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1 Is territory defence related to plumage ornaments in the king penguin *Aptenodytes patagonicus*?

2

3 VANESSA M. VIERA^{1,2}, PAUL M. NOLAN³, STEEVE. D. CÔTÉ¹, PIERRE JOUVENTIN⁴,

4 RENÉ GROSCOLAS²

5

6 ¹Département de Biologie and Centre d'études nordiques, Université Laval, Canada.

7 ²Département d'Ecologie Physiologie et Ethologie, IPHC, CNRS, France

8 ³Department of Biology, The Citadel, USA

9 ⁴Equipe d'Ecologie Comportementale, Centre d'Ecologie Fonctionnelle et Evolutive, France

10

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12

13 Correspondence address : Steeve D. Côté, Département de Biologie, Université Laval, Sainte-

14 Foy, Québec, G1K 7P4, Canada, Email : steeve.cote@bio.ulaval.ca

15

16 Authors addresses : V. M. Viera, Département de Biologie, Université Laval, Sainte-Foy, Québec,

17 G1K 7P4, Canada ; R. Groscolas, Département d' Ecologie Physiologie et Ethologie, IPHC,

18 CNRS, 23 rue Becquerel, 67087 Strasbourg cedex 02, France ; P. M. Nolan, Department of

19 Biology, The Citadel, 171 Moultrie St., Charleston, SC, 29409, USA; P. Jouventin, Equipe

20 d'Ecologie Comportementale, Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, 1919

21 route de Mende, F-34293 Montpellier Cedex 5, France

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1 **ABSTRACT**

2 Colour ornaments in monogamous birds may be directed at potential mates or other conspecifics
3 to signal reproductive status or fighting ability, especially in territorial species. We investigated
4 whether the size of the orange auricular patch may be an indicator of aggressiveness in the king
5 penguin *Aptenodytes patagonicus*, a monogamous and territorial seabird. The relationship
6 between auricular patch size and defence behaviour was explored relative to territory location
7 (centre vs. periphery of the colony), period of reproduction (early vs. late), state of reproduction
8 (incubation vs. brooding) and sex. The proportion of time spent in territorial defence and the rate
9 of aggressive behaviours were positively correlated with auricular patch size, mainly because
10 central birds were more aggressive than peripheral birds and they also had larger patch sizes. The
11 period of reproduction, state of reproduction and sex did not interact with patch size to affect
12 aggressiveness. Our results suggest that the size of the auricular patch in king penguins may be a
13 reliable signal allowing individuals to evaluate the quality of mates or competitors in terms of
14 aggressiveness. Whether aggressiveness is directly linked to patch size or indirectly through body
15 condition, however, remains to be determined. In any event, birds with larger patches seem to
16 gain central territories in the colony, thereby increasing their reproductive success. Our study
17 adds to the growing evidence that the evolution of sexually monomorphic ornaments may stem
18 from mutual mate choice.

19
20 **KEYWORDS**

21 Aggressive behaviour, *Aptenodytes patagonicus*, Defence, Individual quality, King penguins,
22 Ornaments, Patch size, Territory, Mutual ornamentation

1 Sexual selection is thought to explain the evolution of ornamental traits and preference for mates
2 displaying such traits (Andersson 1994). The evolution and function of ornamentation in both
3 sexes, especially in monogamous species, however, are still puzzling (Wachtmeister 2001). Two
4 main hypotheses have been proposed to explain the widespread occurrence of mutual
5 ornamentation: a by-product of genetic constraints on sex-limited trait expression (Lande 1980),
6 or sexual selection on females as well as on males (Amundsen 2000). In addition, the functional
7 interpretation of ornamentation in both sexes might be to signal phenotypic quality to
8 conspecifics (Zahavi 1975; Hamilton & Zuk 1982; Kodric-Brown & Brown 1984; Møller &
9 Jennions 2001).

10 Carotenoid and melanin pigmentation (either the colour intensity or the extent of the
11 coloured area) correlate with aspects of individual quality, such as immunocompetence, fighting
12 ability, parental quality, general health, breeding performance or even offspring quality (Hill
13 1991; Hill & McGraw 2006a,b). Furthermore, conspicuous patches of colour mediate aggressive
14 interactions in many vertebrates, including birds (Lemel & Wallin 1993; Pryke et al. 2001; 2002),
15 lizards (Lopez et al. 2004; Huyghe et al. 2005; Whiting et al. 2006), and fish (Horth 2003).
16 Models suggest that the evolution of ornaments in socially monogamous and sexually
17 monochromatic species could be driven by mutual mate choice or by intra-sexual signalling
18 within both sexes (Johnstone et al. 1996; Kokko & Johnstone 2002). Many monogamous species
19 are territorial and what appears to be signalling between the pair members may in reality be
20 directed at other conspecifics as signals of status or fighting ability (Enquist & Leimar 1983;
21 Andersson 1994). It has been suggested that the biological function of the strikingly coloured
22 feathers and bill spots of penguins is related to mate acquisition (Massaro et al. 2003; Jouventin
23 et al. 2005; 2006; in press). A pioneering experiment manipulating plumage of three penguin
24 species (*Aptenodytes patagonicus*, *Eudyptes chrysocome*, and *E. chrysolophus*) found that the

1 removal of yellow feathers from the head resulted in males having difficulty acquiring a mate,
2 although it was unclear if those males fared poorly in mate choice or in male-male competition
3 (Jouventin 1982).

4 The king penguin (*Aptenodytes patagonicus*) is a territorial seabird in which both sexes
5 are characterized by permanent bright auricular and breast patches of yellow-orange feathers
6 (Jouventin 1982), and an orange beak horn reflecting intensely in the ultraviolet (UV)
7 wavelengths (Jouventin et al. 2005; Dresp et al. 2005). King penguin feathers lack carotenoids
8 and contain only a small amount of melanin pigments; the feathers on their breast and auricular
9 regions appear coloured by an undescribed pterin pigment (McGraw et al. 2004).

10 King penguins nest in dense colonies where pairs vigorously defend a small territory of
11 approximately 0.5 m² during incubation and brooding (Côté 2000). Aggressive behaviour varies
12 significantly depending on territory location within the colony (central birds are more aggressive
13 than peripheral birds) or the state of reproduction (aggressiveness during incubation is lower than
14 during brooding), but both sexes are equally aggressive (Côté 2000). Moreover, breeding birds
15 experience differential reproductive success depending on the period of reproduction (early
16 breeders had a three-fold higher success than late breeders) and territory location (central
17 territories have a higher success than those on the edge; Weimerskirch et al. 1992; Côté 2000).
18 Territory defence may represent the degree of parental investment or parental quality of breeding
19 birds and consequently may play a crucial role in reproductive success in this species.

20 Despite extensive studies on the evolution and role of colour ornaments, monomorphic
21 seabirds like penguins are still poorly known, even though those species exhibit strikingly
22 coloured feathers and their breeding and behavioural ecology suggest a sexually-selected role for
23 their plumage ornaments. Because auricular feathers play a role in mate choice in king penguins
24 (Jouventin 1982; Jouventin et al. in press), we investigated whether the size of the orange

1 auricular patch may be an indicator of aggressiveness in this monochromatic species. We tested
2 the relationship between auricular patch size and defence behaviour according to the territory
3 location (centre vs. periphery), period of reproduction (early vs. late), state of reproduction
4 (incubation vs. brooding), and sex of breeding pairs.

5

6

METHODS

7 King penguins are pelagic seabirds that breed throughout the subantarctic islands. We studied
8 king penguins in a sub-colony of ca. 16 000 pairs in “La Baie du Marin”, Possession Island,
9 Crozet Archipelago (46°25’S, 51°45’E). The laying period extends from November to March and
10 hatching occurs on average 54 days after the beginning of incubation (Stonehouse 1960), i.e.
11 starting at the beginning of January at Crozet. King penguins do not build a nest, and therefore
12 incubate a single egg on their feet (Stonehouse 1960). Male and female king penguins share
13 incubation and chick-rearing duties. The male performs the first shift, which typically lasts about
14 two weeks, whereas the duration of each remaining incubation shift lasts 5 to 15 days
15 (Stonehouse 1960).

16 **Data collection**

17 We collected data during the austral summers of 2004 and 2005. We located pairs on their
18 breeding territory during pair formation, sprayed them from a distance with a non-permanent blue
19 dye (PORCIMARK®, Kruuse) on their white breast, and then flipper-banded males and females
20 with a plastic tag during their first incubation shift. The dye on the chest lasted 1 to 15 days
21 depending on the rain, and disappeared completely after going to sea. Flipper length was also
22 measured at capture. Sex was known for all birds, because the male always performs the first
23 incubation shift (Stonehouse 1960; Weimerskirch et al. 1992). The exact day of laying was
24 known for each pair and birds were surveyed daily during incubation and brooding to measure

1 shift durations and to record hatching dates. Early breeders lay their egg in late November-early
2 December (Weimerskirch et al. 1992). Those that laid after the first hatching was observed were
3 considered late breeders (Côté 2000). We defined peripheral territories as those situated within
4 approximately 2 m of the colony edge (Côté 2000). Peripheral individuals were therefore the first
5 birds to interact with predators attempting to enter the colony (Côté 2000).
6 Between December and February, we performed 278 focal animal samples of 15 min each on 74
7 marked birds from different pairs (2 to 11 focals/individual; 1 to 4 shifts/bird) to study their
8 aggressive behaviour (Altmann 1974; Côté 2000). Observations were conducted between 0630 to
9 2030 hours and were carried out from outside the colony at distances of 10-250 m, using
10 binoculars and spotting scopes when necessary to avoid disturbing the birds. We recorded
11 territorial defence as the following aggressive behaviours: beak pointing (no vocalization, beak
12 closed, body stretched out), gaping (pointing but with bill open and vocalizing, body stretched
13 out), pecking and flipper blows (Côté 2000). Number of direct neighbours of the territory, i.e.
14 those close enough to allow interactions with body contact, was noted for each focal sample
15 (Côté 2000).

16

17 We took digital photographs of the heads of all marked individuals (44 males, 30
18 females), using a Canon digital camera (EOS 300D). We captured all birds once and held them
19 briefly inside a nearby field hut, to obtain similar light conditions and standard background. We
20 used a standardised posture: birds in profile, head lightly extended and bill pointing up at 30
21 degrees from the horizontal. Photographs were taken from 40 cm away and using 50 mm as the
22 focal distance (Canon EF-S 18-55 lens / f5.6). In each photograph, we hold a ruler in the same
23 plane as the plumage badge, to allow measurement of the patch size. Badge sizes were measured

1 from digital images on a Macintosh computer using the public domain NIH Image software
2 (<http://rsb.info.nih.gov/nih-image>).

3 **Statistical analyses**

4 We estimated the proportion of time spent in territory defence and the rates of threat displays
5 involving 1) no body contact (beak pointing and gaping) and 2) with body contact (pecking and
6 flipper blows). The proportion of time spent defending the territory was arcsine square-root
7 transformed, while the rates of threat displays and aggressive interactions with body contact were
8 square-root transformed to satisfy normality (Sokal & Rohlf 1995). Mixed GLMs (GLMM) with
9 individual as a random factor were used to assess the relationships between patch size and the
10 different measures of aggressive behaviour (dependent variables). Because the number of
11 neighbours and body size (as indexed by flipper length) may affect aggressiveness or patch size,
12 we considered them as covariates in the models. Sex, territory location (central vs. peripheral),
13 period of reproduction (early vs. late laying), state of reproduction (incubation vs. brooding), and
14 all two-way interactions with patch size were included in the mixed models. We also tested the
15 effects of sex, territory location, period of reproduction, and state of reproduction on measures of
16 patch size. Models took into account the dependence between observations from the same subject
17 with a compound symmetry structure (Littel et al. 2006). All statistical analyses were performed
18 with SAS statistical software (SAS Institute, Cary, N.C.; version 9.1). Means are reported \pm 1 SE
19 and the significance level was set at 0.05.

20 **Ethical Note**

21 We captured penguins from a sector of the colony inhabited by about 1600 pairs, and placed a
22 hood over the heads of captured birds to keep them calm during handling, which lasted 5 to 10
23 minutes. To minimize disturbance, we only took a picture of the right profile of each bird.
24 Removing the birds from the colony to standardize conditions for pictures and limit the

1 disturbance of neighbours did not result in any egg lost and, after releasing birds, no predation
2 was observed in the colony. When focal observations were conducted at short distances, we
3 observed the birds from behind a low wall. Birds were banded at the onset of the breeding season
4 and tags were removed before the winter. Capture and tagging procedures were approved by the
5 Ethical Committee of the Institut Polaire Français – Paul-Emile Victor and the experiments
6 comply with the current laws of France.

7 **RESULTS**

8 The covariates in the models were not significant: flipper length, an index of body size, was not
9 related to auricular patch size (GLMM: $F_{24,227} = 0.82$, $P = 0.71$) or aggressiveness (rate of threat
10 displays, rate of body contacts and time spent in territory defence; all P 's > 0.4). Moreover, the
11 number of neighbours did not affect any measures of aggressiveness (all P 's > 0.3).

12 Time spent in territory defence increased with patch size ($F_{1,228} = 141.9$, $P < 0.001$,
13 $R^2=0.34$; Fig. 1). Similarly, the rate of threat displays ($F_{1,228} = 9.91$, $P = 0.002$) and body contact
14 interactions ($F_{1,228} = 5.88$, $P = 0.01$) increased with patch size. There was also an interaction
15 between patch size and territory location (proportion of time spent in defence: $F_{1,224} = 6.95$, $P =$
16 0.009 ; threat displays: $F_{1,224} = 8.90$, $P = 0.003$; body contacts: $F_{1,224} = 29.14$, $P < 0.001$),
17 indicating that aggressiveness increased more rapidly with patch size for birds on central
18 territories than for birds on peripheral territories (Fig. 1). Moreover, aggressiveness was higher
19 for central birds than for birds occupying the periphery of the colony (all P 's < 0.02; Table 1).
20 The interactions between patch size and either the period of reproduction, the state of
21 reproduction or sex did not affect measures of aggressiveness (all P 's > 0.2).

22 Similarly to aggressiveness, patch size was larger in central birds than in peripheral birds
23 ($F_{1,224} = 18.90$, $P = 0.001$; Table 1), but it did not differ between early and late breeders ($F_{1,224} =$

1 1.80, $P = 0.18$), incubating and brooding birds ($F_{1,224} = 3.39$, $P = 0.07$) or between sexes ($F_{1,224} =$
2 0.63, $P = 0.43$).

3 DISCUSSION

4
5 Our study demonstrated that auricular patch size can convey information on the aggressive
6 behaviour of both sexes. West-Eberhard (1983) suggested that bright coloration in both sexes of
7 many bird species may occur because the two sexes perform aggressive displays. Very few
8 studies on birds, however, have shown that an ornament may be involved in aggressive displays
9 in both sexes (Jones & Hunter 1999; Kraaijeveld et al. 2004). Male and female king penguins
10 share territory defence. The risk of injury in aggressive interactions involving body contacts is
11 therefore high in both sexes, favouring the evolution of badges of status (Jones & Hunter 1999).
12 As a result, both sexes are similarly ornamented in king penguins and, therefore, we argue that
13 our results add to the emerging evidence that selection for social signalling in both sexes could be
14 the product of mutual sexual selection rather than genetic correlation between the sexes (Jones &
15 Hunter 1993; Kraaijeveld 2003; Komdeur et al. 2005). Kraaijeveld et al. (2004) showed that
16 ornamental feathers of monomorphic black swans (*Cygnus atratus*) function as a signal of social
17 dominance which is highly correlated with reproductive success in both sexes. Others have also
18 recently investigated how ornaments were associated with reproductive performance in both
19 sexes of different bird species. Komdeur et al. (2005) found positive relations between
20 ornamentation of European starlings (*Sturnus vulgaris*) and fitness correlates such as laying date,
21 clutch size, and relative hatching success, whereas Velando et al. (2001) showed that ornaments
22 indicated parent and chick quality in Inca terns (*Larosterna inca*). To better understand the
23 evolution of mutual ornamentation in king penguins, it remains to be tested whether patch size is
24 related to reproductive success in both sexes.

1 Patch sizes of birds in the centre of the colony were larger than those of birds at the edge
2 of the colony. Reproductive success of penguins varies according to their territory location
3 mainly because of higher protection from avian predation in the centre of the colony than on the
4 edge (Emslie et al. 1995; Côté 2000). For king penguins, it has been suggested that the first birds
5 to arrive in the colony (early breeders) choose the central locations (Côté 2000; Bried &
6 Jouventin 2001). However, our results indicate that patch size did not vary with the period of
7 reproduction so that birds with larger patches seem to move into central territories when they
8 arrive, even if they are late in the breeding season. Such a hypothesis emphasizes the importance
9 of territory location for king penguins because it suggests that the benefits of being in the centre
10 of the colony outweigh the costs of being more aggressive. As a consequence, it seems
11 reasonable that the relationship between aggressiveness and patch size is related to territory
12 location as birds in good condition are likely to gain access to central territories because of their
13 aggressive behaviour. Ornamentation thus predicted status, with smaller ornamented king
14 penguins less capable of obtaining high quality central territories. The higher aggressiveness of
15 birds on central territories towards territorial neighbours and intruders, compared to peripheral
16 birds (Table 1; Côté 2000), supports this idea.

17 In many bird species, breeding success declines seasonally (Moreno 1998) and often early
18 breeders are more ornamented than late breeders (Møller 1994; Daunt et al. 2003). As the general
19 pattern of other birds, early breeders have higher reproductive success than late breeders in king
20 penguins (Weimerskirch et al. 1992). However, king penguins are unique among penguins in that
21 a successful reproductive cycle requires an average of 14 months (Stonehouse 1960). Such a long
22 breeding cycle means that individuals cannot breed early two years in a row if they have fledged
23 a chick one year. In other words, king penguins can alternate early and late breeding years
24 independently of their condition (Weimerskirch et al. 1992). This may help explain why we did

1 not find any relationship between auricular patch size and the timing of breeding, or between
2 brooding and incubating birds.

3 Mate choice based on the size of a phenotypic trait, such as bill or body size, can also be
4 explained by a positive relation between age and the trait, especially in long-lived species where
5 the expression of a trait often increases with age (Kokko 1997). Therefore, an alternative
6 explanation for the relationship we observed between aggressive behaviour and ornament
7 expression could be that patch size is related to age. However, Nicolaus et al. (unpublished data)
8 tested this hypothesis for king penguins at the same study site and found no difference in mean
9 patch size for birds of 2 to >7 years of age.

10 Individuals best able to assess the quality of potential mates or competitors using colour
11 signals should be favoured by natural selection, which should lead to the display of condition-
12 dependent traits such as colourful plumage patches. Along these lines, Nolan et al. (2006)
13 showed that hue of the breast plumage patch of king penguins reflected their innate, genetically-
14 based immune response. Jouventin (1982) and Jouventin et al. (in press) found evidence of sexual
15 function of patch size and our study demonstrated that patch size may a reliable cue of
16 aggressiveness and indicates an individual's ability to gain and/or defend a territory. The next
17 step is to determine whether aggressiveness is linked to patch size directly or if body condition
18 determines aggressiveness and patch size independently.

19 In conclusion, our results suggest that auricular ornaments signal aggressiveness in both
20 sexes in king penguins and could be influenced by mutual sexual selection. Patch size provides
21 reliable information on aggressive behaviour and perhaps also on individual quality (Kristiansen
22 et al. 2006; Velando et al. 2006; Tibbetts & Curtis 2007). In monogamous bird species, mutual
23 mate choice by males and females is expected to result in assortative pairing for characters linked
24 to individual quality (Andersson 1994).

1

2

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1 Table 1: Aggressiveness (proportion of time spent in defence and rate of aggressive behaviours)
 2 and auricular patch sizes according to territory location in breeding king penguins
 3 (*Aptenodytes patagonicus*) from the Crozet Archipelago

	Central birds (N=40)	Peripheral birds (N=34)
Proportion of time spent in defence (%)	16.6 ± 1.8	13.1 ± 1.9
Threat displays (beak pointing and gaping/h)	95.4 ± 1.7	82.4 ± 1.0
Body contact interactions (pecking and flipper blows/h)	21.4 ± 1.0	11.3 ± 0.6
Auricular patch size (cm ²)	15.1 ± 0.5	13.9 ± 0.5

4

5

- 1 Figure 1: Relationship between percent of time spent in territory defence and auricular patch size
- 2 in breeding king penguins from the Crozet Archipelago. Filled circles are birds on central
- 3 territories and empty circles birds occupying territories on the edge of the colony.

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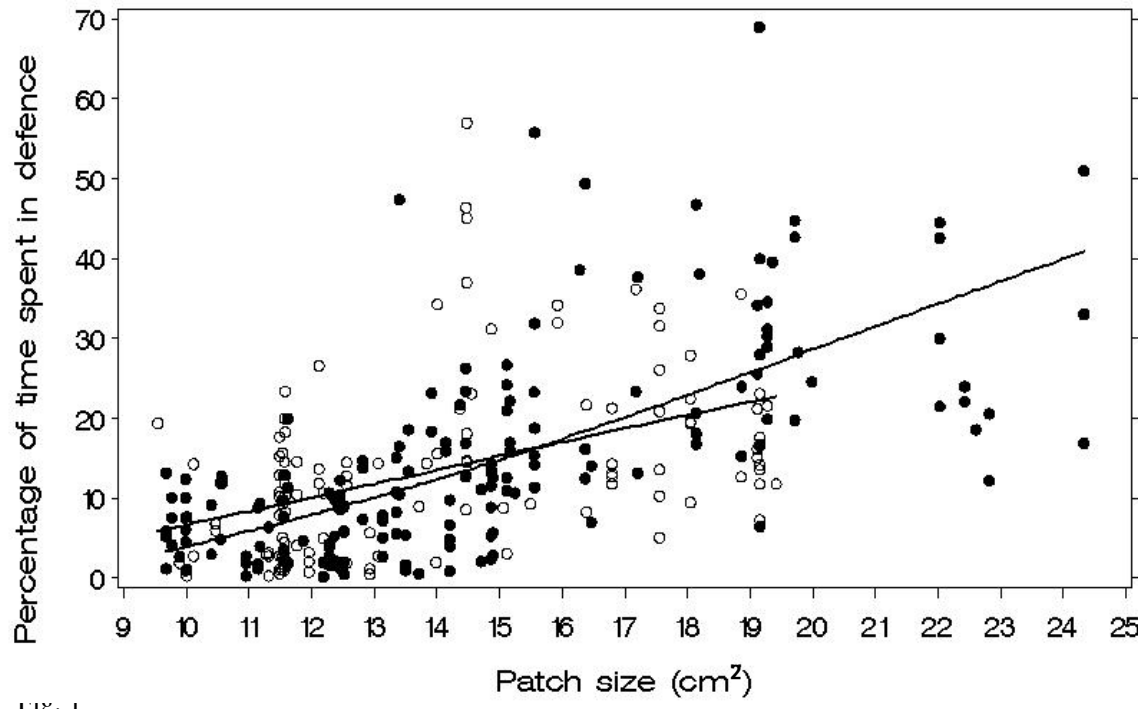


Fig. 1