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RESEARCH ARTICLE

Uropygial gland size: a marker of phenotypic quality that shows no senescence in a long-lived seabird

Janek Urvik · Kalev Rattiste · Peeter Hõrak · Richard Meitern · Tuul Sepp

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Abstract Studies of senescence in the wild have traditionally focused on traits like survival or fecundity. Although efforts to measure other salient phenotypic traits and markers of relevant physiological processes are rapidly increasing, traits related to self-maintenance remain understudied in the context of aging. Uropygial or preen gland is a holocrine gland, exclusive to birds, directly linked to self-maintenance of the quality of plumage. We measured the size of uropygial glands of common gulls (*Larus canus*) in a cross sectional manner in order to test whether it shows the similar age-related decline as reproductive traits previously recorded in this species. Gulls with larger glands started breeding earlier in the season, indicating that gland size is a marker of individual phenotypic quality. We found a senescent decline in the onset of breeding and the size of white wing patches, a sexually dimorphic ornamental trait, while in contrast, preen gland increased with advancing age. This finding supports the view of life-history theory that in long-lived species whose lifetime reproductive success depends heavily on lifespan, self-maintenance is prioritized over reproduction. Altogether our results support the concept that senescence in the wild can be asynchronous for traits related to maintenance versus reproduction.

Keywords Aging · Aging asynchrony · Common gull · Phenotypic quality · Preen gland · Senescence

Introduction

Recent field studies and reviews have indicated that senescence, the gradual deterioration of function with age, is common in wild animals (Nussey et al. 2013). There is considerable variation in the course of aging and trajectories of senescence by traits across species, depending mainly on levels of environmentally imposed mortality (Roach 2016). Slower rates of aging are expected in populations or species with low rates of extrinsic mortality, for example in species such as turtles, which have protective shells (Warner et al. 2016), or seabirds, that are better protected against predation, contagious disease, starvation, and weather-related stress than most terrestrial animals (Holmes and Austad 1995; Moe et al. 2007). Species with different rates of extrinsic mortality and different lifespans are expected to have different optimal

J. Urvik (✉) · P. Hõrak · R. Meitern · T. Sepp
Institute of Ecology and Earth Sciences, University of Tartu, Vanemuise 46, 51014 Tartu, Estonia
e-mail: urvik.janek@gmail.com

K. Rattiste
Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 1, 51006 Tartu, Estonia

T. Sepp
School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501, USA

investment in somatic maintenance and repair (Moe et al. 2007). Long-lived species are therefore excellent model systems for understanding the patterns of age-dependent investment in self-maintenance in relation to the senescent decline in physiological functions in natural environment. In this context, birds deserve special attention because they have longer lifespans and fewer signs of ageing than expected from their body size and rates of energy metabolism (Holmes and Ottinger 2003).

Studies of senescence patterns in the wild have mostly concentrated on traits most proximate to fitness (i.e. survival and fecundity). While efforts to measure other salient phenotypic traits (e.g. body mass, secondary sexual characters, parental investment, foraging behaviour) and markers of relevant physiological processes (e.g. endocrine function, sarcopenia, oxidative stress, telomere length) are rapidly increasing (Nussey et al. 2013), traits related to self-maintenance remain understudied in the context of aging.

Here we focus on a measure of uropygial gland size as a trait directly linked to self-maintenance, quality of plumage-based sexual signals, and defence against parasites. Uropygial or preen oil gland is a holocrine gland that is exclusive to birds and is located in the integument above the posterior free caudal vertebrae. While preening, birds squeeze the sebaceous secretion from the gland and transfer it across the entire body (Jacob et al. 1997). The uropygial gland size is positively correlated with the quantity of produced secretion (Martín-Vivaldi et al. 2009). Preen oil has been hypothesised to have several non-exclusive functions, including plumage maintenance (Giraudeau et al. 2010) water repellence (reviewed by Moreno-Rueda 2017) and defence against bacteria (Shawkey et al. 2003), ectoparasites (Moreno-Rueda 2010) and fungi (Jacob et al. 1997). Uropygial gland size has been shown to correlate positively with residual body mass and an index of immune function (a swelling response to intradermally injected antigen), being therefore related to bird health and condition (Moreno-Rueda 2010).

Since preen oil has numerous functions, it is reasonable to assume that maintaining uropygial gland function would have major fitness benefits for an individual. However, to our best knowledge, no studies on wild bird species have considered uropygial gland size as a potential marker of physiological condition in relation to age. For that matter, we measured uropygial gland size in male and female common gulls (*Larus canus*), aged from 2 to 28 years, in a cross-sectional manner. Previous studies in this species have indicated that reproductive senescence is common in this colony, with old birds starting breeding later and having lower breeding success (Brommer and Rattiste 2008), lower investment into egg quality (Urvik et al. 2018) and having smaller ornamental white wing patches (Sepp et al. 2017) than middle-aged birds. At the same time, traits related to physiological condition (telomere length and skin pentosidine concentration; Rattiste et al. 2015), and indices of oxidative and nutritional state (Urvik et al. 2016), do not show consistent age-related patterns. These findings are compliant with the prediction of the life-history theory that in long-lived species whose lifetime reproductive success depends heavily on lifespan, self-maintenance is prioritized over reproduction (Nussey et al. 2013).

The main purpose of this study is to test whether the size of uropygial gland (1) shows senescence, (2) correlates with other condition dependent traits such as the breeding onset, and a sexually dimorphic plumage ornament, the size of a white wing patch that have previously shown age-related decline in the studied population. We further asked (3) whether any of these potential links is expressed in a sex-specific manner, as to test for the occurrence of possible sex-specific senescence patterns. We start with testing for the occurrence of senescence in all measured traits (to be revealed as a quadratic relationship with age in case of condition-dependent traits) and continue by examining the associations between uropygial gland size versus plumage ornaments and breeding date.

Materials and methods

The study was conducted on a population located on Kakrarahu islet in Matsalu National Park on the west coast of Estonia (58°46′N, 23°26′E), in a breeding colony of common gulls with known ages (see Rattiste 2004). Data for the study, including 109 birds (54 males and 55 females, gland measurements missing for 2 females and breeding age missing for 1 male and 3 females), were collected in May 2016. Birds were caught from nests using spring traps, and to avoid nest abandonment, all birds were caught after the tenth day of incubation. The study protocol complies with the laws of the Republic of Estonia.

Laying date of the first egg was determined by daily inspections of the nests. In common gulls clutch size is invariant (three eggs), and laying date is thus presumably a key reproductive trait in this species. We consider the date of laying of the first egg as a proxy of both male and female reproductive success, because there is a strong selection for early laying in this population and female's laying date depends on the male's ability to arrive early to the colony and quickly establish and defend a breeding territory, his ability for courtship feeding, and his timing of spermatogenesis and copulation prowess (Brommer and Rattiste 2008).

All birds were photographed with their right wing pressed against a flat surface with a ruler placed next to it for scale (Fig. 1, see Sepp et al. 2017 for method details). White wing patch area, a sexually dimorphic measure of wing ornamentation, was measured in mm^2 from digital photographs using IMAGEJ software (http://rsbweb.nih.gov). To assess the repeatability of the measurements, a subsample of 56 birds were measured twice from the same photograph and another subsample of 8 was photographed twice. Repeatability of the measurements was high (0.99, $F_{55,56} = 176.5$, $p < 0.0001$ and 0.95, $F_{7,8} = 38.5$, $p < 0.0001$ respectively), so only the first measurement was used for the analyses.

Diameter of uropygial gland was measured with a dialed caliper to the nearest 0.1 mm. For repeatability, 19 birds were caught and measured twice, trapping events usually separated by at least one day. Repeatability of gland diameter was 0.86 ($F_{16,19} = 14.25$, $p < 0.0001$). For birds with multiple measurements, average gland diameter was used in the analyses.

As the exact age was not known for all birds and since common gulls are highly faithful to their breeding colony (Rattiste 2004), breeding age (defined as a 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 these analyses to reduce the risk of underestimation of breeding age. Age and breeding age correlated strongly ($r = 0.98$, $p < 0.0001$, $n = 88$) in a subsample of birds for which both parameters were known.

All dependent variables used in the analyses (uropygial gland diameter, wing patch area and laying date) were normally distributed, allowing to use parametric statistical analyses (t-tests for comparing

Fig. 1 Measures of white wing patch area 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

trait values between sexes, ANCOVA-s for testing the sex-specific associations between breeding age or uropygial gland size vs. dependent variables). Occurrence of age-related patterns in gland diameter, wing patch area, and laying date was tested by examining the significance of square of breeding age as a predictor variable. Occurrence of sex differences in the rate of trait senescence was tested by examining the interactions between the sex and squared breeding age. Occurrence of sex differences in the linear age-related changes in trait values was tested by examining the interactions between the sex and linear effect of breeding age. The P value for accepting statistical significance was 0.05. Statistical analyses were performed with a software package STATISTICA version10 (StatSoft, Inc. 2011; www.statsoft.com).

Results

We did not detect sex differences in the diameter of uropygial gland (males: 5.15 ± 0.99 mm, females: 4.96 ± 1.01 mm, $t_{53,52} = 0.97$, $p = 0.335$) while males had 14% larger white wing patches than females (males: 1368 ± 258 mm^2, females 1153 ± 227 mm^2, $t_{54,55} = 4{,}62$, $p = 0.00001$; mean ± SD presented). Laying date showed similar concave relationship with breeding age among both males and females (Fig. 2a; breeding age squared: $F_{1,104} = 38.4$, $p < 0.000001$; sex × breeding age squared: $F_{1,102} = 0.87$, $p = 0.352$). Wing patch size showed similar convex relationship with breeding age in both sexes (Fig. 2b; breeding age squared: $F_{1,103} = 6.9$, $p = 0.010$; sex × breeding age squared: $F_{1,102} = 0.4$, $p = 0.505$).

Uropygial gland increased with advancement of breeding stage and age (Fig. 2b, Table 1. No significant quadratic terms for age could be detected ($F_{1,101} = 1.2$, $p = 0.271$)).

Birds with larger uropygial glands started breeding earlier (Table 1, Fig. 3). We did not detect any sex-specific patterns in associations between uropygial gland diameter versus age, laying date or wing patch size (Table 2).

Discussion

Irrespective of sex, laying date and the size of white wing patches showed clear age-related patterns. Middle-aged birds started egg-laying and had larger wing patches than young and old individuals. This result is consistent with the previous findings of the longitudinal studies from the same population, demonstrating senescence in annual fitness (Rattiste 2004; Brommer and Rattiste 2008) and wing patch size (Sepp et al. 2017). Previous study in the same population (Sepp et al. 2017) suggested that size of the white wing patch in common gulls may serve as an honest handicap signal of individual quality: possessing unpigmented areas in the tip of the wing is probably costly as feather breakage is more likely in the sites that lack protection by melanin (reviewed by Burtt 1986). Thus only individuals in superior condition (that being, for example, stronger feather structure, more protective preen gland, or ability to avoid situations where feathers may break) can afford large unpigmented areas in wingtips, and the size of these areas enables them to signal their prime condition (Zahavi 1975). Consistent with signalling function of white wing patches are the findings that their size was positively related to survival and that individuals with larger white wing patches experienced lower extent of abrasion of wing tips (Sepp et al. 2017). It is thus most likely that the later start of breeding and smaller wing patches of old common gulls reflect senescence of reproductive and signal traits. Alternative explanation would be selective disappearance of early breeders and birds with the large wing patches among the oldest age classes. However, such a scenario would be difficult to reconcile with widely established condition-dependency of reproductive and signal traits (van Noordwijk and de Jong 1986; Andersson 1994; Rowe and Houle 1996).

In contrast to laying date and wing patch size, diameter of the uropygial gland showed monotonous increase with age (Fig. 2b). Notably, gland diameter also correlated strongly with laying date, so that birds with larger uropygial glands started breeding earlier. Given that early onset of breeding is a major determinant of annual reproductive success in the studied colony and that survival selection favours early-breeding females (Brommer and Rattiste 2008), our findings suggest that diameter of uropygial gland is an excellent marker of individual phenotypic quality in breeding common gulls. In this context, absence of decline in preen gland diameter in old birds is notable. Although the cross-sectional design of the current study does not enable to demonstrate directly the

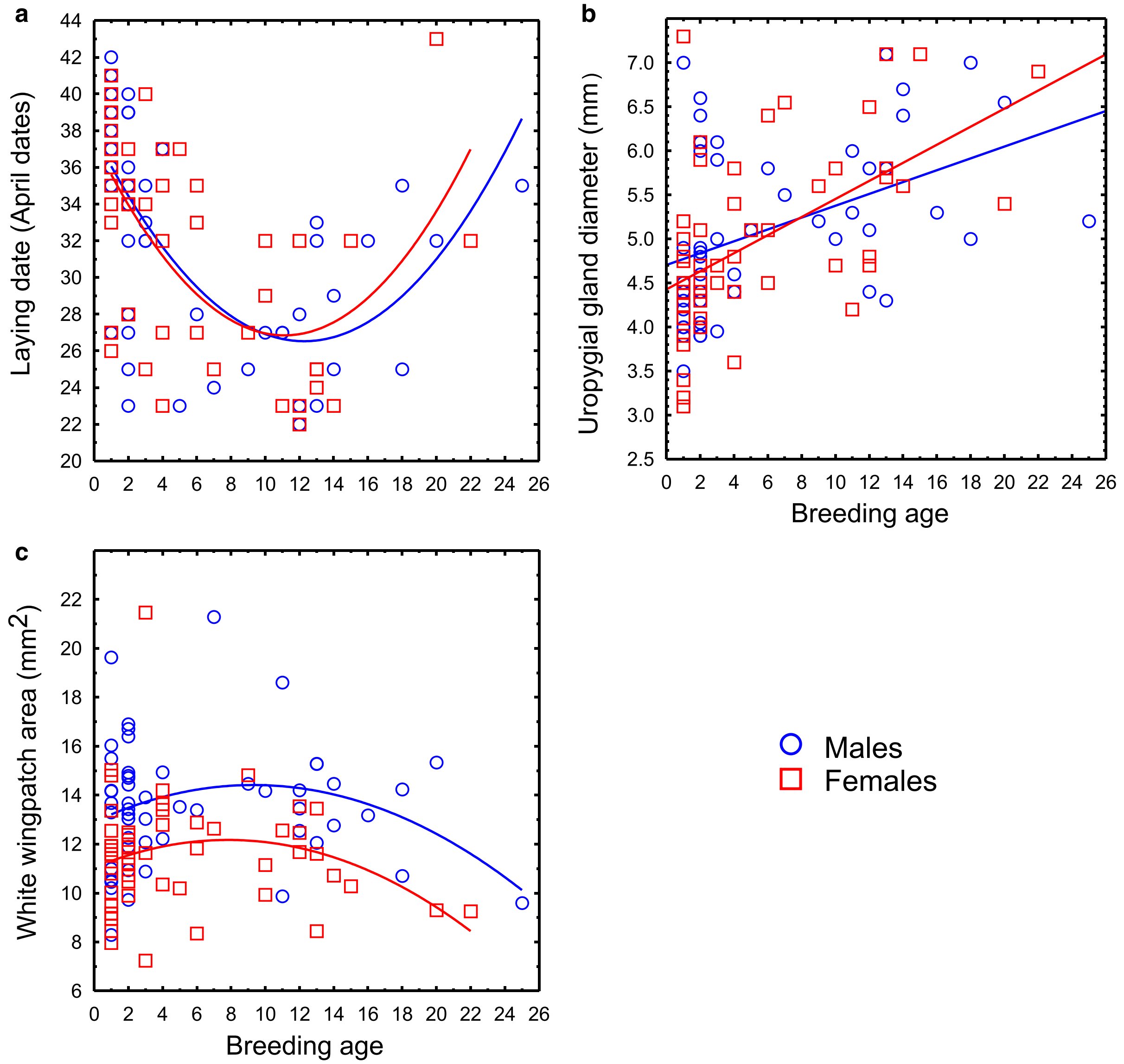

Fig. 2 Age-related changes in **a** laying date, **b** diameter of uropygial gland, **c** wing patch area. Second order polynoms are fitted if squared term for breeding age is statistically significant; otherwise lines for linear regression are presented. Squares and red lines denote females and circles and blue lines denote males. Laying date is expressed in April dates (day 1 = 1st April)

absence of senescence in preen gland diameter, we suggest that monotonous increase of the preen gland size with age can be best explained by selective disappearance of the birds with smaller preen glands (and thus less capable of maintaining plumage in prime condition) from the older age cohorts. Consistent with such a scenario, a recent study in house martins (*Delichon urbica*) showed that malaria-infected birds with larger uropygial glands were better able to survive to the next breeding season, while infected birds with small uropygial glands were not (Magallanes et al. 2017).

Absence of age-related decline in uropygial gland size in old birds compares favourably with results of previous studies (Rattiste et al. 2015; Urvik et al. 2016; Sepp et al. 2017), indicating that older common gulls do not show physiological indication of senescence in traits other than reproduction, prioritizing self-maintenance over reproduction in older age. Occurrence of different age-related patterns among (intercorrelated)

Table 1 Predictors of the diameter of uropygial gland in the multiple regression analysis

Trait	F	P	η^2	β (SE)
Breeding stage	29.4	< 0.0001	0.23	− 0.67 (0.12)
Breeding age	13.4	0.0004	0.12	0.27 (0.08)
Laying date	56.9	< 0.0001	0.36	− 0.99 (0.13)
Wing patch size	0.2	0.287	0.0	0.03 (0.07)

Adjusted R^2 for the model = 0.51. Breeding stage denotes time interval between the onset of laying and measurement of the gland (the number of days passed between the laying of first egg and catching the bird for gland measurement). η^2 stands for partial η^2, a measure of effect size (variance explained by a given variable of the variance remaining after excluding variance explained by other predictors). β is standardized regression coefficient. DF = 1 and 100 for all variables

indices of physiological condition is consistent with the concept that aging is multidimensional and can be asynchronous in wild animals (Hayward et al. 2015). For instance, it has been shown, that in wild ungulates reproductive senescence may start later and progress more rapidly, than age-related declines in survival probability (Nussey et al. 2013) and in some mammal species even post-reproductive survival has been documented (Croft et al. 2015).

Differentiation of male and female reproductive strategies is expected to produce sex-specific optima for traits that affect longevity and ageing rate, often favouring a 'live fast, die young' strategy in males, relative to females, although numerous exceptions to this pattern are observed and sex-differences in ageing rate, in particular, remain poorly understood (Bonduriansky et al. 2008). Within literature of aging in the wild, there is mounting evidence for both differences in ageing rates between the sexes and asynchrony among phenotypic traits within sexes in the way they change with age in later life (Nussey et al. 2013). Previous studies have revealed sex-specific temporal patterns in preen gland size, with females reaching a maximum gland size later in the breeding season than

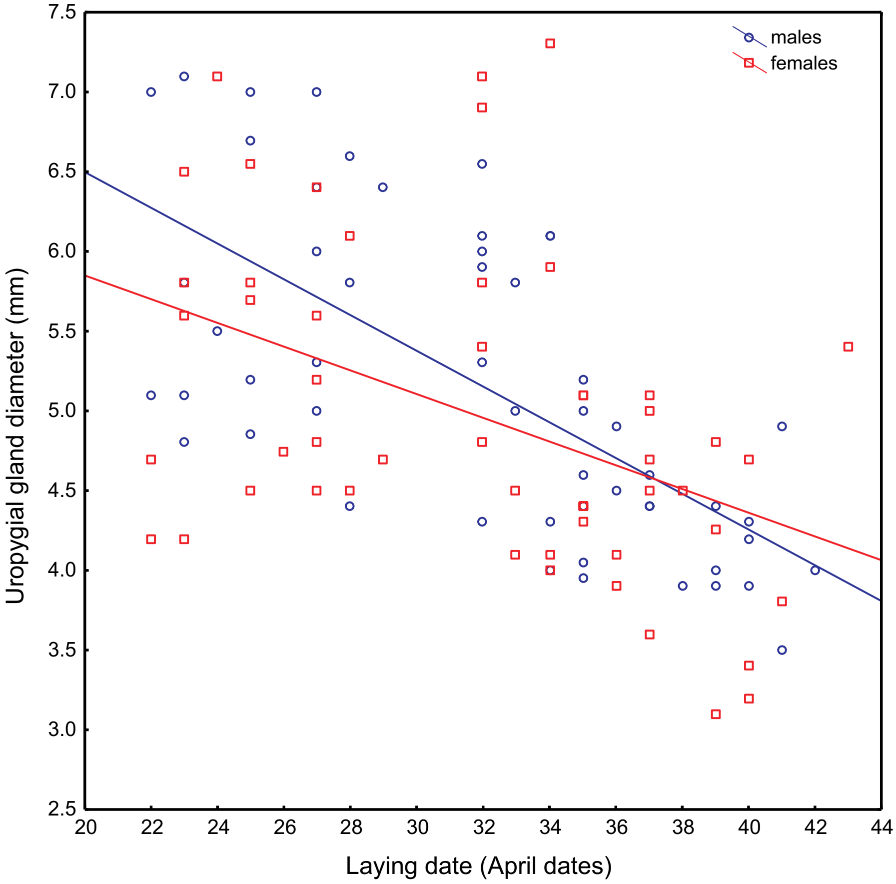

Fig. 3 Associations between the diameter of uropygial gland size and laying date. Laying date is expressed in April dates (day 1 = 1st April)

Table 2 ANCOVAs for sex-specific associations between uropygial gland diameter versus breeding age, laying date and white wing patch size

Trait	F_{DF}	P	η^2	β (SE)
Sex	$1.4_{1,101}$	0.246	0.01	0.14 (0.12)
Breeding age	$33.0_{1,101}$	< 0.0001	0.25	0.50 (0.09)
Sex × breeding age	$1.1_{1,101}$	0.234	0.01	− 0.14 (0.12)
Sex	$2.3_{1,103}$	0.125	0.02	0.70 (0.46)
Laying date	$44.9_{1,103}$	< 0.0001	0.30	− 0.54 (0.08)
Sex × laying date	$1.8_{1,103}$	0.179	0.02	− 0.61 (0.46)
Sex	$3.0_{1,103}$	0.088	0.03	− 0.97 (0.56)
Wing patch size	$0.7_{1,103}$	0.402	0.00	0.09 (0.11)
Sex × wing patch size	$3.2_{1,103}$	0.077	0.03	1.03 (0.57)

Adjusted R^2 for the model with age is 0.23, for the model with laying date 0.31 and for the model with wing patch size 0.03

males (Golüke and Caspers 2017, but see also Pap et al. 2010 for the contrary). In the current study, we failed to detect any sex-specific relationships between uropygial gland size versus age and laying date; nor did we detect any associations between gland size and sexually dimorphic wing ornaments. Absence of the association between the size of preen gland and white wing patches is notable, given that in this population survival selection favours both male and female gulls with larger white wing patches. One might thus speculate that expression of this type of ornaments is independent of the maintenance function provided by the preen gland.

In conclusion, we showed that preen gland is an age-related quality indicator in a long-lived bird, since common gulls with larger glands have reached older age and can start breeding earlier in the season. Supporting our previous findings in the same colony, this long-lived species seems to prioritize self-maintenance over reproduction, since a trait related to self-maintenance (preen gland size) did not show senescence, while a trait related to reproductive success, the date of laying the first egg, did. Our study supports the understanding that senescence in the wild can be asynchronous, and more attention should be directed towards age-dependence of life-history trade-offs and sex-specific investment in life-history traits in relation to aging.

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Authors' contribution KR, TS and PH designed the study. JU, TS, RM and KR carried out the fieldwork. JU analyzed photos. PH, RM and JU carried out statistical analyses. TS, PH and JU drafted the manuscript. All authors gave final approval for publication.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Data accessibility All the data used for the study will be available through Dryad data repository after the manuscript's acceptance.

References

Andersson M (1994) Sexual selection. Princeton University Press, Princeton

Bonduriansky R, Maklakov A, Zajitschek F, Brooks R (2008) Sexual selection, sexual conflict and the evolution of ageing and life span. Funct Ecol 22:443–453

Brommer JE, Rattiste K (2008) "Hidden" reproductive conflict between mates in a wild bird population. Evolution 62:2326–2333

Burtt EH Jr (1986) An analysis of physical, physiological, and optical aspects of avian coloration with emphasis on wood-warblers. Ornithol Monogr 38:1–128

Croft DP, Brent LJN, Franks DW, Cant MA (2015) The evolution of prolonged life after reproduction. Trends Ecol Evol 30:407–416

Giraudeau M, Duval C, Guillon N, Bretagnolle V, Gutierrez C, Heeb P (2010) Effects of access to preen gland secretions on mallard plumage. Naturwissenschaften 97:577–581

Golüke S, Caspers BA (2017) Sex-specific differences in preen gland size of Zebra Finches during the course of breeding. Auk 134:821–831

Hayward AD, Moorad J, Regan CE, Berenos C, Pilkington JG, Pemberton JM, Nussey DH (2015) Asynchrony of senescence among phenotypic traits in a wild mammal population. Exp Gerontol 71:56–68

Holmes DJ, Austad S (1995) Birds as animal models for the comparative biology of aging: a prospectus. J Gerontol Biol Sci 50A:B59–B66

Holmes DJ, Ottinger MA (2003) Birds as long-lived animal models for the study of aging. Exp Gerontol 38:1365–1375

Jacob J, Eigener U, Hoppe U (1997) The structure of preen gland waxes from pelecaniform birds containing 3,7-dimethyloctan-1-ol—an active ingredient against dermatophytes. Z Naturforsch C 52:114–123

Magallanes S, García-Longoria L, López-Calderón C, Reviriego M, de Lope F, Møller AP, Marzal A (2017) Uropygial gland volume and malaria infection are related to survival in migratory house martins. J Avian Biol 48:1355–1359

Martín-Vivaldi M, Ruiz-Rodríguez M, Soler JJ, Peralta JM, Méndez M, Valdivia E, Martín-Platero AM, Martínez-Bueno M (2009) Seasonal, sexual and developmental differences in hoopoe preen gland morphology and secretions. Evidence for a role of bacteria. J Avian Biol 40:191–205

Moe B, Angelier F, Bech C, Chastel O (2007) Is basal metabolic rate influenced by age in a long-lived seabird, the snow petrel? J Exp Biol 210:3407–3414

Moreno-Rueda G (2010) Uropygial gland size correlates with feather holes, body condition and wingbar size in the house sparrow Passer domesticus. J Avian Biol 41:229–236

Moreno-Rueda G (2017) Preen oil and bird fitness: a critical review of the evidence. Biol Rev Camb Philos Soc 92:2131–2143

Nussey DH, Froy H, Lemaitre J-F, Gaillard JM, Austad SN (2013) Senescence in natural populations of animals: widespread evidence and its implications for biogerontology. Ageing Res Rev 12:214–225

Pap PL, Csongor IV, Gergely O, Cosmin M, Zoltan B (2010) Seasonality in the uropygial gland size and feather mite abundancein house sparrows Passer domesticus: natural covariationand an experiment. J Avian Biol 41:653–661

Rattiste K (2004) Reproductive success in presenescent common gulls (Larus canus): the importance of the last year of life. Proc R Soc Lond B Biol Sci 271:2059–2064

Rattiste K, Klandorf H, Urvik J, Sepp T, Asghar M, Hasselquist D, Cooey C, Horak P (2015) Skin pentosidine and telomere length do not covary with age in a long-lived seabird. Biogerontology 16:435–441

Roach DA (2016) Uncovering variation in the patterns of aging. Proc Natl Acad Sci USA 113:6328–6329

Rowe L, Houle D (1996) The lek paradox and the capture of genetic variance by condition dependent traits. Proc R Soc Lond B 263:1415–1421

Sepp T, Rattiste K, Saks L, Meitern R, Urvik J, Kaasik A, Hõrak P (2017) A small badge of longevity: opposing survival selection on the size of white and black wing markings. J Avian Biol 48:570–580

Shawkey MD, Pillai SR, Hill GE (2003) Chemical warfare? Effects of uropygial oil on feather-degrading bacteria. J Avian Biol 34:345–349

Urvik J, Meitern R, Rattiste K, Saks L, Hõrak P, Sepp T (2016) Variation in the arkers of nutritional and oxidative state in a long-lived seabird: associations with age and longevity. Physiol Biochem Zool 89:417–440

Urvik J, Rattiste K, Giraudeau M, Okuliarova M, Hõrak P, Sepp T (2018) Age-specific patterns of maternal investment in common gull egg yolk. Biol Lett 14:20180346

van Noordwijk A, de Jong G (1986) Acquisition and allocation of resources: their influence on variation in life history tactics. Am Nat 128:137–142

Warner DA, Miller DAW, Bronikowski AM, Janzen FJ (2016) Decades of field data reveal that turtles senesce in the wild. Proc Natl Acad Sci USA 113:6502–6507

Zahavi A (1975) Mate selection: a selection for a handicap. J Theor Biol 53:205–214