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RESEARCH ARTICLE

Raising offspring increases ageing: Differences in senescence among three populations of a long-lived seabird, the Atlantic puffin

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Abstract

1. Actuarial senescence, the decline of survival with age, is well documented in the wild. Rates of senescence vary widely between taxa, to some extent also between sexes, with the fastest life histories showing the highest rates of senescence. Few studies have investigated differences in senescence among populations of the same species, although such variation is expected from population-level differences in environmental conditions, leading to differences in vital rates and thus life histories.
2. We predict that, within species, populations differing in productivity (suggesting different paces of life) should experience different rates of senescence, but with little or no sexual difference in senescence within populations of monogamous, monomorphic species where the sexes share breeding duties.
3. We compared rates of actuarial senescence among three contrasting populations of the Atlantic puffin *Fratercula arctica*. The dataset comprised 31 years (1990–2020) of parallel capture–mark–recapture data from three breeding colonies, Isle of May (North Sea), Røst (Norwegian Sea) and Hornøya (Barents Sea), showing contrasting productivities (i.e. annual breeding success) and population trends. We used time elapsed since first capture as a proxy for bird age, and productivity and the winter North Atlantic Oscillation Index (wNAO) as proxies for the environmental conditions experienced by the populations within and outside the breeding season, respectively.
4. In accordance with our predictions, we found that senescence rates differed among the study populations, with no evidence for sexual differences. There was no evidence for an effect of wNAO, but the population with the lowest productivity, Røst, showed the lowest rate of senescence. As a consequence, the negative effect of senescence on the population growth rate (λ) was up to 3–5 times smaller on Røst ($\Delta\lambda = -0.009$) than on the two other colonies.

5. Our findings suggest that environmentally induced differences in senescence rates among populations of a species should be accounted for when predicting effects of climate variation and change on species persistence. There is thus a need for more detailed information on how both actuarial and reproductive senescence influence vital rates of populations of the same species, calling for large-scale comparative studies.

KEYWORDS
actuarial senescence, capture–mark–recapture, environmental conditions, intraspecific variation, life-history trade-offs, long-term data, population viability, seabirds

1 | INTRODUCTION

Declining survival with increasing age, namely actuarial senescence (hereafter senescence; Gaillard et al., 2017; Monaghan et al., 2008), has been documented in a wide range of taxa, especially in birds and mammals (Gaillard & Lemaître, 2020; Nussey et al., 2013). Several theories have been proposed to explain the evolution of senescence (Kirkwood, 1977; Medawar, 1952; Williams, 1957), but fundamental to all is that the strength of natural selection declines with increasing age (Hamilton, 1966; Kirkwood & Rose, 1991). The pattern of senescence, both in terms of onset and strength, varies between species across the slow–fast continuum of life histories, where species at the fast end experience senescence earlier and at a higher rate than those at the slow end (Colchero et al., 2019; Jones et al., 2008). However, differences in senescence among populations within a species have rarely been investigated (but see Bleu et al., 2015; Cayuela et al., 2020; Holand et al., 2016; Loison et al., 1999).

Populations of the same species are exposed to different environmental conditions, leading to age-specific differences in their vital rates (i.e. survival and reproduction; Cayuela et al., 2020). Life-history theory predicts that a decrease in adult survival should lead to higher rates of senescence (Monaghan et al., 2008; Williams, 1957). This is corroborated by studies showing that some insects and large herbivores undergo more rapid senescence in the wild than in captivity (Kawasaki et al., 2008; Lemaître et al., 2013), indicating the importance of more frequent mortality events (i.e. higher hazard rates; Ergon et al., 2018) in natural environments, although the opposite difference has been found for longer-lived mammals, possibly due to their earlier onset of reproduction in zoos (Tidière et al., 2016). Variation in environmental conditions such as food availability, predation and weather conditions will affect both reproduction and survival and may, therefore, also impact senescence (Monaghan et al., 2008). A trade-off between survival and reproduction might, for example, be apparent only under harsh environmental conditions (Garnier et al., 2016; Reznick, 1985), acknowledging also that the survival costs of reproduction to some extent can be counteracted by skipping breeding or abandoning the offspring at an early stage. Under more favourable environmental conditions, increased allocation to reproduction might increase the cost of reproduction until a certain threshold (Erikstad et al., 1998).

Differences among individuals within a population, for example, between males and females, may also affect the onset and rate of senescence (Pardo et al., 2013; Tompkins & Anderson, 2019; Williams, 1957). Williams (1957) predicted that the sex with the higher mortality rate should have a steeper rate of senescence. Such differences may arise from sex-biased reproductive allocation, often linked to mating systems. Males experience higher rates of senescence in polygynous species, whereas little or no difference between the sexes is expected in monogamous and non-dimorphic species (Clutton-Brock & Isvaran, 2007, but see Lemaître et al., 2020). Given the basic differences between the sexes in their reproductive allocation (e.g. in producing the offspring), it is still impossible to rule out any sexual differences in senescence in response to shifting environmental conditions, even for monogamous species.

Seabirds are under pressure from a multitude of factors (Dias et al., 2019), and are experiencing widespread reproductive problems and population declines worldwide (Croxall et al., 2012; Sydeman et al., 2021). Given the projections for future climate change and seabirds' role as sentinels of marine environments, it is critical to understand how environmental conditions impact seabird population dynamics. When breeding success declines, the importance of age-specific survival for population persistence increases (Caswell, 2001). However, to what extent variation in rates of senescence can affect the persistence of populations is less well known (but see Robert et al., 2015). Opportunities to study senescence in long-lived seabirds with delayed maturity and potentially high natal dispersal are severely limited because large-scale marking of chicks over many years is required to build a long-term dataset of known age breeders (Fay et al., 2018). Data on seabird survival are therefore often restricted to adults of unknown age.

Many seabirds are characterized by high adult survival, a key demographic parameter in their life history. The population growth rate of long-lived species is most sensitive to variation in adult survival (Sæther & Bakke, 2000) and seabirds often avoid jeopardizing survival by foregoing reproduction when conditions for breeding are unfavourable, to maximize their life-time reproductive output (Weimerskirch, 2002). A typical example is the

Atlantic puffin *Fratercula arctica* (hereafter puffin), a medium-sized auk (Alcidae) breeding in colonies spread across the North Atlantic. Puffins are monogamous (Anker-Nilssen et al., 2008) and both male and female share parental duties, albeit in unequal proportions, with females spending more time on incubation and chick provisioning and males more time on burrow maintenance and defence (Creelman & Storey, 1991; T. Anker-Nilssen et al., unpubl. data). Previous studies have not found evidence of sex-specific differences in survival of puffins (Erikstad et al., 2009; Harris et al., 1997, 2005) and there are few morphological differences between the sexes in the study colonies except that, on average, the male is 8%–10% heavier, has a 5%–7% larger bill and slightly (≈1%) longer wing cords than the female (Anker-Nilssen et al., 2018; Barrett et al., 1985).

Temporal variation in adult survival of puffins has been linked to various environmental factors, including the winter North Atlantic Oscillation Index (wNAO) (Gimenez et al., 2012; Grosbois et al., 2009; Harris et al., 2005; Sandvik et al., 2005) but age-specific survival has only been documented for puffins in one colony, the Isle of May, where annual survival rate dropped gradually with age from more than 0.95 to around 0.70 over a 20-year period after first-time capture of the birds as adults (Harris et al., 1997). Although no large differences in survival rates between colonies in the north-east Atlantic have been documented (Harris et al., 2005; but see Reiertsen et al., 2021), populations of puffins have been shown to differ in terms of several other aspects of their biology, including productivity, diet, non-breeding conditions, wintering areas and, ultimately, population trends (Barrett et al., 1987; Fayet et al., 2017; Harris et al., 2005; Harris & Wanless, 2011; Reiertsen et al., 2021).

To explore whether such differences influence senescence, we used 31 years of capture–mark–recapture (CMR) data for adult puffins in three colonies with contrasting productivity and population trends, using time elapsed since first capture (TFC) as a proxy for age. We hypothesized that senescence rates would differ among these populations, and that the differences would be explained by local-scale conditions for breeding (using population-level productivity as a proxy) and/or larger-scale variation in winter climate (using wNAO as a proxy). Without individual-level data on reproductive effort, it is difficult to differentiate between the effects of environmental factors and individual attributes on productivity. Long-lived birds are however, expected to maximize their fitness by a trade-off between reproductive effort and chances of own survival (Cairns, 1987; Stearns, 1989). Consequently, reproductive allocation may come with a significant cost in terms of both survival (e.g. Erikstad et al., 1998) and senescence (Boonekamp et al., 2020), indicating the trade-off is also likely to interact with the conditions experienced outside the breeding season (i.e. through carry-over effects from breeding to winter or from winter to breeding). Against this background, we predicted that populations showing higher productivity, that is those experiencing favourable environmental conditions, should also exhibit higher rates of senescence. Furthermore, we expected to find a negative direct effect of wNAO on senescence, especially for the populations with high productivity. We did however, expect little or no difference in senescence between the sexes, given that puffins are highly monogamous (Anker-Nilssen et al., 2008) with males and females being relatively monomorphic and sharing most breeding duties (Creelman & Storey, 1991; Harris & Wanless, 2011).

2 | MATERIALS AND METHODS

2.1 | Study populations and data collection

Annual data on puffin survival and productivity (i.e. breeding success) were collected in 1990–2020 at three different colonies: Isle of May in southeast Scotland, North Sea (56° 11' N, 2° 34' W), Hernyken in the Røst archipelago, Norwegian Sea (67° 26' N, 11° 52′ E, hereafter 'Røst') and Hornøya in the Barents Sea (70° 27' N, 31° 9′ E) (see map in Supporting Information S1, Figure S1). These populations showed contrasting population changes over the study period with an overall increase on the Isle of May and a relatively stable population on Hornøya, while the Røst population decreased markedly (Harris & Wanless, 2011; SEAPOP data portal at www.seapop.no/en). They also differ with respect to environmental conditions such as the prey types and availability during the breeding season and the climatic conditions encountered during and outside the breeding season (Fayet et al., 2017; Harris et al., 2005; Reiertsen et al., 2021). In general, birds breeding on Isle of May and Hornøya usually benefitted from good access to several local prey stocks (sandeels *Ammodytidae* at both colonies, and sprat *Sprattus* and capelin *Mallotus villosus* at Isle of May and Hornøya respectively; e.g. Barrett, 2015; Harris & Wanless, 2011), whereas those on Røst depended on a highly variable and often failing supply of first-year herring *Clupea harengus* (e.g. Cury et al., 2011; Saraux et al., 2021). Although average survival rates of the three populations were not found to differ in 1990–2002 (Harris et al., 2005), Hornøya birds experienced lower and more variable survival than the two other populations in 2007–2019 (Reiertsen et al., 2021). While the Isle of May and Hornøya populations had high and relatively stable breeding success over the study period, the Røst population showed extreme variation in productivity, with numerous seasons with total breeding failure (Barrett, 2015; Cury et al., 2011; Harris & Wanless, 2011).

Capture–mark–recapture data for puffins on the Isle of May ($n = 605$ individuals), Røst ($n = 569$) and Hornøya ($n = 927$) were collected annually during the study period as integral parts of long-term national monitoring schemes for seabirds. Breeding puffins were captured either in the nest burrow (Isle of May, Hornøya), with noose traps (Hornøya) or in mist nets erected on the colony surface (Røst). Individuals were marked with a numbered metal ring and either a unique combination of colour rings or an individually coded colour ring. Marked individuals were then visually resighted in subsequent breeding seasons.

Information about sex was available for all individuals from Røst and 43% of individuals from Isle of May but was not available for the Hornøya birds. Individuals from Røst were either sexed by molecular DNA ($n = 317$, see Anker-Nilssen et al., 2017 and Griffiths et al., 1998 for methods), or by using a colony-specific discriminant function based on the length of head+bill and bill depth at gonys ($n = 252$) that was shown to classify sex correctly for 86.8% of the individuals (Anker-Nilssen & Brøseth, 1998). Similar sexing techniques were used on the Isle of May with morphological sex sometimes confirmed by observations of the birds' mating behaviour. The sex ratio among the study individuals was close to one on the Isle of May ($n_{\text{female}} = 132$, $n_{\text{male}} = 130$) but skewed towards females on Røst ($n_{\text{female}} = 337$, $n_{\text{male}} = 232$).

Puffins lay a single-egg clutch and colony-specific productivity was measured annually by monitoring breeding success for a sample of study burrows containing an egg or a chick (average sample sizes with ranges: Isle of May 176 (132–196); Røst 103 (34–284); Hornøya 42 (22–68)). The definition of breeding success differed between the colonies and was calculated as chicks fledged per egg laid on the Isle of May and Hornøya, and as chicks fledged per egg hatched on Røst. Data on productivity were not available for 3 years on Hornøya (1991, 1994, 1999). As the modelling of the CMR data required annual values for all covariates, the mean value of breeding success on Hornøya was used for the missing years.

In Norway, all handling, ringing and sexing of the birds was approved by the Norwegian Environment Agency (latest permit ref. No 2018/607), in later years also by the Norwegian Food Safety Authority (latest permit FOTS ID 23280). In the United Kingdom, similar permits were granted by the British Trust for Ornithology (personal permits A400 and A2332).

2.2 | Age determination

Time elapsed since first capture as an adult was used as a proxy for the birds' age, since most puffins were marked as adults and their true age was therefore unknown. Most puffins start breeding around 6 (4–8+) years old (Harris & Wanless, 2011); hence, this can be considered a useful proxy for the minimum age for all individuals when entering the analysis. As the birds did not enter the study at the same age, the TFC approach is likely to increase the uncertainty of the estimates (Péron et al., 2010). The approach did, however, prove sufficient to detect senescence in a population of common guillemots *Uria aalge* on the Isle of May (Crespin et al., 2006). Given the resighting rates and samples sizes involved in our data set, we also assessed that TFC could be used as a reasonable proxy for age to estimate senescence rates in our study populations (see Supporting Information S2).

2.3 | Environmental variables

The variation in annual environmental conditions experienced by birds from the different colonies was accounted for by including two variables in the survival model, the wNAO and the colony-specific productivity. wNAO is a climatic index measured as the average difference in air pressure between Iceland and Portugal, that is known to reflect weather conditions in the north Atlantic during the winter. As winter conditions have previously been shown to affect puffin survival in several colonies, including Røst and Hornøya (Reiertsen et al., 2021; Sandvik et al., 2005), we used the station-based wNAO for December–March (Hurrell & National Center for Atmospheric Research Staff, 2020), since puffins from the three colonies show no overlap in their distribution during these months (Fayet et al., 2017). Colony-specific productivity was used as a proxy for environmental conditions encountered in the breeding season assuming that favourable environmental conditions increase the chances of successful reproduction, whereas unfavourable conditions decrease success.

2.4 | Age-specific survival analyses

The capture histories of the birds were modelled in a Cormack–Jolly–Seber (CJS) framework. Prior to the analyses, a goodness of fit test was conducted using programme RELEASE implemented in programme MARK (White & Burnham, 1999) to examine whether the data fitted a CJS reference model. Trap happiness (i.e. that individuals seen in year *t*, have a higher probability to be seen in year *t*+1 than those not seen in year *t*) was present in all colonies (Supporting Information S3, Table S1). This was accounted for by incorporating trap dependence (1 year) in the resighting model as suggested by Pradel (1993).

All modelling was performed in R (version 4.0.3; R Core Team, 2020). We modelled the CMR data in RMark (Laake, 2013), an R interface of programme MARK. To estimate age dependence of apparent adult survival (hereafter survival, φ), a Gompertz mortality model (Gompertz, 1825) was used to model the effect of senescence (Gaillard et al., 2004):

$$\phi(a_i) = \exp(-\alpha \times \exp(\beta \times a_i)),$$

where $\varphi(a_i)$ is the age-specific survival at age a_i, α is the baseline mortality (i.e. initial mortality experienced by individuals at the age of first reproduction, $a_i = 0$) and $\beta > 0$ is the rate of senescence. Hence, this model assumes senescence to start at the age of first reproduction. To use this in the context of CMR modelling, the model was rewritten, following Gaillard et al. (2004):

$$\log(-\log(\phi(a_i))) = \log(\alpha) + \beta \times a_i.$$

To implement this model in RMark, a loglog link was used, and age was included as a continuous linear effect.

As senescence may not set in until several years after the age at first reproduction (e.g. Jones et al., 2008), a threshold modelling approach was used to estimate the onset of senescence that best fitted the data for each study population separately (e.g. Koons et al., 2014). The best fitting onset (assessed from TFC = 0 to TFC = 12) was identified based on the Akaike information criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002).

2.5 | Model selection

First, all three populations were modelled separately in a simple model only including age as a categorical variable to investigate the general pattern of age-specific survival in each colony with resighting rate depending on year and age. For each case, a Gompertz model was applied to examine the fit of the model. To test whether the strength of senescence differed between populations, all populations were modelled in a joint model, with age, wNAO, productivity and colony as covariates and applying all relevant two-way interactions. If a two-way interaction improved the model, we also tested the relevant three-way interaction. In addition, for Isle of May and Røst, age- and sex-specific survival rates were modelled to test for sex-specific senescence within colonies. Here, each colony was modelled separately with age and sex as additive or interaction effects, with year, age and sex in the resighting model. Resighting rates for the joint model including all colonies were modelled with year, colony and age as additive effects, successively removing colony and/or age. For all models including age, model selection was done based on AICc. If competing models were within Δ2AICc, the model with fewest parameters (i.e. the most parsimonious) was chosen.

2.6 | Consequence of varying senescence rates on population growth rate

We used an age-structured Leslie matrix model to assess how senescence affected population growth rates (see details in Supporting Information S4). For each colony, we contrasted age-structured models with and without senescence (the latter assuming that the baseline survival was survival at the onset of senescence), using estimates of pre-breeding survival from an integrated population model (K. Layton-Mathews et al., unpubl. data), and letting fledging success vary over the observed range of variation. We used the dominant eigenvalue of the Leslie matrix as a measure of population growth rate (e.g. Caswell, 2001).

3 | RESULTS

3.1 | Colony-specific senescence

Puffins in all three colonies showed senescence as survival of adults decreased with age (TFC; Figure 1). Onset of senescence varied between the colonies with Isle of May, Røst and Hornøya having an onset of senescence at TFC = 6, 0 and 1, respectively (Supporting Information S5, Table S2). The best supported model with all populations together included the three-way interaction between age, colony and productivity and all lower-order term interactions (Table 1; Supporting Information S5, Table S3). This model indicated that senescence rate differed between the populations, as did baseline survival (Table 2). This was also in accordance with the general models when colonies were modelled separately (Figure 1). The effect of productivity (abbreviated fs = fledging success) differed with age and between colonies. Increasing productivity had a strong negative effect on age-dependent survival on Røst, in contrast to a positive effect on the Isle of May and to a lesser extent on Hornøya (Figure 2; Supporting Information S5, Table S2). The model including wNAO as an additive effect performed less well (ΔAICc > 2) than the model without this effect, with no evidence of wNAO having an effect on survival (loglog: −0.001, 95% CI: −0.034, 0.032). Each recapture (i.e. resighting) model, including year, colony and age as additive effects, was consistently better than the simpler recapture models, with a decreasing probability of resighting with increasing age (Supporting Information S6, Table S3).

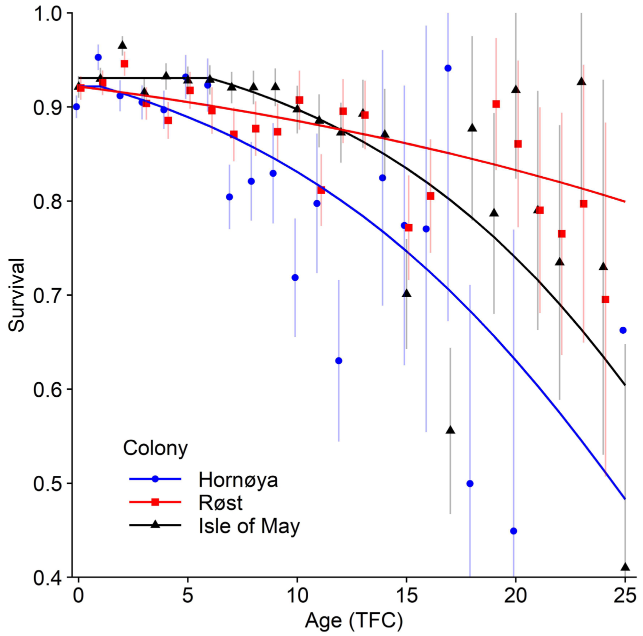

FIGURE 1 Age-specific survival of adult Atlantic puffins in each study colony. Colonies were modelled separately with age (time elapsed since first capture [TFC]) as a categorical factor, i.e. $\varphi(A)p(t+A)$. Chronological age is ≥TFC + 6 years (see text). All symbols are point estimates with error bars indicating ±1 SE. Missing symbols indicate the estimates did not converge. Lines show the best Gompertz model fit for each colony.

3.2 | Sex-specific senescence

As no interaction of sex and age was included in the best models, there was no statistical support for a difference in senescence between males and females at either colony, although the model including the interaction was within Δ2AICc of the best model for Røst (Table 3). In both populations, the simplest model including only sex as an additive effect was marginally better than the model with a sex–age interaction, showing only a slight tendency for higher survival of males than females (difference in loglog estimates: Røst 0.173, 95% CI: −0.020, 0.366; Isle of May 0.128, 95% CI: −0.135, 0.391).

TABLE 1 Model selection table showing the 10 best survival (φ) and recapture (p) models

Model (φ)	Model (p)	k	ΔAICc	Weight	Deviance
A+col+fs+A×col+col×fs+A×fs+A×fs×col	t+A+col	46	0.00	0.726	19,638.43
A+col+fs+wNAO+A×col+col×fs+A×fs+A×fs×col	t+A+col	47	2.01	0.266	19,638.42
A+col+fs+A×col+col×fs	t+A+col	43	9.84	0.005	19,654.30
A+col+fs+wNAO+A×col+col×fs	t+A+col	44	11.85	0	19,654.30
A+col+fs+wNAO+A×col+col×fs+col×wNAO	t+A+col	46	13.07	0	19,651.49
A+col+fs+A×col+col×fs+A×fs+A×fs×col	t+col	45	45.67	0	19,686.11
A+col+fs+wNAO+A×col+col×fs+A×fs+A×fs×col	t+col	46	47.68	0	19,686.11
A+col+fs+A×col+col×fs	t+col	42	56.69	0	19,703.17
A+col+fs+wNAO+A×col+col×fs	t+col	43	58.71	0	19,703.17
A+col+fs+wNAO+A×col+col×fs+col×wNAO	t+col	45	60.15	0	19,700.58

Note: See full model selection table in Supporting Information S6, Table S3.

Abbreviations: A, age as a linear effect; col, colony; fs, productivity; wNAO, winter North Atlantic Oscillation; t, year; k, number of estimated parameters.

TABLE 2 Estimates of baseline survival and senescence rates for each population derived from the best model (Table 1). Estimates are given at the median colony-specific productivity.

Colony	Baseline survival[a] (95% CI)	Baseline survival[b] (95% CI)	Senescence rate[c] (95% CI)	Median productivity (range)
Isle of May	2.69 (2.57, 2.82)	0.935 (0.926, 0.942)	0.078 (0.052, 0.104)	0.670 (0.300, 0.840)
Røst	2.33 (2.14, 2.52)	0.907 (0.888, 0.922)	0.015 (−0.007, 0.036)	0.086 (0.000, 0.959)
Hornøya	2.53 (2.39, 2.67)	0.924 (0.913, 0.933)	0.110 (0.089, 0.131)	0.772 (0.129, 0.925)

[a] Loglog scale.

[b] Back-transformed to probability scale.

[c] Estimated from β in Equation (1).

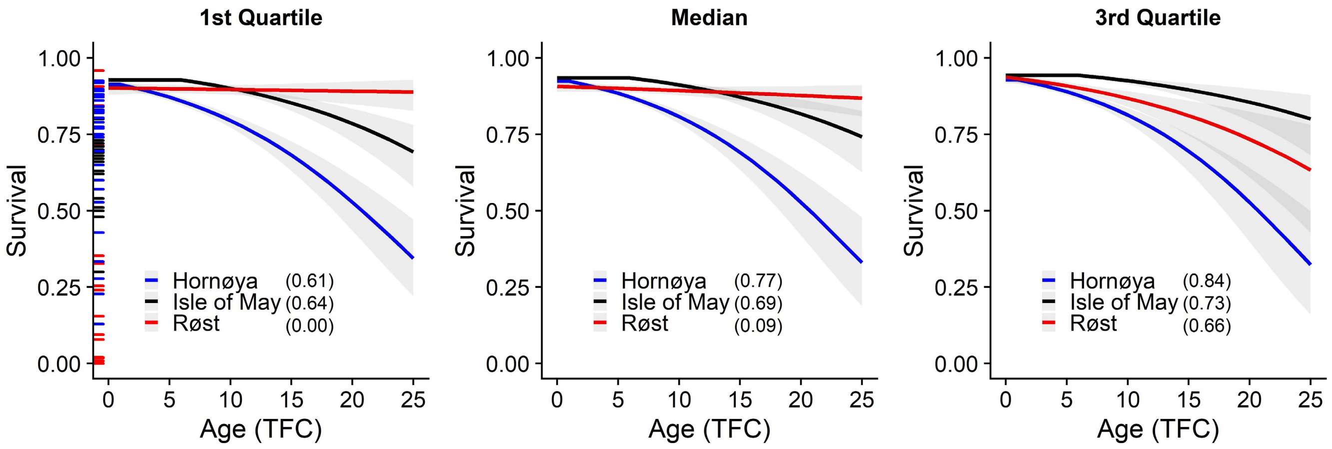

FIGURE 2 Predicted age-specific survival for adult Atlantic puffins in the study colonies at three different colony-specific levels of observed productivity during the study period, the 1st quartile, the median and 3rd quartile (the corresponding estimates of fledging success are indicated in parentheses for each colony). Grey shading represents the 95% confidence intervals of predicted survival. Rug bars on the y-axis indicate the annual colony-specific productivity estimates during the study period (1990–2019).

3.3 | Effects of senescence on population growth rate

As expected, senescence affected the population growth rate (λ) negatively in all colonies, but the strength of the effect differed between the populations and was highly dependent on environmental conditions as measured by productivity. Under the lowest quartile of observed conditions experienced at each colony, the negative effect of senescence on λ was estimated to be twice as strong on Hornøya ($\Delta\lambda = -0.018$) than on Røst (−0.009), and about six times

TABLE 3 Model selection table evaluating sex-specific senescence for the Isle of May and Røst populations

Colony	Model (φ)	Model (p)	k	ΔAICc	Weight	Deviance
Isle of May	Age	t + age + sex	34	0.00	0.48	2503.107
	Age + sex	t + age + sex	35	1.15	0.27	2502.146
	Age × sex	t + age + sex	36	1.30	0.25	2501.427
Røst	Age + sex	t + age + sex	36	0.00	0.48	5419.143
	Age	t + age + sex	35	1.06	0.28	5422.250
	Age × sex	t + age + sex	37	1.43	0.24	5418.536

stronger than on Isle of May (−0.003). Furthermore, in the extreme case of sustained zero productivity at all colonies, the model predicted the effect to be three and five times stronger on Isle of May and Hornøya, respectively, than on Røst (Supporting Information S4, Figures S3 and S4).

4 | DISCUSSION

This study is one of the few exploring within-species differences in actuarial senescence, and, to our knowledge, the first to document this in seabirds. Using 30 years of CMR data, we show that rates of senescence differed among three populations of Atlantic puffins breeding in three geographically distinct sea areas. We also demonstrate that this was linked to corresponding differences in local breeding conditions, as reflected by contrasting levels of productivity at the three colonies and by colony-specific effects of annual productivity on senescence. As predicted for a monogamous species and sexual similarities in morphology, breeding duties and survival rates, we found no differences in the degree of senescence between males and females.

Our results need to be interpreted with some caution, as several assumptions were made. One obvious limitation is that the exact age of the individuals was unknown. Although this would act to reduce the precision of the estimates, our approach should be sufficiently robust to capture the differences in senescence rates between the study populations. We do however believe that the estimated differences in onset of senescence, which started much earlier at Røst (at TFC = 0) and Hornøya (at TFC = 1) than at Isle of May (at TFC = 6), were mainly caused by differences in actual age at first capture rather than genetic differences. This assumption is supported by the contrasting trends in breeding numbers and productivity at the three colonies in the decade before colour ringing was started, when the Røst population decreased by 65% (Anker-Nilssen & Røstad, 1993) and had many failed seasons (Anker-Nilssen, 1987), Hornøya increased by 69% (Krasnov & Barrett, 1995) and had high breeding success (Barrett, 2002), and the Isle of May population underwent an extraordinary nine-fold increase and also reproduced well (Harris & Wanless, 2011). As a consequence, recruitment rates of first-time breeders were likely to be equally different among these colonies at the start of our study, when most of the birds with the longest resighting records were ringed. Thus, we cannot conclude that the onset of senescence differed between the colonies.

Furthermore, we did not have the data to control for individual heterogeneity, such as age-specific differences in individual quality (Hamel et al., 2018). For example, older age classes might have a higher proportion of high-quality individuals, due to selective disappearance of the lower quality individuals, which may have been strongest on Røst where conditions for breeding were extremely poor. We were unable to quantify the importance of this effect for our study populations, but such heterogeneity may act to mask senescence (Gaillard et al., 2017; Gimenez et al., 2018), and several studies have therefore emphasized the importance of accounting for heterogeneity in CMR studies of senescence (e.g. Cam et al., 2002; Fay et al., 2018; Péron et al., 2010).

Understanding the mechanisms affecting the age structure of populations is an important aspect of ecology and conservation. The presence of senescence in populations experiencing prolonged periods of unfavourable conditions that negatively affect their vital rates might be critical if it acts to accelerate population decline, thereby slowing down population recovery (see Supporting Information S4 for details). Consequently, it is important to document how shifting conditions in key habitats may affect senescence and potentially alter the age structure and, therefore, the resilience of a population.

Williams (1957) predicted that an increase in mortality should lead to more rapid senescence and a faster pace of life. As allocation of resources to survival or reproduction is expected to shift in response to variable environmental conditions (Kirkwood & Rose, 1991; Stearns, 1989), the slow–fast continuum can be used to explain variation in senescence across species (Jones et al., 2008; but see Jones et al., 2014). There are many studies demonstrating differences in vital rates among populations of the same species (e.g. Frederiksen et al., 2005; Reiertsen et al., 2021), but few explore the consequences of such differences on senescence (but see Bleu et al., 2015; Cayuela et al., 2020; Loison et al., 1999) or document effects of environmental factors in this context. Holand et al. (2016) found evidence of spatial variation in senescence rates in a house sparrow *Passer domesticus* metapopulation but found no link to environmental differences between the populations investigated.

Our three study populations all showed senescence and the rates of late-life decline were highest in the two populations with the highest productivity (Isle of May and Hornøya). This accords well with our expectation that the differences were caused by differences in allocation of resources between survival and reproduction (Kirkwood & Rose, 1991). The effect of productivity, here used as a proxy for environmental conditions in the breeding season, on senescence rates did indeed differ markedly between the populations. For the population breeding on the Isle of May, where breeding success was usually high, the rate of senescence increased under poor environmental conditions, the opposite was true for the population on Røst, where breeding failure was the norm, while there was no clear trend for Hornøya. Although successful breeding was probably more costly for the puffins on Røst, as indicated by the steep increase in their senescence at high levels of productivity, reproductive allocation per breeding attempt was probably lower there, as reflected by senescence effects being marginal when productivity and environmental conditions were poor. This indicates an important difference for the Røst population, which to some extent seems able to buffer the low productivity with lower rates of senescence. The existence of such a flexible strategy is supported by an experimental study of reproductive allocation in puffins, which showed that they are prudent parents, able to adjust their allocation based on both their own and their chick's condition (Erikstad et al., 2009). The more able puffins are to limit their allocation of energy to reproduction when environmental conditions are too poor for successful breeding, the higher are their chances of post-breeding survival. This flexible strategy can confer big advantages, especially when breeding in a highly stochastic environment (Erikstad et al., 1998).

As argued in the Introduction, productivity is an ambiguous proxy for environmental conditions in the breeding season if it also correlates with the birds' reproductive effort. Clearly, individual-level data are needed to quantify fitness-related trade-offs between survival and reproduction. An experimental study of brood size in jackdaws *Coloeus monedula* found that increasing reproductive effort accelerated senescence (Boonekamp et al., 2020). This was probably also the case for our study populations, with increased effort used to sustain the single offspring increasing senescence. As we measured productivity at the population level, it is reasonable to expect that it reflected the general conditions for breeding, which is also corroborated by studies showing that breeding success in each colony was closely linked to the availability of key prey (e.g. Barrett, 2015; Cury et al., 2011; Harris & Wanless, 2011). It may still be that the relationship between environmental conditions and senescence for long-lived species is U-shaped rather than linear (see also Erikstad et al., 1998), with senescence peaking under intermediate conditions when the consequences of a trade-off decision between survival and productivity is less predictable. This theory warrants further research but would not contradict our results, given that the Hornøya birds experienced the highest senescence and, in the last half of the study, more frequent seasons of intermediate breeding success than at the two other colonies.

Using wNAO as a proxy, we failed to find evidence for an effect of large-scale variation in environmental conditions outside the breeding season on senescence. Nevertheless, given their highly different winter distributions (Fayet et al., 2017; Reiertsen et al., 2021) and the unlikeliness that wNAO, a fixed-site climate signal, reflects population-specific differences in winter conditions, it may well be that such variation also affects their senescence. To what extent this was the case and potentially affected the populations differently, is beyond the scope of this paper but is an important question for better understanding the importance of senescence for seabird demography. The same goes for effects of reproductive senescence as indicated by decreasing resighting rate with age in all colonies, suggesting that the likelihood of skipping or abandoning breeding attempts increased with age (e.g. Reed et al., 2008).

As predicted for a monogamous species like the puffin (Clutton-Brock & Isvaran, 2007), we found no detectable difference in senescence between males and females at the two colonies where birds were sexed. This finding is in accordance with Williams' (1957) predictions, given the lack of evidence for sex-specific survival in puffins (Erikstad et al., 2009; Harris et al., 1997, 2005). Although the evidence was not strong, female survival was, however, consistently lower than that of males at both colonies in the current study. This is interesting in the light of sexual differences in breeding effort, including not only the obvious difference in egg production, but also the apparently condition-dependent sharing of other tasks such as nest defence and chick feeding (Creelman & Storey, 1991, T. Anker-Nilssen et al., unpubl. data) that may affect both the survival and senescence of the sexes differently.

The limited effect of senescence on population growth rate on Røst compared to the other populations suggests that the Røst birds might be making more conservative decisions when allocating resources between survival versus reproduction, possibly influenced by their longer experience of breeding failure. The magnitude of this effect has obvious consequences for the resilience of the Røst population by considerably reducing its risk of extinction under prolonged periods of unfavourable conditions. Nevertheless, from the same line of arguments we would expect similar responses to appear in the two other populations, if they were subjected to equally bad conditions. This expectation is indeed supported by the increasing senescence observed at Røst with improving conditions (Figure 2, 3rd quartile), reaching approximately the same level as on Isle of May under comparable conditions (Figure 2, first quartile). Thus, even if senescence rates differed, we still believe the driving mechanisms of senescence were the same across colonies. During our study, the Røst population experienced, on average, almost total breeding failure every second year, and colony size dropped by 62%. In contrast, puffins in the two other populations bred successfully in most years and over the study period their breeding populations increased in size by 12% (Hornøya) and 100% (Isle of May), although at the latter there was a major decline in the mid-2000s (Norwegian seabird monitoring programme, unpubl. data; UK CEH Isle of May long-term studies, unpubl. data).

5 | CONCLUSIONS

Long-lived species such as seabirds are known to avoid jeopardizing their survival by adjusting reproductive effort (Gaillard & Yoccoz, 2003; Weimerskirch, 2002). Hence, differences in environmental conditions experienced by the populations during the breeding season were expected to be the driving force behind the differences in senescence rates among our study populations. The high incidence of breeding failure in the Røst population was partly counteracted by a lower rate of senescence, while the other two populations, where productivity was much higher, had higher rates of senescence.

Understanding why life-history traits vary among populations and species is a central goal of evolutionary theory, and our findings provide novel and valuable insight for further investigations on within-species differences in senescence in general, particularly in seabirds. However, with data from only three locations and productivity data at the population level, care is needed before drawing robust conclusions on the mechanisms explaining these differences. Our findings do, however, show that generalizing senescence patterns across populations of the same species should be done with caution, as differences in environmental context and phenotypic quality, and interactions between them, may have contrasting effects on senescence in different populations.

Senescence is undoubtedly a widespread phenomenon, possibly having important consequences for population dynamics. For seabirds, where many species are now globally red-listed (Dias et al., 2019), consideration of environmentally induced changes in senescence rates may prove to be crucial for developing effective conservation strategies and predicting the demographic consequences of climate variation and change. Thus, to accurately model the performance of seabird populations, and populations of species in general, there is a need for more detailed information on how both actuarial and reproductive senescence influence their vital rates. In this context, comparative, individual-based studies across multiple populations and species are urgently needed.

AUTHOR CONTRIBUTIONS

Tycho Anker-Nilssen conceived the study, which was further designed by Terje L. Landsem, Tycho Anker-Nilssen and Nigel G. Yoccoz; Data were collected by Michael P. Harris and Sarah Wanless (Isle of May), Kjell E. Erikstad and Tone K. Reiertsen (Hornøya), and Tycho Anker-Nilssen assisted by Terje L. Landsem and Christoffer H. Hilde (Røst); Terje L. Landsem analysed the data with special guidance from Kate Layton-Matthews, Nigel G. Yoccoz, Christoffer H. Hilde and Tycho Anker-Nilssen; Terje L. Landsem and Tycho Anker-Nilssen drafted the paper with input from all authors.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.3xsj3txkz (Landsem et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Map of study locations.

Appendix S2. TFC-validating simulations.

Appendix S3. Goodness of fit tests.

Appendix S4. Population matrix modelling.

Appendix S5. Tests for onset of senescence.

Appendix S6. Full model selection of the joint modelling.

Appendix S7. Output of the best supported model.

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