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Mutually honest? Physiological 'qualities' signalled by colour ornaments in monomorphic king penguins

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Abstract :

Mate choice is expected to be important for the fitness of both sexes for species in which successful reproduction relies strongly on shared and substantial parental investment by males and females. Reciprocal selection may then favour the evolution of morphological signals providing mutual information on the condition/quality of tentative partners. However, because males and females often have differing physiological constraints, it is unclear which proximate physiological pathways guarantee the honesty of male and female signals in similarly ornamented species. We used the monomorphic king penguin (Aptenodytes patagonicus) as a model to investigate the physiological qualities signalled by colour and morphological ornaments known to be under sexual selection (coloration of the beak spots and size of auricular feather patches). In both sexes of this slow-breeding seabird, we investigated the links between ornaments and multiple indices of individual quality; including body condition, immunity, stress and energy status. In both sexes, individual innate immunity, resting metabolic rate, and the ability to mount a stress response in answer to an acute disturbance (capture) were similarly signalled by various aspects of beak coloration or auricular patch size. However, we also reveal interesting and contrasting relationships between males and females in how ornaments may signal individual quality. Body condition and oxidative stress status were signalled by beak coloration, although in opposite directions for the sexes. Over an exhaustive set of physiological variables, several suggestive patterns indicated the conveyance of honest information about mate quality in this monomorphic species. However, sex-specific patterns suggested that monomorphic ornaments may signal different information concerning body mass and oxidative balance of males and females, at least in king penguins.

Keywords : body condition, king penguin, monomorphic seabird, mutual mate choice, ornament, oxidative stress, sexual selection, ultra-violet signals

INTRODUCTION

The evolutionary explanation for conspicuous and similar ornaments in both sexes (i.e. in sexually monomorphic ornamented species) has been a long-standing quandary in evolutionary biology (reviewed by Kraaijeveld et al. 2007). Two main hypotheses have been proposed to explain mutual ornamentation. The first suggests that female ornaments are non-functional, but arise as a by-product of genetic correlations between the sexes (Lande 1980, Price 1996). The second, mutual selection, suggests that functional ornaments may result from selection on their expression in both sexes. Processes that may select for both male and female ornaments include mimicry to conceal sexual identity (Burley 1981), mutual sexual selection for high quality partners (Hooper and Miller 2008), or social competition over non-mate resources in both sexes (West-Eberhard 1979, Tobias et al. 2012). As pointed out by Kraaijeveld et al. (2007), these processes are not mutually exclusive, as traits may be used in several contexts, for instance both in contests over resources (either mates or non-mate resources) and mate choice (Berglund et al. 1996).

Mutual sexual selection is expected when variance in reproductive success is similar between males and females, and when mate quality is an important predictor of variation in male and female success (Trivers 1972, Clutton-Brock and Vincent 1991), such as in slow breeding seabirds (e.g. Velando et al. 2001). Where both sexes should be choosy in their pairing preferences, ornaments may be favored because they assist the individual expressing them in acquiring a high quality mate, whereas preferences for ornaments may do the same for receivers (Johnstone et al. 1996, Kokko and Johnstone 2002, Hooper and Miller 2008). Furthermore, mating systems with extended mate-sampling periods are expected to lead to reduced mutual ornamentation ("dull monomorphism"; Badyaev and Qvarnström 2002, Badyaev and Hill 2003), whereas mating systems with short mate-sampling periods should favor extravagant "bright" monomorphism (Fitzpatrick 1994). However, because males and

76 females often differ in physiological constraints, the aspects of individual quality signaled and
77 of interest to receivers may differ between the sexes (Alvarez et al. 2005, Lopez et al. 2008).
78 For instance, in goldfinches (*Spinus tristis*), monomorphic bill coloration is correlated with
79 acquired immunity in females but not males, probably linked to the different functional roles
80 of beak coloration in male and female social communication (Kelly et al. 2012).

81 King penguins (*Aptenodytes patagonicus*) are monomorphic seabirds, where both
82 sexes experience a highly energy demanding breeding cycle (Groscolas and Robin 2001) and
83 cooperate for as long as 14 months to successfully raise a single chick (Stonehouse 1960).
84 Both males and females display conspicuous color ornaments including auricular feather
85 patches that only reflect yellow-orange colors, a breast feather patch that reflects yellow to
86 rusty-brown colors (Pincemy et al. 2009), and keratin beak spots on their lower mandibles
87 that reflect yellow-orange *and* UV color (Jouventin et al. 2005). Although it has been
88 previously demonstrated that feather and beak spot colorations are used in mate choice
89 (Pincemy et al. 2009, Nolan et al. 2010), little is known on the information carried by those
90 ornaments. We tested whether the ornaments of king penguins convey similar information in
91 both sexes in order to determine whether the condition-dependence of ornamental features
92 occurs only in one sex, suggesting that selection operates primarily in that sex and that
93 monomorphism is the outcome of genetic correlation between the sexes; or whether
94 condition-dependence occurs in both sexes (though not necessarily on the same ornaments
95 nor related to the same qualities) supporting the idea of mutual sexual selection. We aimed at
96 providing an extensive list of quality measures choosing key mediators of vertebrate life
97 histories expected to exhibit important associations with fitness. Those included body
98 condition, immune status, energy expenditure, hormonal stress status, hormonal and heart rate
99 stress responsiveness, and oxidative status (e.g. Norris and Evans 2000, Monaghan et al.
100 2009).

Because beak UV is important to pairing decisions for both male and female king penguins (Nolan et al. 2010), we expected it to reflect information on individual quality in both sexes. In contrast, larger auricular patches are more important to females during mate choice (Pincemy et al. 2009, Dobson et al. 2011), but have also been positively linked to social aggressiveness in both sexes (Viera et al. 2008). Thus, we expected auricular patch size to yield information on male quality, or non-exclusively to signal male and female abilities to cope with their aggressive colonial environment, including via physiological stress responses (e.g. Parker et al. 2002, Bortolotti et al. 2009). Social competition has been suggested to favor the evolution of ornaments as 'badges of status' that are used in alternative contexts to mate choice (West-Eberhard 1979, Kraaijeveld et al. 2007). King penguins are known to aggressively compete over breeding sites, and thus colored ornaments might convey information about social dominance or aggressiveness (Viera et al. 2008, Keddar et al. 2015a). Specifically, given that males perform the first and longest reproductive fast of the breeding cycle (typically 1-mo. including courtship and incubation; Stonehouse 1960), information on body condition should be more important to females. We predicted that ornamental features should be associated with body condition, especially in males. In contrast, information relating to immunity should be particularly relevant to both sexes in this species, since ticks (*Ixodes uriae*) are prevalent in king penguin colonies and detrimentally affect adult and offspring fitness (Mangin et al. 2003, Bize P., Schull Q., Pardonnet S., Handrich Y., Criscuolo F., Viblanc V.A., Robin J.P., unpubl. data). Finally, stress status (including oxidative stress; von Schantz et al. 1999) in relation to mate choice (e.g. parental breeding quality; Angelier and Chastel 2009) or social territory acquisition should be mutually important to males and females, and associated with ornamental traits in both sexes.

METHODS

126 **Field site and study species**

127 This study was conducted in the king penguin colony of *La Baie du Marin* (Possession Island,
128 Crozet Archipelago; 46°25'S, 51°45'E) during the 2011-2012 breeding season (Dec.–Mar.).
129 After an initial courtship period (~15 days), male and female penguins alternate periods
130 fasting on-land and foraging at sea during incubation and chick-brooding (Stonehouse 1960).
131 Hatching occurs after approximately 54-days and both parents alternate feeding and guarding
132 duties on-land during most of the austral summer.

133 In early November (breeding onset), we captured 31 penguin pairs and marked them
134 with non-permanent animal dye (Porcimark; Kruuse, Langeskov, Denmark) and plastic
135 flipper-bands. Because of logistical constraints, all birds were caught after courtship, and had
136 already undergone the mate choice and the pairing processes. We assumed that ornaments at
137 mate choice were correlated with the moment at which we measured them, after birds had
138 paired (see below). Accordingly, the size of the ear patch is determined at molt and beak
139 measures at the start of breeding showed little within-individual variation compared to
140 between individual variation (Schull Q., Viblanc V.A., Dobson F.S., Bize P., unpubl. data).
141 Males (N = 31) were tagged during the first incubation shift, shortly after the female had
142 departed to feed at sea. Females (N = 30) were tagged upon return from their foraging trip.
143 Birds were observed daily from a distance, during the entire breeding season (Nov.–Mar.), to
144 monitor their breeding status and determine sex-specific breeding shifts. All plastic flipper-
145 bands were removed at the end of the study.

146

147 **Morphometric measures**

148 Flipper (± 1 mm) and beak length (± 0.1 mm) were measured using a solid metal ruler and
149 dial calipers (Stonehouse 1960). Body girth (thoracic circumference) was measured (± 1 mm)
150 with a flexible tape-ruler just below the upper articulation of the flippers to the body (Viblanc

et al. 2012a). Birds were measured at the onset of incubation shift 2 for females and incubation shift 3 for males, to insure that both males and females had experienced similar minimal fasting durations (2-3 days) on land.

Ornament measures

Standardized measures of the width and height of the right and left auricular feather patches were performed using a flexible tape-ruler (see online supporting information S1). Left and right distances were averaged and the surface of the patch was calculated as *width x height* (mm^2).

Reflectance measurements of the beak spot were obtained using a portable JAZ spectrophotometer (Ocean Optics Inc., Dunedin, FL, USA) with a spectral resolution of 0.3 nm across the spectral range 320-700 nm. The spectrophotometer contained a pulsed-xenon light module and was calibrated against a white Spectralon standard. All measures were performed using a 200 µm fiber probe with a 90° angle window. Measures were repeated 3 times across each bill plate (in the orange region from bill tip to base) and spectra were averaged using an R script adapted from Montgomerie (2008). From spectral data, we calculated tri-stimulus color variables: mean brightness, hue and chroma. We considered the spectral range 320-700 nm, given the range of spectral sensitivity in birds (Cuthill 2006). The reflectance of king penguin beak spots is characterized by a bimodal pattern including a reflectance peak in UV and a peak/plateau in the yellow-orange (YO) portion of the spectrum (see Fig. 1). Thus, we calculated color variables over wavelength sub-regions of interest. For yellow-orange colors, we focused on the 500-700 nm portion of the spectrum. For the UV peak, we focused on the range 320-450 nm. Although this region extends beyond UV coloration *per se*, the choice was deliberate to account for the UV peak of king penguin beak spots in its entirety (Jouventin et al. 2005). Mean brightness is a measure of spectral intensity

of the ornament, and yellow-orange and UV mean brightness were calculated by averaging reflectance over wavelengths 500-700 nm and 320-450 nm, respectively (Montgomerie 2006). Hue is a measure of color appearance (e.g. 'blue', 'yellow', etc.). For the YO plateau portion of the spectrum, it was calculated as the wavelength at which the reflectance was halfway between its maximum and minimum (Keddar et al. 2013). For the UV peak, hue was calculated as the wavelength of maximum reflectance between 320 and 450 nm. Finally, chroma is a measure of color purity and was calculated as the difference between maximum and minimum reflectance over the mean reflectance for that particular region (formula S_8; Montgomerie 2006).

Body condition

We used a principal component analysis to calculate a structural size index (SSI), which explained 86% of the variation in beak size and flipper length (SSI = 0.95 x flipper + 0.31 x beak). We then regressed body girth on this SSI ($F_{1,59} = 18.87$, $P < 0.001$, $R^2 = 0.24$) and used the residuals as an index of body condition. This method yields condition indices very similar to classical mass/size regressions (correlation, r = 0.92; Viblanc et al. 2012a), but is more practical than weighing birds within the breeding colony.

Immunity measures

Immune status was assessed from blood samples collected during the second incubation shift of males and females. Blood (1 mL) was collected within 3-minutes of capture (see stress protocol below) from the marginal flipper vein using a 0.7*40 mm, 22G needle fitted to a 5 mL heparinized syringe. Within 10 min of sampling, blood was centrifuged at 3000xg for 5 min separating plasma and blood cells. Samples were kept at -18°C until the end of the day before being transferred at -80°C until lab-analyses. Constitutive innate humoral immunity

was determined using the hemolysis-hemagglutination assay described for birds (including seabirds) by (Matson et al. 2005). This assay evaluates natural antibody (NAb) levels and associated complement activation potential in plasma. Briefly, NAbs are innate non-specific antibodies encoded by the germ line that react with virtually any antigen. They are naturally present in antigen-naïve individuals, form a large portion of serum immunoglobulin, and initiate the complement enzyme cascade that ends in cell lysis (Matson et al. 2005). We exposed 25µL of penguin plasma (serially diluted from 1 to 1/1024) to 25µL of a 1% rabbit blood cell suspension and scored lysis (Lysis titers) and agglutination (NAb titers) for each sample. All assays were run on the same day and scored by the same observer (AS). Within and among-assay variation was 2.4% and 7.5% for lysis, and 3.0% and 4.1% for agglutination titers, respectively.

Resting metabolic rate

An estimate of bird's resting metabolic rate was obtained by measuring their daily resting heart rate (rHR). The conversion of HR to VO_2 (the classic measure of metabolic rate) using previously established calibrations is complicated by various issues including error measurement (for a discussion see Green 2011). Thus, we used raw HR data as a qualitative rather than quantitative index of metabolic rate in king penguins (Viblanc et al. 2014). We attached external HR-loggers (Polar® RS800 and RS800CX, Polar Electro Oy, Kempele, Finland) to breeding birds on the 6^{th} day of their second incubation shift (shift 3 for males, N = 26; shift 4 for females, N =24). Details on logger attachment, technology and accuracy of HR measurement are provided elsewhere (Groscolas et al. 2010). Birds' HR was recorded for 48 hours (until day 8 of their incubation shift) at a rate of 1 value every 5 or 2 seconds (depending on the logger model and memory). HR typically recovered to resting levels within 30 minutes of the initial capture stress (Viblanc et al. 2012b). We thus systematically

discarded the first 60 minutes of each recording to avoid confounding our calculations with handling stress. We calculated daily rHR using moving averages to determine the 10 consecutive minutes where HR was lowest over 12-h periods. Daily rHR values were highly repeatable (r = 0.95; Lessels & Boag 1987) and were averaged (Viblanc et al. 2014).

Stress status

We assessed penguins' stress status by measuring plasma total corticosterone (CORT), the main glucocorticoid stress hormone in birds. We determined both basal total CORT levels and acute total CORT increase to a standardized capture stress on the 8^{th} day of second incubation shift, at the same time that HR-loggers were removed. The capture stress was a standardized approach starting > 25m away from the bird, before hooding and capturing it. At the start of the approach, the experimenter insured that the bird was resting. The time at which it became vigilant to the approaching experimenter was considered T_0 and a first blood sample (as previously described) was made within the following 3-5 minutes. In king penguins, plasma CORT levels do not significantly increase due to a capture-handling stress within this time period (Ménard 1998). After initial blood sampling, the experimenter loosely maintained the bird captive for 30 min and performed a second blood-sample at T_{30}. Concentrations of plasma CORT were measured in duplicate using a quantitative competitive sandwich enzyme immunoassay technique according to guidelines provided by the manufacturer (ELISA Corsticosterone kit, Enzo Life Sciences, Farmingdale, NY, USA, ADI-900-097). Kit sensitivity was 27.0 pg/mL, intra- and inter-assay variation were 7.6% and 13.3%, respectively. The CORT response to acute stress was calculated as $100*(CORT_{30} - CORT_0)/CORT_0$.

During the standardized capture protocol we also measured HR response. We defined the initial resting HR (HR_i) as the HR at the moment preceding a rapid constant increase in

HR due to the approaching experimenter (Viblanc et al. 2012b). Maximal HR (HR_{max}) in response to the capture corresponded to the maximal HR achieved in the 3 minutes following the onset of the stress. The maximum increase in HR was then calculated as $100*(HR_{max} - HR_i)/HR_i$. HR-loggers were removed at the end of the stress.

Oxidative status

On the 8th day of the second incubation shift, we determined plasma oxidative status as previously described for king penguins (Geiger et al. 2012). The antioxidant capacity of penguin's plasma (OXY) and its concentration of reactive oxygen metabolites (ROM; a measure of exposure to oxidative stress) were respectively measured using commercially available OXY adsorbent and dROM kits (Diacron International srl, Grosseto, Italy). Intra- and inter-assay variation was 7.4% and 7.0% for OXY, and 6.4% and 7.9% for ROM.

Data analyses

Analyses were performed using R v.3.0.2. All individuals only appeared once in the data set and we had no repeated measures. First, we investigated male and female dimorphism by considering the effect of sex on structural size, beak color variables and auricular patch surface in linear models. For auricular patch surface, we also considered sexual dimorphism controlling for structural size (specified as a covariate in the analysis). We then investigated whether ornaments reflected physiological variables (*i.e.* could the birds "predict" physiological quality from the ornaments) by running separate models for each physiological trait and specifying beak color traits (hue, chroma and brightness) and auricular patch size as predictor variables in our models. Sex was included as a cofactor in the analyses and its interactions with beak coloration variables and auricular patch size were considered. The area of the colony in which the bird was sampled (close to the beach or further up the valley) was

fixed as a cofactor in all analyses to account for known colony-related differences in parasites and stress responses (Viblanc et al. 2012b). Independent variables were standardized prior to analyses, so that model estimates were comparable (Schielzeth 2010). We used multi-model inference with Akaike's Information Criterion corrected for small sample size to identify the best model (AICc and AIC weights) for each physiological parameter considered ('dredge' package in R; Bartoń 2015). We retained the most parsimonious model within potential candidates (ΔAICc < 2). Models were compared using Maximum Likelihood. Because most color variables were correlated to some extent (see online supporting information S2), we insured collinearity was not an issue before performing model selection in our analyses. We checked for variance inflation factors (VIFs) in the full model (suggested cut-off = 5; Zuur et al. 2007). Yellow hue was the only variable which appeared problematic in all models, with 7.2 < VIF < 9.4. Thus, we removed it from all analyses, and subsequent collinearity was low (1.2 < VIFs < 5.2). Due to sampling and slight variations in success of laboratory analyses, sample sizes varied across physiological measures. Diagnostic plots and the Shapiro-Wilk normality test were used to inspect model residuals for normality and potential outliers. When necessary (i.e. for resting HR and the acute CORT response), data were transformed prior to analyses using Box-Cox power transformations (Viblanc et al. 2012b) to insure residual normality. For each model, we calculated effect sizes (ES, Hedges' unbiased d and z-transformed r) and their associated 95% confidence intervals based on respective t-statistics using equations 10, 11, 14, 15, 17 and 19 from (Nakagawa and Cuthill 2007). We use the benchmarks r = 0.1, 0.3, 0.5 and d = 0.2, 0.5, 0.8, to discuss small, medium and large effect sizes (Nakagawa and Cuthill 2007).

RESULTS

Male and female dimorphism in sexual ornaments

Males were slightly but significantly larger than females (3-4% for flipper and beak, respectively; Fig2; online supporting information S3), and had significantly larger auricular patches (14%), even when accounting for structural size as a covariate in the model (Fig. 2). Sexes did not differ significantly in terms of ornamental colors, except for UV chroma, which was slightly higher in males (Fig. 2).

Body condition and ornaments

The most parsimonious model explaining body condition in breeding birds with the lowest AICc and highest AIC weight retained beak UV brightness, yellow orange chroma, and their interactions with sex as important factors (Table 1, see online supplementary material S4). Patterns of association between beak UV brightness, yellow-orange chroma, and body condition were different in males and females (Fig. 3, Table 1). Beak UV brightness was weakly positively ($\mathcal{Z}r$ = +0.29; CI_{95} = [-0.00, 0.58]) related to body condition in males, but moderately negatively in females ($\mathcal{Z}r$ = -0.51; CI_{95} = [-0.22, -0.80]) (Fig. 3A). Beak yellow-orange chroma was moderately positively related to body condition in females ($\mathcal{Z}r$ = +0.53; CI_{95} = [0.24, 0.82]), but not in males ($\mathcal{Z}r$ = -0.06; CI_{95} = [-0.35, 0.23]) (Fig. 3B).

Oxidative status and ornaments

UV hue, sex and their interaction were selected by AICc as important variables related to ROM levels (Table 2, online supplementary material S5). In females, beak UV hue was strongly negatively related to ROM levels ($\mathcal{Z}r$ = -0.59; CI_{95} = [-0.20, -0.99]), whereas the association was positive in males, though the effect was weak as CI barely overlapped zero ($\mathcal{Z}r$ = +0.37; CI_{95} = [-0.02, 0.77]) (Fig. 4). In contrast, OXY levels were not related to beak coloration or auricular patch surface, *i.e.* only the intercept was retained in the best model (online supplementary material S6).

326

327 **Immunity and ornaments**

328 The most parsimonious model retained YO beak chroma as a feature explaining variation in
329 lysis scores in both sexes, but no sex interaction (Table 3, online supplementary material S7).
330 YO chroma was weakly negatively ($\mathcal{Z}r$ = -0.24; CI_{95} = [-0.54, 0.05]) related to lysis titers
331 (Fig. 5A). NAb titers were moderately negatively ($\mathcal{Z}r$ = -0.42; CI_{95} = [-0.72, -0.12]) related to
332 patch surface in both sexes (again, no sex interaction) (Table 4, online supplementary material
333 S8) (see Fig. 5B).

334

335 **Resting metabolic rate and ornaments**

336 Model selection retained UV brightness as a variable related to daily resting HR, but no sex
337 interaction (Table 5, online supplementary material S9). UV brightness was moderately
338 positively ($\mathcal{Z}r$ = +0.35; CI_{95} = [0.05, 0.66]) associated with daily resting HR levels (Fig. 6).

339

340 **Stress and ornaments**

341 Beak and patch ornaments did not relate to basal total CORT levels, as the best and most
342 parsimonious model only retained colony area as an important factor explaining CORT levels
343 (d_{unbiased} = +0.94; CI_{95} = [0.29, 1.59], see online supplementary material S10). Birds breeding
344 further up the valley had significantly higher basal CORT (3.56 ± 0.35 $ng.mL^{-1}$) levels than
345 birds breeding close to the beaches (2.15 ± 0.23 $ng.mL^{-1}$). For the birds' acute CORT
346 response to a standardized 30-min capture, model selection retained UV hue as a variable
347 explaining variation in the CORT response, but no sex interaction (Table 6; see online
348 supplementary material S11). UV hue ($\mathcal{Z}r$ = -0.37; CI_{95} = [-0.69, -0.06]) was moderately
349 negatively related to the acute CORT response (Fig. 7). Finally, birds' HR response to capture
350 did not appear to be related to beak or auricular patch ornaments. Indeed, the best and most

parsimonious model only retained colony area as an important factor explaining variation in birds' acute HR response to stress (d_{unbiased} = +0.59; CI_{95} = [-0.09, 1.26]; see online supplementary material S12). Birds breeding up the valley had slightly higher HR responses to captures (132.6 ± 8.1 %) than birds breeding close to the beaches (113.8 ± 11.6 %).

DISCUSSION

The two main hypotheses proposed to explain the evolution of elaborate ornamentation in males and females are the 'genetic correlation' and the 'mutual selection' hypotheses (Kraaijeveld et al. 2007). The former proposes that showy ornaments are functional in males, but evolve as non-functional by-products of genetic correlations between the sexes in females (Lande 1980). Selection then operates in males and the condition-dependence of ornaments should be primarily related to the male sex. The latter proposes that ornaments are functional in both sexes, evolving as honest signals of individual quality related to sexual or other, not mutually-exclusive, forms of social selection (e.g. social competitiveness for breeding sites) (Johnstone et al. 1996, Kokko and Johnstone 2002, Hooper and Miller 2008, Tobias et al. 2012). Although the genetic correlation hypothesis predicts that ornaments should convey information mostly in males, the mutual selection hypothesis predicts that ornament should convey information in both sexes.

In agreement with the mutual selection hypothesis, in king penguins we found that the showy ornaments used in mate choice were related to various aspects of physiological quality in both sexes. Successful breeding in this species involves obligate bi-parental care over an extended 14-mo. period (Stonehouse 1960). Adults experience high annual divorce rates (up to 81%; Olsson 1998) and courting birds encounter prospective mates at a high rate. Such conditions provide scope for mutual choosiness (Johnstone et al. 1996, Kokko and Johnstone 2002) and are indeed expected to favor the evolution of ornamental signals reflecting

individual quality in both sexes (Kraaijeveld 2003, Kraaijeveld et al. 2007). However, we also found that not all facets of physiological quality were similarly related to ornamentation in both sexes, suggesting that mutual ornamentation may be maintained by varying selective pressures in males and females (e.g. Murphy 2007).

Mutual ornamentation and immunity

One important cost of colonial breeding is parasitism (Mangin 2003). The immunocompetence hypothesis predicts that, given limited resources (energy, nutrients, protein), trade-offs occur between energy allocations to immunity or to the production and maintenance of ornamentation (Saino et al. 1997, Verhulst et al. 1999). Consistently, we found weak to moderate negative associations between measures of innate immunity and ornamental features in both sexes. Lysis and NAb titers were negatively related to YO beak chroma and auricular patch surface respectively suggesting that investing into larger auricular patches and more YO beaks may incur a cost in terms of immunity. Interestingly, Nolan et al. (2006) previously documented a link between the PHA skin test and breast coloration in males, although they failed to detect an association with beak coloration or auricular patch size. Unlike the PHA-test that measures a wide range of immune responses involving both innate and acquired immunity (Tella et al. 2008), NAb titers reflect a well-defined component of the innate immune response not induced by an experimental infection (Matson et al. 2005). These findings support the notion that different ornaments may signal different components of immunity in breeding birds (Kelly et al. 2012).

Mutual ornamentation and body condition

Acquiring information on body condition should be especially important to mate choice in breeding seabirds that undergo extended periods of fasting while caring for the egg or chick

401 (Groscolas and Robin 2001). Surprisingly, we found that body condition was related to beak
402 spot coloration differently in males and females. Better body condition was associated with
403 lower UV brightness and higher YO chroma (both strong effects) in females, but higher UV
404 brightness (moderate effect) in males. These results are consistent with previous findings of
405 lower UV brightness for females in better body condition (Dobson et al. 2008), but at odds
406 with the idea that mutual selection for high UV reflectance occurs in both sexes (Nolan et al.
407 2010, Keddar et al. 2015b). One explanation is that males and females use beak spot signals
408 differently. As males have to endure the longest reproductive fast (Stonehouse 1960),
409 including courtship and the first incubation shift, choosing mates of high body condition
410 should be especially important for females. In females, poor body condition to an extent could
411 reflect greater investments into reproduction to the detriment of self-maintenance, which
412 should be favored by males. In females, body condition was negatively associated with
413 increasing UV brightness but positively associated with increasing YO chroma, raising
414 questions about the interactions between carotenoid and structural signals (Shawkey and Hill
415 2005, Mougeot et al. 2007, Dugas and McGraw 2011). For instance, in red grouse (Mougeot
416 et al. 2007) and nestling house sparrows (Dugas and McGraw 2011), carotenoid pigments
417 appear to act as a mask, decreasing UV reflectance in soft structures. There is some
418 suggestion that carotenoid pigments are also found in the beak of king penguins (see McGraw
419 et al. 2007), and similar interactions might explain the opposite relationships we find for beak
420 YO chroma and UV brightness. Further, only high condition females may have been able to
421 allocate carotenoid pigments to their beak spots to function as signals (Blount et al. 2003,
422 Mougeot et al. 2010).
423
424 **Mutual ornamentation and metabolic rate**

We found that beak UV brightness was positively (medium effect size) associated with resting HR levels (a proxy for resting metabolic rate; Viblanc et al. 2014) in both sexes. High resting metabolic rates may reflect increased capacities to engage in a suite of challenging activities such as foraging, caring for the young or competing for ressources, and might be honestly reflected by color ornaments (Biro and Stamps 2010, Kelly et al. 2012). The links between UV coloration and metabolic rate may lie within the energy costs of producing/maintaining structural colors (Siefferman and Hill 2005, Doutrelant et al. 2012). For example, Siefferman and Hill (2005) showed that experimentally reducing the energy cost of reproduction by reducing brood size in bluebirds (*Sialia sialis*) allowed males to increase their investment into plumage UV in the subsequent year. Rather than a long-term energy trade-off between competing functions (conserving energy for ornament production vs. expanding it for current reproduction), our results suggest possible indirect metabolic costs, such as keeping the beak clean, for UV maintenance.

Mutual ornamentation and stress

Glucocorticoid hormones (GC) play key roles in mediating physiological trade-offs and energy allocation, and baseline GC levels have been suggested to ensure signal honesty (Husak and Moore 2008, Weiss et al. 2013). Whereas we found no link between baseline CORT and ornaments in our study, UV hue was moderately and negatively associated with the birds' CORT response to acute stress ($\mathcal{Z}r$ = -0.37; CI_{95} = [-0.69, -0.06]). Birds with more UV hued beaks mounted a greater stress response to capture. Because stress responses are energy costly, this is consistent with the idea that the ability to mount stress responses while fasting is reflected in ornamentation, which may be particularly relevant in the context of colonial breeding during exposure to overt social aggressiveness (Côté 2000). In contrast, we did not observe a link between ornaments and the acute HR response to stress, suggesting that

450 HPA and sympathetic stress pathways may be modulated and signaled independently in
451 breeding birds (e.g. Nephew et al. 2003). We found that birds up the valley mounted slightly
452 higher HR responses to capture, and had higher baseline CORT levels than birds breeding
453 close to the beach. These results suggest two alternatives: that birds breeding close to the
454 beach might have habituated to chronic human disturbance (Viblanc et al. 2012b), and that
455 birds up the valley may have been more exposed to parasites (Bize P., Schull Q., Pardonnet
456 S., Handrich Y., Criscuolo F., Viblanc V.A., Robin J.P., unpubl. data), Manipulating
457 circulating CORT levels in breeding birds may allow further exploration of the interplay
458 between ornamentation, glucocorticoids, and cardiovascular function. For instance, chronic
459 experimental increases in baseline stress levels (via CORT implants) have been shown to
460 negatively affect UV and orange-red reflectance in female striped plateau lizards (*Sceloporus*
461 *virgatus*) (Weiss et al. 2013).
462
463 **Mutual ornamentation and oxidative stress**
464 We observed sex-related differences in UV advertising for oxidative stress. In females, lower
465 UV hue (i.e., hue more strongly embedded in the peak UV wavelengths) was strongly and
466 positively associated with higher pro-oxidant levels (higher ROM but not higher OXY levels),
467 whereas the opposite occurred in males (a moderate effect and the CI overlapped zero). This
468 result was surprising for a structural color, as links between ornamentation and oxidative
469 status are expected for yellow-orange colors, because of the allocation trade-off of carotenoid
470 pigments to either anti-oxidant or ornamental functions (von Schantz et al. 1999, Mougeot et
471 al. 2010). However, the interplay between UV and yellow-orange color reflectance might also
472 convey information on carotenoid availability (Jacot et al. 2010). Carotenoids absorb
473 wavelengths of short to medium wavelengths (400-515 nm), and greater deposition of
474 carotenoids in feathers has been experimentally shown to cause a shift in the UV peak to

475 shorter wavelengths in great tits (Jacot et al. 2010). The precise link between carotenoid
476 concentration and beak reflectance both in UV and YO wavelengths remains to be determined
477 in king penguins. But our result may suggest that females depositing more carotenoids in their
478 beak suffered from greater oxidative stress, highlighting a trade-off between pigment
479 allocation to anti-oxidant defenses or beak coloration. The exhaustive measurement of
480 oxidative status of breeding birds requires supplementary markers of oxidative damage and
481 antioxidant defense (*e.g.* lipid peroxidation, antioxidant enzymatic activity), and preferentially
482 in different tissues (Selman et al. 2012). However, our results add to the evidence that
483 condition-dependent UV signals indeed occur in many bird species (Keyser and Hill 2000,
484 Bize et al. 2006, Mougeot et al. 2010), likely in interaction with carotenoid signaling.
485
486 **Conclusion**
487 Taken together our results suggest that monomorphic ornamentation reflects several aspects
488 of physiological quality in king penguins, supporting the mutual selection hypothesis.
489 Interestingly, the qualities signaled by mutual ornamentation may nonetheless differ (in fact
490 be opposite) between the sexes, likely due to physiological differences and varying selection
491 pressures. Because we collected the physiological and ornamental measures only at only one
492 point in time, it remains to be explored if some of those traits are dynamic (e.g. beak
493 coloration: Faivre et al. 2003, Pham et al. 2014) and whether birds may use them for short-
494 term behavioral decisions. The further study of monomorphic species should shed new
495 insights on the maintenance, information and costs of sexual signals.
496
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FIGURE CAPTIONS

Fig 1. Reflectance curve obtained from the beak spot of a breeding king penguin (*Aptenodytes patagonicus*). Note the typical bi-modal pattern with a UV-peak around 380-390 nm and a yellow-orange plateau from 500-700 nm.

Fig 2. Effect sizes and 95% confidence intervals for ornamental and structural size dimorphism between king penguin males and females. Effect sizes and 95% CI were calculated after Nakagawa & Cuthill 2007. Effects are considered significant if their 95% CI does not overlap zero.

Fig 3. Relationships between beak coloration and body condition in breeding king penguins. Relationships are given for (A) beak UV brightness, and (B) beak yellow-orange chroma. Females are depicted by open circles and a full line, males by filled circles and a dashed line. The right panel provides effect sizes and 95% CI calculated after Nakagawa & Cuthill 2007. Effects are considered significant if their 95% CI does not overlap zero.

Fig 4. Relationship between beak coloration and standardized plasma concentration of reactive oxygen metabolites [ROM] in breeding king penguins. Females are depicted by open circles and a full line, males by filled circles and a dashed line. The lower panel provides effect sizes and 95% CI calculated after Nakagawa & Cuthill 2007. Effects are considered significant if their 95% CI does not overlap zero.

Fig 5. Relationship between beak coloration, auricular patch surface and innate immunity in breeding king penguins. Relationships are given for (A) plasma lysis titers and yellow-orange chroma, and (B) plasma Nab titers and auricular patch surface. On the left panel, males are depicted by filled circles, females by open circles. The right panel provides effect sizes and 95% CI calculated after Nakagawa & Cuthill 2007. Effects are considered significant if their 95% CI does not overlap zero.

Fig 6. Relationship between beak UV brightness and daily resting HR levels (bpm) in breeding king penguins. On the left panel, males are depicted by filled circles, females by open circles. The right panel provides effect sizes and 95% CI calculated after Nakagawa & Cuthill 2007. Effects are considered significant if their 95% CI does not overlap zero.

Fig 7. Relationship between the relative corticosterone increase in response to a standardized 30 minute capture and beak UV hue in breeding king penguins. On the left panels, males are depicted by filled circles, females by open circles. The right panel provides effect sizes and 95% CI calculated after Nakagawa & Cuthill 2007. Effects are considered significant if their 95% CI does not overlap zero.

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TABLES

	Estimate	Std. Error	t value
Intercept	-2.00	0.53	-3.73
Sex[M]	2.46	0.55	4.45
UV brightness	-1.59	0.45	-3.51
YO chroma	1.71	0.47	3.61
Colony area [A1]	0.82	0.58	1.41
Sex[M]*UV brightness	2.34	0.59	3.99
Sex[M]*YO chroma	-1.85	0.59	-3.11

Table 1. Model estimates for the influence of beak color variables on body condition in breeding king penguin (*Aptenodytes patagonicus*). The sex effect is given in reference to the female level [F]. The colony area effect is given in reference to area [A2]. See Fig. 3 for effect sizes with 95% CI.

	Estimate	Std. Error	t value
Intercept	2.43	0.20	12.10
Sex[M]	0.18	0.27	0.66
UV hue	-0.50	0.16	-3.20
Sex[M]*UV hue	0.93	0.27	3.48

Table 2. Model estimates for the influence of beak UV hue on plasma reactive oxygen metabolite levels in breeding king penguin (*Aptenodytes patagonicus*). The sex effect is given in reference to the female level [F]. See Fig. 4 for effect sizes with 95% CI.

	Estimate	Std. Error	t value
Intercept	3.33	0.14	23.13
YO chroma	-0.15	0.09	-1.70
Colony area [A1]	-0.65	0.18	-3.55

Table 3. Model estimates for the influence of beak YO chroma on plasma lysis titers in breeding king penguin (*Aptenodytes patagonicus*). The colony area effect is given in reference to area [A2]. See Fig. 5A for effect sizes with 95% CI.

	Estimate	Std. Error	t value
Intercept	5.46	0.24	22.32
Patch surface	-0.47	0.16	-2.94
Colony area [A1]	-0.85	0.31	-2.70

Table 4. Model estimates for the influence of auricular patch surface on plasma NAb titers in breeding king penguin (*Aptenodytes patagonicus*). The colony area effect is given in reference to area [A2]. See Fig. 5B for effect sizes with 95% CI.

	Estimate	Std. Error	t value
Intercept	5.97	0.07	83.36
UV brightness	0.11	0.05	2.40
Colony area [A1]	-0.07	0.09	-0.72

Table 5. Model estimates for the influence of UV brightness on daily resting heart rate in breeding king penguin (*Aptenodytes patagonicus*). The colony area effect is given in reference to area [A2]. See Fig. 6 for effect sizes with 95% CI.

	Estimate	Std. Error	t value
Intercept	2.42	0.24	10.25
UV hue	-0.36	0.15	-2.45
Colony area [A1]	-1.16	0.31	-3.74

Table 6. Model estimates for the influence of beak UV hue on the acute relative increase in plasma total corticosterone levels in response to a standardized 30-min capture in breeding king penguin (*Aptenodytes patagonicus*). The colony area effect is given in reference to area [A2]. See Fig. 7 for effect sizes with 95% CI.

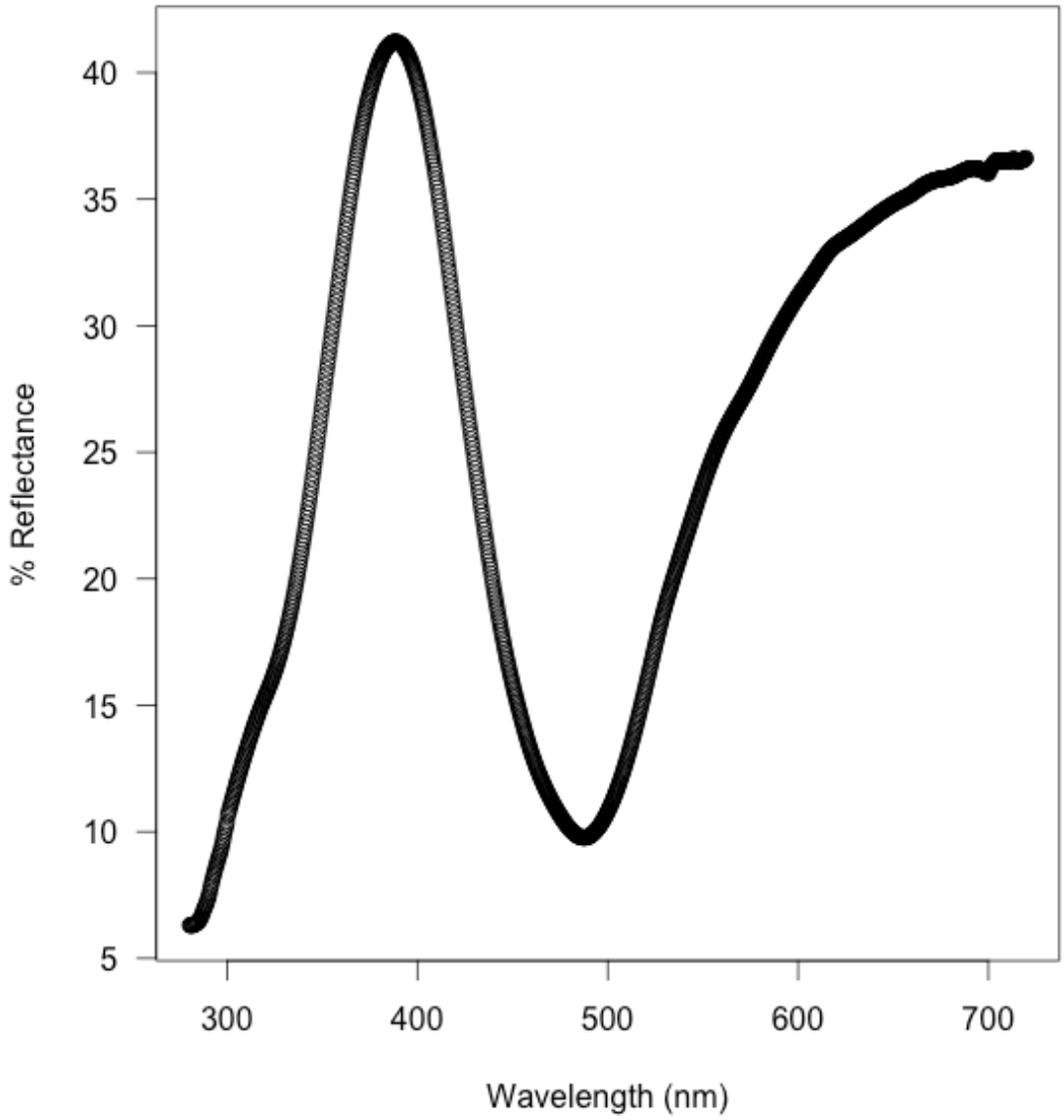

% Reflectance
40
35
30
25
20
15
10
5
300
400
500
600
700
Wavelength (nm)

Fig 1.

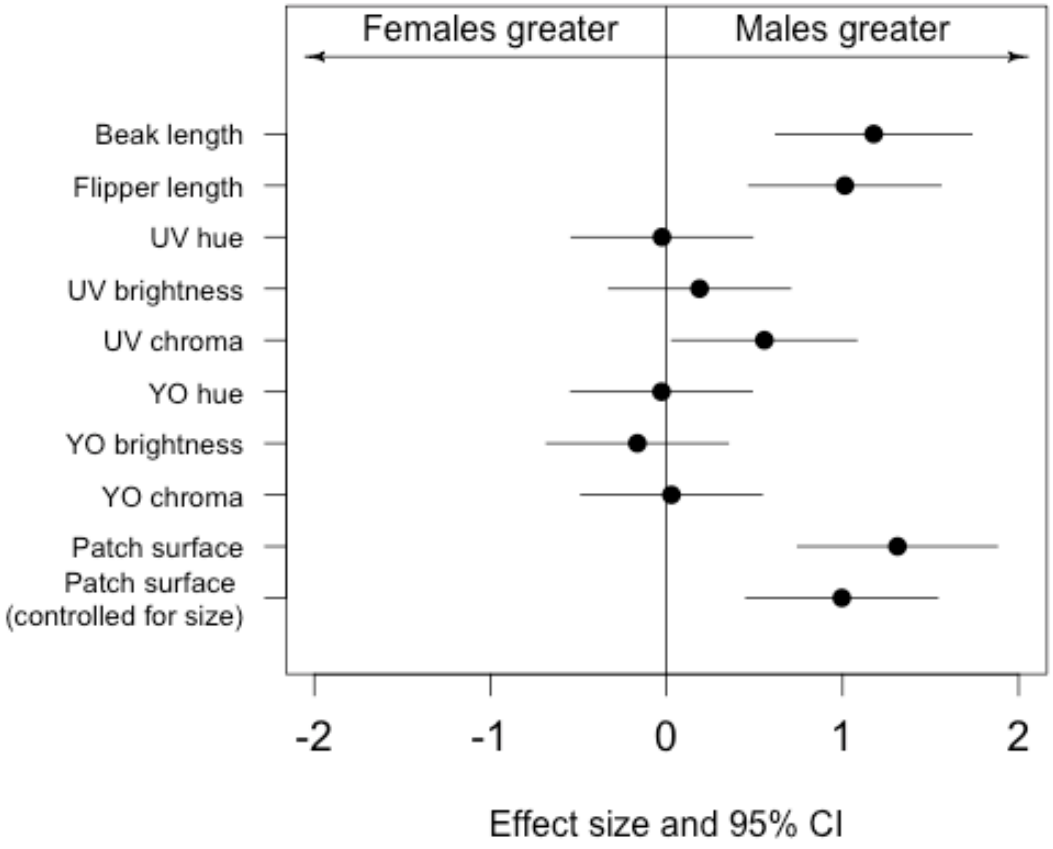

Females greater
Males greater
Beak length
Flipper length
UV hue
UV brightness
UV chroma
YO hue
YO brightness
YO chroma
Patch surface
Patch surface
(controlled for size)
-2
-1
0
1
2
Effect size and 95% CI

Fig 2.

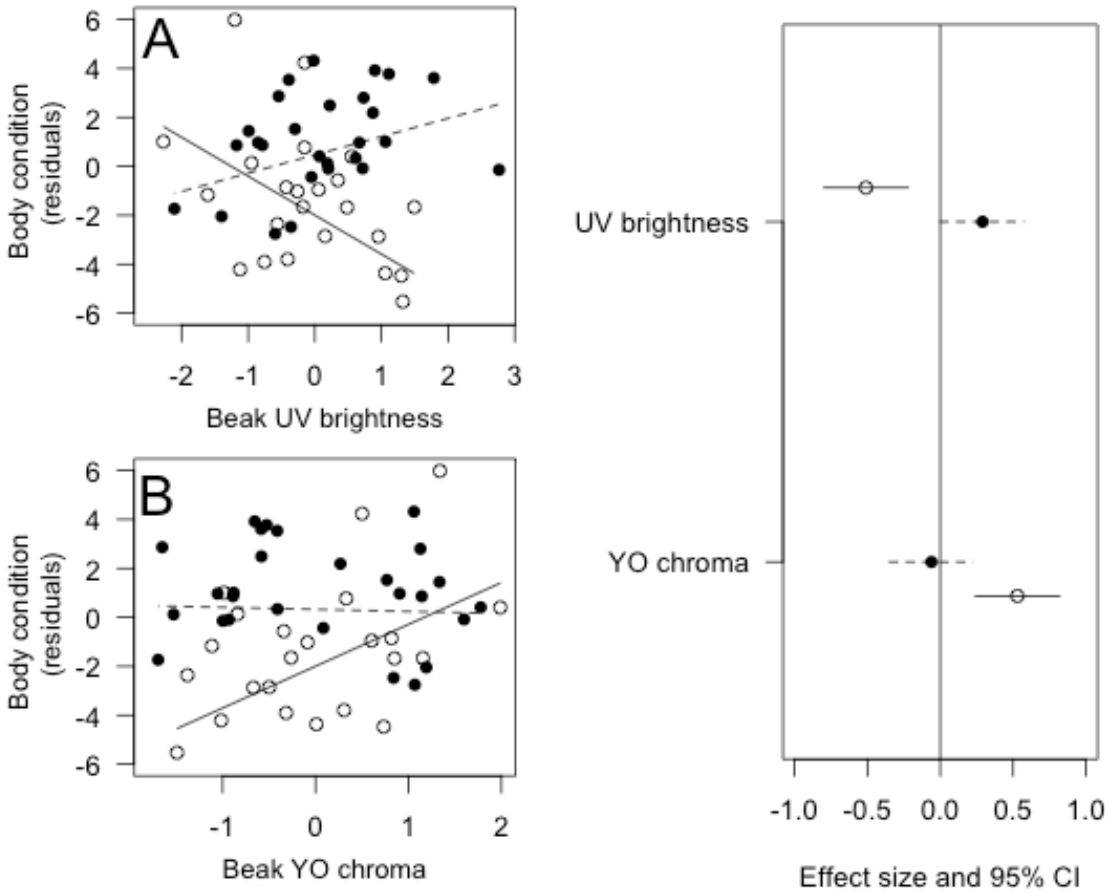

A
Body condition (residuals)
Beak UV brightness
B
Body condition (residuals)
Beak YO chroma
UV brightness
YO chroma
Effect size and 95% CI

Fig 3.

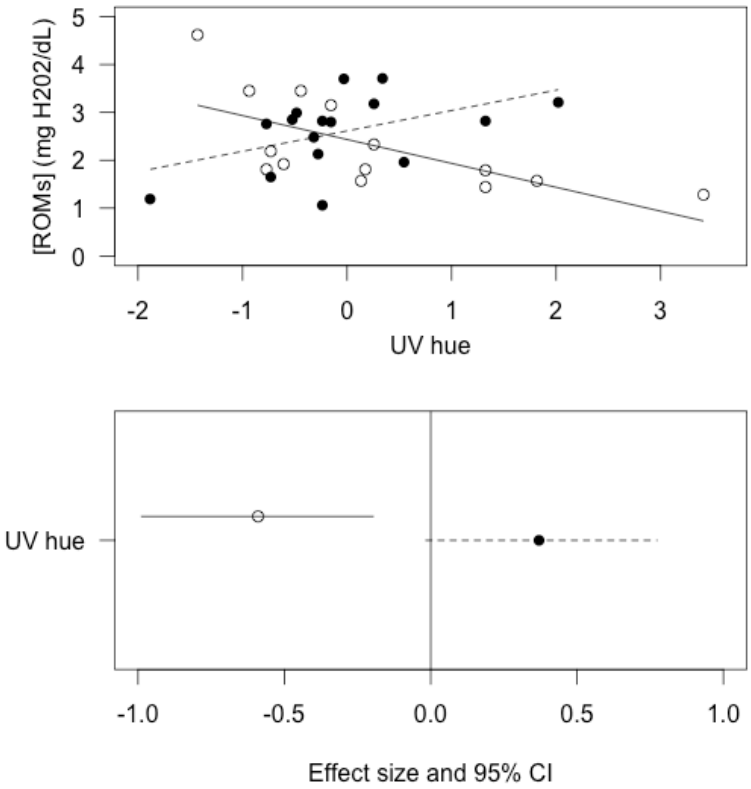

[ROMs] (mg H202/dL)
0
1
2
3
4
5
-2
-1
0
1
2
3
UV hue
UV hue
-1.0
-0.5
0.0
0.5
1.0
Effect size and 95% CI

Fig 4.

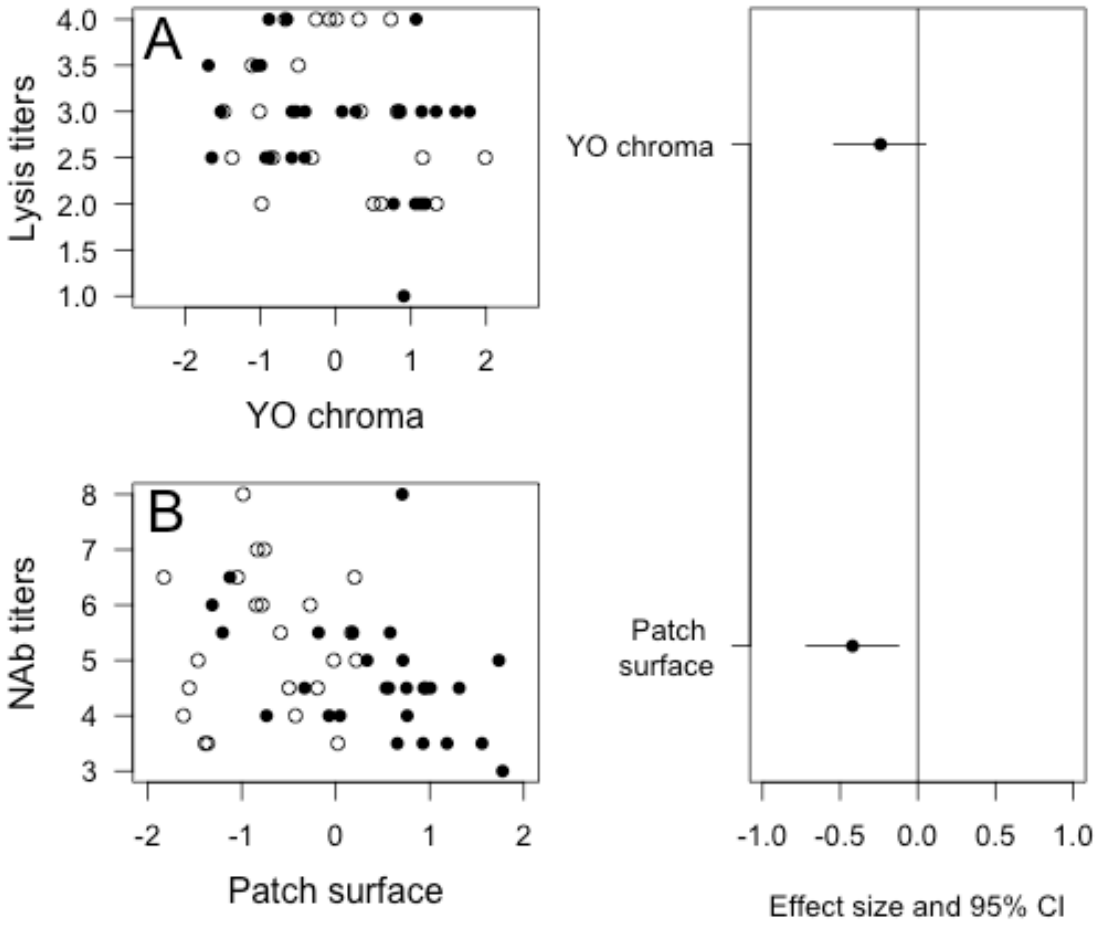

A
Lysis titers
4.0
3.5
3.0
2.5
2.0
1.5
1.0
-2
-1
0
1
2
YO chroma
B
NAb titers
8
7
6
5
4
3
-2
-1
0
1
2
Patch surface
YO chroma
Patch surface
-1.0
-0.5
0.0
0.5
1.0
Effect size and 95% CI

Fig 5.

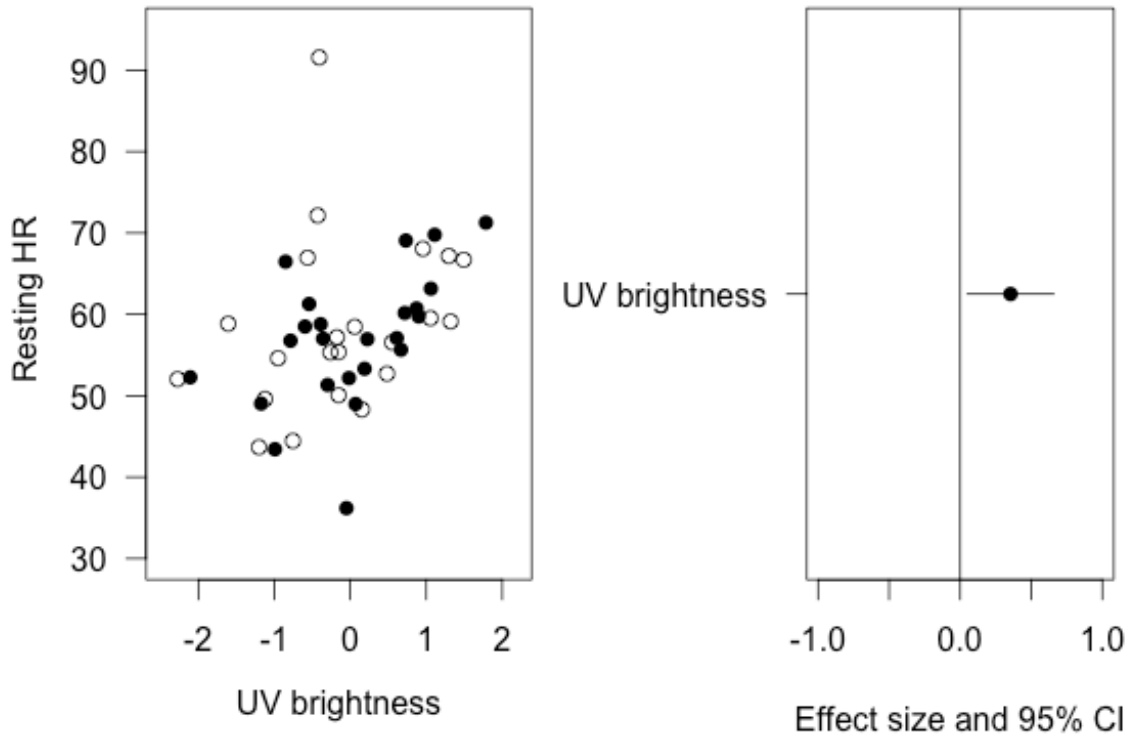
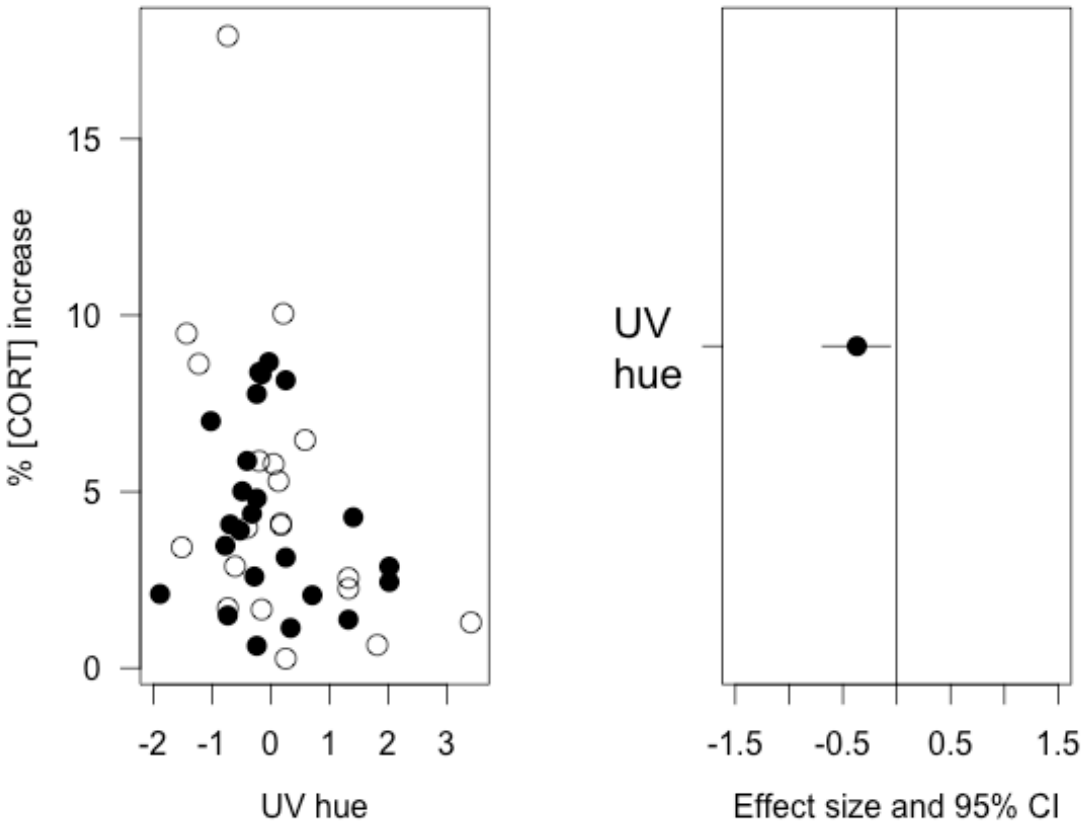

Resting HR
90
80
70
60
50
40
30
-2
-1
0
1
2
UV brightness
UV brightness
-1.0
0.0
1.0
Effect size and 95% CI

Fig 6.

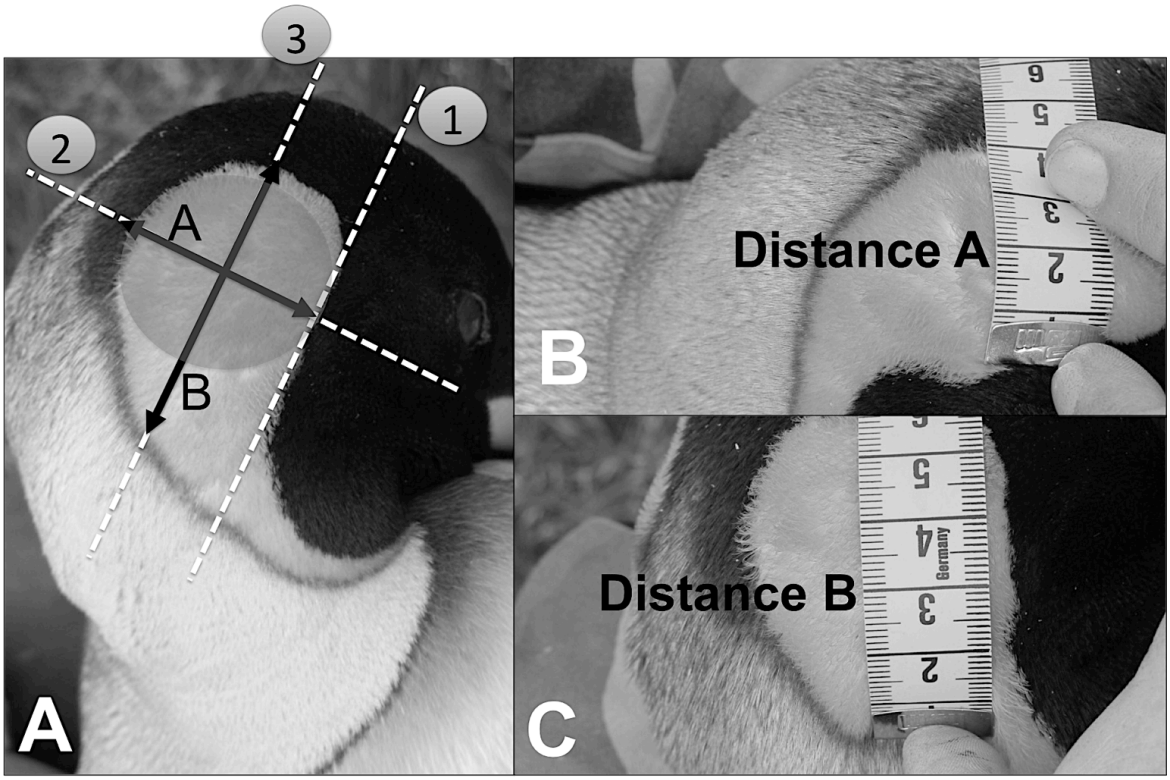

% [CORT] increase
15
10
5
0
-2
-1
0
1
2
3
UV hue
UV
hue
-1.5
-0.5
0.5
1.5
Effect size and 95% CI

43

44 **Fig 7.**

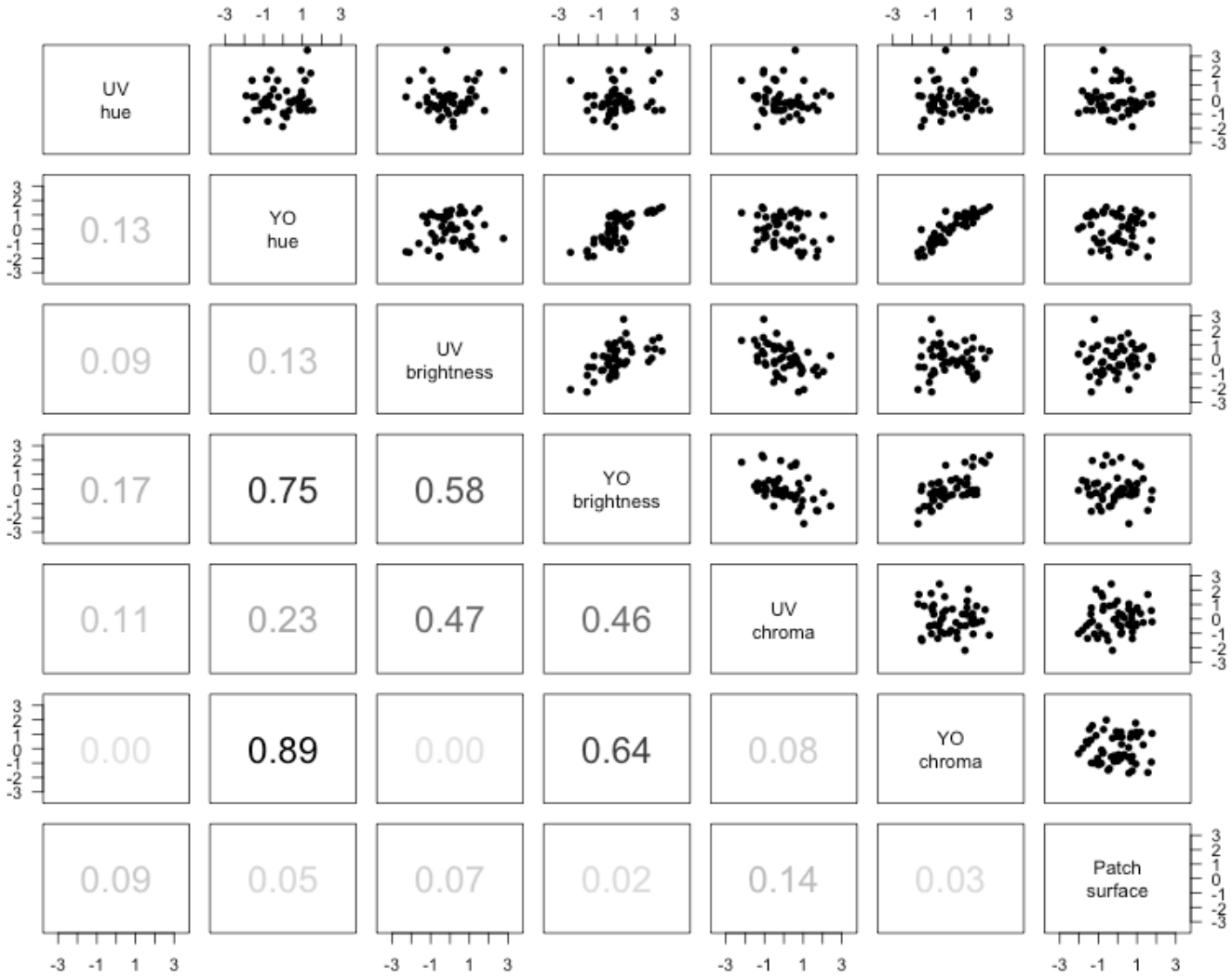
Online supporting information S1:

Standardized measures of the auricular patches of breeding king penguin (*Aptenodytes patagonicus*). The head of the bird was held such that its beak rested on the shoulder opposite to the side of the body where the auricular patch was measured (Fig. 1A). A virtual line was pictured along the side of the auricular patch closest to the eye (line 1; Fig 1A). Then, a second perpendicular line reaching the most distant point of the circle (diameter) was pictured (line 2; Fig 1A), and the width of the auricular patch was measured (distance A; Fig 1B). From the center of distance A (line 3; Fig 1A), the height of the auricular patch was measured at a 90° angle (distance B; Fig 1C).



Online supporting information S2:

Correlation matrix for the ultraviolet (UV) and yellow-orange (YO) beak coloration measures (hue, brightness and chroma), and auricular patch surface, of breeding king penguins (*Aptenodytes patagonicus*). The upper right panel presents the standardized data, the lower left panel the correlation value (colors from light grey to black representing weak to strong correlations).



Online supporting information S3:

Summary statistics of the structural size and ornamental data of breeding king penguin (*Aptenodytes patagonicus*) used in the study. Sample size is indicated in parentheses and varies across measures due to constraints during field sampling. The average percent difference between males and females is given. Beak mean brightness, hue and chroma were calculated both across the UV-blue peak and yellow-orange regions characteristic of king penguin beak spots (Jouventin et al. 2004).

			FEMALES	MALES	
		Variable	**Mean ± SD**	**Mean ± SD**	**% Difference males - females**
Structural size		Flipper length	317.4 ± 9.5 (30)	327.1 ± 9.6 (31)	3%
		Beak Length	124.2 ± 3.8 (30)	129.7 ± 5.4 (31)	4%
	Beak UV-blue	Mean brightness (% reflectance)	18.1 ± 3.4 (23)	18.8 ± 3.6 (27)	4%
	(320-450 nm)	Hue (nm)	388.5 ± 9.9 (23)	388.3 ± 7.8 (27)	-0%
		Chroma (ratio, % reflectance)	1.26 ± 0.17 (23)	1.35 ± 0.14 (27)	7%
Ornaments	Beak yellow-orange	Mean brightness	31.1 ± 6.7 (23)	30.1 ± 5.6 (27)	-3%
	(550-625 nm)	Hue	575.4 ± 26.8 (23)	574.7 ± 24.0 (27)	-0%
		Chroma	1.13 ± 0.22 (23)	1.14 ± 0.25 (27)	1%
	Auricular patch	Surface (mm^2)	1744.0 ± 185.0 (30)	1995.0 ± 198.3 (31)	14%

Online supporting information S4:

Model selection for the effects of beak coloration and auricular patch surface on body condition (residuals, see Methods) in breeding king penguin (*Aptenodytes patagonicus*). Colony area in which the bird was sampled was fixed in all models to account for known differences in parasite loads and stress responses that may affect body condition. All models with a ΔAICc <2 compared to the best model are presented. The most parsimonious model retained is indicated in bold.

#	Model	R^2	F	df	logLik	AICc	delta	weight
1	UV brightness + YO chroma + patch surface + sex + sex*UV brightness + sex*YO chroma + sex* patch surface + colony area	0.58	7.06	10	-97.06	219.77	0.00	0.45
2	**UV brightness + YO chroma + sex + sex*UV brightness + sex*YO chroma + colony area**	**0.52**	**7.75**	**8**	**-100.38**	**220.27**	**0.50**	**0.35**
3	UV brightness + UV chroma + YO chroma + sex + sex*UV brightness + sex*YO chroma + sex* UV chroma + colony area	0.57	6.67	10	-97.88	221.41	1.64	0.20

Online supporting information S5:

Model selection for the effects of beak coloration and auricular patch surface on plasma reactive oxygen metabolite (ROM) levels in breeding king penguin (*Aptenodytes patagonicus*). Colony area was not included in this analyses as ROM levels were only determined for birds in one location of the colony. All models with a ΔAICc <2 compared to the best model are presented. The most parsimonious model retained is indicated in bold.

#	Model	R^2	F	df	logLik	AICc	delta	weight
1	**UV hue + sex + sex*UV hue**	**0.37**	**5.04**	**5**	**-31.34**	**75.20**	**0.00**	**0.71**
2	UV hue + YO chroma + sex + sex*UV hue + sex*YO chroma	0.46	4.1	7	-28.94	77.00	1.78	0.29

Online supporting information S6:

Model selection for the effects beak coloration and auricular patch surface on plasma antioxidant capacity (OXY) in breeding king penguin (*Aptenodytes patagonicus*). Colony area was not included in this analyses as OXY levels were only determined for birds in one location of the colony. All models with a ΔAICc <2 compared to the best model are presented. The most parsimonious model retained is indicated in bold.

#	Model	R^2	F	df	logLik	AICc	delta	weight
1	**Intercept only**	**0.00**		**2**	**-146.00**	**296.30**	**0.00**	**0.70**
2	UV hue	0.02	0.76	3	-145.60	298.00	1.66	0.30

Online supporting information S7:

Model selection for the effects of beak coloration and auricular patch surface on plasma lysis titers in breeding king penguin (*Aptenodytes patagonicus*). Colony area in which the bird was sampled was fixed in all models to account for known differences in parasite loads and stress responses that may affect immune status. All models with a ΔAICc <2 compared to the best model are presented. The most parsimonious model retained is indicated in bold.

#	Model	R^2	F	df	logLik	AICc	delta	weight
1	YO brightness + YO chroma + colony area	0.33	7.26	5	-42.87	97.1	0.00	0.29
2	UV chroma + YO chroma + colony area	0.31	6.68	5	-43.52	98.4	1.29	0.15
3	UV brightness + YO brightness + YO chroma + colony area	0.34	5.61	6	-42.44	98.9	1.74	0.12
4	**YO chroma + colony area**	**0.26**	**8.20**	**4**	**-45.07**	**99.0**	**1.91**	**0.11**
5	YO brightness + YO chroma + patch surface + colony area	0.33	5.55	6	-42.54	99.1	1.94	0.11
6	YO brightness + YO chroma + UV hue + colony area	0.33	5.54	6	-42.56	99.1	1.97	0.11
7	YO brightness + YO chroma + UV chroma + colony area	0.33	5.53	6	-42.57	99.1	2.00	0.11

Online supporting information S8:

Model selection for the effects of beak coloration and auricular patch surface on plasma NAb titers in breeding king penguin (*Aptenodytes patagonicus*). Colony area in which the bird was sampled was fixed in all models to account for known differences in parasite loads and stress responses that may affect immune status. All models with a ΔAICc <2 compared to the best model are presented. The most parsimonious model retained is indicated in bold.

#	Model	R^2	F	df	logLik	AICc	delta	weight
1	**Patch surface + colony area**	**0.24**	**7.31**	**4**	**-71.14**	**151.2**	**0.00**	**0.68**
2	Patch surface + UV hue + colony area	0.26	5.15	5	-70.67	152.7	1.54	0.32

Online supporting information S9:

Model selection for the effects of beak coloration and auricular patch surface on daily resting heart rate in breeding king penguin (*Aptenodytes patagonicus*). Colony area in which the bird was sampled was fixed in all models to account for known differences in parasite loads and stress responses that may affect energy expenditure. All models with a ΔAICc <2 compared to the best model are presented. The most parsimonious model retained is indicated in bold.

#	Model	R^2	F	df	logLik	AICc	delta	weight
1	**UV brightness + colony area**	**0.14**	**3.61**	**4**	**-9.84**	**28.6**	**0.00**	**0.71**
2	UV brightness + sex + colony area	0.15	2.62	5	-9.47	30.4	1.78	0.29

Online supporting information S10:

Model selection for the effects of beak coloration and auricular patch surface on baseline plasma total corticosterone levels in breeding king penguin (*Aptenodytes patagonicus*). Colony area in which the bird was sampled was fixed in all models to account for known differences in parasite loads and stress responses that may affect corticosterone levels. All models with a ΔAICc <2 compared to the best model are presented. The most parsimonious model retained is indicated in bold.

#	Model	R^2	F	df	logLik	AICc	delta	weight
1	Patch surface + sex + colony area	0.29	5.54	5	-76.26	164.1	0.00	0.23
2	Patch surface + sex + UV chroma + colony area	0.33	4.73	6	-75.21	164.7	0.59	0.17
3	Sex + colony area	0.23	6.28	4	-78.03	165.1	0.99	0.14
4	Patch surface + sex + UV brightness + colony area	0.32	4.56	6	-75.46	165.2	1.10	0.13
5	UV chroma + sex + colony area	0.27	5.02	5	-76.88	165.3	1.24	0.12
6	**Colony area**	**0.18**	**9.32**	**3**	**-79.50**	**165.6**	**1.50**	**0.11**
7	UV brightness + sex + colony area	0.26	4.79	5	-77.16	165.9	1.80	0.09

Online supporting information S11:

Model selection for the effects of beak coloration and auricular patch surface on the relative corticosterone increase in response to a standardized 30 minute capture in breeding king penguin (*Aptenodytes patagonicus*). Colony area in which the bird was sampled was fixed in all models to account for known differences in parasite loads and stress responses. All models with a ΔAICc <2 compared to the best model are presented. The most parsimonious model retained is indicated in bold.

#	Model	R^2	F	df	logLik	AICc	delta	weight
1	UV chroma + UV hue + YO brightness + colony area	0.43	7.46	6	-57.96	130.2	0.00	0.24
2	UV choma + UV brightness + UV hue + YO brightness +colony area	0.46	6.47	7	-56.91	130.9	0.75	0.16
3	**UV hue + colony area**	**0.35**	**11.05**	**4**	**-60.98**	**131.0**	**0.79**	**0.16**
4	UV hue + YO chroma + colony area	0.38	8.13	5	-59.99	131.6	1.37	0.12
5	UV chroma + UV hue + YO chroma + colony area	0.41	6.90	6	-58.69	131.7	1.47	0.11
6	UV chroma + UV hue + colony area	0.38	8.07	5	-60.05	131.7	1.49	0.11
7	UV brightness + UV hue + YO brightness + colony area	0.41	6.79	6	-58.83	131.9	1.74	0.10

Online supporting information S12:

Model selection for the effects of beak coloration and auricular patch surface on the relative heart rate increase in response to a standardized capture in breeding king penguin (*Aptenodytes patagonicus*). Colony area in which the bird was sampled was fixed in all models to account for known differences in parasite loads and stress responses. All models with a ΔAICc <2 compared to the best model are presented. The most parsimonious model retained is indicated in bold.

#	Model	R^2	F	df	logLik	AICc	delta	weight
1	Patch surface + colony area	0.11	2.27	4	-193.8	396.9	0.00	0.44
2	**Colony area**	**0.05**	**1.87**	**3**	**-195.2**	**397.1**	**0.20**	**0.40**
3	UV hue + colony area	0.07	1.26	4	-194.8	398.9	2.00	0.16