CHICAGO JOURNALS

American Society of Naturalists

The University of Chicago

Reproductive Senescence in a Long-Lived Seabird: Rates of Decline in Late-Life Performance Are Associated with Varying Costs of Early Reproduction

Thomas E. Reed,[1,2,*] Loeske E. B. Kruuk,[1,†] Sarah Wanless,[2,‡] Morten Frederiksen,[2,3,§] Emma J. A. Cunningham,[1,‖] and Michael P. Harris[2,#]

1. Institute of Evolutionary Biology, King's Buildings, University of Edinburgh, Edinburgh EH9 3JT, United Kingdom;
2. Centre for Ecology and Hydrology, Bush Estate, Penicuik, Midlothian EH26 0QB, United Kingdom;
3. National Environmental Research Institute, Department of Arctic Environment, University of Aarhus, Frederiksborgvej 399, DK-4000 Roskilde, Denmark

ABSTRACT: Evolutionary theories of senescence predict that rates of decline in performance parameters should be shaped by early-life trade-offs between reproduction and somatic maintenance. Here we investigate factors influencing the rate of reproductive senescence in a long-lived seabird, the common guillemot *Uria aalge*, using data collected over a 23-year period. In the last 3 years of life, individual guillemots had significantly reduced breeding success and were less likely to hold a site or attempt to breed. Females senesced at a significantly faster rate than males. At the individual level, high levels of reproductive output earlier in life were associated with increased senescence later in life. This trade-off between early- and late-life reproduction was evident independent of the fact that as birds age, they breed later in the season. The rate of senescence was additionally dependent on environmental conditions experienced earlier in life, with evidence that harsh conditions amplified later declines in breeding success. Overall, individuals with intermediate levels of early-life productivity lived longer. These results provide support for the antagonistic-pleiotropy and disposable-soma theories of senescence and

* E-mail: tom.reed@ed.ac.uk.

† E-mail: loeske.kruuk@ed.ac.uk.

‡ E-mail: swanl@ceh.ac.uk.

§ E-mail: mfr@dmu.dk.

‖ E-mail: e.cunningham@ed.ac.uk.

E-mail: mph@ceh.ac.uk.

demonstrate for the first time in a wild bird population that increased rates of senescence in reproductive performance are associated with varying costs of reproduction early in life.

Keywords: senescence, reproductive performance, trade-off, disposable soma, guillemot.

Senescence is an innate deterioration in physiological condition and cellular functioning in old age, which leads to reductions in survival and/or breeding success and ultimately to the death of the organism. Once thought to be something rarely encountered in the wild (Comfort 1979), there is now convincing evidence that senescence is a widespread and fundamental phenomenon in natural populations (Keller and Genoud 1997; Ricklefs 1998; Berube et al. 1999; Ericsson et al. 2001; Bonduriansky and Brassil 2002; Reznick et al. 2004). The majority of investigations to date have focused on documenting and describing increases in mortality in old age, known as actuarial senescence, with an emphasis on the need to explain interspecific variation in incidence and rates of actuarial senescence (Promislow 1991; Holmes and Austad 1995; Ricklefs 2000; Ricklefs and Scheuerlein 2001). In contrast, investigating whether reproductive performance declines with age has proved more difficult, and empirical studies are rare. Analyses of senescence (both actuarial and reproductive) are problematic because of the inherent problems involved in obtaining large enough samples of the oldest cohorts and in following individuals of known age (which must be marked at birth or at recognizable ages) throughout their entire life spans. In addition, differential mortality rates of phenotypes associated with variation in individual quality may either obscure or falsely amplify reproductive senescence effects at the population level (Forslund and Pärt 1995; Nisbet 2001). Recent methodological and analytical advances, however, in combination with accumulating data from more and more long-term studies on marked individuals, are making the reliable detection and report-

ing of age-related declines in performance parameters at the individual level increasingly possible (Reid et al. 2003; Catry et al. 2006; Crespin et al. 2006; Nussey et al. 2006; van de Pol and Verhulst 2006).

Senescence entails a loss in fitness to the organism; its widespread occurrence is therefore challenging to explain from an evolutionary perspective, and several theories have been advanced. Evolutionary theories of senescence are based on the premise that the strength of natural selection declines with age, as dictated by levels of extrinsic mortality (Medawar 1952; Hamilton 1966; Charlesworth 1980; Partridge and Barton 1993). In the mutation accumulation theory for the evolution of aging, harmful mutations with late-acting effects amass in older age classes as a result of reduced effective population size and the consequent relative inefficiency of selection at purging mutations effected at these later stages (Medawar 1952). Similarly, the theory of antagonistic pleiotropy postulates that genotypes that increase early-life fecundity or fitness at the expense of later-life fitness (via the action of pleiotropic genes or linkage disequilibrium) can be selected for if selection is much stronger earlier in the life history, so that early benefits outweigh later costs (Williams 1957). Related to antagonistic pleiotropy is the concept of the disposable soma, which proposes that senescence is the outcome of a balance of trade-offs between increased investment in early reproduction at the expense of future survival and future reproduction, and particularly at the expense of somatic maintenance, which would favor increased survival and longevity (Kirkwood 1977; Kirkwood and Rose 1991).

Central to the theories of antagonistic pleiotropy and disposable soma is the notion that reproduction is costly (Williams 1966). In natural situations, organisms are usually limited in their abilities to acquire and utilize resources (energy and nutrients). Resources invested in reproduction, which is energetically highly expensive, are not then available for allocation to other functions such as growth, cellular repair, and immune function (Nur 1984; Reznick 1985; Gustafsson and Sutherland 1988; Gustafsson et al. 1994; Hanssen et al. 2003). Individuals investing heavily in reproduction at early stages are thus more likely to exhibit increased senescence and/or reduced longevity. Such energetic trade-offs provide a physiological framework through which the action of genes with antagonistic early- versus late-life fitness effects could be mediated (Partridge 1987). Antagonistic pleiotropy and disposable soma therefore both make similar predictions, namely, that increases in reproductive investment early in life should be accompanied by reductions in late-life performance and/or survival. Empirical evidence for the existence of such trade-offs in natural populations is, however, sparse, and support for both theories derives mainly from laboratory studies on insects (Rose and Charlesworth 1980; Partridge

and Barton 1993; Service 1993). Little research has been carried out on intraspecific variation in rates of senescence related to costs of reproduction in natural populations, and very few studies have provided clear evidence of a link between the two (Gustafsson and Pärt 1990; Reid et al. 2003; Nussey et al. 2006). Moreover, costs are likely to vary depending on prevailing environmental conditions, and it is therefore plausible that different experiences of early-life environmental conditions may generate variation in senescence rates. Importantly, investigations of senescence require appropriate ecological contexts, a fact that is difficult to address in laboratory studies.

Birds, for their body size, live remarkably long compared to mammals and in general are expected to senesce at slower rates (Williams 1957; Holmes and Austad 1995; Ricklefs and Scheuerlein 2001). Compelling evidence for reproductive senescence, in particular, has been difficult to obtain (Coulson and Fairweather 2001; Catry et al. 2006). Seabirds are among the longest-lived of all birds and constitute excellent models for research into both the evolutionary ecology and physiological basis of aging (Holmes et al. 2001; Ricklefs 1998; Monaghan and Haussmann 2006). In this article we examine rates of reproductive senescence in a population of common guillemots (*Uria aalge*) breeding on the Isle of May in Scotland. The guillemot is a long-lived, colonial, sexually monomorphic seabird. Individuals form multiyear pair bonds, and females lay a single egg clutch. Previous work on this population showed both actuarial and reproductive senescence, with reduced average survival prospects and average breeding success apparent in the older age classes (Crespin et al. 2006). In this earlier study, time elapsed since first capture (TFC) was used as a proxy for age, since birds in the population are largely marked as breeding adults of unknown age. Simulation models showed that TFC could be used as a reliable surrogate measure for age, and employing TFC in models using data from known individuals did not introduce any biases or significantly reduce the probability of being able to detect senescence (Crespin et al. 2006). This approach, however, cannot fully discount the possibility of covariation between probability of survival (and therefore longevity) and individual quality, which would result in progressive changes in the phenotypic composition of older age classes (van de Pol and Verhulst 2006). For example, if poor reproducers die younger, they will progressively disappear from the population such that the oldest cohorts will always contain a higher proportion of good-quality individuals (the selective-disappearance hypothesis; Forslund and Pärt 1995; Cam and Monnat 2000; Reid et al. 2003; van de Pol and Verhulst 2006). This would have the effect of increasing average breeding success in the oldest age classes, thus decreasing

the probability of detecting reproductive senescence through a consideration of age.

Here we utilize a novel technique to describe and quantify the extent of reproductive senescence in individual common guillemots. The approach relies on considering the relationship between breeding success and years before death (YBD) as a means of detecting senescence, where senescence is defined as a progressive reduction in breeding performance in the years leading up to the death of an individual. The use of YBD as an alternative to age or age proxies has two main advantages, since it (1) allows for the reliable detection of within-individual senescent declines in breeding success in individuals whose exact age is unknown and (2) avoids the problems of selective disappearance because, by definition, all individuals eventually disappear from the sample in question. Our first objectives were to quantify within-individual senescent declines in breeding success, to determine at what stage of the life span senescence effects become important, and to establish whether rates of senescence differ between the sexes in guillemots. For example, sex differences in mortality regimes, if present, could lead to the sex with higher mortality also exhibiting more rapid senescence (Williams 1957). To the best of our knowledge, no study has specifically tested for sex differences in reproductive senescence rates before, despite the clear prediction made by Williams's theory. Second, we explored the extent to which early-life reproduction and the environmental conditions experienced early in life influence individual rates of senescence. Third, we aimed to identify whether longevity (reproductive life span) is also affected by early-life reproductive effort, and finally, we quantified the impact of senescence on lifetime reproductive success.

Material and Methods

Study Population and Data Collection

We studied common guillemots (*Uria aalge*) breeding on the Isle of May, Firth of Forth, Scotland (56°11′N, 2°33′W) each year from 1982 to 2004. Individual breeding guillemots of unknown age were marked with unique metal and colored rings. Ringing commenced in 1982, and each subsequent year, additional breeding adults were caught and ringed in an effort to increase numbers of individually identifiable birds and to replace marked birds that had disappeared from the population, thereby sustaining comprehensive sampling in the study areas. Searches for these birds were carried out on an almost daily basis during the breeding season to determine survival, whether a breeding site was held, laying date relative to when birds in the same area laid (relative laying date; Reed et al. 2006), and breeding success, that is, whether they reared a chick that left

the colony at the normal age (for further details on study population and methods, see Harris and Wanless 1988). The analysis was based on 115 females and 123 males.

Variables Used in Analyses

The following variables were used in analyses to test our main hypothesis that rates of within-individual decline in reproductive performance may be associated with early-life reproduction and with environmental conditions experienced early in life.

Measures of Reproductive Performance. Guillemots have a single egg clutch and can raise a maximum of one chick per year. Breeding success in a given year was therefore defined as a binary response variable, with 1 indicating successful (i.e., raised a chick to the age at which it would leave the colony; chicks are taken to sea by the male parent after ∼3 weeks and are still flightless) and 0 indicating failure (i.e., did not raise a chick to leaving the colony that year, regardless of whether the individual actually bred or even held a site). This measure took account of the 5%–10% of birds observed alive in the study colonies that do not breed (lay an egg) in any year (Harris and Wanless 1995), primarily because of eviction from breeding sites by other guillemots, although some birds (∼1%) occupy sites but do not produce an egg (Harris and Wanless 1995; Kokko et al. 2004). Because competition for available sites was fierce, we predicted that if birds lose their competitive edge in old age, there will be a higher incidence of site loss and/or nonbreeding in the years leading up to death of individuals. For this reason, we also consider (1) the probability of individuals attempting to breed and (2) the probability of individuals holding a site in relation to years before death (YBD). We also tested whether the probability of changing site increased in the years leading up to the death of birds.

Years before Death. We quantified senescence from the relationship between breeding success and YBD as an alternative measure to age. When a bird disappeared from the study population and did not return in subsequent years, it was presumed to be dead. However, resighting probabilities, although very high (98%), decline in old age, probably because older individuals come back to the colony to breed less regularly than younger birds (Crespin et al. 2006), so the possibility that birds had changed colonies or were simply not detected within the study plots could not be excluded, although this was considered unlikely. Breeding success of all individuals was considered in relation to YBD, with 1 denoting the final year of life before disappearance. Initial analysis (plotting breeding success against YBD) suggested that declines in breeding success
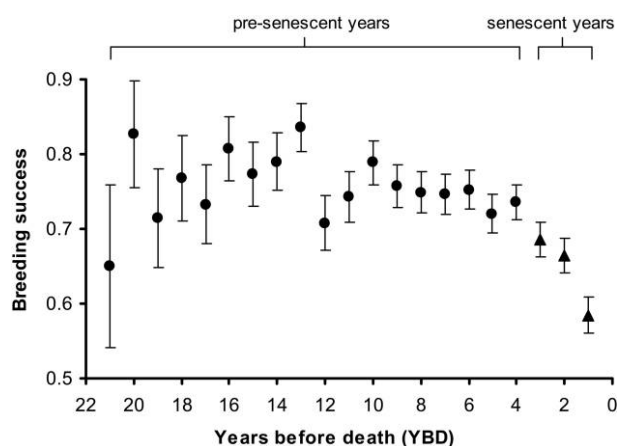
Figure 1: Relationship between years before death and breeding success (the proportion of occasions where a chick was successfully raised to depart the colony). Data points are mean ± SE; $n = 238$ individuals. The last 3 years are termed the senescent years (*triangles*) and all previous years the presenescent years (*circles*). Breeding success was significantly lower in the senescent years (0.646 ± 0.018) than in the presenescent years (0.744 ± 0.001; $\chi^2 = 21.55$, df $= 1$, $P < .001$).

were most apparent in the last 3 years of life, whereas there was no obvious trend in years before these (fig. 1). Hence a dummy variable termed "senescence class" was created, with 1 = the ultimate year of life, 2 = the penultimate year of life, 3 = the third-to-last year of life, and 4 = all other years combined (these are given negative signs in the full model so that senescence effects can have a negative direction, for ease of interpretation). Levels 1–3 are referred to as the "senescent years"; these were the years in which declines in breeding success were significant in a cross-sectional analysis of average breeding success across all individuals (fig. 1, statistics provided in legend). Level 4 combined information on breeding success in all other years previous to these last 3 years of life (when declines are not apparent), collectively referred to as the "presenescent years."

Reproductive Life Span. Reproductive life span (RLS) was the number of years from marking until disappearance (death). Since exact age of ringed birds was not known, we cannot know the true RLS. Birds were marked in five areas on the island; in four of these, the majority of birds were caught in the first 1 or 2 years of the study and are therefore likely to be a representative sample of ages in the population. Ringing effort was then focused on new birds as they entered the breeding population (these recruits can be assumed to be a minimum age of 6 years, the average age at first breeding in this population; Harris et al. 1994). The analyses were repeated excluding the birds marked at the beginning of the study and in the one area

where only a minority of the population was ringed. None of the conclusions changed, so we report the results using the full data set of 115 females and 123 males. The average length of the RLS (for birds included in the analyses) was 15 years (range 8–24 years).

Our analysis of senescence presumes that all individuals die of old age. In reality, some individuals will not reach the age at which senescence effects become apparent but will die from accidents or disease much earlier. Therefore we also examined declines in breeding success in the last 3 years of life, relative to earlier breeding success, in relation to RLS. An initial analysis found no difference in average breeding success between the last 3 years of life and the presenescent years (fig. 2) for individuals that were present for <8 years. In contrast, there were marked differences in average breeding success between the last 3 years of life and the presenescent years for individuals with an RLS of ≥8 years (statistics provided in fig. 2 legend). The shorter-lived group may have contained birds that either died suddenly at a young age, for whatever reason, or were of low quality and never survived to reach senescent ages. Furthermore, they may already have been old when marked, and in this case, the number of years we recorded these individuals as having been alive would not have been a reliable approximation of RLS. We therefore take a conservative approach and restrict subsequent analyses to birds present for ≥8 years.

Early-Life Reproductive Output. An index of early-life reproductive output was obtained by totaling the number of chicks that an individual raised during the first half of its time at the colony and dividing by the number of years
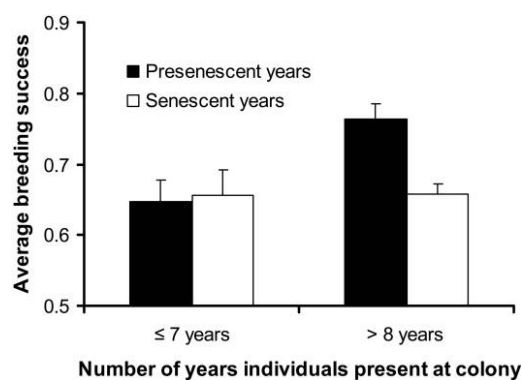
Figure 2: Average breeding success in the last 3 years of life (senescent years) and presenescent years for individuals recorded in <8 years ($n = 123$) versus individuals recorded in ≥8 years ($n = 238$). Difference was highly significant for ≥8-year group ($\chi^2 = 21.55$, df $= 1$, $P < .001$), whereas no difference was found between presenescent and senescent breeding success for individuals in the short-lived group ($\chi^2 = 0.19$, df $= 1$, $P = .86$).

in this period, thus giving mean annual breeding success in an individual's early life. We then tested to see how this measure of early-life effort was associated with individual rates of senescence.

Environmental Conditions Experienced Early in Life. We tested the hypothesis that the environment experienced by individuals early in life may also affect the rate at which they senesce in later life, if the magnitude of costs incurred through early reproduction depends on prevailing environmental conditions. We used two different summary measures of environmental quality to quantify early conditions: (1) a direct measure of climatic conditions, the winter North Atlantic Oscillation index (NAO), and (2) mean annual breeding success in the colony as whole. The NAO is a well-known climate measure based on deviations from long -term average pressure differences in the northern Atlantic. The winter index (wNAO) strongly predicts large-scale climatic conditions and weather patterns in northwestern Europe (Hurrell 1995): positive wNAO values indicate warm, wet winters dominated by westerly winds, and negative values indicate the opposite. The NAO is frequently used in ecological studies across a range of species as an environmental correlate of biological traits (Stenseth et al. 2003). In this population, wNAO is correlated with breeding time, an important fitness determinant; breeding is earlier in strongly positive NAO years when conditions are generally more favorable (Frederiksen et al. 2004; Reed et al. 2006). For each individual, wNAO values were averaged across the first half of its time at the colony to give a single index of weather conditions experienced early in life for each bird in the analysis (hereafter termed "early-life NAO"). The second measure, mean breeding success in the whole colony each year, was obtained from a much larger sample of marked breeding sites ($n = 1{,}412$; includes sites of both marked individuals and nonmarked individuals) that were also followed throughout the study, thereby giving a measure of annual mean breeding success with high resolution. In years where general conditions, such as food availability, weather, availability of good-quality breeding sites, and so on, are poor, this will be reflected in reduced overall breeding success at the colony level (Aebischer et al. 1990). In contrast, years of high breeding success represent situations where conditions were favorable, for example, where food was relatively abundant and easily available. For each individual, annual mean values of colony breeding success were averaged across the first half of the individual's time at the colony to give a single index of general conditions experienced early in life for each bird in the analysis (hereafter referred to as "early-life colony success"). Although both wNAO and mean colony success were correlated with mean laying date in the colony, they were not correlated

with each other ($r = 0.24$ for $n = 23$ years), and so they encapsulate different aspects of overall environmental conditions. We predicted that if individuals experienced on average poor conditions early in life (negative or low wNAO index or low colony success), this would result in higher costs of early reproduction and thus increased rates of senescence later in life.

Temporal Changes in Breeding Success. Average breeding success in the whole colony changed over time during the study, with two distinct periods: 1981–1996, when breeding success remained relatively constant, and 1997–2004, when there was a marked decline in breeding success (fig. 3). Such temporal trends in breeding success may complicate the detection of senescence if, for example, individuals that reach senescence age toward the end of the study period also experience degraded environmental conditions. Furthermore, this may generate false or inflated associations between senescence rates and early-life environment for these individuals. To account for this potentially confounding source of variation, we controlled for the temporal changes by fitting a main effect of period (1981–1996 vs. 1997–2004) and a nested effect of year within period. Year was also included as a random effect in the mixed model, to further correct for temporal variation in breeding success. (The mixed-model analysis was repeated with and without the effects of period and year nested within period and also with year as a factor in the fixed model rather than the random model. These alternative ways of specifying the model did not significantly change the results or conclusions, and hence all reported effects are robust to model restructuring.)
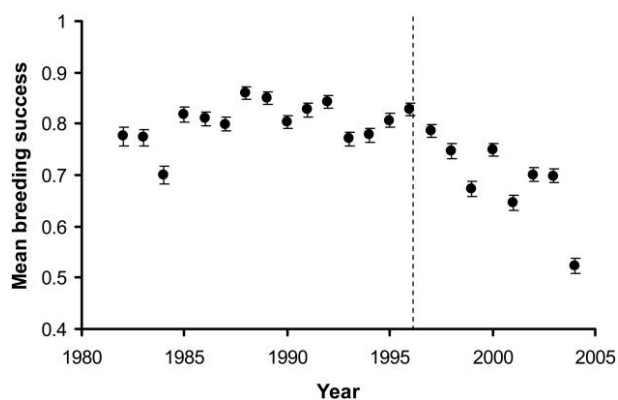

Figure 3: Temporal trends in average breeding success in the colony across the study period. There are two distinct periods, as indicated by the dashed dividing line: 1982–1996, where productivity remained relatively stable, and 1997–2004, where productivity declined sharply.

Statistical Analyses

Testing for Within-Individual Declines in Performance and Factors Associated with These Declines

Within-individual declines in breeding success in the years before death were tested for with a generalized linear mixed-effect model (GLMM), taking into account other important sources of variation that might have had an effect on breeding success. The model had breeding success as a binary response (successful or unsuccessful) and period (early/late), year as a continuous variable nested within period (to reflect the differing temporal trends shown in fig. 3), senescence class, early-life reproductive output, early-life NAO, early-life colony success, sex, and TFC as fixed effects. TFC was included to account for the fact that declines in breeding success may become apparent at different (estimated) ages. Period and sex were factors, while all other terms were continuous variables. Senescence class (a summary version of YBD) was treated as a continuous variable in the model because we were interested in how breeding success declines linearly in the years leading up to the death of individuals and how this decline (slope) might vary between the sexes and among individuals. To answer these latter questions, we fitted interaction terms between senescence class and sex, between senescence class and early-life reproductive output (to determine whether individuals that invested varying amounts in reproduction early in life senesced at different rates), and between senescence class and early-life environment (to test whether conditions experienced early in life, assessed by either wNAO or mean colony success, influenced the rate of senescence). Individual identity and year as factors were fitted as random effects to account for nonindependence of repeated measures on individuals across years. Thus the initial full model was breeding success = period + period/ year + sex + early-life reproductive output + early-life NAO + early-life colony success + senescence class + TFC + senescence class × (sex + early-life reproductive output + early-life NAO + early-life colony success) + individual ID + year.

This initial model was then simplified by progressively removing nonsignificant terms in order of least significance until all remaining terms (or interactions involving nonsignificant terms) were significant. The significance of terms was assessed using Type III tests (as when added last to the model, using Wald statistics compared against a χ^2 distribution with the appropriate degrees of freedom), with the significance of main effects assessed after first dropping associated interactions from the model. The GLMM had a logit-link function and a binomial error structure (Crawley 2002).

As individuals get older, there is a tendency to breed later in the season, and late laying is associated with re-duced breeding success (Wanless and Harris 1988). To check whether within-individual senescent declines in breeding success later in life could simply be driven by older birds breeding later, we repeated the GLMM with relative laying date of individuals each year included as a continuous fixed effect.

Testing for Declines in Probability of Breeding or Holding a Site

The significance of differences between senescence classes in the proportion of individuals attempting to breed and the proportion of individuals holding sites was also assessed using a GLMM, with binary measures of performance (bred/not bred, site held/site not held) as the response variables in each case, senescence class as the only (continuous, ranging from -4 to -1) fixed effect, and random effects for individual identity and year in each. A GLMM was also similarly used to test whether the probability of individuals changing site (binary variable) increased in the years approaching death.

The Effect of Early-Life Reproductive Output on RLS and Lifetime Breeding Success

The full mixed model tested for factors associated with individual rates of decline in breeding success in the senescent years. We also assessed the extent to which these factors influenced components of overall lifetime fitness, RLS and lifetime breeding success (LBS). To test for the effect of early-life reproductive output on RLS, for instance, whether individuals that invest heavily in reproduction early in life also die earlier, we performed a regression analysis of RLS on early-life reproductive output and (early-life reproductive output)^2. The quadratic term was included to determine whether there was some optimum level of early investment in terms of future life span. We then performed a multiple-regression analysis using overall LBS as the response to determine the relative importance for LBS of the various fitness components: early-life reproductive output, (early-life reproductive output)^2, output in senescent years, and RLS (Brown 1988). Each term was added sequentially in this order (the same order in which the events occur within an individual's life) as explanatory variables, and their significance was assessed using Type I (i.e., sequential) tests. All models were fitted using restricted maximum-likelihood (REML) and least-squares methods in GENSTAT (8th ed.; VSN International).

Table 1: Results of final reduced mixed model (generalized linear mixed-effect model) showing variables with significant effects on annual breeding success

Effect	Estimate	SE	df	Wald statistic	P value
Fixed effects:					
Intercept	1.204	.133			
Period:					
1981–1996	.000				
1997–2005	.351	.474	1	.55	.459
Period/year:					
1981–1996	.042	.064	2	5.50	.004
1997–2005	−.166	.064			
Sex:					
Females	.000		1	2.97	.085
Males	.017	.100			
Early-life reproductive output	3.476	.219	1	226.67	<.001
Early-life wNAO	−.001	.089	1	.19	.664
Senescence class	−.221	.068	1	9.98	.002
TFC	.034	.017	1	4.20	.040
Senescence class × sex:					
Females	.000	.082	1	3.99	.046
Males	.164	.082			
Senescence class × early-life reproductive output	−1.376	.174	1	62.48	<.001
Senescence class × early-life wNAO	.186	.070	1	6.98	.008
Random effects:					
Bird identity	.177	.054			
Year (factor)	.087	.045			
Residual variance	.909	.023			

Note: Breeding success in a given year was scored as a binary response, with $n = 238$ individuals breeding in multiple years. Relative laying date is not included in this model. Significance of fixed effects was assessed using Type III tests and Wald statistics. Variance components plus their standard errors are shown for random effects. A binomial error structure was specified with a logit-link function. TFC = time elapsed since first capture; wNAO = winter North Atlantic Oscillation index.

Results

Declines in Reproductive Performance in Years Leading up to Death of Birds

There was a clear trend toward a reduction in breeding success in the 3 years leading up to the death of individuals (fig. 1), with mean breeding success notably much lower in the ultimate year of life. In addition, the proportion of individuals attempting to breed was significantly lower in the senescent years, with ∼84% of individuals attempting to breed in the ultimate year of life compared to an average of ∼93% in the presenescent years (effect of senescence class in GLMM of bred/not bred: Wald = 44.15, df = 1, $P < .001$). Individuals were also less likely to hold a site in the last 3 years of life compared to presenescent years (effect of senescence class in GLMM of site held/not held: Wald = 42.76, df = 1, $P < .001$). Individuals were no more likely to change site in the senescent years; the incidence of site change remained constant in the years lead-

ing up to the death of individuals (Wald = 0.51, df = 1, $P = .475$).

Within-Individual Senescent Declines

The results of the final reduced model of changes in annual breeding success are given in table 1. The random effect for bird identity accounted for a significant portion (15.1%) of the total variance in breeding success (calculated as the sum of the bird identity and year variance components plus the residual variance), indicating significant variation between individuals in average breeding performance. Breeding success declined linearly with year in the latter period of the study, whereas there was no effect of year within the first period. Overall breeding success was lower in the latter period (GLMM including main effect of period but excluding effect of year within period: predicted mean success in first period = 0.932, in second period = 0.565; Wald = 3.67, $P = .055$). TFC had a

marginally significant positive effect in the full GLMM. Inclusion of TFC in the model does not significantly alter the parameter estimates of other terms, and the conclusions of the model remain the same independent of TFC, so TFC was retained in the model.

There was a strong negative effect of senescence class, implying that breeding success became significantly reduced as individuals approached the final years of life. This demonstrates that within-individual senescent declines in reproductive performance are evident for common guillemots in this population. The effect was particularly marked in the ultimate year of life (mean breeding success of males and females combined of 0.54, compared to an average of 0.74 in the presenescent years; fig. 4) but was also significantly lower in the penultimate year of life (0.68) and somewhat lower in the third-to-last year (0.71). There were no overall differences in breeding success between males and females, but there was a significant interaction between sex and senescence class, indicating that females senesce at slightly faster rates than males (table 1; fig. 4). Females performed consistently worse than males in the last 3 years of life and particularly worse in the ultimate year of life (fig. 4). Females also had lower average early-life reproductive output than males (mean females = 0.724, mean males = 0.765; two-tailed t-test: $t = -5.08$, $P < .001$).

Factors Influencing the Rate of Senescence

Individuals that performed well in the first half of their breeding life span had significantly higher breeding success on average throughout the full breeding life span. However, individuals that had higher early-life reproductive output also senesced faster, with a highly significant interaction between early-life output and senescence class in the final model (table 1). Figure 5A illustrates this trade-off, showing how individuals that were highly successfully at raising chicks during the first half of their reproductive lives (high-output individuals) had significantly lower breeding success in their senescent years compared to presenescent years. In contrast, the difference in breeding success between senescent and presenescent years was not as pronounced for birds with lower early-life reproductive output (i.e., those that were less successful during early life).

Early environmental conditions also had a significant impact on the rate of senescence. There was a highly significant interaction between senescence class and early-life NAO: individuals that experienced on average lower wNAO (i.e., poorer climatic conditions) early in life senesced at faster rates (fig. 5B). Interactions between senescence class and early-life NAO and senescence class and early-life colony success were both included in the full model. Neither was significant when in the model together, and the interaction
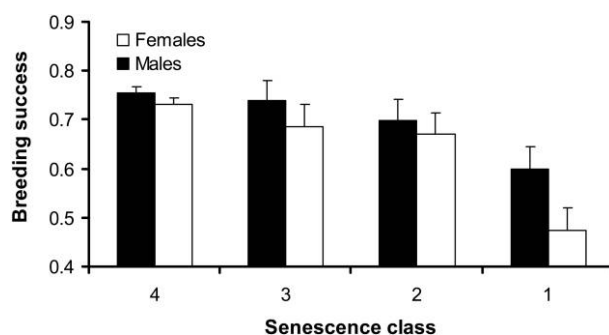

Figure 4: Breeding success (the proportion of occasions where a chick was raised) of males and females in relation to senescence class (mean ± SE).

with early-life colony success was less significant (effect of senescence class × early-life colony success in full model: estimate = 4.344 ± 3.666, Wald = 1.40, df = 1, P = .236). This interaction term and the main effect of early-life colony success, which was also not significant, were therefore removed from the model, to give the final model (table 1), in which the interaction between senescence class and early-life NAO had a significant effect. Alternatively, when the interaction with early-life NAO was removed and the interaction with early-life colony success was retained, the latter remained significant (effect of senescence class × early-life colony success in model without early-life NAO or its interaction with senescence class: estimate = 7.469 ± 2.879, Wald = 6.73, df = 1, P = .009). This effect was also in the predicted direction (individuals experiencing poorer early conditions subsequently senesce faster; fig. 5C). The final model reported in table 1 presents the results for the model using early-life NAO only.

The GLMM including relative laying date showed a highly significant negative effect of relative laying date on breeding success, confirming that late-breeding birds perform consistently poorer (relative laying date = -0.081 ± 0.009, Wald = 80.81, $P < .001$). However, after inclusion of relative laying date in the model, the main effect of senescence class was no longer significant (senescence class = -0.069 ± 0.065, Wald = 1.14, $P = .286$), nor were the interactions between senescence class and sex (males relative to females: senescence class = -0.019 ± 0.101, Wald = 0.04, $P = .849$) and senescence class and early-life NAO (-0.065 ± 0.083, Wald = 0.62, $P = .433$). Nevertheless, the interaction effect between senescence class and early-life reproductive output remained highly significant, implying that high-quality individuals performed worse in the senescent years relative to the presenescent years, independent of time of the season at which they bred (senescence class × early-life reproductive output effect in model in-
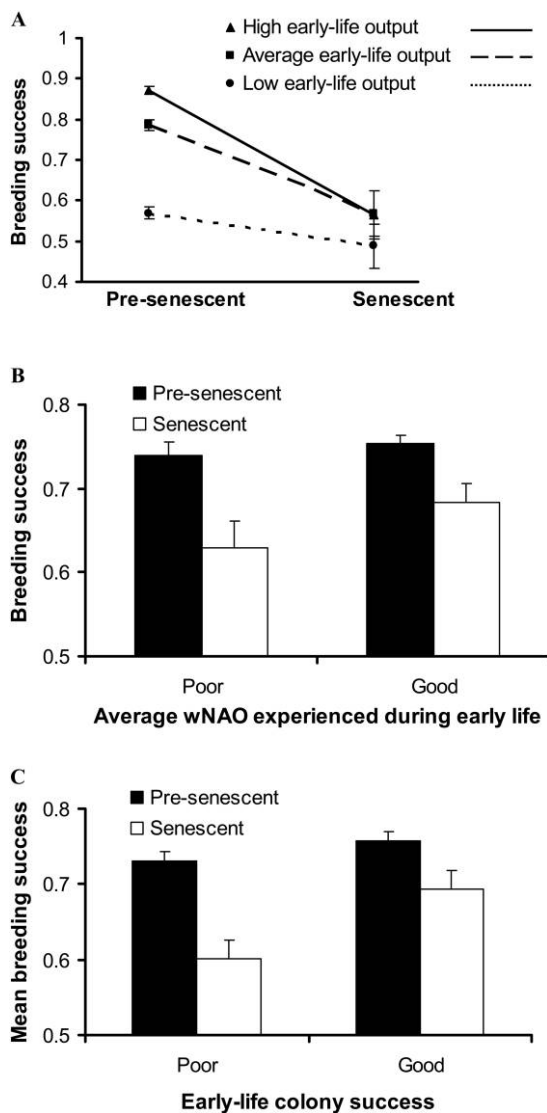
Figure 5: *A*, Senescent declines, as represented by the difference in annual breeding success (±SE) between presenescent and senescent years, in relation to early-life reproductive output. Early-life reproductive output was fitted as a continuous variable in the mixed model but divided into groups here for convenience: low = bottom third of range (0–0.60 chicks/year), average = middle third of range (0.61–0.80 chicks/year), high = top third of range (0.81–1 chicks/year). *B*, Differences in annual breeding success (±SE) between presenescent years and senescent years in relation to general weather conditions experienced early in life (average early-life winter North Atlantic Oscillation [wNAO]). Average early-life wNAO was fitted as a continuous variable in the mixed model but divided into groups here for convenience: poor = bottom half of range (−0.39 to 1.89), good = top half of range (1.90–3.24). *C*, Differences in breeding success between presenescent years and senescent years in relation to general environmental conditions experienced early in life. Mean colony breeding success averaged across the first half of individuals' lives was fitted as a continuous variable in the mixed model but divided into groups here for convenience: poor = bottom half of range, good = top half of range.

cluding relative laying date: −1.478 ± 0.219, Wald = 44.58, $P < .001$). None of the interactions between relative laying date and other terms was significant.

Effect of Early-Life Output on RLS and LBS

Analysis of the relative overall importance of the different fitness components revealed a significant quadratic effect of early-life reproductive output on RLS (fig. 6*A*). Individuals with intermediate values for early-life reproductive output (~0.8, i.e., successfully raised chicks 80% of the time) bred for longer than individuals with either lower or higher early-life output. Early-life reproductive output and its quadratic term also had significant effects on LBS (the number of chicks successfully raised across the whole life span; fig. 6*B*; table 2) in the multiple regression, independent of other terms when added first to the model. This relationship was best described by a decelerating function: the effect of early-life reproductive output on LBS was stronger for lower values of early-life reproductive output (fig. 6*B*). There were also strong positive effects of reproductive output in the senescence years and RLS on LBS, independent of early-life reproductive output (table 2).

Discussion

Here we provide clear evidence for within-individual reproductive senescence in a long-lived seabird species, with declines in reproductive performance in the final years of life. Senescent individuals were less likely to hold a breeding site, to attempt to breed, and to raise a chick. Detecting reproductive senescence in wild bird populations is difficult, and few studies have unequivocally demonstrated its existence at the level of the individual (Nisbet 2001; Reid et al. 2003; Catry et al. 2006). The recent studies of Ricklefs (2000) and Coulson and Fairweather (2001) suggest that the primary reason reproductive senescence is so rarely detected in birds is that in general, birds manage to maintain their bodies in a state of high physiological condition right up until the end of life. For example, Ricklefs (2000) drew attention to the fact that intrinsic rates of age-related mortality are broadly similar between captive and wild birds, suggesting that progressive reproductive senescence is not necessarily something we expect to observe in nature (Ricklefs 2000). A sudden drop in physiological condition (and hence reproductive output) observed at the very end of life, therefore, could be viewed as the result of pathological terminal illness rather than conventional senescence, that is, a general and progressive decline in performance in the years leading up to the death of individuals. In our study, however, reductions in breeding performance became apparent in guillemots 2–3 years
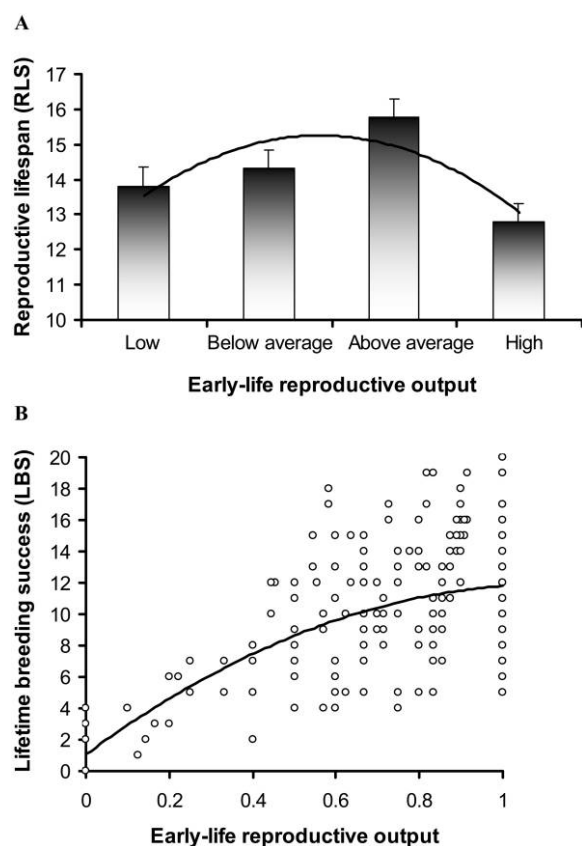
Figure 6: *A,* Effect of early-life reproductive output on reproductive life span. Early-life reproductive output was a continuous variable but here is divided into quartiles: low = 0–0.6 chicks/year raised on average, below average = 0.6–0.8 chicks/year, above average = 0.8–0.92 chicks/year, high = 0.92–1 chicks/year (regression analysis: reproductive life span = $7.46 + 1.92 \times$ early-life reproductive output $- 8.14 \times$ (early-life reproductive output)^2, $n = 238$ individuals; quadratic effect: $F = 351.83$, df $= 1$, $P < .001$). Curve is quadratic fit as predicted from regression. *B,* Effect of early-life reproductive output on lifetime breeding success (regression analysis: lifetime breeding success $= 1.06 + 19.53 \times$ early-life reproductive output $- 8.79 \times$ (early-life reproductive output)^2, $n = 238$ individuals; quadratic effect: $F = 9.32$, df $= 1$, $P = .002$).

before the death of individuals, suggesting a more progressive senescence. This contrasts with the situation described by Coulson and Fairweather (2001) for black-legged kittiwakes *Rissa tridactyla* breeding in northeast England, where individuals seemed to perform significantly worse on their final breeding attempt, irrespective of age, but no worse in their penultimate or third-to-last attempts. We could not detect senescence effects in younger birds (birds breeding for <8 years) in this study, in the ultimate year or any other year preceding the death of individuals; declines in breeding success were apparent only for older birds (in the last 2–3 years of life), again pointing toward progressive senescence rather than terminal illness. Fur-

thermore, senescent effects may be subtle and may affect other aspects of performance such as foraging, as highlighted by a recent study on gray-headed albatrosses (*Thalassarche chrysostoma*) by Catry et al. (2006), and hence they may not necessarily result in complete breeding failure of older pairs but rather progressive reductions in breeding success. We do not know the mechanism driving the declines in guillemots, but foraging capabilities and chick-feeding rates may well be important determinants of late-life success. It is of course possible that old guillemots begin to suffer from impaired locomotory or cognitive capacities, for example, from a much earlier stage but manage nevertheless to maintain high levels of productivity by compensating, that is, by investing relatively more energy and resources in reproduction as they age (e.g., Velando et al. 2006). Further studies on the more subtle effects of aging in birds will be important in testing these ideas.

The analytical technique employed in this study of quantifying senescent reductions in breeding success in the years leading up to death of individuals represents a novel approach to tackling the problem of senescence. Selective disappearance after survival selection is a long-standing general problem in studies of age-related breeding performance and can hamper the detection of senescent declines (Cam and Monnat 2000; Nisbet 2001; Reid et al. 2003; van de Pol and Verhulst 2006). Our method circumvents this pitfall by effectively aligning individual life histories so that progressive differences in the average quality of age cohorts due to selective disappearance are no longer an issue; all individuals now "disappear" at the same point. There may still be quality differences between individuals, and this may affect how long they live, but it will not impede the detection of senescence using this procedure. In general, mixed models represent a powerful approach to the study of senescence because they can control for between-individual variation in quality, thereby enabling within-individual senescent declines to be measured independently (Nussey et al. 2006; van de Pol and Verhulst 2006). Furthermore, our mixed-model approach allows senescence to be modeled without prior knowledge of true age, which is often necessary in studies of birds that are difficult or impossible to age once mature (see also Crespin et al. 2006). Our results were also in concordance with a previous analysis of reproductive senescence in this population (Crespin et al. 2006) that employed a different methodology through the use of a surrogate measure for age (TFC). Inclusion of TFC in our models does not change our conclusions, implying that information on age is not necessary for senescence to be adequately described by the current method.

Female guillemots were found to senesce at a significantly faster rate than males. This is the first demonstration, to our knowledge, of sex differences in within-

Table 2: ANOVA table for multiple regression analysis of lifetime breeding success showing significant effects

	df	SS	*F*	*P* value
Early-life reproductive output	1	3,108.96	2,345.9	<.001
(Early-life reproductive output)^2	1	95.71	72.2	<.001
Output in senescent years	1	410.08	309.4	<.001
Reproductive life span	1	78.78	59.4	<.001
Residual	233	308.79		

Note: Early-life reproductive output and output in senescent years were both measured here as number of chicks successfully raised in these periods. Significance of terms was assessed using Type I tests, that is, when added sequentially to the model in the order specified (the order in which events occur during life).

individual rates of reproductive senescence in a wild vertebrate. Evolutionary theories of senescence (antagonistic pleiotropy and disposable soma) predict that the sex with the higher rate of mortality will suffer more rapid senescence because selection for increased investment in early reproduction over somatic repair (or for genes with antagonistic early- and late-life fitness effects) will be stronger in this sex, with negative knock-on effects on late-life vigor (Williams 1957). Males and females may thus exhibit different allocation strategies based on mortality risk, which may affect the degree to which senescence is manifested in each sex. However, there do not appear to be overall sex differences in mortality rate in this population (annual survival of males = 95.4% ± 0.9% [± SE], females = 95.3% ± 0.6%; Harris et al. 2000). We found no evidence for increased investment in early reproduction by females relative to males; rather, we found the opposite, since females appeared to have lower average reproductive output in the first half of their lives. Thus, our finding of sex differences in senescence rate in guillemots could not be explained by our current understanding of mortality differences or differences in levels or costs of early reproduction. Cumulative reproductive costs, for example, due to egg production or higher chick-feeding rates (Wanless and Harris 1986), over the entire presenescent period could nevertheless be greater for females, and this could result in reduced condition of females relative to males in the senescent years. An alternative explanation could be that males switch partner more frequently as they get older in favor of better-quality (perhaps younger) females; however, previous work on this population suggests that mate switching is costly for males rather than beneficial (Lewis et al. 2006).

Individual rates of senescence were associated with levels of early-life reproductive effort. Guillemots investing heavily in reproduction during the first half of their reproductive careers had significantly reduced breeding success in the senescent years. This demonstration of a trade-off between early- and late-life reproduction provides rare evidence in favor of the antagonistic-pleiotropy and dis-

posable-soma theories for the evolution of aging (although it does not exclude the possibility of other mechanisms also contributing to senescence). Despite a large body of theory, empirical tests of this key prediction have seldom been carried out, particularly in free-living vertebrate populations. Nussey et al. (2006) provided the first test in mammals, showing that female red deer *Cervus elaphus* reproducing more frequently in early life subsequently exhibit stronger declines in offspring birth weight and delayed calving dates in old age. Trade-offs between early- and late-life reproductive performance have also been shown to exist in birds (Gustafsson and Pärt 1990; Reid et al. 2003). Gustafsson and Pärt (1990), for example, demonstrated that female collared flycatchers (*Ficedula albicollis*) laid smaller clutches late in life when subjected to experimentally enlarged broods early in life. Similarly, reductions in late-life survival resulting from heightened levels of early reproduction have been detected in passerine birds (McCleery et al. 1996; Orell and Belda 2002) and humans (Pettay et al. 2005). In this study, however, we focus on rates of decline in reproductive performance, rather than absolute performance levels late in life, and provide a clear demonstration of a trade-off with early reproduction. Furthermore, we show that rates of reproductive senescence are also dependent on environmental conditions experienced early in life; individuals that faced poorer general conditions during their early years subsequently senesced at faster rates. We suggest that this increased rate of senescence associated with poorer early environmental conditions results from the increased costs of reproduction under such circumstances. If, for example, food was generally less available for these birds, producing and feeding a given number of chicks during early life would have been relatively more costly than producing and feeding the same amount under more favorable conditions. We controlled for differences between individuals in the number of chicks produced during early life in our model as well as for other potentially confounding sources of variation, such as temporal deteriorations in the environment and sex effects, and we were still able to dem-

onstrate this independent effect of early environment on rate of senescence. These delayed costs of early energy expenditure thus provide a direct illustration of how patterns of senescence invoked by the disposable-soma hypothesis might be modulated. This important phenomenon is largely ignored in laboratory studies, where environmental variation is kept to a minimum. It is thus crucial to also examine senescence within the natural ecological context under which it evolved, and further detailed studies exploring potential environmental effects will be essential in determining the generality of this result. Furthermore, our results highlight the fact that if conditions continue to deteriorate at this colony (2004 and 2006 were the worst breeding years on record since 1980), then these residual effects of early conditions will continue to impact the dynamics of the colony over the next 20 years or so as current cohorts age.

Finally, we have shown that life span in guillemots is also dependent on the level of early-life reproductive output: individuals with very high levels of early reproductive effort did not live as long. Reproductive life span is the most important component of lifetime breeding success in this population and is generally considered to be of key importance in seabird life histories, which are characterized by low annual reproductive output and high survival (Moreno 2003). The hardest-working individuals (those that invested most in early reproduction) exhibited more senescence in the last 3 years of life and also died sooner, and both of these factors explain why birds obtain increasingly less advantage, in terms of lifetime breeding success, from having very high fecundity early in life. We also show that individuals with high early-life reproductive output have reduced breeding success late in life regardless of when in the season they lay, implying that delayed costs of reproduction are associated with increased intrinsic (physiological) senescence and loss of function late in life independent of breeding time. These results have implications for the optimization of individual life-history strategies and highlight the value of long-term, individual-level data from wild populations in developing a more comprehensive understanding of the ecological causes and evolutionary consequences of senescence.

Acknowledgments

Literature Cited

Aebischer, N. J., J. C. Coulson, and J. M. Colebrook. 1990. Parallel long-term trends across four marine trophic levels and weather. Nature 347:753–755.

Berube, C. H., M. Festa-Bianchet, and J. T. Jorgenson. 1999. Individual differences, longevity, and reproductive senescence in bighorn ewes. Ecology 80:2555–2565.

Bonduriansky, R., and C. E. Brassil. 2002. Rapid and costly ageing in wild male flies. Nature 420:377.

Brown, D. 1988. Components of lifetime reproductive success. Pages 439–453 *in* T. H. Clutton-Brock, ed. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago.

Cam, E., and J.-Y. Monnat. 2000. Apparent inferiority of first-time breeders in the kittiwake: the role of heterogeneity among age classes. Journal of Animal Ecology 69:380–394.

Catry, P., R. A. Phillips, B. Phalan, and J. P. Croxall. 2006. Senescence effects in an extremely long-lived bird: the grey-headed albatross *Thalassarche chrysostoma*. Proceedings of the Royal Society B: Biological Sciences 273:1625–1630.

Charlesworth, B. 1980. Evolution in age-structured populations. Cambridge University Press, Cambridge.

Comfort, A. 1979. The biology of senescence. 3rd ed. Churchill Livingstone, Edinburgh.

Coulson, J. C., and J. A. Fairweather. 2001. Reduced reproductive performance prior to death in the black-legged kittiwake: senescence or terminal illness? Journal of Avian Biology 32:146–152.

Crawley, M. J. 2002. Statistical computing: an introduction to data analysis using S-Plus. Wiley, New York.

Crespin, L., M. P. Harris, J. D. Lebreton, and S. Wanless. 2006. Increased adult mortality and reduced breeding success with age in a population of common guillemot *Uria aalge* using marked birds of unknown age. Journal of Avian Biology 37:273–282.

Ericsson, G., K. Wallin, J. P. Ball, and M. Broberg. 2001. Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. Ecology 82:1613–1620.

Forslund, P., and T. Pärt. 1995. Age and reproduction in birds: hypotheses and tests. Trends in Ecology & Evolution 10:374–378.

Frederiksen, M., M. P. Harris, F. Daunt, P. Rothery, and S. Wanless. 2004. Scale-dependent climate signals drive breeding phenology of three seabird species. Global Change Biology 10:1214–1221.

Gustafsson, L., and T. Pärt. 1990. Acceleration of senescence in the collared flycatcher *Ficedula albicollis* by reproductive costs. Nature 347:279–281.

Gustafsson, L., and W. J. Sutherland. 1988. The costs of reproduction in the collared flycatcher *Ficedula albicollis*. Nature 335:813–815.

Gustafsson, L., D. Nordling, M. S. Andersson, B. C. Sheldon, and A. Qvarnstrom. 1994. Infectious diseases, reproductive effort and the cost of reproduction in birds. Philosophical Transactions of the Royal Society B: Biological Sciences 346:323–331.

Hamilton, W. D. 1966. The moulding of senescence by natural selection. Journal of Theoretical Biology 12:12–45.

Hanssen, S. A., I. Folstad, and K. E. Erikstad. 2003. Reduced im-

munocompetence and cost of reproduction in common eiders. Oecologia (Berlin) 136:457–464.

Harris, M. P., and S. Wanless. 1988. The breeding biology of guillemots *Uria aalge* on the Isle of May over a 6 year period. Ibis 130:172–192.

———. 1995. Survival and non-breeding of adult common guillemots *Uria aalge*. Ibis 137:192–197.

Harris, M. P., D. J. Halley, and R. L. Swann. 1994. Age of first breeding in common murres. Auk 111:207–209.

Harris, M. P., S. Wanless, and P. Rothery. 2000. Adult survival rates of shag *Phalacrocorax aristotelis*, common guillemot *Uria aalge*, razorbill *Alca torda*, puffin *Fratercula arctica* and kittiwake *Rissa tridactyla* on the Isle of May 1986–96. Atlantic Seabirds 2:133–150.

Holmes, D. J., and S. N. Austad. 1995. The evolution of avian senescence patterns: implications for understanding primary aging processes. American Zoologist 35:307–317.

Holmes, D. J., R. Fluckiger, and S. Austad. 2001. Comparative biology of aging in birds: an update. Experimental Gerontology 36:869–883.

Hurrell, J. W. 1995. Decadal trends in the North-Atlantic Oscillation: regional temperatures and precipitation. Science 269:676–679.

Keller, L., and M. Genoud. 1997. Extraordinary lifespans in ants: a test of evolutionary theories of ageing. Nature 389:958–960.

Kirkwood, T. B. L. 1977. Evolution of ageing. Nature 270:301–304.

Kirkwood, T. B. L., and M. R. Rose. 1991. Evolution of senescence: late survival sacrificed for reproduction. Philosophical Transactions of the Royal Society B: Biological Sciences 332:15–24.

Kokko, H., M. P. Harris, and S. Wanless. 2004. Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the common guillemot *Uria aalge*. Journal of Animal Ecology 73:367–376.

Lewis, S., S. Wanless, D. A. Elstono, M. D. Schultz, E. Mackley, M. Du Toit, J. G. Underhill, et al. 2006. Determinants of quality in a long-lived colonial species. Journal of Animal Ecology 75:1304–1312.

McCleery, R. H., J. Clobert, R. Julliard, and C. M. Perrins. 1996. Nest predation and delayed cost of reproduction in the great tit. Journal of Animal Ecology 65:96–104.

Medawar, P. B. 1952. An unsolved problem in biology. Lewis, London.

Monaghan, P., and M. F. Haussmann. 2006. Do telomere dynamics link lifestyle and lifespan? Trends in Ecology & Evolution 21:47–53.

Moreno, J. 2003. Lifetime reproductive success in seabirds: interindividual differences and implications for conservation. Scientia Marina 67:7–12.

Nisbet, I. C. T. 2001. Detecting and measuring senescence in wild birds: experience with long-lived seabirds. Experimental Gerontology 36:833–843.

Nur, N. 1984. The consequences of brood size for breeding blue tits. I. Adult survival, weight change and the cost of reproduction. Journal of Animal Ecology 53:479–496.

Nussey, D. H., L. E. B. Kruuk, A. Donald, M. Fowlie, and T. H. Clutton-Brock. 2006. The rate of senescence in maternal performance increases with early-life fecundity in red deer. Ecology Letters 9:1342–1350.

Orell, M., and E. J. Belda. 2002. Delayed cost of reproduction and senescence in the willow tit *Parus montanus*. Journal of Animal Ecology 71:55–64.

Partridge, L. 1987. Is accelerated senescence a cost of reproduction? Functional Ecology 1:317–320.

Partridge, L., and N. H. Barton. 1993. Optimality, mutation and the evolution of ageing. Nature 362:305–311.

Pettay, J. E., L. E. B. Kruuk, J. Jokela, and V. Lummaa. 2005. Heritability and genetic constraints of life-history trait evolution in preindustrial humans. Proceedings of the National Academy of Sciences of the USA 102:2838–2843.

Promislow, D. E. L. 1991. Senescence in natural populations of mammals: a comparative study. Evolution 45:1869–1887.

Reed, T. E., S. Wanless, M. P. Harris, M. Frederiksen, L. E. B. Kruuk, and E. J. A. Cunningham. 2006. Responding to environmental change: plastic responses vary little in a synchronous breeder. Proceedings of the Royal Society B: Biological Sciences 273:2713–2719.

Reid, J. M., E. M. Bignal, S. Bignal, D. I. McCracken, and P. Monaghan. 2003. Age-specific reproductive performance in red-billed choughs *Pyrrhocorax pyrrhocorax*: patterns and processes in a natural population. Journal of Animal Ecology 72:765–776.

Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos 44:257–267.

Reznick, D. N., M. J. Bryant, D. Roff, C. K. Ghalambor, and D. E. Ghalambor. 2004. Effect of extrinsic mortality on the evolution of senescence in guppies. Nature 431:1095–1099.

Ricklefs, R. E. 1998. Evolutionary theories of aging: confirmation of a fundamental prediction, with implications for the genetic basis and evolution of life span. American Naturalist 152:24–44.

———. 2000. Intrinsic aging-related mortality in birds. Journal of Avian Biology 31:103–111.

Ricklefs, R. E., and A. Scheuerlein. 2001. Comparison of aging-related mortality among birds and mammals. Experimental Gerontology 36:845–857.

Rose, M., and B. Charlesworth. 1980. A test of evolutionary theories of senescence. Nature 287:141–142.

Service, P. M. 1993. Laboratory evolution of longevity and reproductive fitness components in male fruit-flies: mating ability. Evolution 47:387–399.

Stenseth, N. C., G. Ottersen, J. W. Hurrell, A. Mysterud, M. Lima, K. S. Chan, N. G. Yoccoz, et al. 2003. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. Proceedings of the Royal Society B: Biological Sciences 270:2087–2096.

van de Pol, M., and S. Verhulst. 2006. Age-dependent traits: a new statistical model to separate within- and between-individual effects. American Naturalist 167:766–773.

Velando, A., H. Drummond, and R. Torres. 2006. Senescent birds redouble reproductive effort when ill: confirmation of the terminal investment hypothesis. Proceedings of the Royal Society B: Biological Sciences 273:1443–1448.

Wanless, S., and M. P. Harris. 1986. Time spent at the colony by male and female guillemots *Uria aalge* and razorbills *Alca torda*. Bird Study 33:168–176.

———. 1988. The importance of relative laying date on breeding success of the guillemot *Uria aalge*. Ornis Scandinavica 19:205–211.

Williams, G. C. 1957. Pleiotropy, natural selection, and the evolution of senescence. Evolution 11:398–411.

———. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's Principle. American Naturalist 100:687–690.