A small badge of longevity: opposing survival selection on the size of white and black wing markings

Tuul Sepp, Kalev Rattiste, Lauri Saks, Richard Meitern, Janek Urvik, Ants Kaasik and Peeter Hõrak

T. Sepp (tuul.sepp@ut.ee), R. Meitern, J. Urvik, A. Kaasik and P. Hõrak, Dept of Zoology, Univ. of Tartu, Tartu, Estonia. – K. Rattiste, Dept of Zoology, Inst. of Environmental and Life Sciences, Estonian Univ. of Life Sciences, Tartu, Estonia. – L. Saks, Estonian Marine Inst., Univ. of Tartu, Tartu, Estonia.

According to handicap principle, exaggerated ornamental traits are supposed to exert costs on their bearers. However, there is much less theoretical and practical consensus about whether and under which conditions ornament expression should positively correlate with survival. We measured age-related variation and survival selection on the size of white wing patches and black wing tips in a long-lived monogamous seabird, the common gull *Larus canus*. Males had larger white patches than females but patch size showed concave relationship with age irrespective of sex, suggesting that white patch size was prone to senescence in both sexes. Extent of wing tip abrasion correlated negatively with the size of white patch, suggesting, in agreement with the Zahavian handicap hypothesis that only individuals with largest ornaments are able of maintaining them and not paying cost of displaying them. Areas of white wing patches and black wing tips correlated negatively. Irrespective of sex, survival selection favored birds with larger white wing patches and smaller black wing tips, which suggests that white and black wing markings may have coevolved as reverse components of a single ornament. Altogether, our results provide an evidence for the case where survival selection on ornamental traits in females is not weaker than in males. Absence of sex differences with respect to most of observed patterns is consistent with a prediction that among monogamous long-lived species with biparental care, mutual mate choice leads to evolution of elaborate ornamental traits in both sexes.

Function of ornamental plumage coloration belongs to the most thoroughly studied topics in behavioral ecology. According to Hill (2011, 2014) the signaling value of ornamental traits is based on their integration with the functionality of vital cellular processes. Such condition-dependence of plumage coloration has been well documented (reviewed by Niecke et al. 2003, Hill and McGraw 2006, McGraw 2008, Svensson and Wong 2011, Piault et al. 2012). However, the question about associations between ornaments and fitness is more complicated. First, there is much less theoretical consensus about whether and under which conditions ornament expression should positively correlate with components of fitness (Kokko 1997, Höglund and Sheldon 1998, Getty 2002, 2006, Morehouse 2014, Ercit and Gwynne 2015, Galván et al. 2015, see also the discussion about possible pleiotropic effects in Ducrest et al. 2008). Second, although the associations between color-based signals and reproductive success are quite well established (Yezerinac and Weatherhead 1997, Siefferman and Hill 2003, Komdeur et al. 2005, Doutrelant et al. 2008), much less is known about the associations between color-based signals and life span in birds. Studies on short-lived species have shown that the extent of expression of

potentially costly color traits is associated with increased survival (Jennions et al. 2001, Griffith et al. 2003, Galván and Møller 2013, Galván et al. 2014, Hõrak and Männiste 2016). However, at least two studies have also detected viability selection against conspicuous coloration (Keyser and Siefferman 2005, Moore et al. 2015) and some studies found stabilizing selection on conspicuousness (Gregoire et al. 2004, Figuerola and Senar 2007, but see also Acker et al. 2015 for disruptive viability selection on a plumage trait), suggesting that the sign and magnitude of selection exerted on coloration might be species- or trait-specific (Meunier et al. 2011). It is also suggested that at least in case of heritable melanin-based colouration, selection may not always be directional, but may be conditional to environmental conditions (Senar et al. 2014, Roulin 2016). Among long-lived birds, significant viability selection on plumage coloration has been demonstrated only in south polar skua *Catharacta maccormicki* (Hanssen et al. 2009) and barn owl *Tyto alba* (Roulin et al. 2010, Emaresi et al. 2014).

There is reason to predict that selection for signal traits reflecting the potential for longer life span should be particularly strong in species that form monogamous pair bonds lasting for years or even decades and where both

adults provide parental care for an extended period. In such species life span is often the most important determinant of lifetime reproductive success (Annett and Pierotti 1999, Kruger and Lindstrom 2001, Rattiste 2004, Altwegg et al. 2007). It would be expected that (sexual) selection favors signals which enable to choose a mate on the basis of cues that predict the potential for remaining alive and healthy long enough to successfully complete the rearing of current and future offspring.

In the current study, we test whether the size of white wing patches is sexually dimorphic, changes and covaries with age and predicts life expectancy in a long-lived monogamous seabird, the common gull *Larus canus*. Wing tip patterns of several gull species are highly variable, age dependent and sometimes also sexually dimorphic (Coulson et al. 1982, Allaine and Lebreton 1990). All these properties are characteristics to sexually selected traits (Andersson 1994), however, selection on the wing tip pattern of gulls has never been investigated. In other bird species, white plumage regions are often viewed as traits with little utilitarian function and thus, serving as sexually selected signals of individual quality (Kose and Møller 1999, Moreno-Rueda 2005, Hanssen et al. 2006, 2008, Blanco and Fargallo 2013, Saino et al. 2015). The condition dependence of white plumage patches has gained ample support across species although the proximate mechanisms ensuring their honesty may vary in different ecological settings. White patches have been suggested to reliably advertise parasite resistance, because they are strongly affected by chewing lice (Kose et al. 1999, Moreno-Rueda and Hoi 2012) or feather-degrading bacteria (Ruiz-De-Castaneda et al. 2012, 2015). This resistance may be partly mediated by uropygial gland functioning (Roulin 2007, Moreno-Rueda 2010, Saag et al. 2011). Due to protective role of melanin pigments, white patches can also be viewed as costly signals because of their weaker resistance to abrasion (Barrowclough and Sibley 1980, Mackinven and Briskie 2014), especially when located in body parts that are most exposed to wear and tear, such as tail or wing feathers.

Male common gulls are larger than females (Larsson et al. 1997) and the onset of breeding is affected by sexually antagonistic genetic effects (Brommer and Rattiste 2008). When sexes have different optima for shared traits, sexually antagonistic selection generates intralocus conflict that is thought to be resolved through the evolution of sexual dimorphism (Cox and Calsbeek 2009). We thus asked whether the size of white wing spot appears such a sexual signal trait. Under this scenario, we predicted sex differences in the size and age-dependence of wing patch, as well as different associations between wing patch size and life expectancy among males and females. Alternatively, long-lived monogamous species may practice mutual mate choice (Jones and Hunter 1993, Johnstone et al. 1996, Kraaijeveld et al. 2007), so we considered also the possibility that the size of white wing patches is similarly condition-dependent in both sexes. Under the latter scenario, we predicted that patterns of covariation between wing patch size vs age and survival do not differ between males and females.

We tested first whether wing patch size appears sexually dimorphic under the assumption that if it is a sexual ornament, males have larger patches than females. We also tested for a presence of sexual dimorphism in a control trait, the size of black patch in the tip of first two primaries under the assumption that it is an utilitarian trait which serves to protect wing tips from abrasion, since colour pigments help resist abrasive agents (Roulin et al. 2013). In contrast, white wing patches do not seem to serve any utilitarian function. It is generally predicted that ornaments differ from ordinary morphological traits by showing a larger variation (Cuervo and Møller 2001). Smaller variation in the utilitarian trait – the black wing tip – would therefore support the assumption that white wing patches serve as sexual signals. We predicted that under such scenario, black wing tips of males will be either of similar size or smaller than those of females. Alternatively, if the black wing tip also serves as part of the signal trait, the variation in black wing tip size should be comparable to that of the white patch size. According to findings in other bird species, we expected that as a signal trait, larger white patches are indicative of better individual quality in terms of life expectancy.

To assess the potential costs of having large white wing patches we tested whether their size correlates with the extent of abrasion of feather tips. The direction of such correlation could be both negative (if only birds with more abrasion-resistant feathers can allow prominent white patches) or positive (if feather abrasion is the price that birds have to pay for more conspicuous signal traits).

Our dataset included a subsample of birds measured twice over a 9 or 10-yr interval, which enabled assessment of individual consistency (repeatability) and longitudinal changes in wing patch size. Because little is known and hypothesized about the lifetime changes in ornamental traits in long-lived species, we had no predictions about the direction of changes in wing patch size with age. We would expect a within-individual decrease in wing patch size with age if this trait shows senescent decline similarly to reproductive success in common gulls (Rattiste 2004). For example, synchronous age-related decline in reproductive traits and sexual signal traits has been previously demonstrated in male fowls *Gallus gallus* (Cornwallis et al. 2014) and collared flycatchers *Ficedula albicollis* (Evans et al. 2011). Alternatively, increase towards the end of life can be expected if gulls increase their investment in ornament expression as their residual reproductive value declines and selection favors increased investment in ornamentation that may increase present mating opportunities (Kokko 1997). This hypothesis has been successfully tested in fish and insects (Candolin 2000, Miller and Brooks 2005, Sadd et al. 2006) and short-lived birds (Evans et al. 2011, Grunst et al. 2014, Kervinen et al. 2015), but whether it holds in other contexts, for example in long-lived monogamous species, remains unknown. Absence of life-time changes in wing patch size can be predicted if this trait primarily reflects genetic composition or persistent epigenetic effects (Walker et al. 2013). The age-specific patterns in patch size were also studied in the larger, cross-sectional sample. Although cross-sectional analysis does not enable to distinguish effects of selective mortality from within-individual changes, this information is still valuable for testing for occurrence of sex-specific patterns of senescence.
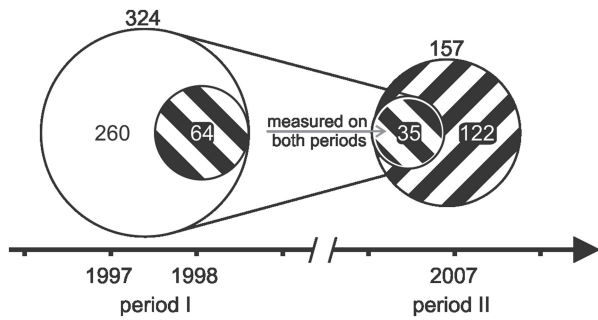
Figure 1. Sampling timeline and sample sizes for different analyses. Striped circles indicate the sub-sample where both white and black wing patch size was measured. White area means that only white wing patch was measured. Circle sizes (and numbers) denote sample sizes. Total sample size was 446 birds, from which 35 were measured twice.

Methods

Study population and general procedures

The study was conducted in a population located on the islet of Kakrarahu in Matsalu National Park, on the west coast of Estonia (58°46′N, 23°26′E). This colony has been studied since 1962, so the population's demographic structure is well known. It has been previously found (Rattiste 2004) that 50% of males and 10% of females return to their birth colony to breed. However, due to predation by herring gulls *Larus argentatus* in other colonies, those numbers are up 89 and 44% in males and females, respectively (KR unpubl). Common gulls start breeding at age 3 or 4 and breed on average 5–6 yr. After the tenth breeding year, there is a notable decline in breeding success, indicating the start of reproductive senescence (Rattiste 2004).

Data for the current study, including 446 birds (216 females and 230 males) were collected from 1997 to 2015 to record survival. Wing patch data were collected in two periods: 1997 and 1998, and 2007 (Fig. 1). Different individuals were sampled in 1997 and 1998. 35 of these birds (16 females and 19 males) were subsequently recaptured in 2007. Adult birds were caught, sexed and individually marked both with metal and plastic rings at their first

breeding attempt, to enable their later identification. Birds were caught from nests using spring traps. To avoid nest abandoning, all birds were caught after the tenth day of incubation. Head length – the distance from the back of the head to the tip of the bill – was measured with a calliper to the nearest 0.1 mm. The study protocol complies with the laws of the Republic of Estonia.

At least 94% of nest owners (both males and females) were identified each year. As the exact age was known only for birds ringed as chicks, the breeding age (defined as number of years since the first breeding attempt) was used in analyses as an approximation for age. Birds known to have bred previously outside the study area were excluded from analyses. This reduced the risk of underestimation of a bird's breeding age. Because common gulls do not skip breeding seasons (KR unpubl.) and breeding birds are highly faithful to their colony (less than 3% change colonies between years, moving mostly to neighboring colonies, Rattiste 2004), if an individual was not observed breeding, it was considered dead. Survival data were used only for birds measured in 1997 and 1998, because more than half of the birds captured on 2007 were still alive in 2015. Measuring selection on these birds would have thus excluded the most viable individuals from the 2007 sample.

Wing patch measurement

To characterize the individual wing tip pattern, we summed the measurements of the areas of the white spots on five to six (some birds had a white spot on the 6th feathers, some did not) outermost primaries on the right wing of the bird (Fig. 2). The wing patch data were collected using different methods on separate periods. On 1997 and 1998, the area of spots was measured as follows: the wing was placed in its natural position on the flat surface so that the edges of all white spots on the feathers were visible. Transparent plastic sheet with a grid of 5×5 mm (25 mm^2) cells was placed on the wing and the areas of spots were estimated as the number of squares with the precision of 1/4 cell, which was thereafter multiplied by 25 to obtain the measurement in square millimeters. If a spot had visible signs of abrasion, this was taken into account during the measuring procedure, and the abraded area was manually extrapolated to

Figure 2. Individual wing tip pattern variation in common gulls. White wing patch size was calculated as the summed area of distinctive white spots on outermost 1st–5th (6th) primaries on the right wing. If a spot had visible signs of abrasion, the measured area was manually extrapolated to represent the undamaged state. Areas surrounded with red line denote measured area size. Black wing patch size was calculated as the summed area of black on the tips (distal to the white patch) of 1st and 2nd primaries. Left: bird with feather abrasion score of 0 and white spots on 6 primaries; right: bird with feather abrasion score of 3 (maximum) and white spots on 5 primaries.

represent the undamaged state. At the time, the method was preferred because its relative simplicity, low cost and reasonably low measurement error, as the repeatability (Lessells and Boag 1987) of the measurements of different wing spots, based on two consecutive measurements, was 0.99 ($F_{15,16} = 165.4$; $p < 0.0001$). All the wings were measured by the single person (LS). In 1998, wings of 64 individuals were also photographed, with their right wing placed on the millimeter paper for scale.

In 2007, all birds were photographed with a ruler placed next to their right wing for scale. Patch size was measured as the white area in mm² from digital photographs using IMAGEJ software (<http://rsbweb.nih.gov>). Again, if a spot had visible signs of abrasion, this was taken into account during the measuring procedure by manually extrapolating to represent the undamaged state (Fig. 2). To compare two methods, IMAGEJ was also used to measure wing patches of ten birds photographed on year 1998. The correlation between wing patch size estimates with different methods was extremely strong ($r = 0.98$, $p < 0.0001$). Black patch area on the tips (distal to the white patch) of first and second primaries was also measured from birds photographed in 1998 and 2007 (Fig. 1 and 2).

The photographs taken in 1998 and 2007 also allowed estimating the level of abrasion on the tips of the primaries. Abrasion level was estimated on a scale of 0–4, with 0 representing no visible abrasion and 4 representing missing feather tips on several feathers (Fig. 2). Feather abrasion was estimated independently by four persons. Repeatability for feather abrasion level estimates was 0.67 ($p < 0.0001$, $F_{212,671} = 6.7$). Averages of four raters were used in calculations.

Statistical analyses

Most of the measured variables were nearly normally distributed in a range of skewness from –0.05 to 0.53. Two traits were strongly right skewed: breeding age (females: skewness = 0.94 ± 0.17 (SE), males: 1.05 ± 0.16) and the size of the white wing spot (females: skewness = 2.72 ± 0.17 (SE), males: 1.11 ± 0.16), hence we checked whether comparing the sexes with non-parametric U-test would give different results from parametric tests. In none of the cases did significance of the results change, hence results of the t-tests along with means and SD are presented for all variables in Table 1.

For analyzing age-related patterns of wing patch size we used linear mixed-effects models, with individual identity as a random factor and wing patch size as a dependent variable. Models were fit using maximum likelihood. Type III tests were used for testing fixed effects. Breeding year (as a proxy of age) was included in models as a continuous independent variable to describe associations between measured parameters and age. To describe possible parabolic relations of measured parameters and age, all models were also tested for significance of the square of breeding year. Models were ran using R ver. 3.2.2 and the package nlme.

An individual's life span is an outcome of its cumulative annual survival probabilities, and its variation can therefore be attributed to consistent between-individual variation in mortality risk, as well as variation in changes in within-individual risk of mortality over life (Zhang et al. 2015). Neither the between- nor within-individual variation in mortality risk can be observed directly, but can be captured in the instantaneous rate of death (i.e. mortality risk) calculated in Cox models (Zhang et al. 2015), which we used to test whether any of the recorded variables predicts survival, using R ver. 3.2.2 and the package survival (Therneau 2015). In our study, we define survival as a trait that indicates if the bird is alive on year 2015 and specifies the lifespan from first breeding year to death or year 2015. The model was right censored (i.e. for some individuals the exact life spans were not known) as 19 of 324 birds were still alive in 2015 in the case of white wing patch and 4 of 64 birds were alive in the case of black wing tip area. In survival analyses, sizes of black and white wing markings and their ratios were standardized to z-scores (mean = 0, SD = 1) within sex because these traits were sexually dimorphic and such a standardization enabled to analyse survival of both sexes in the same model. P-value of 0.05 was considered as a criterion for significance.

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.gc60p> (Sepp et al. 2016).

Results

Male common gulls were 14% heavier and had 7% longer heads than females (Table 1). White wing patches of males were 14% larger than those of females; however the overlap (and coefficients of variation) of patch size between sexes

Table 1. Comparison of morphological and demographic parameters of male and female common gulls. Breeding age is number of years since first breeding when an individual was captured. Breeding life span is a number of breeding years and it is given for individuals captured at 1997 and 1998 and whose age of death was known. Wing tip abrasion is assessed on the four point scale from 0 (no abrasion) to 3. For the birds measured twice (35 individuals), first or second measurement was chosen randomly, except for head length, where mean values of two measurements were used. Variances did not differ between sexes for any of the traits (p always > 0.06). p-values are from t-tests.

| | Mean ± SD (CV) n | | | |
Trait	Females	Males	t	p
Head length (mm)	87.5 ± 1.9 (0.02) 198	94.0 ± 2.1 (0.02) 218	−32.6	< 0.0001
Body mass (g)	400.9 ± 22.2 (0.06) 54	455.5 ± 26.9 (0.06) 61	−11.8	< 0.0001
White wing patch size (mm²)	1343.5 ± 307.1 (0.23) 216	1513.1 ± 270.9 (0.18) 230	−6.2	< 0.0001
Black wing tip size (mm²)	192.6 ± 53.5 (0.28) 105	180.3 ± 53.3 (0.30) 108	1.7	0.10
Black/white area ratio	0.151 ± 0.058 (0.38) 105	0.127 ± 0.049 (0.39) 108	3.3	0.001
Wing tip abrasion score	1.62 ± 0.78 (0.48) 105	1.57 ± 0.75 (0.48) 108	0.6	0.54
Breeding age (years)	6.40 ± 5.18 (0.81) 215	5.88 ± 5.01 (0.85) 223	1.07	0.29
Breeding life span (years)	12.36 ± 5.63 (0.46) 182	12.78 ± 6.05 (0.47) 188	−0.7	0.49
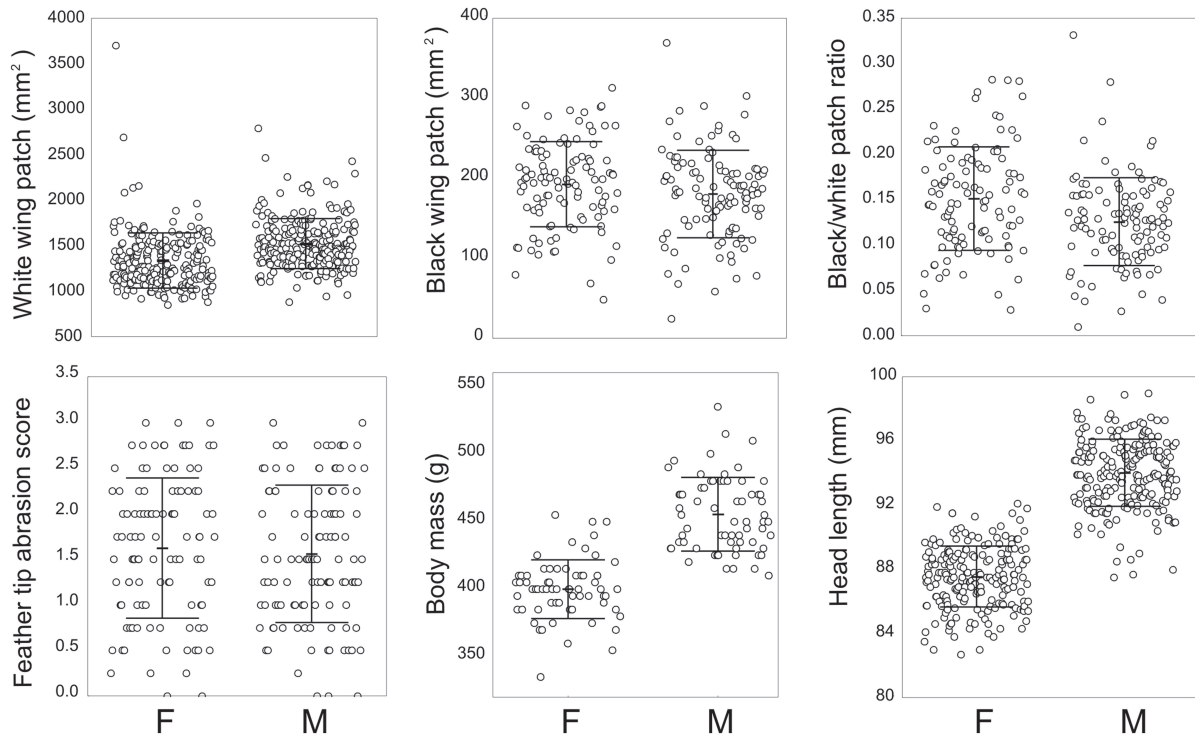
Figure 3. Comparison of plumage traits and morphological traits of female and male common gulls. Whiskers indicate means and standard deviations. See Table 1 for additional information.

was higher than that of head length and body mass (Fig. 3, Table 1). Size of the black wing tip and the extent of wing tip abrasion did not differ between sexes; average ages and life expectancies of males and females were similar (Table 1). Size of a white wing patch was individually highly repeatable over decade (females, $F_{18,19} = 17.7$, $R = 0.89$; males, $F_{15,16} = 11.4$, $R = 0.84$).

Area of black wing tip correlated negatively with that of white patch in sexes combined ($r_s = -0.30$, $p < 0.00001$, $n = 221$) and in females ($r_s = -0.30$, $p = 0.002$, $n = 107$) and males separately ($r_s = -0.25$, $p = 0.005$, $n = 114$). Wing patch size tended to decrease with age in most females except the ones measured at younger age ($r = -0.61$, $p = 0.012$, $n = 16$), while males showed no consistent age-dependent changes ($r = -0.02$, $p = 0.94$, $n = 18$, Fig. 4). However, these correlation coefficients did not differ significantly in a two-tailed test ($z = -1.82$, $p = 0.069$). Analysis of cross-sectional data showed that the birds in the middle of their reproductive age had largest white wing patches. This pattern was similar in both sexes (Table 2, Fig. 5). Size of black wing tips, black/white ratio and wing tip wear did not associate with age in mixed effects model accounting for linear and quadratic effects of breeding age, sex or their interaction (all p-values > 0.4; Supplementary material Appendix 1, Table A1–A3).

Females with smaller white wing patches and higher proportion of black in relation to white had higher wing abrasion scores ($r_s = -0.21$, $p = 0.028$ and $r_s = 0.21$, $p = 0.032$, $n = 107$, respectively). Black wing tip area was not associated with abrasion ($r_s = 0.14$, $p = 0.149$, $n = 107$). No significant associations between any measures of pigmentation and abrasion emerged in males ($r_s = 0.05$ to -0.12, $p = 0.22$ to

0.59, $n = 114$). When correlations between wing coloration and abrasion were pairwise compared between females and males, all 95% CI values for Spearman r-s overlapped).

In the whole dataset, birds with larger white wing patches had generally higher chances of survival, irrespective of sex (Table 3, Fig. 6a). In the subsample of data for 64 birds for which we had measures of black wing tip area, absolute and relative (to white patch area) size of the black wing tips significantly predicted survival (Table 4, Fig. 6b).
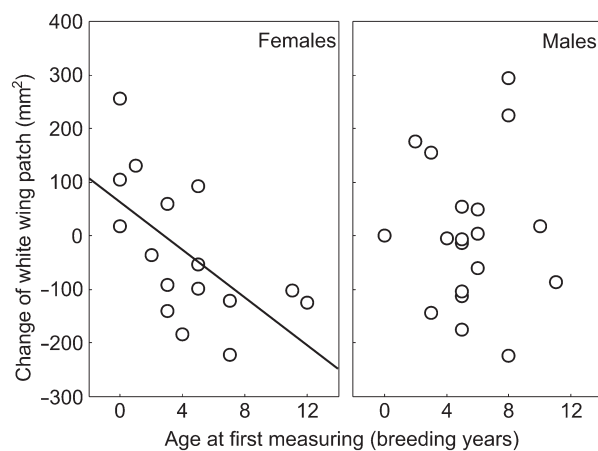

Figure 4. Age-dependent changes in white wing patch sizes in females and males in relation to age at first measuring. The difference between two measurements of individual birds is 9–10 yr. In all figures, age at measuring is given in years since first breeding event. Both linear (p = 0.019) and quadratic (0.015) effect remained significant after the female outlier was removed from the model.

Table 2. White wing patch size in relation to sex and breading year. Linear mixed-effects model fit by maximum likelihood with individual identity as random effect. In total 477 measurements from both sampling periods (422 unique individuals). Model simplification did not reduce goodness of fit (likelihood ratio test L = 2.96, DF = 2, p = 0.23). B is regression coefficient and SE its standard error.

	B	SE	denDF	F	p
Full model					
Breeding year	23.7	8.1	31	8.7	0.006
Sex	201.0	47.6	440	17.8	< 0.0001
Breeding year^2	−1.4	0.4	31	10.2	0.003
Sex × Breeding year	−14.1	12.5	31	1.3	0.27
Sex × Breeding year^2	0.9	0.6	31	2.1	0.15
Simplified model					
Breeding year	17.1	6.3	33	7.3	0.011
Breeding year^2	−0.9	0.3	33	7.6	0.009
Sex	174.2	27.5	440	40.1	< 0.0001

Table 3. Survival in relation to white wing patch size. Cox proportional hazards test, n = 320. Model simplification did not reduce goodness of fit (likelihood ratio test, X^2 = 3.8, DF = 2, p = 0.14).

	B	SE(β)	exp(β)	p
Full model				
White patch size (z-score)	0.07	0.08	0.93	0.3743
Sex	0.20	0.12	0.82	0.0776
Breeding year	−0.07	0.01	1.07	< 0.0001
White patch × Sex	0.10	0.12	0.90	0.3771
Simplified model				
White patch size (z-score)	0.12	0.06	0.88	0.0303
Breeding year	−0.07	0.01	1.07	< 0.0001

Irrespective of sex, birds with smaller black wing tips had higher survival chances than the birds with larger black wing tips. When the areas of white wing patch and black tip were simultaneously entered into a model predicting survival, neither was significant. However, the value of β for black was more than three times higher than that of white and close to significance (Table 5). When the area of black wing tips was dropped from the model, size of the white wing patch nearly significantly predicted survival (β = 0.28 ± 0.15 (SE), p = 0.064), in a model accounting for breeding year (β = 0.09 ± 0.03, p = 0.009) in the sample of 64 birds for which we had data on selection on black wing tips. In the same sample, wing tip abrasion did not predict survival (β = 0.06 ± 0.17, p = 0.711) in a model accounting for breeding year (β = 0.08 ± 0.04, p = 0.024).

Discussion

White wing patch

The most clear cut findings of this study relate to variation in white wing patch size. Male common gulls had 14% larger white wing patches than females. The variation in wing patch
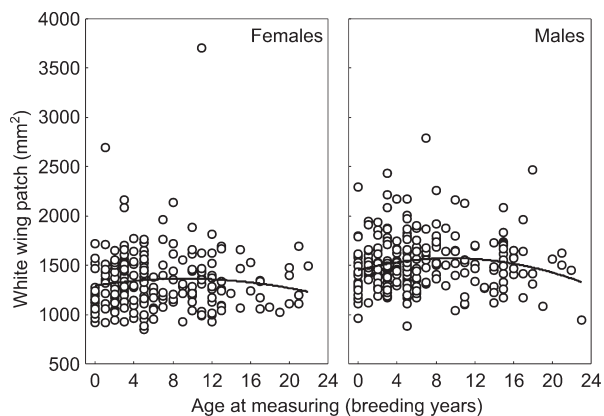

Figure 5. Relationship between age and white wing patch size in a cross-sectional sample in female and male common gulls. Age at measuring is given in years since first breeding event.

size among females and males was of comparable magnitude (CV = 0.23 in females and 0.18 in males) and remarkably higher than variation in body mass or head length (CV = 0.02 to 0.06: Table 1). High within-population variation in trait values has been traditionally considered as characteristic to ornamental traits (Alatalo et al. 1988, Møller and Pomiankowski 1993). Ornamental function of white wing patches is also suggested by the findings that 1) patch size showed a concave age-dependency in cross-sectional sample and that 2) the same trait was positively associated with survival. Both patterns were similar in males and females. Altogether these findings suggest that large white wing patches in common gulls signal viability, irrespective of sex.

Smaller wing patches of old birds can result either from individual decline of patch size after midlife or selective disappearance of senescent individuals with large wing patches. Our sample size for repeatedly measured individuals was too small for partitioning the age-related changes in patch size into within- and between-individual components. However, the sample of 16 individual females captured over decade clearly showed decline of patch size with age. No such pattern emerged in males. We lacked sufficient test power to detect whether this sex difference in age-related pattern was statistically significant, so we cannot exclude the possibility that males possessing large white wing patches after midlife were selected against.

Concave relationship between white wing patch size and age indicates that it is a condition-dependent trait. Consistent with this, previous studies in the same colony have shown that middle-aged birds start their annual breeding attempts earlier (Rattiste et al. 2015), lay heavier eggs (Urvik et al. 2016) and their breeding success exceeds that of young and old individuals (Rattiste 2004). Also consistent with an idea of condition dependency is the finding that females with larger white wing patches experienced lower extent of abrasion of wing tips. Although the repeatability of wing abrasion measurement was moderate (0.67) and it's correlation with patch size was not very high (−0.21), these patterns can still be interpreted to support an idea that at least in female common gulls, the size of white wing patch could serve as a Zahavian handicap (Zahavi 1975). For instance, Kose and Møller (1999) showed that both male and female barn swallows *Hirundo rustica* with long tails had larger white tail spots than short-tailed individuals, tail spots appear to be preferred sites for feeding by Mallophaga, and that feather breakage is more likely in the white tail spots. In our study, the relationship between wing patch size and abrasion was
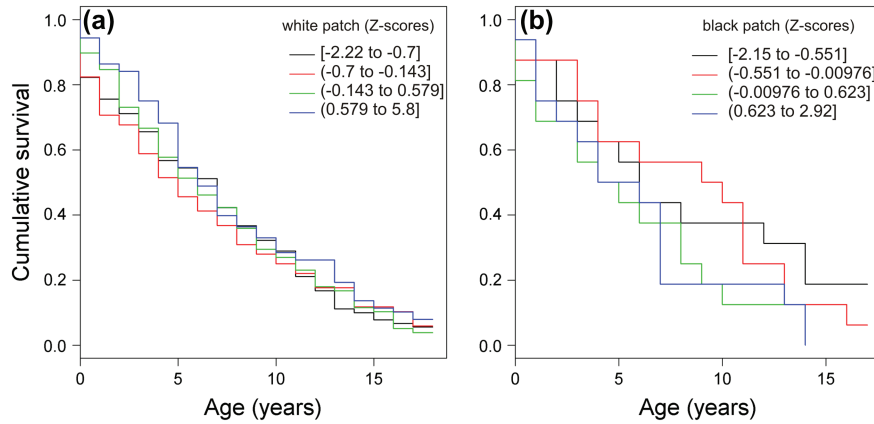
Figure 6. Age-related survival probability of the birds in relation to the size of white wing patches (a) and black wing tips (b). Colours denote quartiles. Sizes of black and white wing markings sre standardized to z-scores (mean = 0, SD = 1) within sex to enable analysing survival of both sexes in the same model.

not significant in males. However, comparison of 95% confidence intervals did not enable to conclude that the correlation in males had differed from that of females significantly. Present data thus do not enable to establish whether the association between white wing patch size and wing tip abrasion actually differed between the sexes. Nonetheless, this finding is interesting in the context of another study of long-lived birds, south polar skuas (Hanssen et al. 2009) showing that females with larger white wing patches laid larger eggs but survived less well than females with small patches, while the whiteness of the patch was positively associated with survival. None of the wing patch characteristics was associated with survival in male skuas. Another study in a long-lived bird, the barn owl, also showed that selection on a plumage trait (size of eumelanic spots) was stronger in females than

in males (Roulin et al. 2010). Altogether these findings are consistent with a prediction that elaborate ornamental traits on both sexes are likely to evolve due to mutual selection, in particular among monogamous long-lived species with biparental care (Johnstone et al. 1996, Kraaijeveld et al. 2007).

Common gulls breed colonially, which provides ample opportunities for mate assessment. Both partners participate in defending territory, incubation and feeding the young. We lack the data for the frequency of extrapair paternity from our population, but elsewhere it has been reported to occur among 8% of broods (Bukacińska et al. 1998). Both females and males have on average two partners during the breeding life span (Brommer and Rattiste 2008). New pairs are formed either due to the death of previous partner or divorce. Frequency of divorce ranges from 20% among inexperienced breeders to 10% among experienced birds and divorce is more common among the birds with poor hatching success in the previous year (Rattiste and Lilleleht 1986). Males also practice forced extra-pair copulations while females still seem to maintain the control over fertilizations (Bukacińska et al. 1998). Pairs that have bred together previously are able to start breeding earlier (KR unpubl.) and earlier breeding is consistently selected for in the studied population (Brommer and Rattiste 2008). Such mating system offers opportunities for both female and male choice and intra-sexual signaling.

Table 4. Survival in relation to (A) black wing tip size and (B) black to white ratio. Cox proportional hazards test, n = 64. Model simplification did not reduce goodness of fit neither for black wing tip area (likelihood ratio test, $X^2 = 0.84$, DF = 2, p = 0.7), nor black to white ratio (likelihood ratio test, $X^2 = 0.62$, DF = 2, p = 0.7).

(A)

	B	SE(β)	exp(β)	p
Full model				
Black wing tip size (z-score)	−0.40	0.21	1.49	0.063
Sex	0.24	0.28	0.79	0.4
Breeding year	−0.10	0.04	1.10	0.008
Black wing tip × Sex	0.07	0.27	0.93	0.8
Simplified model				
Black wing tip size (z-score)	−0.35	0.13	1.42	0.009
Breeding year	−0.09	0.03	1.09	0.012

(B)

	B	SE(β)	exp(β)	p
Full model				
Black/white ratio	−0.28	0.19	1.32	0.15
Sex	0.21	0.27	0.81	0.4
Breeding year	−0.10	0.03	1.10	0.006
Patch size × Sex	−0.06	0.24	1.06	0.8
Simplified model				
Black/white ratio	−0.31	0.12	1.37	0.012
Breeding year	−0.10	0.03	1.10	0.008

Table 5. Test for simultaneous survival selection on areas of white and black wing markings. Cox proportional hazards test, n = 64. Model simplification did not reduce goodness of fit (likelihood ratio test, $X^2 = 3.36$, DF = 3, p = 0.3).

	B	SE(β)	exp(β)	p
Full model				
White patch size (z-score)	−0.18	0.25	1.20	0.5
Sex	0.27	0.28	0.76	0.3
Black wing tip size (z-score)	−0.48	0.24	1.62	0.040
Breeding year	−0.11	0.04	1.12	0.003
White patch × Sex	0.57	0.36	0.57	0.1
Black wing tip × Sex	0.37	0.33	0.69	0.3
Simplified model				
White patch size (z-score)	0.09	0.18	0.91	0.6
Black wing tip size (z-score)	−0.31	0.16	1.36	0.061
Breeding year	−0.09	0.03	1.10	0.01

For instance, studies of carotenoid-based bare-skin ornaments in other seabirds with similar mating systems have shown that females possess ornaments that are highly variable and condition-dependent (Doutrelant et al. 2013) and honestly reflect maternal investment in egg quality (Blount et al. 2002, Kristiansen et al. 2006). Findings of the current study that the size of white wing patch was similarly highly variable and associated with age and survival in both sexes is thus most likely explained by mutual mate choice on this trait. Such mutual mate choice has been experimentally demonstrated with respect to ornamental plumes in crested auklet *Aethia cristatella* (Jones and Hunter 1993) and on foot coloration in blue-footed booby *Sula nebouxii* (Torres and Velando 2005).

Despite similarly high variation in males and females, common gull males in our study still had 14% larger wing patches than females, which suggest that female choice and/or male–male competition have played a role in evolution of this trait (Jones et al. 2000). Alternatively, it may be possible that sexual dimorphism in white wing patch size (similarly to that of body size) reflects the earlier evolutionary origin of this trait, so that its signaling function for females was acquired more recently. Such situation may not be uncommon, given that measures of body size in sexually dimorphic species often reveal smaller variation than ornamental traits (Cuervo and Møller 2001).

Black wing tip

Our sample size for black wing tips (and wing tip abrasion) was considerably smaller than that for white wing patches (Fig. 1, Table 1–4), which might have possibly hampered our ability to detect the association between black wing tip size, age, and wing abrasion. However, the high variation and strong viability selection detected with respect to this trait deserve attention. The size of black wing tip was initially considered as a utilitarian trait because we assumed that its function is to protect wing tips from abrasion. Utilitarian traits are expected to show much smaller within-population variation than ornamental traits because these are supposedly subject to stabilizing selection (Alatalo et al. 1988) and less costly and condition-dependent than ornamental traits (Møller and Pomiankowski 1993, Cuervo and Møller 2001). Contrary to our expectations, coefficients of variation for black wing tip size (0.28 and 0.30) and black/white area ratio (0.38 and 0.39) were considerably larger than those for white wing patch area (0.23 and 0.18). Further, the coefficients of variation for black appeared larger than those for previously published ornamental traits in several bird species, ranging from 0.06 to 0.26 with an average for 0.12 (Alatalo et al. 1988, but see Møller and Petrie 2002). Consistent with high variation, the viability selection on black wing tip size (both absolute and relative to white) was stronger than selection on white wing patch size). Interestingly, survival selection favored birds with smaller black wing tips and the areas of white patches and black tips correlated negatively (Table 3 and 4). This raises the question whether the white and black areas in the wing tips of common gulls should be considered as a single composite trait or if the size of one color patch could serve as an amplifier for another. Answering these questions would require measuring sexual

selection for both patches for which we currently lack data. In any case, detection of viability selection for the smallness of color patch is probably a unique finding which further complicates current understanding about the evolution of ornamental traits.

Assumption that signaling value of ornamental traits is based on their integration with the functionality of some important physiological process (Hill 2011, 2014) requires presence of mechanisms that enhance the quality of birds with smaller black wing tips. We suggest that a possible link here would involve physiological pathways that increase resistance of wing feathers to abrasion. For instance, resistance to feather-degrading bacteria and ectoparasites is likely to be mediated by uropygial gland functioning (reviewed by Ruiz-Rodríguez et al. 2014). This gland produces waxes, sterols and hydrocarbons that are important to maintain the plumage supple, rigid and to protect it against abrasion (Jacob and Ziswiler 1982, Shawkey et al. 2003). Uropygial gland development is costly as shown in tawny owls *Strix aluco* (Piault et al. 2008) and house sparrows *Passer domesticus* (Pap et al. 2013). In house sparrows the size of uropygial gland also correlated positively with body condition, immune responsiveness and resistance of feathers to chewing lice (Moreno-Rueda 2010). Interestingly, the same study found that birds with larger white wing patches had larger uropygial glands. Also barn owls with larger uropygial glands had less eumelanotic plumage (Roulin 2007). The studies cited above point to the possibility that the size of unpigmented plumage patches (in relation to melanic patches) may appear as an honest indicator about the functionality of uropygial gland in protection of feathers from damage. Our finding that common gull females who had lower proportion of black in relation to white had lower wing abrasion scores is consistent with results of these studies. Altogether such findings suggest that co-occurrence of white and dark plumage patches may have evolved as to enable signaling of damage-resistance of white patches.

Conclusions

We found evidence for high variation, age- and condition dependence and viability selection on the size of wing markings in a long-lived monogamous seabird species. Size of white wing patches exhibited concave relationship with age, demonstrating that ornamental traits are prone to senescence in a similar manner to reproductive performance. Most of observed patterns were indistinguishable between males and females, which supports the idea of mutual mate choice and/or intra-sexual selection as predicted for colonial long-lived monogamous species. The most peculiar finding of this study, i.e. superior survival of birds with small black wing tips, suggests that white and black wing markings may have coevolved as reverse components of a single ornament.

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Supplementary material (Appendix JAV-01136 at <www.avianbiology.org/appendix/jav-01136>). Appendix 1.