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ORIGINAL ARTICLE

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Carotenoid-derived ornaments reflect parental quality in male and female yellow-eyed penguins (*Megadyptes antipodes*)

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Abstract The handicap principle suggests that ornamental traits that function as honest signals in mate selection must be costly to be effective. We evaluated in the sexually monochromatic yellow-eyed penguin (*Megadyptes antipodes*) whether the carotenoid-derived plumage and eye coloration predicts parental quality and whether males and females within pairs mate assortatively in relation to these carotenoid-derived ornaments. In addition, we investigated whether age or body condition was related to the coloration of the ornamental traits. In yellow-eyed penguins, parental quality of males and females was predicted by eye and head plumage coloration. Even when we controlled for gender- and age-specific differences, eye and head plumage coloration reflected honestly parental quality. Males and females mated assortatively in relation to these ornamental traits. While age influenced coloration of both the eye and head plumage, body condition was related only to the saturation of plumage coloration. These results provide evidence that the carotenoid-derived ornaments in yellow-eyed penguins reflect the parental abilities of birds and, therefore, may be costly signals. Potentially, female and male yellow-eyed penguins could use eye and plumage coloration as an indirect cue in assessing age and quality of individual birds during mate choice. This is only the second study to examine plumage coloration in relation to sexual selection in penguins, while conspicuous ornamental traits in other species of penguin beg the question whether they also play a role in sexual selection.

Keywords Assortative mating · Carotenoid pigments · Ornamental traits · Sexual selection · Yellow-eyed penguin

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Introduction

The evolution of bright coloration in animals, particularly in birds, has long been the subject of considerable debate (Cronin 1991). Since Darwin (1871) proposed the theory of sexual selection, whereby the choice of mates by females could result in the evolution of elaborate secondary sexual traits, it has been shown that bright coloration, usually in males, functions in intersexual selection (e.g. Hamilton and Zuk 1982; Kodric-Brown and Brown 1984; Hill 1990). Models to explain the evolution of secondary sexual traits disagree about whether these ornamental traits signal the bearer's physical condition (the handicap principle: Zahavi 1975; and the good-parent hypothesis, Hoelzer 1989) or simply the bearer's ability to attract mates (the runaway model: Fisher 1930; Lande 1981). While theoretical work suggests that all evolutionary mechanisms are plausible (Grafen 1990; Iwasa et al. 1991; Pomiankowski et al. 1991), it is virtually impossible to identify and use exclusive predictions that test among these models (Balmford and Read 1991; Kirkpatrick and Ryan 1991). However, the handicap principle suggests that ornamental traits that function specifically as indicators during mate choice must be costly signals, otherwise low quality individuals would be able to cheat by producing showy ornaments (Zahavi and Zahavi 1997; Olsen and Owens 1998). If ornaments are not, on average, trustworthy indicators, then selection for these traits during mate choice should disintegrate (Grafen 1990). Recent work focuses on which traits are 'honest' signals of condition, and which are more likely to be 'arbitrary' cues (Owens and Short 1995).

Carotenoids, which are responsible for the bright yellow, orange and red coloration in birds, are synthesized de novo only by plants, algae, and some bacteria and fungi, so ultimately birds can only obtain carotenoids through their diet (Brush 1981, 1990). Additionally, carotenoids are known to benefit health as they function as precursors of vitamins, boosters of the immune system and antioxidants (Bendich 1989, 1993; Lozano 1994; Rock et al. 1996). In several studies of birds, male carotenoid-based coloration was found to be correlated with the physical condition or associated parasite infection (e.g., Hill 1991; Camplani 1999; Wolfenbarger 1999), and females generally chose their mates accordingly (Hill 1990; Zuk et al. 1990). Carotenoid-derived ornaments have been generally perceived as costly signals, because of the difficulty of obtaining carotenoids through the diet, in particular for predatory birds (Olsen and Owens 1998). In addition, a recent controversial debate arose over whether circulating carotenoid pigments have detrimental or beneficial effects on birds (Olsen and Owens 1998; Hill 1999; von Schantz et al. 1999). High levels of circulating carotenoid levels might be costly for birds through their toxic effects (Zahavi and Zahavi 1997) or, alternatively, beneficial for their overall health and, by depositing carotenoids in ornamental traits for coloration, the maintenance of the immune system and other health functions would be compromised (Negro et al. 1998; von Schantz et al. 1999).

When females exhibit conspicuous ornamental traits, it is unclear whether female ornamentation evolved directly through selection on the female or, alternatively, indirectly as a genetically correlated response to selection on males (Lande 1980). Several empirical studies on birds concluded that female ornamentation is an artifact of selection and a consequence of a genetic correlation between the sexes (e.g., Hill 1993; Cuervo et al. 1996), but others supported the direct selection hypothesis, whereby males chose females according to their ornamental expression (e.g., Jones and Hunter 1993; Møller 1993; Amundsen et al. 1997; Roulin 1999), maybe because the ornament reflected honestly female quality (Møller 1993; Amundsen et al. 1997; Roulin 1999). To evaluate whether males prefer females with conspicuous ornamental traits, researchers have investigated whether males pair non-randomly with females in respect to their ornamental traits (Bortolotti and Iko 1992; Wiebe 2000; Forero et al. 2001). However, some authors have argued that positive assortative mating by a phenotypic trait, such as bill size, can be explained by a positive relation between age and the trait, in particular in long-lived species (Coulson et al. 1981; Reid 1988; Jouventin et al. 1999). Thus, it is necessary to investigate whether individuals mate assortatively in relation to age or to a phenotypic trait.

In this study, we examined the carotenoid-derived plumage and eye coloration in the yellow-eyed penguin (*Megadyptes antipodes*), a socially monogamous and sexually monochromatic bird species (Richdale 1957). A bright yellow eye and a yellow stripe, termed postocular stripe, that extends from behind the eye backwards encircling the crown, distinguishes adults from subadults. We measured the variation of eye and postocular stripe color in adult yellow-eyed penguins and tested whether the coloration of these two carotenoid-derived ornaments reflect honestly parental quality of males and females. Concurrently, we controlled for age- and condition-specific differences that might influence parental quality. In addition, we investigated whether eye and postocular stripe color was influenced by age, sex or body condition of birds and whether birds mated assortatively in relation to age or to the color of these phenotypic traits.

Methods

Field work was conducted from 1980 until 2002 at Boulder Beach, Otago Peninsula (45°50′S, 170°30′E), on the South Island of New Zealand, where yellow-eyed penguins breed annually from September until February (Richdale 1957). Males and females contribute equally to incubation and raising offspring and usually two chicks are raised per pair (Richdale 1957; Darby and Seddon 1990). Annually, an average of 40% of pairs that bred in the previous year divorce or change mates because of the disappearance or death of one partner (Richdale 1957).

Each breeding season, the reproductive performance of penguins was recorded by visiting the nest sites regularly to determine the number of eggs laid, hatched and chicks fledged (for further details see Darby and Seddon 1990). However, during 1998-1999, nests of one section of Boulder Beach were not monitored regularly and breeding success data were unavailable for 12 birds for that year. Breeding adults and fledglings were individually marked using stainless steel flipper bands. Most adults can be reliably sexed by weight and measurements of their head and feet (Darby and Seddon 1990). To measure parental quality, we used mean annual breeding success (number of chicks fledged per year) of each individual bird from its first breeding attempt until its most recent breeding attempt.

During September and October in 2000 and 2001, we took color photographs of the heads of 95 randomly chosen adult yellow-eyed penguins (47 females and 48 males). Of birds that were photographed in both years (15 birds), we randomly chose one photograph to include in the analyses. For photography we used a Canon EOS-1 with a 50 mm Canon Compact-Macro Lens EF 1:2.5 and Fuji Velvia reversal film (RVP-36, ISO 50). Birds were photographed in profile from a distance of approximately 40 cm. For standardizing lighting conditions all natural light was excluded and a Canon Macro Ring Lite ML-3 (flash) was used for all photography. After photographs had been developed and scanned, we standardized color and brightness among scanned images in Adobe Photoshop version 3.0. (Adobe Systems 1994). A rectangle of 14,014 pixels in the gray area of the color scale that had been included in each image (Fig. 1) was calibrated so that the red, green and blue channels (RGB) were set to 185 on a scale from 0 to 255. We placed 16 squares (10×10 pixels each) in the iris and a diagonal row of further 16 squares of the same size in the middle of the postocular stripe in each penguin image (Fig. 1). With the color picker tool, which was set to average the hue and saturation of an area of 5×5 pixels, we took eight randomly chosen samples of coloration: four samples from the eye (iris) and four from the postocular stripe, which were later averaged. To take a sample, the color picker tool was always placed in the middle of a 10×10 square. Colors were evaluated with the color picker tool within Adobe Photoshop (Adobe Systems 1994; see Fitze and Richner 2002 for a similar approach of evaluating color), which gives each color a score for hue (0°=red, 60°=yellow, 120°=green) and saturation (0%=gray and 100%=fully saturated).

Age and sex were known for all photographed birds. With the exception of three birds, all photographed birds were weighed and their head length was measured. Body mass divided by head length was used as an index of their current body condition. Penguins were

Fig. 1 Image of a male yellow-eyed penguin (*Megadyptes antipodes*) (J 13951). A rectangle (14,014 pixels) placed in the gray area of the color scale was used to standardize color and brightness among images. We placed 16 squares (10×10 pixels) in the iris and a diagonal row of 16 squares in the middle of the postocular stripe in each penguin image. Out of these 32 squares we randomly chose four squares from the eye and four from the postocular stripe to take color samples

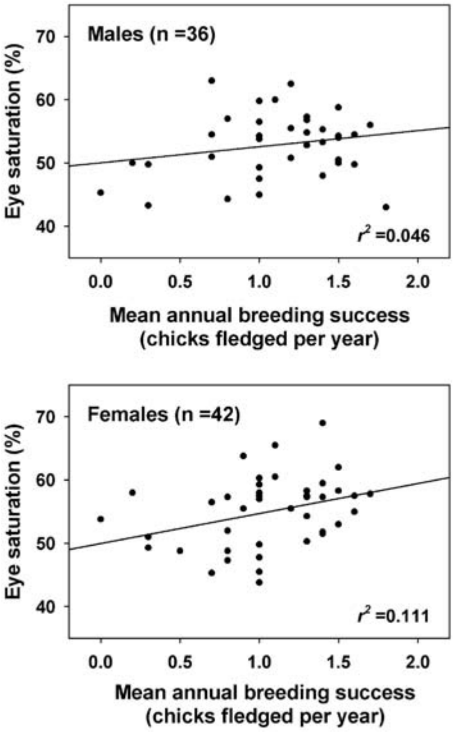

Fig. 2 Eye saturation in relation to mean annual breeding success (as a measure of parental quality) in male and female yellow-eyed penguins

sorted into three body condition categories: (1) birds that had less then 35 g/mm were considered in poor body condition; (2) birds that had between 35 and 38 g/mm were considered in medium condition; and (3) birds that had more then 38 g/mm were considered in good body condition.

We used multi-way ANCOVAs to test whether parental quality (mean annual breeding success) is reflected by eye and postocular stripe color. The models included age, body condition, hue or saturation of the eye or postocular stripe, and all two-way interaction terms as independent variables. For these analyses, we excluded birds from our samples that bred for the first time in the year when their photograph was taken. The data were analyzed separately for males and females. After testing variables for normality we used linear regressions to evaluate whether breeding success was related to hue and saturation of the eye or postocular stripe color within groups of 5-year-old males and 5-year-old females. Multi-way ANCOVAs were used to investigate whether age, sex or body condition or any of the two-way interaction terms influenced eye or postocular stripe color. By using paired sample correlations we tested whether age, eye color and postocular stripe color was related between females and males of pairs. All means are reported ±1 SD and the tolerance for Type I error was set at 0.05 for all statistical tests. SPSS (version 10.0.7a, SPSS 2000) was employed for all statistical analyses.

Results

Parental quality of 36 males was predicted by saturation of the eye ($F_{1,26}=6.8$, $P=0.02$, Fig. 2), their age ($F_{1,26}=6.9$, $P=0.01$), and by the interaction between age and eye saturation ($F_{1,26}=6.1$, $P=0.02$). Eye hue and postocular stripe color did not predict parental quality ($F_{1,26}=0.1$–1.5, $P>0.05$), nor did body condition ($F_{2,26}=0.5$–2.3, $P>0.05$) or any of the other interaction terms. For the 42 females, their parental quality was predicted by saturation of the eye and postocular stripe (eye: $F_{1,32}=6.1$, $P=0.02$, Fig. 2; postocular stripe: $F_{1,32}=12.6$, $P<0.01$), while age also significantly influenced parental quality in three analyses ($F_{1,32}=5.9$–8.0, $P\leq0.02$). The interactions between age and eye hue, eye saturation and postocular stripe saturation also predicted parental quality ($F_{1,32}=5.2$–8.9, $P\leq0.03$). Body condition did not influence parental quality in females ($F_{2,32}=0.6$–1.7, $P>0.05$), nor did any of the other interaction terms.

Within groups of 5-year-old males ($n=8$) and 5-year-old females ($n=9$), eye saturation was significantly related to mean annual breeding success (males: $r^2=0.59$, $P=0.03$; females: $r^2=0.66$, $P<0.01$), while eye hue and hue and saturation of the postocular stripe showed no significant relationship with breeding success (Fig. 3).

Mean values and coefficients of variation for hue and saturation of the eye and postocular stripe are reported in Table 1 for males and females. Hue of the eye color differed significantly between males and females: eye color was orange in males, but yellow in females ($F_{1,82}=5.1$, $P=0.03$). With increasing age, eye color became more yellow in females while it became more red in males (interaction between sex and age: $F_{1,82}=6.3$, $P=0.01$). Age, body condition or any of the other interaction terms did not influence hue of the eye color. Saturation of the eye color increased significantly with age ($F_{1,82}=10.5$, $P<0.01$, Fig. 4). Hue of the postocular stripe was not related to age, sex, body condition or any of the two-way interactions. As birds became older, saturation of the postocular stripe increased significantly ($F_{1,82}=9.4$, $P<0.01$, Fig. 4). Mean saturation of the

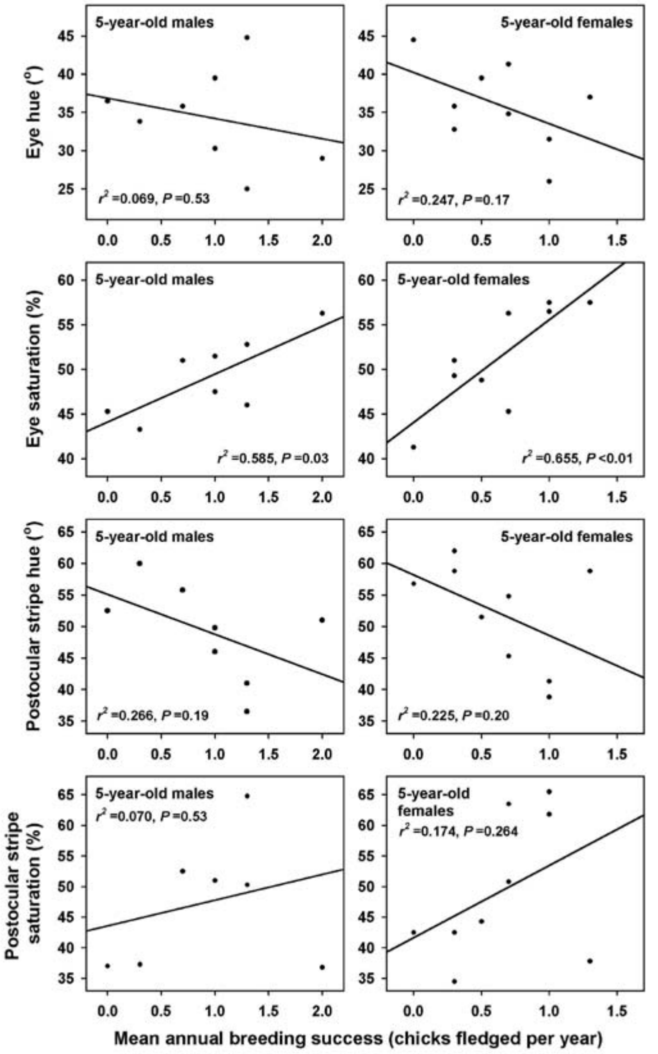

Fig. 3 Hue and saturation of the eye and postocular stripe in relation to mean annual breeding success (as a measure of parental quality) in 5-year-old male and 5-year-old female yellow-eyed penguins

postocular stripe was also significantly higher of birds in medium body condition (55.4%, ±9.2) than of birds in poor condition (50.4%, ±10.8) and in good condition (51.8%, ±8.3, $F_{2,82}$=4.8, P=0.01). Birds in medium and good body condition increased their saturation of the postocular stripe from approximately 50–60% as they became older. However, birds in poor condition had a low saturation of the postocular stripe when they were young (~40%), but a high saturation (>60%) when they were old (interaction between age and body condition ($F_{2,82}$=4.1, P=0.02).

Age of females and males within 40 breeding pairs was not significantly correlated (paired sample correlation 0.304, P=0.06). Hue of the eye was significantly correlated between females and males of pairs (0.577, P<0.01, Fig. 5), but saturation was not (–0.019, P=0.91). Hue (0.490, P<0.01, Fig. 5) and saturation (0.339, P=0.03) of the postocular stripe were significantly correlated between females and males of pairs.

Discussion

As researchers have typically perceived monomorphic appearance of both sexes in birds as an indication of the absence of sexual selection (Amundson 2000), there have been few studies to date that have investigated mutual mate choice in such species (Bortolotti et al. 1996). At first glance, monomorphic penguins seem to lack any conspicuous secondary sexual characteristics, however, bill and body size of males in Adélie (*Pygoscelis adeliae*) and crested penguins (genus *Eudyptes*) have been suggested to be sexually selected traits caused by female choice (Davis and Speirs 1990; Davis 1991) or male-male competition (Ainley and Emison 1972; Warham 1975). Surprisingly, carotenoid-based eye and plumage colorations in penguins (most conspicuous in *Aptenodytes* species, crested and yellow-eyed penguins) have never been investigated before in relation to sexual selection. In yellow-eyed penguins, the extent of variation of the eye and head plumage coloration (CV=10.26–19.60%) is similar to traits, that are assumed to be sexually selected for in other species (mean CV=11.7%, range 6.0–25.6%; Alatalo et al. 1988); variation of traits likely to be influenced by natural selection is much lower (CV for head and foot length =1.5–2.6%; Massaro M, unpublished data). While considerable variation of the thickness of the black pectoral band in Magellanic penguins (*Spheniscus magellanicus*) suggested that this band could be sexually selected for (CV=27.9–30.2), Forero et al. (2001) could not find any correlation between the thickness of the pectoral band and parental performance. Melanin-based plumage coloration, such as the pectoral band in Magellanic penguins, has been suggested to be cheap to produce, because melanin pigments can be readily synthesized by birds from basic dietary components (Hill and Brawner 1998). In Magellanic penguins, the melanin-based pectoral band appears to be an arbitrary cue unrelated to breeding performance, while in yellow-eyed

Table 1 Means, standard deviations (*SD*) and coefficients of variation (*CV*) for hue and saturation of eye and postocular stripe color in male and female yellow-eyed penguins (*Megadyptes antipodes*).

Ornament colour		Adult males (n=48)			Adult females (n=47)		
		Mean	SD	CV	Mean	SD	CV
Eye	Hue (°)	34.75	4.84	13.93	35.27	5.69	16.13
	Saturation (%)	52.20	5.49	10.52	54.88	5.63	10.26
Post-ocular stripe	Hue (°)	50.36	6.66	13.22	49.03	6.67	13.60
	Saturation (%)	49.68	7.10	14.29	55.57	10.89	19.60

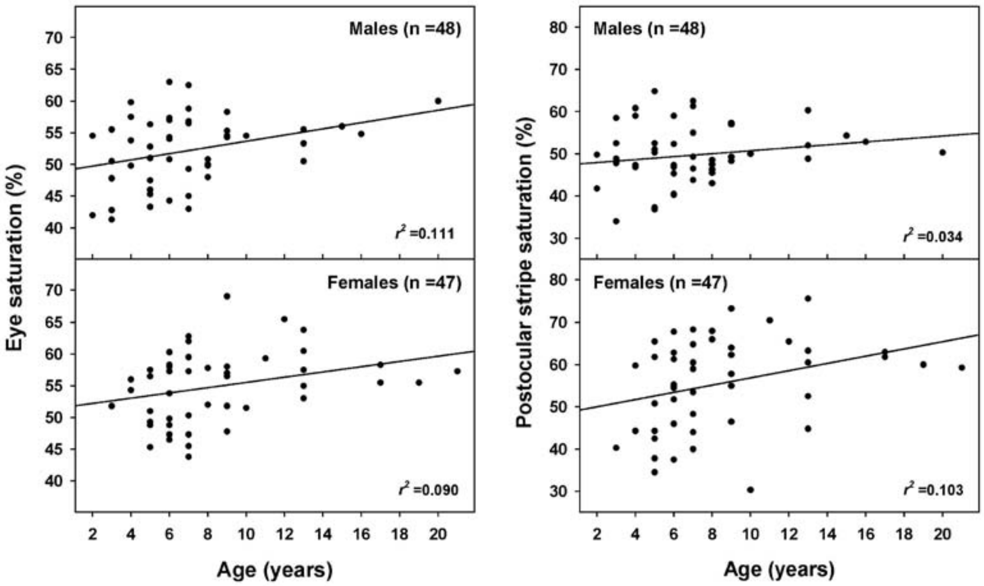

Fig. 4 Eye and postocular stripe saturation in relation to age in male and female yellow-eyed penguins

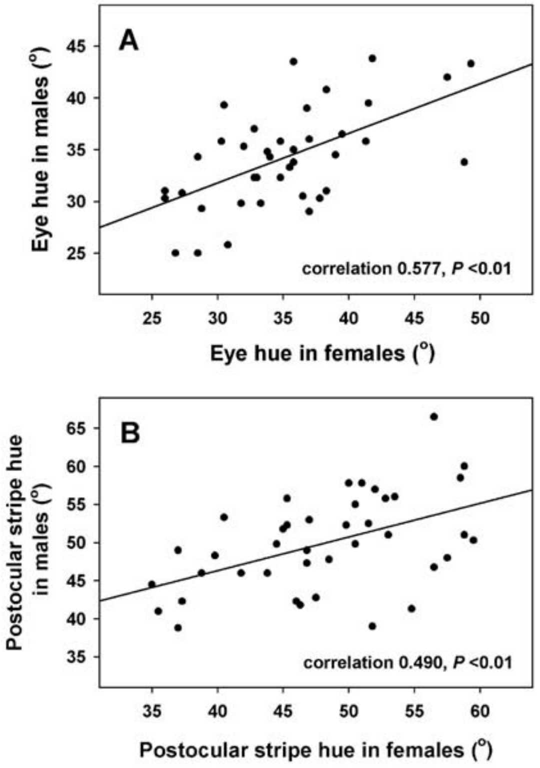

Fig. 5 The within-pair relationship between male and female eye hue (**A**) and postocular stripe hue (**B**) in yellow-eyed penguins

penguins carotenoid-based eye and plumage coloration was an honest signal of parental quality in males and females. Even in birds of the same sex and age we found a strong relation between eye color and parental quality. While yellow-eyed penguins may decide to re-mate with their previous mate as a response to their breeding success in previous years, the assessment of the parental abilities of a potential new mate would have to rely on indirect cues, such as eye color, since parental performance cannot be observed in advance (Saetre et al. 1995). Choosing a suitable partner for breeding is an important aspect for successful reproduction. This is even more so in monogamous seabirds, where levels of female and male parental care are similar and where differences in quality of birds may lead to high levels of both choice and competition in females and males (Johnstone et al. 1996). Since there is considerable variation among yellow-eyed penguins in their ability to raise offspring, we would expect that both males and females should be choosy and select mates with high parental skills as well as high genetic qualities.

We found that in yellow-eyed penguins, pairs mated assortatively in relation to eye and postocular stripe color. These results suggest that yellow-eyed penguins may choose their mates according to these ornamental traits, but explicit mate choice experiments are necessary to confirm our findings. In three penguin species (*Aptenodytes patagonicus, Eudyptes chrysocome and E. chrysolophus*) manipulation of yellow head feathers reduced mating success, which was interpreted as evidence that these feathers function during species recognition (Jouventin 1982). However, these results could also be caused by mating preferences towards brightly ornamented individuals, and thus be consistent with the idea that colorful head plumages are sexually selected traits in penguins. In fact, experiments showed that in a monomorphic, northern hemisphere seabird, the crested auklet (*Aethia cristatella*), elongated crest feathers were favoured by males and females during mate choice (Jones and Hunter 1993, 1999). The authors of these studies concluded that female ornamentation as male ornamentation evolved through direct sexual selection, whereby members of both sexes favor mates with conspicuous ornamental traits. However, other studies, on species where males and females are similarly ornamented, provided evidence that the expression of a trait is advantageous to males, but nonfunctional in females (e.g., Hill 1993; Tella et al. 1997). Whether the maintenance of female ornamentation proceeds from a genetically correlated response to selection on males or from direct sexual selection is not mutually exclusive (Amundsen 2000). Instead, trait expression caused by genetic correlation might trigger further trait exaggeration through sexual selection and produce highly ornamented daughters and sons (Amundsen 2000). The positive relationship between female ornaments and quality suggests that in yellow-eyed penguins female ornaments can be a true quality indicator to males and not a nonadaptive trait caused by a genetically correlated response to male ornaments.

The handicap principle predicts that honest signals should be costly (Zahavi 1975). Since the eye and plumage color appear to be honest signals of quality in the yellow-eyed penguin, producing or carrying those signals must be costly and only those individuals in the best condition are able to maintain a maximum ornament display. However, the factors that may limit the production of carotenoid-derived ornaments are poorly understood (Olsen and Owens 1998; Bortolotti et al. 2000). In contrast to algae, which are the primary producer of carotenoids in the marine environment, fish contain relatively few carotenoids (Fox 1979). Potentially, yellow-eyed penguins could indeed spend considerable time and energy foraging for carotenoid-rich prey. Alternatively, cost may derive from depositing carotenoid pigments in feathers and consequently compromising health-related functions by decreasing levels of circulating carotenoids (Negro et al. 1998; von Schantz et al. 1999).

We found that body condition was related to the postocular stripe color in yellow-eyed penguins. Birds in medium body condition displayed a more saturated postocular stripe than birds in poor and good condition. However, whether depositing carotenoid pigments in the postocular stripe decreases circulating carotenoid levels in yellow-eyed penguins is unknown. In addition, the color of the postocular stripe in yellow-eyed penguins most likely indicates the state of the bird at the time of molt (post-breeding molt in March–April), while we measured body condition in September and October. Eye color, however, may reflect short-term changes of the bird's physical condition (Ligon 1999) and, thus, gives a more up-to-date signal of the bearer's health. Of the four color variables that were measured in this study, eye saturation was the best indicator for parental quality. As it has been previously suggested, eye color is probably an important signal in sexual selection in birds (Ligon 1999); it certainly appears so in yellow-eyed penguins.

In this study, age was an important variable that influenced coloration of ornaments. Because of difficulties obtaining sufficient numbers of known-age birds, few studies were able to test or control for age-specific variation in ornaments in long-lived species (Bortolotti et al. 1996). For example, Forero et al. (2001) showed that Magellanic Penguins paired nonrandomly in relation to bill size but, owing to their lack of information on the age, it is impossible to rule out whether the observed assortative mating is due to assortative mating by age. Yellow-eyed penguins did not mate assortatively in relation to age, but according to coloration of ornamental traits. We have also shown that breeding success or parental abilities increase with age in yellow-eyed penguins (Massaro et al. 2002; this study) and age also influences ornament coloration. While coloration of ornaments even reflected parental quality when age-specific differences were controlled for (in 5-year-old birds), we would expect that older birds, that display bright ornaments, will be favoured as mates because with increasing age many birds may gain experience that may allow them to forage more efficiently and ultimately invest more in reproduction (Weimerskirch 1990).

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