

Geographic variation in beak colouration in gentoo penguins *Pygoscelis papua*

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Abstract Ornamental colouration is often due to carotenoid pigments and varies inter- and intra-specifically. This paper reports on variation in beak colour of the gentoo penguin, *Pygoscelis papua*, corresponding to different geographical locations along a latitudinal gradient in the Antarctic Peninsula (from King George Island (62°15'S–58°37'W) to Rongé Island (64°40'S–62°40'W)). The gentoo penguin has a conspicuous red spot on both sides of the beak that indicates the presence of the carotenoid pigment, astaxanthin. Beak colouration was measured with a portable spectrophotometer for 20 individuals in three locations, along the Western coast of the Antarctic Peninsula. In the study area, marked variation can be found in terms of factors such as parasite load, human impact, variations in UV radiation and the abundance of krill; all possibly affecting carotenoid availability for signalling purposes. Colour traits were expected to be more intense, that is more vivid, saturated and pure, in places where there is diminished pressure from factors such as contamination, parasites or diseases, all

of which may reduce the availability of carotenoids for other functions, such as antioxidant or immune stimulation involving physiological trade-offs. Likewise, colour traits might be predicted to be more intense where carotenoid sources, krill in the case of gentoo penguins, are more available. However, contrary to this initial expectation, our results indicate that northerly penguins' populations, which are in the most polluted and parasitized areas, have more saturated beaks. An alternative hypothesis suggests that environmental constraints relating to the variation in abundance of krill may explain the geographical variation in colour expression found among gentoo penguins.

Keywords Antarctica · Carotenoid · Colour trait · Contaminants · Gentoo penguin · Geographic variation · Krill · Ultraviolet

Introduction

Carotenoid pigments often colour integumentary traits, such as scales, feathers, beaks or skin, in red and yellow (Grether et al. 1999; Hill et al. 2002, but see McGraw et al. 2004). These compounds have to be ingested by the animals in their diet, as they can only be synthesized by plants, fungi, algae and bacteria (Goodwin 1984). Apart from colouration, they are also required in a number of physiological processes for their antioxidant (Burton and Ingold 1984) and immune stimulation properties (Blount et al. 2003).

The intensity of carotenoid-mediated colouration of integumentary traits can vary inter- and intra-specifically (Hill et al. 1994; Hill and McGraw 2006). This variation has been related to the amount of carotenoids present in the diet (Hill et al. 2002), which may depend on habitat

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conditions (Grether et al. 1999) or foraging ability (Hill et al. 1994). Nevertheless, some carotenoid differences that are independent of diet may be explained by physiological differences manifested in the ability to store or metabolize ingested carotenoids (Negro et al. 2001; McGraw 2005). Intra-specific differentiation of colour traits between sexes, or according to age or populations, has also been previously described (Hill et al. 1994; Norris et al. 2007).

At the intra-specific level, geographical variation in carotenoid-mediated colour traits might be predicted in several different ways. Colour traits may be more intense in situations where there are fewer challenges to individual condition (e.g., contamination, parasite or disease pressure) as these will cause carotenoids to be taken up in other functions, such as antioxidant or immune stimulation (Martinez-Padilla et al. 2007). Alternatively, colour traits may depend on geographical differences in carotenoid type or concentration (Hill et al. 1994) and should thus be more intense in places offering more abundant prey which contains carotenoids.

Colour variation in seabirds including penguins has recently attracted the attention of researchers (Massaro et al. 2003; McGraw et al. 2004; Velando et al. 2006; Jouventin et al. 2007, 2008; Perez et al. 2008; Cuervo et al. 2009). Comparison of sexual ornaments in several penguin species shows that colouration (in plumage and beak) may play a role in mate choice (Massaro et al. 2003; Jouventin et al. 2008; Pincemy et al. 2009; Nolan et al. 2010) as well as in territorial defence (Viera et al. 2008).

We studied the geographic variation in beak colour in the gentoo penguin (*Pygoscelis papua*) at different locations on the Antarctic Peninsula, from King George Island ($62^{\circ}15'S$ – $58^{\circ}37'W$) to Rongé Island ($64^{\circ}40'S$ – $62^{\circ}40'W$). The gentoo penguin has a conspicuous red spot on both sides of its beak due to the presence of the carotenoid pigment astaxanthin (A. Barbosa et al. unpublished), which is found in krill (Yamaguchi et al. 1983), the main prey of this species (Croxall and Lishman 1987; Williams 1995). The link between astaxanthin intake and beak colour in gentoo penguins has recently been confirmed in an experiment using dietary supplements (Jouventin et al. 2007). Additionally, gentoo penguin beak colouration has also been related to body condition in males, suggesting that this trait has the potential for serving as a secondary sexual character in males (Cuervo et al. 2009). In the study area, the Western coast of the Antarctic Peninsula, there are strong variations in environmental factors that may affect colour expression. In the northern Antarctic Peninsula, parasites are more frequent (Barbosa and Palacios 2009), there is greater human impact (Tin et al. 2009), increased presence of heavy metals (Jerez et al. 2011), stronger UV radiation (Barbosa et al. 2007b) and abundant krill

(Atkinson et al. 2004), which may affect the availability of carotenoids for signalling.

Our aim is to show how beak colour varies among the different populations of the gentoo penguin.

Materials and methods

In February 2006, we visited several gentoo penguin breeding localities in the South Shetlands (King George Island and Livingston Island) and the Gerlache Strait (Rongé Island) (Fig. 1; Table 1). The distribution of the Gentoo Penguin (*Pygoscelis papua*) ranges between 46° and $65^{\circ}S$, and therefore, the geographical range of this study constitutes the southern part of its area of distribution. Adult penguins were captured during moulting using a long-handled net. A blood sample was taken from the foot vein of each individual immediately after capture, using a heparinized capillary tube. A drop was preserved in alcohol for molecular sexing following Ellegren (1996). Beak colouration was assessed in terms of reflectance spectra using a Konica Minolta Sensing CM-2600d spectrophotometer that measures reflectance at 10 nm intervals from

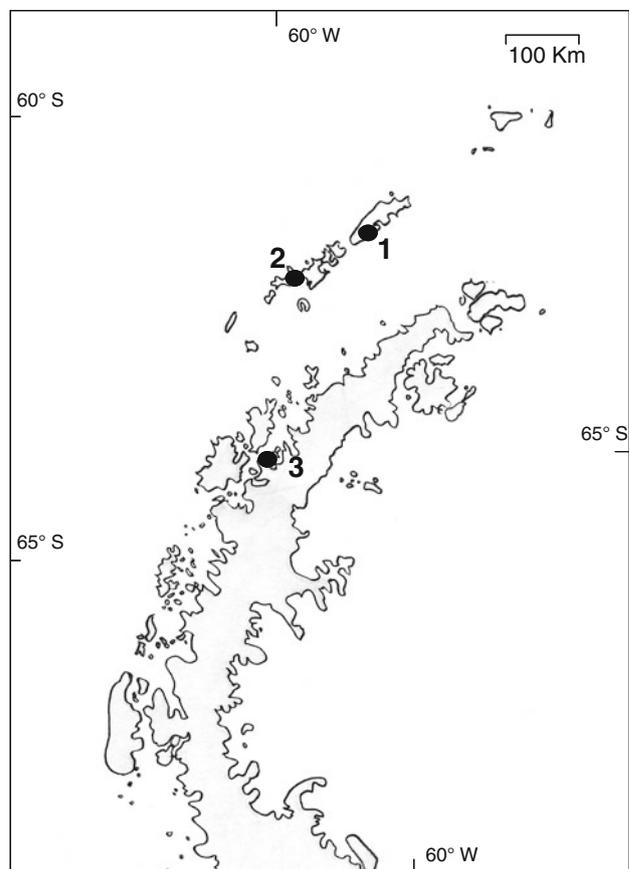


Fig. 1 Localities sampled: 1 Stranger Point (King George Island), 2 Hannah Point (Livingston Island), 3 George Point (Rongé Island)

Table 1 Localities and sample sizes

Localities	Sample size
Stranger Point (King George I) 62°15'S–58°37'W	19 (10F, 6 M) ^a
Hannah Point (Livingston I.) 62°39'S–60°36'W	20 (11F, 9 M)
George Point (Rongé I.) 64°40'S–62°40'W	20 (12F, 8 M)

^a It was not possible to sex three individuals

320 to 700 nm. Two measurements were taken on the right side of the beak, one close to the tip of the beak and one close to the base. The measurements were referenced to a white standard (CM-A145 Konica Minolta Sensing) and to a dark standard (CM-A32, Konica Minolta Sensing). Calibration was implemented for every five individuals measured. All measurements were made by the same person (A. B.).

Colour variables were assessed by reflectance (R) following Montgomerie (2006). Brightness, considered as luminance and defined as the total amount of light reflected from the measured surface (see for instance Saks et al. 2003), was estimated, by adding up all reflectance values between 360 and 700 nm. High brightness indicates that the colour is relatively lighter. Beak colour in the gentoo penguin is mostly reflected in the red wavelength region (see Cuervo et al. 2009); thus, we investigated variation in this part of the spectra with reference to two variables: chroma and hue. Chroma is a measure of the 'purity' or 'saturation' of a colour and was calculated by adding up red region reflectance (630–700 nm) and dividing this figure by the total reflectance. High chroma indicates vibrant colours, whereas low chroma indicates faded and washed out colour. Hue can be understood as the everyday meaning of colour (yellow, green, red) and was defined using the following equation (see Jouventin et al. 2007 for the same approach):

$$\text{HUE} = \arctan \left\{ \frac{[(R_y - R_b)/R_t]}{[(R_r - R_g)/R_t]} \right\},$$

where R_y is equal to the sum of reflectance from 550 to 630 nm R_b from 400 to 480, R_r from 620 to 700; R_g from 470 to 550 and R_t from 360 to 700 nm (Hill and McGraw 2006). Higher reflectance indicates that the colour is redder, whereas less reflectance means less red, that is, more orange. The gentoo penguin beak spot shows a small reflectance peak within the 360–400 nm UV wavelengths (Fig. 2). This peak was also detected by Cuervo et al. (2009). Thus, we also looked for the variation in the UV band among the different populations. UV chroma was estimated by adding up reflectance in the UV band (360–400 nm) and dividing by the total reflectance (360–700 nm). UV hue was defined as the wavelength with the most reflectance in the UV band. Reflectance at 360 nm

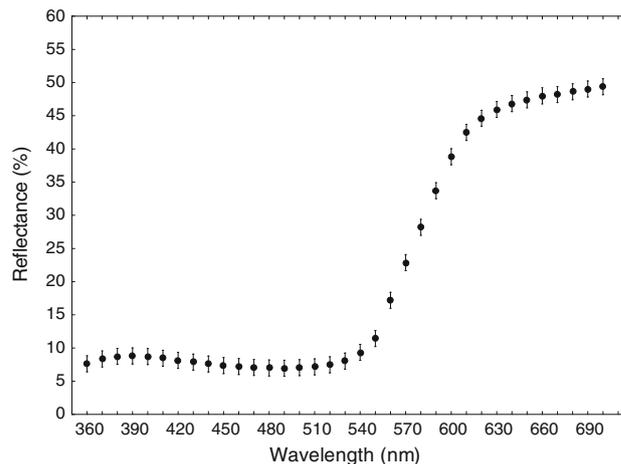


Fig. 2 Mean red beak spot reflectance in gentoo penguin, $n = 59$

was always less than at 370 nm, thus, we are confident that the UV peak was always within our wavelength range (see Cuervo et al. 2009 for the same approach). Repeatability was calculated in a subsample of 19 individuals which involved taken three measurements. Between-individual variation was greater than within-individual variation (i.e., chroma ANOVA $F_{18,38} = 2.20$, $P = 0.02$; repeatability following Lessels and Boag (1987), $r = 0.47$).

All variables except UV hue were normally distributed (Kolmogorov–Smirnov test >0.20). Statistical analyses included the Student's t test and two-way ANOVA with region and sex as the factors. The Kruskal–Wallis and Mann–Whitney tests were performed for testing population and sex differences, respectively, in terms of UV hue. The criterion for removing a variable was set at $P = 0.05$.

Results

Student's t tests indicated that the colour at the base of the beak was significantly more saturated than at the tip, so the measurements at the point with the highest signal (Chroma: $t = 3.61$, $P < 0.0004$, $n = 59$; base: mean = 0.49 ± 0.005 ; tip: mean = 0.47 ± 0.004) were used for further analyses. ANOVA analyses showed that variation in chroma was explained by geographic location ($F_{2,50} = 3.61$, $P = 0.034$, Fig. 3a). Hannah Point (Livingston Island) was the location with the highest scores, whereas George Point (Rongé Island) had the lowest. Stranger Point (King George Island) was in an intermediate position. Neither sex ($F_{1,50} = 1.83$, $P = 0.18$; males: mean = 0.50 ± 0.007 ; females: mean = 0.49 ± 0.007) nor interaction between location and sex ($F_{2,50} = 0.49$, $P = 0.61$) was significant. Differences in brightness were also explained by geographic location ($F_{2,50} = 5.66$, $P = 0.006$, Fig. 3b). The gentoo penguin population at George Point (Rongé Island)

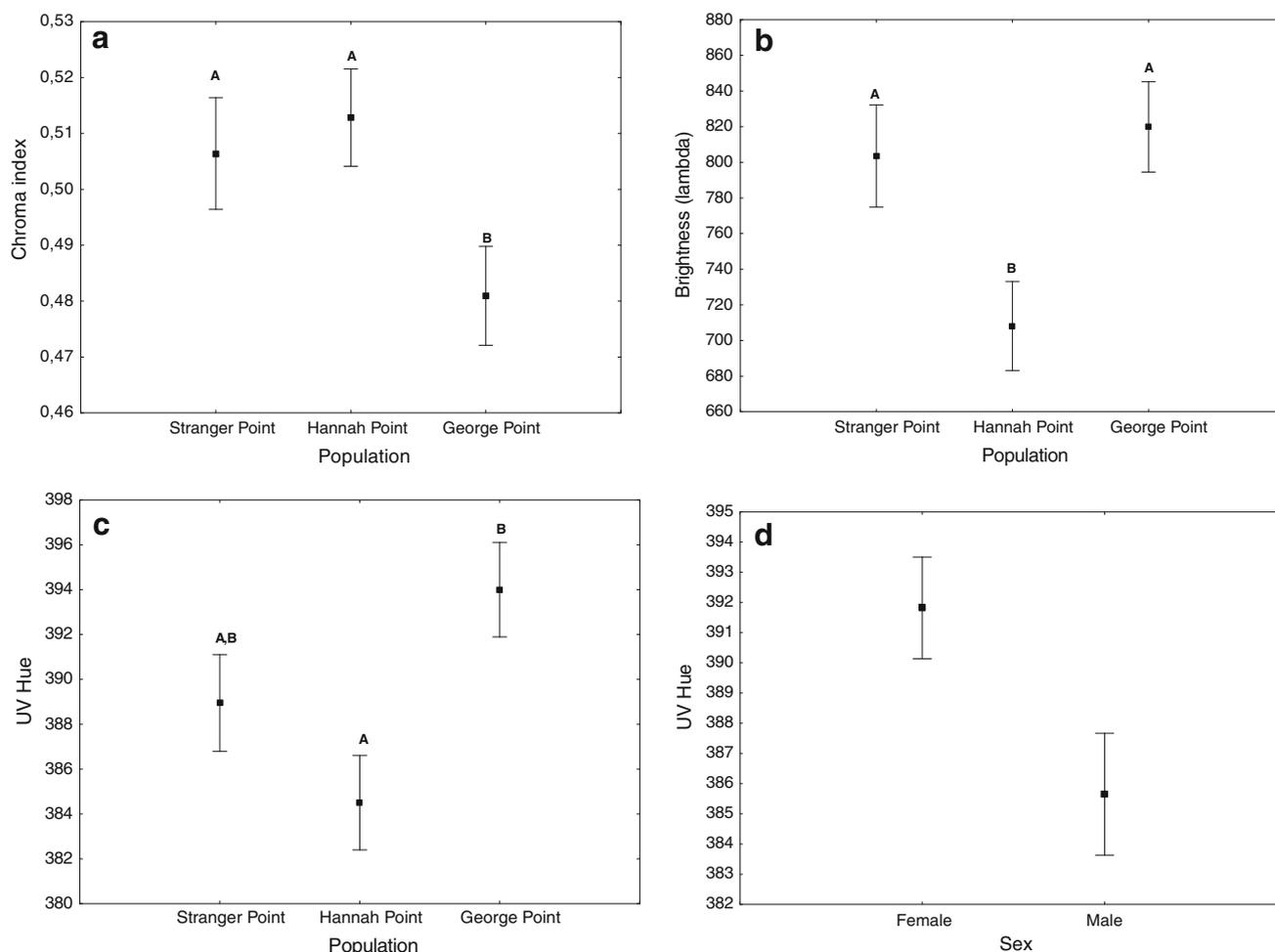


Fig. 3 **a** Differences in red chroma among the studied populations. Letters denote significant differences between groups (post hoc comparisons $P < 0.05$). **b** Differences in red brightness among the studied populations. Values are nm. Letters denote significant differences between groups (post hoc comparisons $P < 0.05$).

c Differences in UV hue among the studied populations. Values are nm. Letters denote significant differences between groups (post hoc comparisons $P < 0.05$). **d** Differences in UV hue between sexes. Values are nm

had the brightest beaks, whereas those at Hannah Point (Livingston Island) had the lowest. Again at Stranger Point (King George Island) scores were intermediate. Neither sex (Sex: $F_{1,50} = 0.85$, $P = 0.36$; males: mean = 785.12 ± 21.80 ; females: mean = 764.92 ± 22.78) nor interaction between location and sex ($F_{2,50} = 0.82$, $P = 0.44$) was significant. Variation in hue did not show significant differences in terms of any of the factors considered (Locality: $F_{2,50} = 1.42$, $P = 0.24$; Stranger Point: mean = 0.53 ± 0.008 ; Hannah Point: mean = 0.54 ± 0.007 ; George Point: mean = 0.55 ± 0.008 ; Sex: $F_{1,50} = 1.55$, $P = 0.21$; males: mean = 0.53 ± 0.006 ; females: mean = 0.54 ± 0.007 ; Interaction: $F_{2,50} = 0.55$, $P = 0.57$).

The UV peak represented 21% of total reflected UV and 1.2% of the total visible reflectance. We did not find any differences in UV chroma depending on location ($F_{2,50} = 1.91$, $P = 0.15$; Stranger Point: mean = $0.05 \pm$

0.003; Hannah Point: mean = 0.05 ± 0.001 ; George Point: mean = 0.05 ± 0.001) or between sexes ($F_{1,50} = 1.58$, $P = 0.21$; males: mean = 0.05 ± 0.001 ; females: mean = 0.05 ± 0.001) nor was interaction significant ($F_{2,50} = 1.44$, $P = 0.24$). Finally, UV hue was significantly different at the various locations ($H_{2,50} = 8.75$, $P = 0.01$ Fig. 3c); scoring highest at George Point (Rongé Island) and lowest at Hannah Point (Livingston Island). Stranger Point (King George Island) was in an intermediate position. UV hue showed differences between sexes and was higher in females (that is, more violet) than males ($U = 250.0$, $P = 0.03$; males = 23, females = 33, Fig. 3d) considering all the localities together.

All the results for hue calculation remained the same when using small variations (± 40 nm) in the range of wavelengths considered for Ry, Rb and Rg or when using the method described by Montgomerie (2006).

Discussion

Our results show differences in beak colouration among gentoo penguins according to the geographical location of the populations studied. Gentoo penguins at Hannah Point (Livingston Island) had a more vibrant, dark beak colour, whereas penguins in the George Point rookery (Rongé Island) had more faded, light beaks. The population at Stranger Point (King George Island) differed neither from Hannah Point in terms of chroma nor from George Point in terms of brightness. On the other hand, we did not find any geographic differences in hue. These results show that penguins in Hannah Point have more saturated red beaks, whereas the George Point population had paler beaks. As Hannah Point and Stranger Point are in the same region (South Shetland Islands), it follows that penguins pertaining to these northern populations have redder beaks. Geographic differences in other variables in this species, such as immunoglobulin and heat shock protein levels, have also been pointed out (Barbosa et al. 2007a, b). This shows that marked environmental variability is evident, relating to only a 2° difference in latitude in the Antarctic Peninsula.

In our study area, the northern population of penguins at Hannah Point (Livingston Island) and Stranger Point (King George Island) is exposed to stronger human impact (Bargagli 2005), more concentrated pollutants such as heavy metals (Jerez et al. 2011) and higher presence of parasites (Barbosa et al. 2011). Several studies have pointed out the negative effects of pollution and parasite pressure on the intensity of colour traits (i.e., Martínez-Padilla et al. 2007, but see Isaksson et al. 2007). However, our results do not seem to support these effects as we found that the localities with darker and more saturated colours are subject to the same high environmental stress from contamination and parasites/diseases.

Alternatively, variation in beak colour may also relate to environmental differences affecting the availability of krill, the main carotenoid resource present in the gentoo penguin diet (Williams 1995). Atkinson et al. (2004) show that the abundance of krill varies in the three locations, being more abundant in Livingston Island and less so in King George Island and Rongé Island. The pattern that emerges concerning the abundance of krill fits seems to be reflected in a similar pattern in red beak colouration, with the reddest beaks found among penguins at Hannah Point (Livingston Island) and those with the least red beaks at George Point (Rongé Island). However, beak colour at Stranger Point does not concur very well with this finding. The distribution and abundance of krill varies both temporally and spatially (Everson and Murphy 1987), and as only rough estimates for krill abundance can be found in databases from 1926 to 2003 (Atkinson et al. 2004), more detailed

information on krill abundance is necessary for testing this hypothesis.

Geographical differences may also occur if populations differ genetically and manifest varying abilities for metabolically appropriating the available carotenoid in their food. However, results from other authors show only very slight genetic differences between two populations (Argentina cove, Livingston Island; and Petermann Island) located very close to ours (Dranitsina et al. 2006). This possibility can therefore be ruled out although more information about the genetic structure of gentoo penguin populations in the Antarctic Peninsula would be pertinent.

As much penguin activity takes place under water, and water tends to absorb longer wavelengths more readily than green or blue wavelengths, small variations in red colouring would be more obvious under water, as in the case of diving birds than they are in the air. This may support the importance of small changes in signalling traits such as the red beak spot in the gentoo penguin.

An alternative, although not mutually exclusive explanation for the geographic variation in colour, may refer to likely differences concerning the intensity of sexual selection in the populations. In this context, carotenoid-mediated colour traits may show geographic variations related to condition-dependence. This has been reported among gentoo penguin males in the Stranger Point population (Cuervo et al. 2009). Nevertheless, more research on the other populations is necessary if this idea is to be confirmed. Interestingly, no sexual dimorphism has been reported in the red chroma, brightness or hue of the beak spot colour in our populations, although sexual differences were found in terms of UV hue (see below and also Cuervo et al. 2009). These results may to some extent reduce the importance of variation in sexual selection intensity as a factor causing variation in beak colour.

We found both geographical and sexual differences in UV hue, but not in UV chroma. UV hue was highest at George Point (Rongé Island), lowest at Hannah Point (Livingston Island), and at Stranger Point (King George Island) it was intermediate. On the other hand, females showed higher values of reflectance in the UV, that is, more violet, than those of males. UV reflectance is produced by a multilayer reflector photonic microstructure by the interference between incident light and that reflected from successive folds in the microstructures (Dresp et al. 2005). It has been demonstrated that this trait plays an important role in sexual signalling and mate choice (i.e., Johnsen et al. 1998; Nolan et al. 2010). Dresp et al. (2005) showed that UV reflectance in king penguins had a structural origin possibly similar to that of the gentoo penguin. Meyer-Rochow and Shimoyama (2008) suggest that reflection of the UV in penguins is of minor biological importance, and stress that caution should be taken when

explaining the biological meaning of this trait to avoid premature conclusions (Meyer-Rochow and Shimoyama 2009; but see Jouventin et al. 2009 for an opposite view). Here we provide additional evidence of UV reflectance variation between sexes and among populations, which could contribute to increase the confidence in the biological role played by UV reflectance in penguins (Cuervo et al. 2009). As far as we know, this is the first demonstration of significant differences in UV among bird populations.

The present study is based on samples from three populations two of which are closer together than the other. Therefore, the north–south comparison is based on a single trial so that there can be no alternative explanation other than the lack of a significant difference. Additional sampling, thus increasing the geographic range (i.e., Sub-Antarctic populations) would be helpful, although the logistic difficulties of simultaneously sampling such a large area during the same breeding season in order to make comparisons preclude such a task.

Finally, we measured the beak colour of gentoo penguins during moulting (no moulting of beak spot was observed). It might be argued that differences in beak colour could exist at different times during the annual cycle because of differences in the need for signalling and that this is reflected in the differences found among the populations. However, we think this is not the case. Firstly, although in one of the study populations (Stranger Point, King George Island), we found that moulting birds had paler beaks than that were breeding (J. J. Cuervo et al. unpublished), actually these differences are also likely to be due to differences in the quality of individuals (see Dobson et al. 2008), as birds that moult early have failed to breed. Secondly, although moulting birds had paler beaks than they had during breeding, there is no reason to think that the extent of colour reduction varied among populations. Likewise, judging from the amount of feathers lost, birds from all the populations were sampled late in moulting, thus ensuring that any observed differences were not due to sampling at different stages during the moult.

In summary, variations in beak colour relating to different populations of gentoo penguins in the Antarctic Peninsula seem to be explained by environmental differences, resulting in variations in the amount of krill. If confirmed, these results may be of interest if it can be shown that changes in krill characteristics are due to global warming and that consequently secondary sexual traits in the gentoo penguin, such as beak colour are affected by food intake. However, this scenario must be treated as a hypothesis until a direct link between environmental factors like pollutants, parasites, krill abundance and variation in beak colour can be established.

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Ethical standards Procedures used in this study comply with the current laws for working in Antarctica. Permission to work in the study area and for penguin handling was granted by the Spanish Polar Committee.

Conflict of interest This study was funded by the Spanish Ministry of Science and Innovation and European Regional Development Fund (grants CGL2004-01348, POL2006-05175 and CGL2007-60369). MJP was supported by a PhD grant from the Spanish Ministry of Science and Innovation (BES2005-8465). AM is grateful for financial support from the Spanish Ministry of Science and Innovation (SAB2006-0192) and DGAPA-UNAM-México. The authors declare that they have no conflict of interest.

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