

Individual quality and reproductive effort mirrored in white wing plumage in both sexes of south polar skuas

Sveinn Are Hanssen,^{a,b,c} Jan O. Bustnes,^a Torkild Tveraa,^a Dennis Hasselquist,^b Øystein Varpe,^{a,d} and John-André Henden^{a,c}

^aNorwegian Institute for Nature Research, Polar Environmental Centre, N-9296 Tromsø, Norway,

^bDepartment of Animal Ecology, Lund University, Ecology Building, S-223 62 Lund, Sweden, ^cBiology Department, Faculty of Science, University of Tromsø, N-9037 Tromsø, Norway, and ^dUniversity Centre in Svalbard, PO Box 156, N-9171 Longyearbyen, Norway

It is well established that female choice may lead to sexual selection on quality-revealing ornaments in males. However, in many species, both sexes display conspicuous characters, which may reflect individual quality and condition. We examined the correlations between measures of individual condition, reproductive performance and variation in size and whiteness of white wing patches in both sexes of the south polar skua (*Catharacta maccormicki*). Females with a whiter patch had a lower mean clutch size and higher survival, and males with whiter patches had higher immune responses against the injected immunogen tetanus. Birds with a larger white patch, on the other hand, had a higher mass loss, and females with large white patches laid larger eggs and had reduced survival probability. Thus, variation in 2 measured aspects of the wing patches in the south polar skua seems to mirror a gradient of reproductive investment strategies; from 1) reduced reproductive investment, better immune defense, and higher survival in birds with more intensely white wing patches to 2) high reproductive investment but survival costs in birds with larger patches. *Key words*: diphtheria, female, immune function, male, ornament, sexual selection, tetanus. [*Behav Ecol* 20:961–966 (2009)]

Charles Darwin (1871) acknowledged sexual selection as a driving force in the evolution of exaggerated ornaments in males, such as the peacocks' tail. Since then the traditional view has been that males compete for females and females assess available males, often by their elaborate ornaments, in order to choose the best direct (e.g., parental care) or indirect (i.e., good genes) benefits for their offspring (Andersson 1994). Most exceptions to this general pattern have been found in species where sex roles are reversed. However, relatively recently, studies of ornamental traits have started to investigate such traits in both sexes, and evidence is starting to accumulate showing that both sexes may carry ornaments that signal some aspect of their quality to potential partners or competitors (for a review, see Kraaijeveld et al. 2007).

Honesty in such traits could stem from the costliness of producing or carrying the character, such as the peacock's tail. However, also conspicuous traits that do not entail such costs may honestly reflect individual quality (e.g., Andersson 1986). Amplifiers are not costly to produce and may reveal the quality of other traits (Hasson 1997). For example, white bird feathers may act as amplifiers because they make feather quality more visible (Fitzpatrick 1998). White feathers are presumably inexpensive to produce in contrast to colored feathers containing costly pigments such as carotenoid and melanin (Badyaev and Hill 2000; Török et al. 2003). However, as depigmented (white) parts on feathers wear faster in birds with inferior feather quality, white feathers may potentially reveal the individual's ability to invest in high-quality feathers (Kose and Møller 1999).

Plumage ornaments, such as white patches, may vary in size (Møller 1988; Yezerinac and Weatherhead 1997) and also in intensity of white (Siitari and Huhta 2002; Safran and McGraw 2004). Such different properties of an ornamental trait may, in turn, contain information about different aspects of the quality/condition of the individual (Møller and Pomiankowski 1993; Johnstone 1996). Ornaments conveying information about multiple quality traits have mostly been shown in males from sexually dimorphic species (Andersson et al. 1998; Møller et al. 1998; Møller and Petrie 2002; Badyaev and Young 2004), but see Roulin et al. (2001, 2003), for a rare female example. There is, thus, a great lack of studies focusing on the significance of traits that appear in both sexes of the same species. This is somewhat surprising since the evolution of mutual ornamentation, reflecting reproductive capacity or genetic quality, is predicted to occur more often in species where both sexes provide parental care (for a review, see Kraaijeveld et al. 2007).

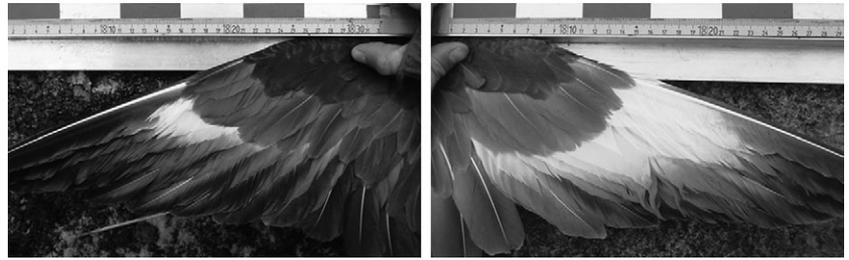
The current study was done in the sexually monomorphic south polar skua *Catharacta maccormicki*, a monogamous bird species where both sexes show a patch of white plumage on the underside of each wing (Furness 1987; Olsen and Larsson 1997). The birds frequently display their underwings during encounters with conspecifics of both sexes (Stonehouse 1956; Burton 1968; Pietz 1985). The function of the wing patches in skuas is currently not known, but they may act as signals in aggressive behavior and pair formation (Spellerberg 1971; Furness 1987), and in the brown skua *Catharacta antarctica lonnbergi*, the white patches seem to increase in size with age (Hahn and Peter 2003). Both sexes contribute to incubation and brood rearing, but the larger females seem to do most of the incubation and nest defense, whereas the slightly smaller males more often bring food to the incubating female and later the chicks (Furness 1987). In this study, 2 properties of the white wing patches, size and whiteness, were measured

Address correspondence to S.A. Hanssen. E-mail: sveinn.a.hanssen@nina.no.

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Figure 1

Picture of the underside of wings from 1 individual with a relatively small white wing patch (left) and 1 with a relatively large white wing patch (right). Photo by JO Bustnes.



and related to measurements of individual quality, reproductive investment, and survival in both males and females of the south polar skua. If the white wing patch is a quality revealing sexually selected trait in males, we predicted that more associations would be found between male quality and white plumage. However, it has been shown for instance in female common eiders that white wing plumage may reveal both individual quality and reproductive capacity (Hanssen et al. 2006, 2008). And as the female skua is performing most of the incubation, in addition to the production of eggs, we expect that female reproductive capacity will be reflected in the white intensity and the size of white wing patches.

METHODS

Study area and general methods

The study was conducted in a breeding colony (~85 pairs) at Svarthamaren (71°53'S, 05°10'E), Dronning Maud Land (Antarctica), during the breeding season (December 2001 to January 2002). Details of the study area are given in Mehlum et al. (1988). Svarthamaren is situated in the interior of Antarctica, approximately 200 km from the ice shelf, and has the largest breeding colony of Antarctic petrels in the world (~200 000 pairs). During the breeding season, skuas feed almost exclusively on eggs and young of petrels (Brooke et al. 1999).

All skua nests were marked shortly after our arrival in mid December. The adults were caught with a nest trap (Helberg et al. 2005) or by using a rod with a snare. Blood was sampled from the wing vein (ca. 10 ml) with a syringe. The whole blood samples were frozen within 2–6 h. All individuals were marked with a letter-coded polyvinyl chloride plastic band and a numbered steel band, and their bill length, bill height (± 0.1 mm), skull length (head + bill), tarsus and wing length (± 1 mm), and body mass (± 5 g) were registered. We performed a principal component (PC) analysis on these measurements except body mass, and used the first PC score as an index of body size (for details, see Bustnes et al. 2007). Eggs were already present in most nests at the time of our arrival, so laying dates could not be recorded directly. Egg length and width (± 0.01 mm) were measured with sliding calipers, and egg volume (ml) was estimated by the formula: Volume = $0.000476 \times \text{Length} \times \text{Width}^2$ (Hoyt 1979). The nests were checked daily to record hatching dates. Nonviable eggs were those not hatching or found to be added during the incubation stage. To record returning adults, the colony was visited 3 years later, when the colony was searched 4 times between 17 and 29 November, and all color-banded individuals were recorded. We were thus able to record the individuals that had survived since January 2002 and returned to breed in November 2004, resulting in data on return rate 3 years after the birds were measured. In the following, we refer to this as return rate, assuming that it reflects survival probability.

Plumage

The underside of the wings of all individuals was photographed. A ruler was placed next to the wing at each photo

in order to standardize the size of the white wing patch (Figure 1). The photos were imported to ArcView and by using the Spatial Analyst module we manually marked the white area and calculated the total area of the white wing patch, hereafter referred to as size. A part (~4 cm²) of 1 of the white feathers in the middle of the wing patch where cut off after the photography was taken during the first capture of the birds. We used a digital spectrometer (Avantes) to measure the “whiteness” of each feather sample. Feathers were measured in constant light in a laboratory without windows. They were placed on a black paper background and the sensor at a 90° angle (see also Hanssen et al. 2006, 2008). These measurements produced 3 variables all describing aspects of the “color” of the white in feathers. The variables were lightness (amount of light reflected, which increases with increasing “whiteness”), hue (i.e., the wavelength of the color), and chroma (i.e., the density of pigmentation; for details, see Hanssen et al. [2006, 2008]). As we expected these 3 color variables to be correlated, we included all variables in a PC analysis in order to simplify analyses. PC1 explained 71% of the variation, whereas PC2 explained 22%. Higher values of PC1 equal higher whiteness in the feather. The factor loadings for each variable were lightness = 0.70, hue = -0.92, chroma = -0.89. PC1 was not related to the size of the white wing patch ($F_{1,134} = 0.008$, $P = 0.93$). We therefore used both size and the first reflectance PC1 (hereafter referred to as “whiteness”) as independent variables describing 2 different aspects of the white wing patch character in south polar skuas. Body size of birds may affect the size of the wing patch, and thus, we tested this in order to evaluate if body size was to be included as a covariate in the analyses. However, body size was not related to white patch size ($F_{1,134} = 0.26$, $P = 0.61$), also, the interaction between sex and patch size was not significant ($F_{1,134} = 0.45$, $P = 0.51$), but females had larger white wing patches than males ($F_{1,134} = 12$, $P = 0.0008$, mean \pm standard error (SE) females 73 ± 3 cm², males 62 ± 2 cm²). Also, male wing patches were on average whiter than those of females ($F_{1,134} = 5.28$, $P = 0.02$, mean \pm SE females -0.3 ± 0.2 , males 0.3 ± 0.2).

Immune responses

A subsample of individuals ($n = 37$) were injected with 150 μ l diphtheria–tetanus vaccine in the pectoral muscle (SBL Vaccin AB, Stockholm; diphtheria toxoid 38 Lf [flocculation entities] and tetanus toxoid 7.5 Lf, mixed with the adjuvant aluminum phosphate 5 mg/ml). In these individuals, we measured the specific antibody responses against the antigens diphtheria and tetanus, respectively. We measured humoral immune system activation as the antigen-specific antibody levels in the skua sera using a standard enzyme-linked immunosorbent assay (ELISA) previously developed for red-winged blackbirds (for details of the methods, see Hasselquist et al. 1999). The assay has been proved to work for other passerines, waders, and gulls (Hasselquist et al. 2001; Bustnes et al. 2004; Mendes, Piersma, Hasselquist 2006; Mendes, Piersma, Hasselquist, Matson, Ricklefs 2006), and in this study, we

found that it works well also for skuas. The ELISA method provides sensitive measures of the amount of antibodies that specifically bind to an antigen. We used a diluent of 1% powdered milk in 0.01 mol/l phosphate-buffered saline (PBS) to produce 1:800 dilutions for the tetanus plates and 1:400 dilutions for the diphtheria plates of the preimmunization and postimmunization serum samples. To avoid between-batch variation, we ran all analyses on 96-well ELISA plates for each of the 2 antigens and analyzed all plates on the same day. Antigens (diphtheria and tetanus toxoid) were diluted to 3 $\mu\text{g}/\text{ml}$ in carbonate buffer (0.15 mol/l, pH 9.6) and added to plates in 100 μl well. After incubation overnight at 4 °C and blocking with 3% milk powder in PBS, 100 μl serum samples (see above) were added to each well and incubated overnight at 4 °C. Plates were then washed in PBS and Tween 20; as a result, only skua antibodies that had specifically bound to the antigen (diphtheria or tetanus) fixed to the sides of the wells remained on the ELISA plate. Next, 100 μl of the secondary antigen, rabbit anti-red-winged blackbird (RaRW) diluted 1:1500 in PBS, were added to each well. The RaRW had previously been produced by immunizing rabbits with purified red-winged blackbird IgM and IgG (Hasselquist et al. 1999, 2001). After a second incubation and wash, a peroxidase-labeled goat anti-rabbit antibody (Kirkegard and Perry, Gaithersburg, MD), diluted 1:2000 in PBS, was added to each well. After a second incubation (1 h at 37 °C) and wash, peroxidase substrate (2,2-azino-bis-3-ethylbenzthiazoline-6-sulfonic acid, catalog no. A1888; Sigma, St Louis, MO) and peroxide were added, and the plates were immediately transferred to a Vmax (Molecular Dynamics, Sunnyvale, CA) kinetics ELISA reader. The plates were read at 30-s intervals for 10 min using a 405-nm wavelength filter. All antibody concentrations are given as the standardized slope of the substrate conversion (in $10^{-3} \times \text{optical densities [ODs]}/\text{min}; \text{mOD} \times \text{min}^{-1}$), with a higher slope indicating a higher concentration of antigen-specific antibodies in a sample. Preimmunization serum samples from each individual were run in duplicate to investigate each individual's background level of antigen-specific antibodies. For each individual, postimmunization serum samples were added to the plate in duplicate, and the average of these was our measure of antibody titer for each dilution. We ran at least 2 wells with blank samples on each plate. These wells were treated in the same way as the test sample wells except that no bird serum was added. As our measure of preimmunization and postimmunization antibody titers of individual birds, we subtracted the mean value of these blanks from the measured antibody concentration. On each plate, we ran 11 standard samples covering the range of antibody titers for the injected birds. The differences between the standard curves were used to adjust preimmunization and postimmunization antibody titers to control for between-plate variations. For each individual, we then subtracted the preimmunization titer from the postimmunization titer to obtain values of the primary antibody response, which we used as a measure of the humoral immune responsiveness in further analyses. Of the 37 inoculated skuas, 15 produced a detectable amount of antibodies against diphtheria and 32 against tetanus. The antibody response was log₁₀ transformed in order to approach a normal distribution.

Statistics

All analyses were performed with SAS version 9.2. Estimates and values are presented as mean \pm SE. We started with saturated models with the 2 wing patch variables (whiteness and size) also including relevant covariates and interaction terms, we then sequentially removed nonsignificant variables based on type III Sums of squares.

RESULTS

Body mass

The adult birds were weighed early and late in the nest period with 14–21 days between. When analyzing mass change, we started with a model including mass change from first until second weighing as dependent variable and initially including days between measurements, body size, whiteness, white patch size, sex, body mass at first weighing, and the interaction terms sex \times whiteness and sex \times white patch size as independent variables. After sequentially removing nonsignificant variables, the remaining model included 4 variables: initial body mass ($F_{1,59} = 18.49$, $P = 0.001$), white patch size ($F_{1,59} = 10.40$, $P = 0.002$), body size ($F_{1,59} = 5.64$, $P = 0.02$), and sex ($F_{1,59} = 7.90$, $P = 0.0067$). Females lost more mass than males (female mass loss 56 ± 8 g, male mass loss 38 ± 10 g). Mass loss was positively related to white patch size (partial estimate 0.89 ± 0.28), which means that individuals with larger white patches lost more mass (Figure 2).

Reproduction

Skuas in the colony produced 1 (16%) or 2 eggs (84%). We started with a full model including body size, patch whiteness, and patch size for each sex separately and then sequentially removed the least significant variable resulting in a model where female patch whiteness and male body size were negatively related to clutch size (female patch whiteness $\chi^2_{1,63} = 7.46$, $P = 0.006$, male body size $\chi^2_{1,63} = 7.34$, $P = 0.007$). Thus, smaller males and females with more grayish wing patches more frequently had nests with 2 eggs.

Egg volume was analyzed by starting with a model including body size, clutch size, patch whiteness, and white patch size for each sex separately and then sequentially removing the least significant variable resulting in a model where female white patch size was positively related to mean egg volume (Figure 3; estimate 0.07 ± 0.03 , $F_{1,66} = 5.66$, $P = 0.02$) and clutch size was marginally negatively related to egg volume (mean egg volume 1 egg clutches: 88.3 ± 1.7 , 2 egg clutches: 84.95 ± 0.69 , $F_{1,66} = 3.83$, $P = 0.055$). Thus, females with

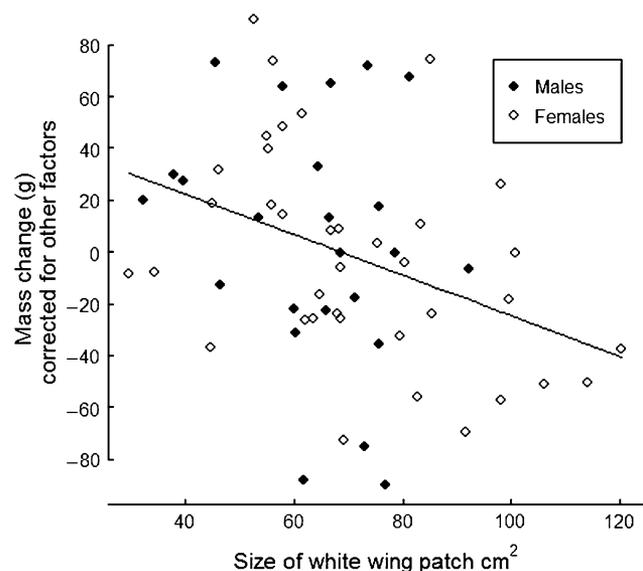


Figure 2

The relationship between whiteness of the wing patch in south polar skuas in relation to sex and mass change during the incubation period.

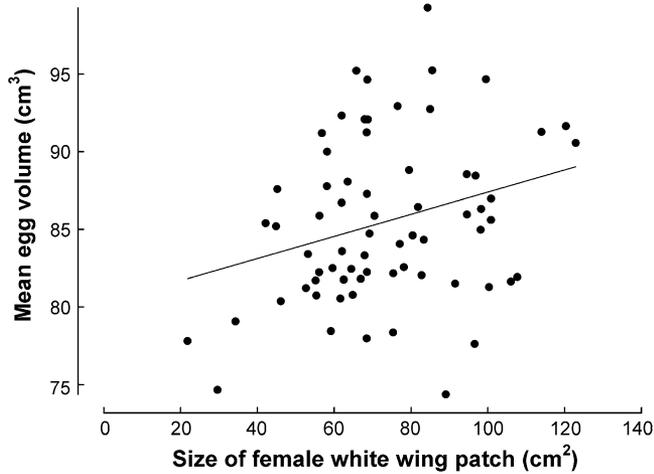


Figure 3
The relationship between size of female white wing patch and mean egg volume in south polar skuas.

larger wing patches produced larger eggs and females with single-egg clutches tended to produce a larger egg compared with 2-egg clutches.

Hatching success was moderately low in the skuas, only 68% of nests hatched at least 1 nestling. The probability of hatching at least 1 nestling was not significantly related to wing patch whiteness or area, although female wing patch whiteness was nonsignificantly positively related to the probability of success ($\chi^2_{1,65} = 2.96, P = 0.09$).

Immune function

The strength of the response against diphtheria was not related to the whiteness (PC1) or the area of the wing patch (patch whiteness $F_{1,28} = 0.84, P = 0.37$, area $F_{1,28} = 0.19, P = 0.67$), and the same was true for sex ($F_{1,28} = 1.02, P = 0.32$) as well as the interaction between sex and patch whiteness ($F_{1,28} = 1.69, P = 0.20$) and sex and patch size ($F_{1,28} = 0.81, P = 0.38$). However, males with deeper white wing patches had a stronger response against the tetanus antigen (Figure 4, patch whiteness $F_{1,8} = 7.08, P = 0.029$), full model: sex

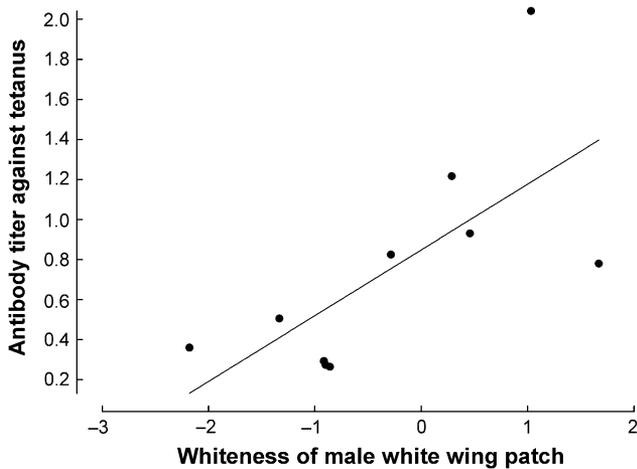


Figure 4
The relationship between whiteness of the wing patch in male south polar skuas in relation to the antibody titer against tetanus antigen.

$F_{1,26} = 0.27, P = 0.61$, patch whiteness: $F_{1,26} = 3.28, P = 0.08$, and the interaction between patch whiteness and sex: $F_{1,26} = 4.30, P = 0.049$. Removed nonsignificant variables were area ($F_{1,24} = 0.16, P = 0.70$) and the interaction between sex and patch size ($F_{1,24} = 0.50, P = 0.49$).

Return rate

An individual was registered as “survived” if observed in the breeding colony 3 years after the wing patch study. The return rate was 63% (87 of 138). The full model showed that the interaction term sex \times whiteness and sex \times patch size was significantly related to the probability of being found in the colony 3 years later (sex $\chi^2_{1,127} = 7.78, P = 0.005$, patch whiteness $\chi^2_{1,127} = 0.47, P = 0.49$, patch size $\chi^2_{1,127} = 1.37, P = 0.24$, body size $\chi^2_{1,127} = 6.14, P = 0.01$, interaction term patch whiteness \times sex $\chi^2_{1,127} = 6.76, P = 0.009$, and interaction term white patch size \times sex $\chi^2_{1,127} = 7.34, P = 0.007$). We therefore analyzed return rate separately for the 2 sexes. For females, birds with smaller patches and birds with whiter patches had a higher return rate (Figure 5; patch whiteness $\chi^2_{1,62} = 4.55, P = 0.03$, white patch size $\chi^2_{1,62} = 7.96, P = 0.005$, and body size $\chi^2_{1,62} = 3.13, P = 0.08$). For males, there were no

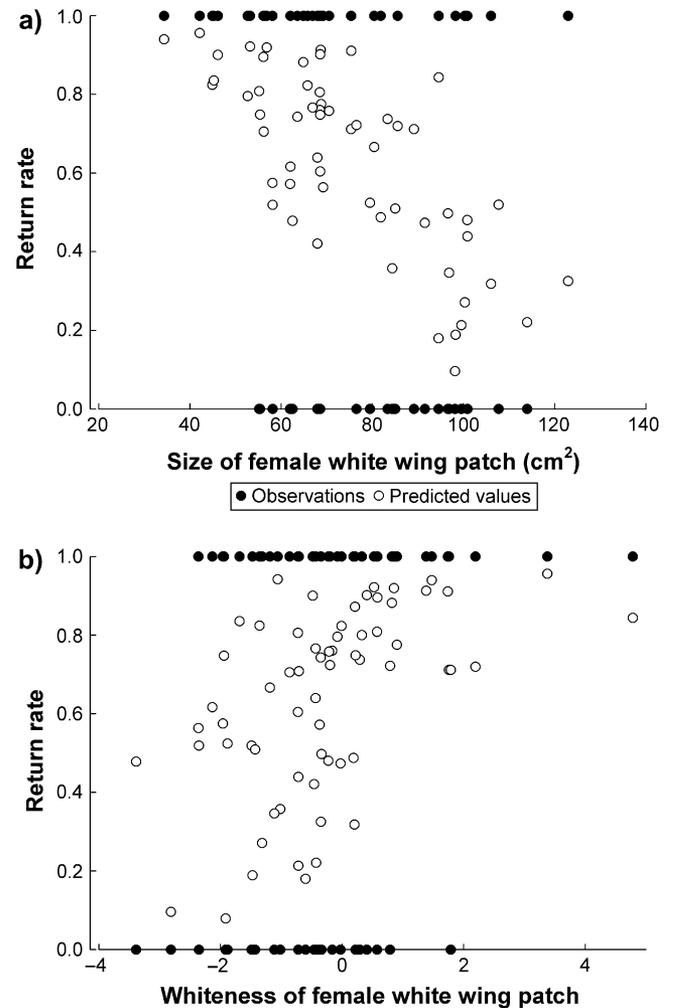


Figure 5
The relationships between return rate and (a) size of the white wing patch and (b) whiteness of the wing patch in female south polar skuas.

significant relationships between wing patch properties and return rate (patch whiteness $\chi^2_{1,63} = 2.19$, $P = 0.14$, white patch size $\chi^2_{1,63} = 1.11$, $P = 0.29$, and body size $\chi^2_{1,63} = 3.01$, $P = 0.08$).

DISCUSSION

In the present study, we found that 2 different properties of the wing patch in the sexually monomorphic south polar skua reflect different individual qualities. A whiter patch was related to a lower mean clutch size and higher survival in females and higher immune responses against the injected immunogen tetanus in males. In contrast, birds with large white patches had a higher mass loss and females with larger patches laid larger eggs but suffered reduced survival probability. Thus, variation in the 2 measured aspects of the wing patches in the south polar skua seems to mirror a gradient of reproductive investment strategies from high reproductive investment but survival costs in birds with larger patches to reduced reproductive investment, better immune defense, and higher survival in birds with more intensely white wing patches.

The size of the white wing patch seems to signal capacity for investment in reproduction, as indicated by a higher body mass loss during breeding in large patched individuals of both sexes, additionally, females with large patches produced larger eggs. In contrast to males, where studies of reproductive investment mostly focus on territorial aggression, number of partners, and gonadal size (see Andersson 1994), relatively few studies have been examining female ornaments and reproductive investment, but a majority of the published studies show associations between ornamental expression and reproductive output (ornamentation and parental care; Møller 1993; Linville et al. 1998, but see Cuervo et al. 1996; Rohde et al. 1999; Smiseth and Amundsen 2000; Hill 1993, ornamentation and hatch date/reproductive success; Ruusila et al. 2002 but see Hill 1993, ornamentation and condition; Johnsen et al. 1996). In females of the sexually dimorphic common eider duck, their white wing feather tips are related to body mass loss and immune function during incubation (Hanssen et al. 2006), and an experimental study has since confirmed that an immune challenge led to reduced expression of white feather tips in the same species (Hanssen et al. 2008). In the skuas, the area of the wing patch was negatively related to return rate in females, indicating a possible survival cost of higher reproductive investment in these birds. To our knowledge, no previous study has found a relationship between a female ornamental trait and survival (for males, see Schantz von et al. 1989); however, studies of the barn owl *Tyto alba* have elegantly demonstrated relationships between expression of plumage characters and immune function (e.g., Roulin et al. 2000, 2001), which could be the proximate cause of increased survival. Several studies on other species have suggested that a trade-off between investment in reproduction and immune function could be mediating survival costs of reproduction (e.g., Sheldon and Verhulst 1996; Hanssen et al. 2004, 2005; Hanssen 2006). In the present study, we found that whiter feathers were related to increased survival in females and increased immune responses in males. The increased survival in birds with whiter feathers could be related to increased investment in immune function, even if we could only demonstrate a higher immune function in males, and/or reduced reproductive effort as females with white feathers laid fewer eggs.

In sum, whiter feathers are related to reduced reproductive investment and increased survival, whereas large white wing patches are related to increased reproductive investment which in turn seems to result in a survival cost of reproduction. As we do not know the age of these birds, it may be that younger

birds with less reproductive experience and higher survival display whiter feathers, whereas older, experienced birds with lower survival chances have larger white patches. In a previous study on another skua from the southern hemisphere, the brown skua *Catharacta antarctica lonnbergi*, Hahn and Peter (2003) found that older skuas had larger white patches. However, they could not find a relationship between patch size and survival in this species. It is possible that older birds (with larger white patches) more often skip breeding and were therefore registered as “not returned” to the colony 3 years after the study. However, older birds often have a drop in reproductive output (senescence), and in this study, we found that birds with larger white patches on the contrary seemed to have a higher reproductive investment. In the present study, we report a return rate after 3 years of 63%, which means a yearly survival rate of 0.86. This seems low for a large seabird with such low reproduction as the south polar skua. In the brown skua, Pietz and Parmelee (1994) reported an annual survival rate of 0.95. The lower return rate in the south polar skua may be caused by lower resighting rate, reflecting abstained breeding in some birds or simply that all breeding birds were not observed.

When both sexes display a similar ornament, this has most commonly been explained by sexual selection for the ornament in the male and the female ornament “hitchhiking” with male ornament evolution. Evidence supporting this hypothesis would be showing that ornamental variation should be more closely associated with male fitness traits. Interestingly, in the present study, we found more associations between female expression of wing patches and both individual quality and reproductive investment. And perhaps even more interesting, there were clear associations between female wing patch variation and a fitness trait such as return rate, whereas no significant associations were found between wing patches and return rate in males. Thus, our study does not support the hypothesis that the trait is developed and maintained mainly as a secondary sexual character in males.

If individuals of south polar skuas use the information in the wing patches as cues when selecting partners, they have the opportunity to select what may be genes for individual quality and survival or they may select partners, which invest more heavily into reproduction, at the expense of survival.

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