for studies of pair formation and sexual selection. They produce a single egg at a time, usually every 2 yr (but with some late production in the year following successful reproduction; Weimerskirch et al. 1992; Olsson 1998). Cooperation between pair members is essential to successful reproduction (Jouventin & Lagarde 1995). After laying, there is alternating care of the egg and young chick on the feet of the parents, with each pair member taking a turn incubating or brooding while its mate is foraging at sea (Stonehouse 1960). Chicks are later semi-independent, standing on the beach while both parents forage at sea and return with food. After a winter fasting period for the chick, the parents return to feed the chick during its pre-fledging molt. The entire sequence takes at least 14 mo, and then parents must molt before breeding again (Weimerskirch et al. 1992). Thus, the choice of a high quality mate should be a very important aspect of reproduction, particularly because the high divorce rate of king penguins means that choice must be made multiple times during life (Olsson 1998).

We worked in a large colony (approx. 16 000 pairs; Delord et al. 2004) of king penguins at Marin Bay, Possession Island, Crozet Archipelago (46°25′S, 51°45′E). Experiments on reduction of male auricular patches and their controls were conducted from Nov. 2001 to Jan. 2002 (described in Jouventin et al. 2008; and below), and the other experiments and their controls were performed from Dec. 2003 to Jan. 2004. For each of the other experiments, all birds were captured and manipulated within three

consecutive days, to minimize any potential seasonal variation in ornament expression. We captured unpaired adult birds after observing each individual perform sex-specific courtship calls for several minutes (Jouventin 1982). In this species, a male and female maintain close physical proximity to each other during the courtship process, as well as during the subsequent selection of a site for egg-laying. Courtship calls are frequent during pair bond formation, but paired birds call infrequently. Therefore, we are confident that our random selection of solitary, calling individuals gave us a sample of unpaired birds. After capturing an unpaired bird, we measured its mass and the length of its right flipper, and attached temporary plastic flipper bands to allow individual identification during the experiment (flipper bands were later removed, so as not to harm birds during foraging trips).

Patch Size Reduction Technique

Experimental (n = 46) and control (n = 30) birds alternated in capture order, and were initially sexed by voice (Jouventin 1982). We reduced auricular patch size of experimental males (n = 28) and females (n = 16) by approximately 50%, by applying a black non-toxic permanent marker along the edges of the orange plumage patch. We used only one marker on any given bird, tracing the marker's full width along the edge of the orange patch, until the orange plumage remaining was approximately equal to the black-marked area. The area covered by the marker was thus contiguous with the normal black plumage surrounding the auricular patch. We also applied the marker to an equivalent area on the heads of control birds (n = 18 males, 12 females), but put the black marker on black plumage surrounding the auricular patch. This treatment of the control birds was intended to serve as an active control for any effects of the marker of which we were not aware. All plumage markings, on both male and female penguins, were performed by the same two field researchers.

UV Reflectance Reduction Technique

We reduced the level of UV reflectance from male (n = 21) and female (n = 16) king penguin beaks by applying a non-toxic solution of clear marine varnish containing finely ground chalk; the varnish was intended as a waterproof, durable carrier for the chalk, which absorbs UV light. We prepared the varnish/chalk mixture fresh daily to prevent any

clumping that could result from the chalk precipitating out of solution. Thus, the varnish/chalk mixture was easily applied and left no obvious signs of its presence once it had dried. Using a small paint brush, we applied four brush strokes of the solution to each of the experimental birds' two beak spots (one beak spot on either side of the mandible), covering the full area of the spot, and also applied one brush stroke of the solution to the beak spots of the control (n = 16 males and 13 females) birds as an active control.

Spectrophotometry

Reflectance measurements were made on penguin beak spots with a USB2000 spectrometer (Ocean Optics), equipped with a PX2 pulsed-xenon flash, and with a resolution of 0.3 nm across the ultraviolet-violet spectral range of 320–450 nm, calibrated against a white standard (WS-2 Spectralon; Ocean Optics). We took all measurements using a fiber-optic cable held at a 90° angle to the area of interest. We collected three measurements of reflectance from the beak spot, removing the probe between each measurement. We defined UV brightness as the total number of counts reflected back to the spectrophotometer across the range of ultraviolet-violet wavelengths, and ultraviolet hue as the wavelength of maximal reflectance within that same range (320–450 nm).

Pairing Assessment Pre- and Post-Manipulation

In this species, a male and female maintain close physical proximity to each other during the courtship process, as well as during the subsequent selection of a site for egg-laying (Jouventin 1982). We captured unpaired adults after observing each individual perform courtship calls for several minutes. We then removed the courting bird from the colony to a field laboratory, where one of the above described treatments was performed (viz. either experimental or control treatments) and described measurements were recorded. Individual penguins were then released back into the colony. The colony was searched daily for marked individuals; we relocated most birds every other day and often saw them 2 d of three. They become easier to find as they got farther into courtship and settled into a part of the colony away from the unpaired birds. We recorded the birds' status as courting or paired whenever we observed them. Courting birds displayed to several potential partners. Paired birds

ceased displaying and calling unless separated in the crowded colony, and moved about the colony together until they located a site for egg-laying. We confirmed the strength of their pair bond by slowly walking between them and causing them to separate by at least 2 m, and then observed their behavior post-separation. Each of the pairs either reunited immediately after we withdrew to a distance of 3–4 m or, if they had lost sight of each other, gave an individually distinct contact call (Jouventin 1982; Aubin & Jouventin 2002) that rapidly led to their reunion.

Latency to Pairing, and Likelihood of Detection

To estimate the time to pairing, we could only measure the number of days that passed between when a bird was manipulated and when we confirmed it to be in a pair, using the technique described above. This measure does not include any time the bird spent courting before we captured it, but Weimerskirch et al. (1992) reported the courting period to be 10.9 ± 4.9 d, which is very similar to the courting periods we observed in our controls. This similarity between the typical courting period and that of the birds in this study suggests that we captured individuals that had only recently begun to court. Furthermore, any variation between individuals in the time they spent courting before our manipulation should be randomly distributed between the experimental and control groups, and therefore unlikely to cause bias. Similarly, any differences in our ability to re-locate birds on a daily basis should not be biased by their treatment category and therefore should not create the patterns we observed.

Statistics

Non-parametric survival tests were used to examine pairing rates (fully explained by Klein & Moeschberger 1997). In these tests, we treated unpaired birds analogously to 'survivors' and pairing as analogous to death in a traditional survival analysis, and compared control and treatment groups. Birds that did not pair during the study were included as 'censored' data. We also tested for differences between the sexes and included sex as a covariate where appropriate when testing treatment effects. We used likelihood-ratio tests (two-tailed) for differences between sexes and Wilcoxon matched-pairs signed-ranks tests (one-tailed) for differences between treatments in survival analyses. These comparisons

included the number of days in which treated and control birds were observed unpaired, even those individuals that did not pair during the study, termed 'censored' individuals. Our experimental manipulations were not expected to speed the rate of pairing for treated birds, only delay them, so we used one-tailed statistical tests. Mean times to pairing were estimated from the latency to pair, the midpoint of curves fit to the survival data. These curve fits do not include time elapsed for censored birds that were greater than the maximum observed time to pairing, and thus are underestimates. We used paired t-tests (one-tailed) to compare UV-reflectance levels before and after application of the varnish/chalk mixture. We used the residuals from a regression of mass on flipper length as an index of **3** body condition (Schulte-Hostedde et al. 2005), then used paired t-tests (two-tailed) to compare mean condition values between control and manipulated birds in each experiment. All statistical tests used the acceptance level of $\alpha \leq 0.05$. Statistical analyses were carried out using SAS statistical software (SAS Institute, Cary, NC, USA).

Results

Natural Variation in Color Traits and Body Condition

Auricular patch size varied from 11.38 to 26.83 cm^2 in males and 10.43 to 23.24 cm^2 in females, and differed significantly between the sexes [$\bar{x}$ ($\pm$ SD) 16.99 $\pm$ 2.75, n = 55; and 15.69 $\pm$ 2.56, n = 40; respectively, t = 2.37, p = 0.02]. The initial UV brightness of the beak spot in males varied from 7885 to 25 082 (in total count), with a $\bar{x}$ ($\pm$ SD) of 16 857 ($\pm$ 4215) for 24 individuals that received the full varnish treatment. In the females, the initial UV brightness of the beak spot varied from 7205 to 24 247 (in total count), with a $\bar{x}$ ($\pm$ SD) of 16 005 ($\pm$ 3829) for 23 individuals that received the full varnish treatment.

The varnish treatment on beak spots of the experimental group resulted in a 30% reduction in brightness of peak UV reflectance, but without a significant change in the wavelength of the peak reflectance. Mean ($\pm$ SD) brightness for males after UV reduction was 11 971 ($\pm$ 3161) (t = 4.54, p < 0.0001; male hue before and after = 387.8 ($\pm$ 8.4) and 384.2 ($\pm$ 8.4) nm, t = 1.46, p = 0.15). Similarly, $\bar{x}$ ($\pm$ SD) brightness for females after UV reduction was 11 142 ($\pm$ 5526) (t = 3.47, p = 0.001; female hue before and after = 389.4 ($\pm$ 14.3) and 388.8 ($\pm$ 12.1) nm, respectively, t = 0.14, p = 0.89).

A separate sample of 20 males (UV brightness = 17 620 $\pm$ 3803) and 20 females (UV brightness = 14 774 $\pm$ 4044) early in the breeding season revealed that the beaks of males reflected significantly more UV light than those of females (t = 2.29, p < 0.05; see also Dobson et al. 2008).

After establishing that mass was significantly positively related to body size ($r^2 = 0.196$, n = 142, p < 0.001), we compared body condition between control and manipulated birds in each experiment but found no significant differences. Manipulated birds in the female auricular patch experiment were not different from their controls (t = −1.24, n = 16, 12, respectively, p = 0.23), nor was body condition different between manipulated and control birds in the female UV reduction experiment (t = 1.14, n = 16, 13, respectively, p = 0.27). Similarly, manipulated and control males did not differ in body condition in the auricular patch or UV reduction experiments (t = −0.34, n = 28, 18, respectively, p = 0.73 and t = 0.40, n = 21, 16, respectively, p = 0.69, respectively).

Patch-Size and Beak Manipulations

In the experiment where auricular patch size was reduced, the control and treatment samples exhibited significantly slower pairing by males than females (Fig. 1; likelihood-ratio test, $\chi^2 = 4.98$, n = 45 males, 28 females, p < 0.03). Mean time to pair was 14.8 $\pm$ 2.1 (SE) d for males and 12.4 $\pm$ 1.4 d for females. In separate tests within the sexes, males showed a significant difference between treatment and control ($\bar{x}$ = 17.3 $\pm$ 2.8 and 8.1 $\pm$ 1.8 d, respectively, $\chi^2 = 3.26$, n = 27, 18, respectively, p = 0.006), but females did not ($\bar{x}$ = 13.1 $\pm$ 1.9 and 10. 7 $\pm$ 1.9 d, respectively, Wilcoxon $\chi^2 = 0.27$, n = 12, 16, respectively, p = 0.30). This difference was held statistically invariant while we tested for a treatment effect of the patch size reduction (Klein & Moeschberger 1997). Reduction of the auricular patch by approximately 50% caused a significant delay in pairing compared to birds subjected to the control treatment. (Wilcoxon test, $\chi^2 = 3.26$, n = 30 control, 43 treatment, p < 0.04). Mean time to pair was 9.5 $\pm$ 1.4 d for the control birds and 19.1 $\pm$ 2.2 d for the birds with reduced auricular patches, a difference of over a week.

There was no significant difference in patterns of pairing by males and females in the control and treatment samples for the reduction in UV reflectance from the beak spot (Fig. 2; likelihood-ratio test; $\chi^2 = 0.06$, n = 37 males, 29 females, p = 0.81).
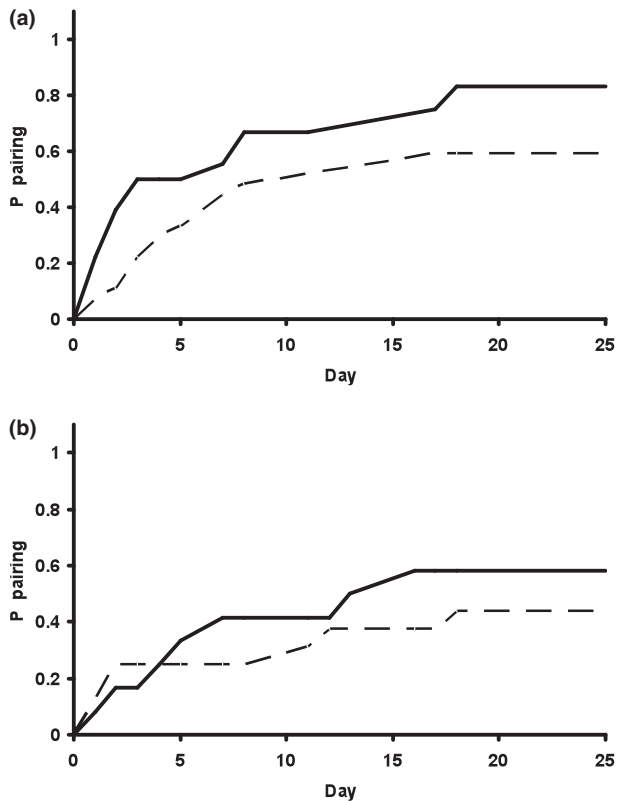
Fig. 1: Probability of pairing in (a) male and (b) female king penguins (*Aptenodytes patagonicus*) after experimental reduction in auricular patch size. Solid lines are control individuals, and dashed lines are with reduced auricular patches individuals. Sample sizes are 18 male controls, 27 male treatment, 12 female controls and 16 female treatment.
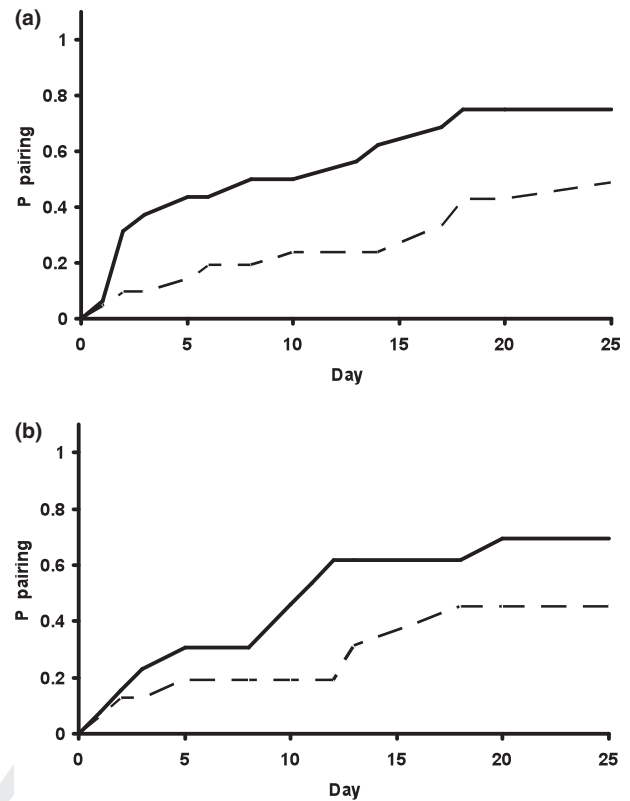
Fig. 2: Probability of pairing in (a) male and (b) female king penguins (*Aptenodytes patagonicus*) after experimental reduction of ultraviolet (UV) reflectance from the beak spot. Solid lines are control individuals, and dashed lines are individuals with reduced UV reflectance. Sample sizes are 16 male controls, 21 male treatment, 13 female controls and 16 female treatment.

Mean time to pair was 15.7 ± 1.6 d for males and 13.9 ± 1.4 d for females. In separate tests within the sexes, males showed a significant difference between treatment and control ($\bar{x} = 18.8 \pm 1.9$ and 10.6 ± 2.0 d until pairing, respectively, $\chi^2 = 3.26$, n = 21, 16, respectively, p < 0.02), and females exhibited a difference that approached significance ($\bar{x} = 14.5 \pm 1.6$ and 11.8 ± 2.1 d until pairing, respectively, $\chi^2 = 0.89$, n = 16, 13, respectively, p = 0.07). Reduction of UV reflectance from the beak spot caused a significant delay in pairing compared to birds subjected to the control treatment (Wilcoxon test, $\chi^2 = 6.94$, n = 29 control, 37 treatment, p = 0.004). Mean time to pair was 11.1 ± 1.4 d for the control birds and 18.6 ± 1.4 d for the birds with reduced UV reflectance, again a difference of over a week.

Discussion

Research in recent years has indicated a strong influence of sexual selection on the evolution and maintenance of ornamental traits, particularly colorful plumage in male birds (Andersson 1994; Hill 2002; Hill & McGraw 2006a,b). A smaller body of work has focused on ornamental traits of females (e.g. Hill 2002), and even fewer studies have examined the possibility of selection for traits with similar elaboration in both sexes (e.g. Velando et al. 2001; Daunt et al. 2003; Kraaijeveld et al. 2004; reviewed by Kraaijeveld et al. 2007). We examined the role that plumage and beak colors play in pairing of male and female king penguins, and provide evidence of selection for the intensity of ultraviolet reflectance from the colored beak spots. Because both sexes had a similar response to the reduced UV-reflectance treatment, this might be an ornament that reflects mutual choice of mates by males and females.

We also examined the size of the colored auricular (ear) plumage patch of king penguins, and it appears to play an important role in pairing. These results were complicated because experiments on males and

females took place in different years. In addition, for both control and treated birds, females appeared to be choosier than males, as shown by the significant differences between the sexes in their preferences for ornamental traits. Pincemy et al. (2009) conducted a similar experiment at Kerguelen Island, and found that female king penguins were significantly choosier than males with respect to the size of the auricular patch. Thus, our evidence for mutual mate choice with respect to this colored ornament is not strong. There are at least two other possible evolutionary mechanisms for the maintenance of mutual male and female ornamentation besides mutual mate choice that seem appropriate for king penguins. The first is strong genetic correlation of ear patch size between males and females, as has been suggested in other species (Møller 1988; [4,5] Price and Burley 1993; Price 1996; Roulin et al. [6] 2001). The second is that the size of auricular patches of males and females are maintained by social competition over resources other than mates. Auricular patch size is associated with social dominance in attaining favorable breeding locations within the colony (Viera et al. 2008).

Our results suggest that both of the ornaments we studied – auricular patches and beak spots – are viewed as honest indicators of male quality (Jouventin et al. 2009). In a previous study, Jouventin et al. [7] (2005) found that the earliest-breeding king penguins had significantly higher ultraviolet reflectance from the beak than those breeding later in the season. Dobson et al. (2008) found an association between UV reflectance from the beak and body condition in males, suggesting a link between UV reflectance and condition as shown with other species (e.g. Doucet & Montgomerie 2003; Griffith et al. 2003). Thus, our experimental result showing increased probability of pairing for males with higher UV reflectance provides at least partial support of the correlation between UV reflectance and pairing speed and body condition, consistent with the idea of selection favoring those courting birds that are in the best condition.

Condition in this case may well be signaled on several time scales, or in different ways. While we do not have data on the rate at which beak spot color changes, it is a tissue-based ornament with at least some access to the blood supply. Therefore, it may mirror changes in physiological states more rapidly than is possible with plumage ornaments. For example, foot color in blue-footed boobies (*Sula nebouxii*; Velando et al. 2006), bill color in mallards (*Anas platyrhynchos*; Peters et al. 2004), and gape color in nestling barn swallows (*Hirundo rustica*; Ayala et al. 2007) all respond within hours or days to physiological conditions, such as changes in nutrition or hormone levels or immune challenges.

Plumage color, on the other hand, represents an integration of the bird's physical state during a previous 6-wk molting period that ended before the pairing process ever began (Weimerskirch et al. 1992). McGraw et al. (2007) showed that the orange ornamental colors on the breast and auricular regions of king penguins are most likely because of a form of pterin pigment. Pterins are important contributors to immunocompetence (Oettl & Reibnegger 2002), so the influence of pterin-based plumage on pairing – like the influence of UV reflectance from the beak – supports the hypothesis that these traits have been selected as honest indicators of male condition (Jouventin et al. 2009). Consistent with this idea, Nolan [8] et al. (2006) showed experimentally that color of the breast patch was significantly related to immune response to a novel antigen in king penguins, and McGraw et al. (2009) showed that plumage color of male Snares penguins (*Eudyptes robustus*) was significantly related to their body condition.

Our results are consistent with those of others studying seabird species in which the parents are limited in their ability to provide food frequently, and in which ornamental traits are assessed during the pairing process. For example, Velando et al. (2001) found that Inca terns (*Larosterna inca*) with the largest plumage ornaments were in the best condition and produced chicks with the strongest immune response. Daunt et al. (2003) found strong evidence of mutual mate choice based on a plumage ornament in European shags (*Phalacrocorax aristotelis*; see also O'Donald 1983). Perhaps most relevant to our study, Jones & Hunter (1999) manipulated the size of a plumage ornament in crested auklets (*Aethia cristatella*) and demonstrated significant preferences for individuals with the augmented plumage character. Thus, there appeared to be mutual mate choice based in part on this color signal. In a review of mutual ornamentation of male and female birds, Kraaijeveld (2003) suggested a positive association with 'divorce rate', the change in mates between breeding seasons. Our experimental results on UV reflectance from the beak spot are in accord with this general pattern, which was attributed to mutual mate choice and sexual selection. King penguins are among the most colorful of penguins (Jouventin 1982), are sexually monomorphic in colored ornaments, and have divorce rates around 80% (Olsson 1998).

The dichotomy in the strength of sexual selection between king penguin males and females for the size of the ear patch (Pincemy et al. 2009), however, is somewhat surprising, given the degree to which bi-parental care is obligate in this species. King penguin chicks are fed by both parents at intervals of 1–2 wk and fast for up to 4 mo during the austral winter if adults are unable to locate and return with food (Jouventin 1982; Weimerskirch et al. 1992). Therefore, selection should strongly favor assessment of a potential mate with regard to their current condition, as a predictor of their ability to compete for increasingly better position within the colony and, later, to provision chicks. Males take the first incubation shift lasting approximately 2 wk, while females return to sea to forage (Stonehouse 1960; Weimerskirch et al. 1992). It may be that this is the period when patch size is most important – as a mediator of aggression (Viera et al. 2008) for maintaining a breeding location within the colony (Côté 2000; Bried & Jouventin 2001b) – and therefore is favored more during pair formation in males than it is in females. This hypothesis yields the prediction that it is more difficult for a king penguin to improve its position within the colony than it is to maintain the position once attained. That prediction has been tested and supported at least indirectly in a variety of species (e.g. felids – Laing & Lindzey 2003; , birds – Tobias 1997; fish – Johnsson & Forser 2002), and represents a potentially productive line of future research for studies of king penguins.

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