Environmental conditions during early life accelerate the rate of senescence in a short-lived passerine bird

J. Balbontín[1,3] and A. P. Møller[2]

[1]*Departamento de Zoología, Facultad de Biología, Edificio Verde, Avda. de Reina Mercedes s/n, E-41012 Sevilla, Spain*
[2]*Laboratoire d'Ecologie, Systématique et Evolution, CNRS UMR 8079, Université Paris-Sud, Bâtiment 362, F-91405 Orsay Cedex, France*

Abstract. Environmental conditions experienced in early life may shape subsequent phenotypic traits including life history. We investigated how predation risk caused by domestic cats (*Felis silvestris catus*) and local breeding density affected patterns of reproductive and survival senescence in Barn Swallows (*Hirundo rustica*) breeding semi-colonially in Denmark. We recorded the abundance of cats and the number of breeding pairs at 39 breeding sites during 24 years and related these to age-specific survival rate and reproductive senescence to test predictions of the life history theory of senescence. We found evidence for actuarial senescence for the first time in this species. Survival rate increased until reaching a plateau in midlife and then decreased later. We also found that survival rate was higher for males than females. Local breeding density or predation risk did not affect survival as predicted by theory. Barn Swallows with short lives did not invest more in reproduction in early life, inconsistent with expectations for trade-offs between reproduction and survival as theory suggests. However, we found that the rate of reproductive decline during senescence was steeper for individuals exposed to intense competition, and predation pressure accelerated the rate of reproductive senescence, but only in sites with many breeding pairs. These latter results are in accordance with one of the predictions suggested by the life history theory of aging. These results emphasize the importance of considering intraspecific competition and interspecific interactions such as predation when analyzing reproductive and actuarial senescence.

Key words: aging; Barn Swallow, Hirundo rustica; *Denmark; density dependence; domestic cat,* Felis silvestris catus; *early-life environment; intraspecific competition; life history theory; life span; longevity; predation risk; senescence.*

INTRODUCTION

Senescence has been defined as an inevitable decrease in physiological functioning with age (Monaghan et al. 2008). Long-term longitudinal studies have shown that reproductive and actuarial senescence (i.e., a decrease in reproductive or survival prospects in late life, respectively) is common in free-ranging wild animals. A recent review showed evidence for senescence in different traits for 175 different animal species from 340 separate studies (Nussey et al. 2013). Although senescence is common, the causes of variation in senescence among species and populations are poorly understood.

Life history theory explained differences in life span across species by arguing that resources are not finite in nature and hence organisms might reach a balance between the resources allocated to current reproduction and those allocated to future reproduction and survival, which results in inevitable trade-offs between these traits (Stearns 1989). Accordingly, individuals investing more in reproduction in early life should decrease reproduc-

tive investment later, decrease their survival prospects, or increase their rate or onset of senescence (Williams 1957, Newton 1989, Stearns 1989, Kirkwood and Rose 1991). There is evidence from laboratory (e.g., Jenkins et al. 2004, Chen et al. 2007) and field studies supporting this central prediction of life history theories of aging (e.g., Gustafsson and Pärt 1990, Reid et al. 2003, Charmantier et al. 2006, Descamps et al. 2006, Nussey et al. 2006, Reed et al. 2008, Peron et al. 2010, Sharp and Clutton-Brock 2011, Hammers et al. 2013). However, there is also contradictory evidence concerning these trade-offs in a number of field studies, above all, when the association between reproduction and survival is investigated. Several studies have emphasized positive rather than negative covariation between early investment in reproduction and survival (Bérubé et al. 1999, McElligott et al. 2002, Beauplet et al. 2006, Moyes et al. 2006). Thus, field studies show evidence consistent with or contrary to these predictions derived from life history theories of aging (Austad 1993, Reznick et al. 2004, Millon et al. 2011). Furthermore, the factors causing variation among individuals and populations in the onset and patterns of senescence are poorly understood (review in Nussey et al. 2013). Currently, many scientists

have accumulated longitudinal data in long-term studies in the wild. Such studies provide high-quality data on phenotypic and fitness traits valuable for testing evolutionary hypotheses of aging (Nussey et al. 2008).

Early-life environmental conditions, such as local density, food availability, or predation risk, have been suggested to affect aging (Austad 1993, Reznick et al. 2004, Nussey et al. 2007, Millon et al. 2011, Hammers et al. 2013). Individuals exposed to hazardous environments, such as those with a high risk of predation, a high local breeding density, or a low-quality environment, are expected to allocate more resources in early life to reproduction at the cost of survival. Recently, it has been shown that Mauritius Kestrels (*Falco punctatus*) have changed their life history strategy by increasing their reproductive investment in early life at the cost of survival, associated with a change in habitat quality from forest to agricultural land due to human transformation (Cartwright et al. 2014). However, detailed studies of the consequences of the environment experienced in early life for rates of aging remain scarce (but see Hammers et al. 2013, Pardo et al. 2013, Oro et al. 2014).

The Barn Swallow (*Hirundo rustica*) is a small passerine bird (~20 g) that breeds semicolonially and feeds on insects while flying. It usually breeds indoors in farms, obtaining permanent access through open doors and windows, and thus is easily captured by humans and cats (*Felis silvestris catus*) alike (Møller et al. 2005). Barn Swallows provide excellent longitudinal data because, once recruited to the breeding population, individuals almost always return to the same colony to breed every year. Repeated mark–recapture sessions every year assured the capture of almost 100% of the individuals at the end of each field season. This, together with the fact that breeding dispersal is very low, allowed us to estimate actuarial survival rather than apparent survival. We studied 39 breeding sites that were exposed to different extrinsic mortality rates and to differences in local breeding density among sites. The domestic cat is a dominant predator in habitats altered by humans (Ewer 1973), and it is known to be an important territorial predator for at least 52 species of birds (Møller et al. 2010). Cats are estimated to annually kill 1.4–3.7 billion birds in North America alone (Loss et al. 2013). Although these direct effects on their own are significant, indirect effects of predators are likely to be even greater than the direct predation costs (Abrams 1984, Lima and Dill 1990, Lima 1998).

A previous study demonstrated the existence of reproductive senescence in two European populations of Barn Swallows, including the Danish population that is the focus of this paper (Møller and de Lope 1999, Balbontín et al. 2007, 2012). For this Danish Barn Swallow population, breeding success measured as annual number of eggs and fledglings declined when swallows reached the age of four years (Balbontín et al. 2012). Here, we focus on how predation pressure caused

by domestic cats and local breeding density experienced in early life affected the rate of reproductive senescence and actuarial survival of Barn Swallows in Denmark. These two factors could interact in nature if, for instance, individuals living at high density suffered less from predators. To our knowledge, no single study has so far focused on how these two factors interact to affect aging in nature. We investigated for the first time in this species the existence of actuarial senescence. Furthermore, according to life history theory of aging we predicted that:

1) Early-life environmental conditions would predict age-related survival rate, with individuals from sites subject to a high predation pressure or with a high number of breeding pairs showing a reduction in age-related survival rate compared to individuals from less stressful sites.
2) Investment in reproduction in early life would reduce life span; those individuals that invest more in reproduction would live shorter lives.
3) Early-life environmental conditions would affect life span, with individuals from sites subject to a high risk of predation or with a large number of breeding pairs living shorter lives.
4) Early-life environmental conditions would predict the rate of senescence, with individuals from sites subject to a high risk of predation or with a large number of breeding pairs showing an accelerated rate of senescence.

METHODS

Field procedures

We studied Barn Swallows at Kraghede, Denmark (57°12′ N, 10°00′ E) during 1988–2011. The study area consisted of farms, plantations, ponds, and hedgerows (for more details, see Møller 1994). We conducted our studies at 39 sites (nearest neighbor distance between sites was 1101 ± 1089 m, mean $\pm$ SD; range 75–3400 m) that differed in predation risk and local breeding density. Every breeding season, we visited each site weekly to obtain records of laying date, clutch size (i.e., number of eggs laid), and brood size (i.e., number of chicks in the nest). Survival rate for chicks from the age of 12 days to the age of fledging is very high (>98%) (Møller 1994). Thus, we estimated fecundity as the number of 12-day-old nestlings. Because this species frequently produced second clutches, we summed all eggs laid and all fledglings produced in first and second clutches for each individual adult throughout its life. From mid-April, we captured adults by using mist nets across windows and doors at the breeding sites. We made weekly captures of birds during every breeding season until 98–100% of breeding individuals were captured. Capture–mark–recapture analyses have shown that >97% of all adults were captured each year (Møller and Szép 2002). We searched each farm for feathers of

Barn Swallows, indicating successful cat predation, and farmers collected such feathers and bands to allow us to identify Barn Swallow prey. In total, 29 out of 34 dead Barn Swallows were observed to have been killed by cats. Each offspring was identified with a numbered metal band at the age of 12 days after careful observation of the breeding phenology of the parents. Captured adults were provided with a metal band and a combination of color PVC bands at first capture. All adults were also provided with an individual combination of color markings on their belly feathers using stamp ink with the aim to assign them to their nest site. Individuals were sexed from the presence (females) or absence (males) of a brood patch and from observation of breeding behavior during courtship and incubation. On each visit to the breeding sites, we recorded the number of adult cats in each farm. The total number of cats present in a colony of Barn Swallows was estimated as the maximum number recorded at the end of the field season. Local breeding density was the total number of breeding pairs of Barn Swallows at each colony.

Age and life span determination

We calculated the age of Barn Swallows with confidence because this species exhibits high breeding-site fidelity and because first recruitment occurs at an age of one year (for details, see Møller 1992, Møller et al. 2005, Balbontín et al. 2009). Briefly, in our study sites, breeding dispersal is negligible; <0.1% of breeding individuals (i.e., those ≥1 year old) of the more than 10 000 adults banded in Italy, Spain, and Denmark during more than 30 years ever moved to another farm in the same or subsequent years (N. Saino, F. de Lope, and A. P. Møller, *unpublished data*). Moreover, age at first reproduction occurred at the age of one year for the majority of individuals because all but one of more than 600 local recruits (i.e., more than 99% of individuals) were captured in their first year of life. Thus, we could assign the age of individuals with accuracy, assuming unbanded birds to be yearlings at first capture originating from outside the study area, and assuming that disappearance of color-banded breeders from colonies indicated mortality rather than dispersal. The last year that an individual was recorded breeding at a given site was the age at last reproduction (hereafter, ALR), which was used as a reliable estimation of life span. We eliminated from our data all adult individuals that were still alive at the end of the study and from which we could not calculate ALR, and this constituted 271 individuals.

Statistical analyses

To test our hypotheses of how environmental conditions during early life affected age-related survival rate, we evaluated all possible candidate models obtained from a generalized linear mixed model. We defined a global model that included the number of cats found in a given breeding site (hereafter, cats) when swallows were first captured at the breeding sites, the size of the colony (i.e., the number of breeding pairs; hereafter, colony size), sex, age, and the quadratic effect of age as input variables. Because first recruitment occurs at one year of age, early-life environmental conditions (i.e., number of cats and number of breeding pairs) were measured at the age of one year for all individuals. We included in the global model all two-way interactions between main input variables. In total, we included in the global model 11 predictor terms that resulted in $2^{11} = 2048$ candidate models. We did not include the interaction between the quadratic term of age with the other input variables because it would result in over-parameterization. The response variable was the survival of individuals from one year to the next. Survival was coded as 1 if the individual survived to the next year or 0 if it did not survive. The global model was a linear mixed-effect model in which we included these predictors as fixed effects and individual identity, the year at first capture, and breeding site as random effects (intercepts). We first standardized the input variables entering the global model, scaling them by centering their mean (dividing by two standard deviations), which allowed comparison on the same scale of coefficients of binary factors (e.g., sex), and covariates. Therefore, the parameter estimates are standardized effect sizes and are on a comparable scale (Gelman 2008, Grueber et al. 2011). Top models of all possible candidate models were determined using Akaike's information criterion with a correction for small sample size (AIC_c). We calculated the Akaike weight (w) for each candidate model (i); w_i can be interpreted as the probability that i is the best model, given the data and set of candidate models (Burnham and Anderson 2002). The reference level of the fixed factor "sex" was "female" in all models. The final model was obtained by averaging the parameter estimates from top models at a cutoff criterion of $AIC < 6.0$ (Richards 2008). We employed the library MuMIn (Bartón 2009) and the library lme4 (Bates and Maechler 2009) using R version 2.15.1 (R Development Core Team 2012). The confidence intervals (95% CI) were calculated from the final model using the parameter estimated effect size and associated SE obtained after model averaging. It has the same meaning as any other confidence interval: if the procedure is repeated over and over, 95% of the time the value of the parameter will lie within that interval. We assumed that a predictor term significantly contributed to explain the response variable when the 95% CI for the estimated parameter excluded zero (Grueber et al. 2011). In this model, a significant effect of the number of cats or colony size on survival would support prediction (1). Likewise, a significant effect of the interaction term between cats and age, or between density and age, would also support prediction (1).

We also used linear mixed models by adopting a similar approach to test how environmental conditions during early life (i.e., predation risk and density) and

investment in early reproduction affected ALR. In these analyses, the response variables were ALR and investment in early reproduction (i.e., E1Y, E12Y, F1Y, F12Y), the number of cats, colony size, and all two-way interactions between these input variables were included as explanatory variables. E1Y was defined as the annual number of eggs produced at the age of one year. E12Y was defined as the annual number of eggs produced at the age of one year plus the annual number of eggs produced at the age of two years. Likewise, F1Y was defined as the annual number of fledglings produced at the age of one year and F12Y as the annual number of fledglings produced at the age of one year plus the annual number of fledglings produced at the age of two years. We ran four different models with ALR as the dependent variable, each of them with just one input variable related to investment in early reproduction (i.e., E1Y, E12Y, F1Y, or F12Y). In the model, investment in early reproduction was estimated as the number of eggs; only females were included because clutch size is a female trait. In the models, we included E12Y or F12Y for all individuals living just one year, or life span was excluded from the analyses. We assumed a normal distribution because diagnosis plots on the global model indicated that the residuals fitted well with the normal distribution. The global model was a linear mixed-effect model in which we included these predictors as fixed effects and the year at first capture and breeding site as random effects (intercepts). In these specific analyses, it was not necessary to include individual identity as a random factor to control for pseudoreplication because we used only one observation for all individuals included in the analyses. In the analyses of which the number of fledglings was the measure of early-life investment in reproduction, we also included as an input variable the factor sex, because males and females were analyzed in the same data set. In these models, a significant negative effect of early-life investment in reproduction on ALR would be consistent with the existence of trade-offs between reproduction and survival, because ALR is a good proxy of life span in Barn Swallows and hence would support prediction (2). Likewise, a significant negative effect of early-life environmental condition (i.e., number of cats or colony size) on ALR would support prediction (3).

We analyzed breeding records of individuals aged 4 years or older because that is the age when a leveling off in reproductive performance has been detected in a previous study of the same Barn Swallow population (Balbontín et al. 2012). We tested if there were a significant main effect of age on the number of eggs and fledglings in this subset of individuals reaching old age, while only taking into account breeding records obtained during this period of their life. In case a significant main effect of age arose, this would indicate the existence of reproductive senescence (e.g., Bouwhuis et al. 2009). In order to test if variation in predation risk and density affected reproductive senescence, we also

included the number of cats and the number of breeding pairs and tested whether there was a significant effect of the interaction term between age and environmental conditions during early life (i.e., predation and density). If this significant interaction were to be found, it would support prediction (4). In these models, we included ALR to separate within-subject from between-subject effects of age on breeding performance (van de Pol and Verhulst 2006). The global model was a linear mixed-effect model in which we included these predictors as fixed effects, as well as all two-way interactions. Individual identity, the year at first capture, and breeding sites were included as random effects (intercepts). The number of fledglings and clutch size were modeled, assuming a normal distribution of errors because diagnosis plots indicated that this was the more appropriate distribution for these response variables in our data set. The procedure of model selection was the same as that described for modeling survival.

Results

Environmental conditions during early life and survival

Over the 39 sites, the average number of cats per site was 2.12 ± 2.33 cats, mean $\pm$ SD (range 0–12 cats). The number of cats per site across years was highly consistent (intraclass correlation coefficient $r_i = 0.99$). Although cats prey on Barn Swallows, only 34 Barn Swallows were killed during 1988–2011, as revealed by feathers left on the floor in farms. We found no other predators of adult Barn Swallows during the study. The number of breeding pairs at the 39 sites was 8.21 ± 8.47 pairs, mean $\pm$ SD (range 1–48 pairs). Among breeding sites, the mean number of breeding pairs was positively correlated with the mean number of domestic cats (Spearman correlation coefficient $r_S = 0.527$, $n = 39$ breeding sites, $P < 0.001$).

Life span was 1.43 ± 0.87 years, mean $\pm$ SD (range 1–8 years; $n = 2930$ individuals). There was a slight difference in life span between sexes: male Barn Swallows had a life span of 1.47 ± 0.89 years (range 1–7 years; $n = 1420$ individuals), whereas females had a life span of 1.40 ± 0.84 years (range 1–8 years; $n = 1510$ individuals; two-sample t test, $t = -1.955$, df $= 2928$, $P = 0.05$).

The final model obtained from the analysis of the survival probability of adult Barn Swallows showed a curvilinear relationship of survival with age, with an increase in survival from the age of one year to three years and a subsequent decrease in the probability of survival, demonstrating actuarial senescence. Age and its quadratic term had a relative importance of 1.0. Confidence intervals for these two parameters excluded zero, which indicated that they had an effect on survival probability. In this model, sex had a 99% relative importance effect on age. Confidence intervals for this factor also excluded zero, suggesting that sex affected the probability of survival, with males surviving better
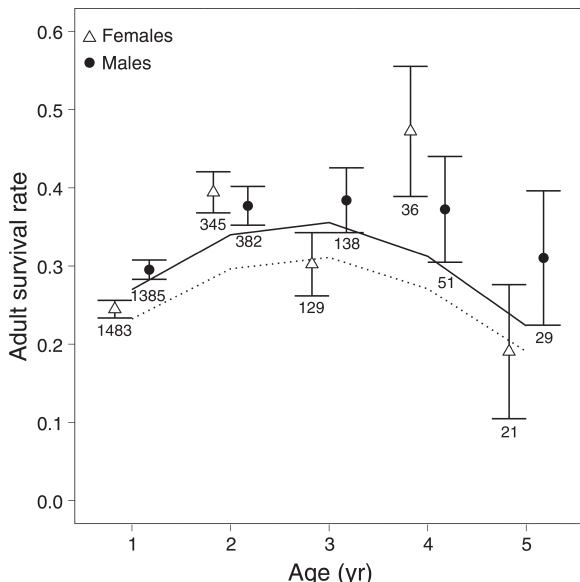
FIG. 1. Annual adult survival rate (mean ± SE, with sample size below error bar) in relation to age of male (solid line) and female (dotted line) Barn Swallows (*Hirundo rustica*) from Denmark. The lines represent the predicted values at average values for other predictors included in the model obtained from a final model after averaging the top models obtained from 2048 candidate models (final model in Table 1 and top models in Appendix A). The sample size is 3999 observations of 2915 individuals.

than females (Fig. 1, Table 1). The interaction term between the number of cats and colony size had a relative importance of 76% to age, and the confidence interval for this predictor also did not include zero, suggesting that this predictor affected the probability of

TABLE 1. Summary results after model averaging of the effects of sex, age, and environmental conditions (predation risk and colony size) during early life on adult survival in Barn Swallows (*Hirundo rustica*) in Denmark.

Parameter	Estimate†	SE	95% CI	RI
Intercept	−1.019	0.124	(1.262, 0.775)	
Sex	**0.2**	**0.072**	**(0.058, 0.342)**	**0.99**
Age	**0.579**	**0.124**	**(0.334, 0.823)**	**1.00**
Age^2	**−0.362**	**0.089**	**(−0.539, −0.186)**	**1.00**
Cats	−0.076	0.158	(−0.387, 0.234)	0.98
CS	0.164	0.108	(−0.048, 0.377)	0.89
Cats × CS	**0.625**	**0.279**	**(0.078, 0.172)**	**0.76**
Sex × Age	−0.107	0.144	(−0.390, 0.176)	0.28
Age × Cats	0.122	0.155	(−0.182, 0.428)	0.22
Sex × CS	0.057	0.144	(−0.226, 0.340)	0.21
Age × CS	−0.055	0.167	(−0.383, 0.272)	0.22
Sex × Cats	−0.018	0.16	(−0.032, 0.295)	0.21

Notes: Parameters include CS, colony size (the number of breeding pairs in a given breeding site), and Cats (the number of cats at breeding sites the year when swallows were one year old). Parameters estimated for predictors with confidence intervals that do not include zero are highlighted in bold. CI is confidence interval and RI is relative importance.

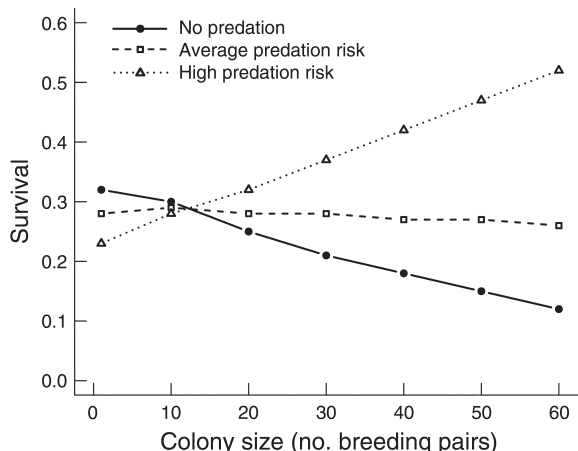† Effect sizes were standardized with 2 SD following Gelman (2008).

FIG. 2. Annual adult survival rate in relation to colony size (number of breeding pairs) and predation risk in Barn Swallows. The lines represent the predicted values for different colony sizes at different levels of predation risk (no predation, 0 cats; average predation risk, 1.84 cats; high predation, 4 cats). These predictions were obtained from a final linear mixed-effect model after averaging top models obtained from 2048 candidate models (final model in Table 1 and top models in Appendix A). The sample size is 3999 observations of 2915 individuals.

survival. Specifically, the final model showed density-dependent survival at sites free of predation, with the probability of survival decreasing with an increasing number of breeding pairs. In contrast, the tendency was reversed and survival increased as colony size increased at sites with high predation pressure. There was no significant trend between density and survival at average predation pressure (Fig. 2). Model selection resulted in 43 top models among the 2048 candidate models, using ΔAIC < 6 as a cutoff criterion. The list of top models and the estimated variance for random effects are reported in Appendix A: Tables A1 and A2. Weighted averages of parameters estimated from the top models are shown in Table 1.

Reproductive investment in early life and early environmental conditions

We investigated how reproductive performance in early life and environmental conditions during early life affected ALR to test for the existence of trade-offs between reproduction and survival (prediction 2) and the existence of an effect of early-life environmental condition on ALR (prediction 3). Our results did not support prediction 2 because we did not find an effect of the annual number of eggs or fledglings produced in early life on ALR (Tables 2–4). Confidence intervals for early-life investment in reproduction (i.e., E1Y, E12Y, F1Y, F12Y) included zero and its relative importance was always below 62% relative to the most important predictor in all analyses. However, we found an effect on ALR of the interaction term between colony size and the number of cats (Tables 2–4). The confidence interval of

TABLE 2.   Summary results after model averaging of the effects of early environmental conditions (predation risk and colony size) and investment in reproduction (number of eggs) on age at last reproduction (ALR) of female Barn Swallows from Denmark.

Parameter	Estimate†	SE	95% CI	RI
No. eggs, first year (E1Y)				
Intercept	1.487	0.041	(1.405, 1.568)	
Cats	−0.007	0.162	(−0.325, 0.311)	0.90
CS	0.013	0.084	(−0.151, 0.178)	0.69
E1Y	−0.079	0.099	(−0.274, 0.115)	0.44
Cats × CS	**0.685**	**0.283**	**(0.130, 1.240)**	**0.59**
CS × E1Y	−0.094	0.169	(−0.426, 0.238)	0.09
Cats × E1Y	−0.070	0.266	(−0.593, 0.452)	0.11
No. eggs, first two years (E12Y)				
Intercept	2.559	0.083	(2.395, 2.723)	
Cats	0.006	0.260	(−0.504, 0.518)	0.84
CS	−0.155	0.189	(−0.526, 0.216)	0.84
E12Y	0.113	0.182	(−0.244, 0.471)	0.41
Cats × CS	**1.933**	**0.748**	**(0.467, 3.399)**	**0.72**
CS × E12Y	0.228	0.322	(−0.403, 0.859)	0.10
Cats × E12Y	0.635	0.423	(−0.194, 1.466)	0.17

Notes: Sample size was 631 observations from females of known reproductive output (number of eggs) in their first year of life (E1Y), and 108 observations from females of known reproductive output in their first two years of life (E12Y). Parameters estimated for predictors with confidence intervals that do not include zero are highlighted in bold. Abbreviations are as in Table 1.
† Effect sizes were standardized with 2 SD following Gelman (2008).

this predictor excluded zero in the four models in which we investigated the effect of early-life conditions on ALR for different levels of reproductive investment. This interaction indicated that, in sites with high predation risk, there was a positive density-dependent effect on ALR. Specifically, in sites with many cats, ALR increased with density. In contrast, at sites with low predation risk, ALR decreased slightly as density increased. There was no clear relationship at average predation pressure (e.g., in sites with six cats) (Fig. 3). Therefore, prediction 3 was not supported by these results. None of the other predictors included in the global model affected ALR when E1Y, E12Y, and F1Y

were the predictors included in the global model (Tables 2 and 3). Finally, in the model in which early-life investment in reproduction was investigated using F12Y, and therefore only individuals living two or more years were included in the analyses, we found an effect of the interaction term of sex with cats. The confidence interval for this interaction term excluded zero (Table 4). This interaction indicated that ALR increased with predation risk (i.e., number of cats), and this was more evident for males than for females (Fig. 4). These results were in the opposite direction of prediction 3. The procedure of model selection that we employed on the models for the effect of early-life investment in

TABLE 3.   Summary results after model averaging of the effects of environmental conditions (predation risk and colony size) and investment in reproduction (number of fledglings produced during the first year of life, F1Y) on age at last reproduction (ALR) of Barn Swallows from Denmark.

Parameter	Estimate†	SE	95% CI	RI
Intercept	1.480	0.054	(1.374, 1.586)	
Cats	−0.063	0.150	(−0.357, 0.230)	0.98
CS	−0.002	0.081	(−0.161, 0.155)	0.69
F1Y	0.079	0.066	(−0.050, 0.209)	0.61
Sex	0.074	0.055	(−0.034, 0.182)	0.64
Cats × CS	**0.548**	**0.256**	**(0.046, 1.050)**	**0.56**
CS × F1Y	0.012	0.127	(−0.237, 0.262)	0.10
Cats × F1Y	0.180	0.182	(−0.177, 0.538)	0.22
Sex × CS	−0.037	0.119	(−0.271, 0.196)	0.11
Sex × Cats	0.034	0.116	(−0.193, 0.263)	0.15
Sex × F1Y	−0.001	0.124	(−0.246, 0.243)	0.09

Notes: Sample size was 1205 Barn Swallows. Parameters estimated for predictors with confidence intervals that do not include zero are highlighted in bold. Abbreviations are as in Table 1.
† Effect sizes were standardized with 2 SD following Gelman (2008).

TABLE 4.   Summary results after model averaging of the effects of environmental conditions (predation risk and colony size) and investment in reproduction (number of fledglings produced during the first two years of life, F12Y) on age at last reproduction (ALR).

Parameter	Estimate†	SE	95% CI	RI
Intercept	2.607	0.068	(1.374, 1.586)	
Cats	0.253	0.216	(−0.170, 0.678)	0.81
CS	−0.166	0.150	(−0.461, 0.128)	0.83
F12Y	0.124	0.152	(−0.174, 0.423)	0.53
Sex	0.103	0.122	(−0.136, 0.342)	0.70
Cats × CS	**1.363**	**0.626**	**(0.136, 2.590)**	**0.62**
CS × F12Y	0.183	0.273	(−0.352, 0.719)	0.11
Cats × F12Y	0.593	0.355	(−0.103, 1.289)	0.25
Sex × CS	0.014	0.260	(−0.495, 0.523)	0.13
Sex × Cats	**0.713**	**0.298**	**(0.129, 1.298)**	**0.59**
Sex × F12Y	−0.023	0.257	(−0.528, 0.481)	0.07

Notes: Sample size was 228 Barn Swallows. Parameters estimated for predictors with confidence intervals that do not include zero are highlighted in bold. Abbreviations are as in Table 1.
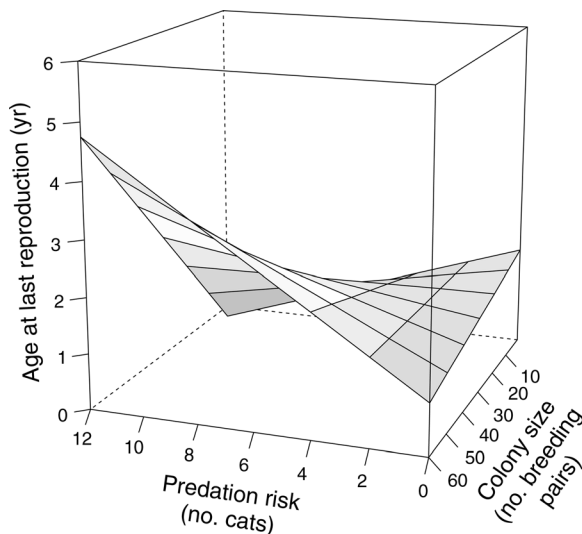† Effect sizes were standardized with 2 SD following Gelman (2008).

FIG. 3. Effects of the interaction term of predation risk (i.e., number of cats) and density (i.e., colony size) on age at last reproduction (ALR) in Barn Swallows. The lines represent the predicted values for different levels of predation risk and density. These predictions were obtained from a final linear mixed-effect model presented in Table 2 for the model in which early-life investment in reproduction was measured as the number of eggs produced during the first year of life (i.e., E1Y). Note that this relationship was consistent for the rest of the models in which different measurements of early-life environmental conditions (e.g., E12Y, F1Y, and F12Y) were used as predictors of ALR. The list of top models is reported in Appendix B.

reproduction on ALR selected 13, and 12 top models among the 64 candidate models when number of eggs was the measure of investment in reproduction; and selected 60, and 48 top models among the 1024 candidate models when number of fledglings was the measure of investment in reproduction. The list of top models obtained from these analyses and the estimated variance for random effects are reported in Appendix B: Tables B1–B8.

Reproductive senescence and environmental conditions during early life

We investigated how reproductive performance in late life was affected by environmental conditions during early life, and we tested for the existence of reproductive senescence by including age as a predictor term in these models. We found a negative effect of age on the annual number of eggs and fledglings produced in late life (i.e., age ≥ 4 years old), as reflected by the exclusion of zero from the confidence interval estimated for this predictor. Rate of senescence, estimated as the slope of age on fitness, was a decrease of 1.01 eggs for an increase of one year of age (i.e., 1.82 eggs for each 1.8 years of age, which corresponded to 2 SD where SD for input age = 0.9 years; after Gelman [2008] standardization; see Table 4). Likewise, estimated rate of senescence for the number of fledglings was a decrease of 0.91 fledglings

for an increase of one year of age. In these models, we included ALR to test for the possibility that disappearance of individuals differing in quality could mask senescence patterns. We did not find an effect of ALR on the annual number of eggs or fledglings produced in late life. Confidence intervals for ALR included zero, and its relative importance was below 36% relative to the most important predictor in all analyses performed. The inclusion of ALR indicated that the effect of age was a within-individual change and therefore demonstrated the existence of reproductive senescence in this short-lived species. Environmental conditions during early life affected senescence patterns. Specifically, we found a negative effect of the interaction term between colony size and age on clutch size, because the confidence interval for this predictor excluded zero (Table 5). Specifically, the rate of senescence (i.e., the slope of age on clutch size) increased as density increased (Fig. 5). This supported prediction (4). Likewise, in the analysis of the annual number of fledglings produced, we found a negative effect of colony size. Specifically, during senescence there was a decrease by 2.50 fledglings with an increase of 33 breeding pairs, as SD for colony size was 16.47 breeding pairs; after Gelman [2008] standardization), which supported prediction (4). In the analyses of senescence rates on clutch size, we also found an effect of the interaction term between colony size and the number of cats on annual number of eggs produced in late life because the estimated confidence interval for this predictor excluded zero. This interaction term indicated that clutch size produced by old females decreased as predation risk increased only, or more steeply, at sites with a large or moderate number of breeding pairs. Thus, clutch size did not change or increased weakly as predation risk increased at sites with fewer than 10 breeding pairs. However, the annual number of eggs produced by old females decreased with
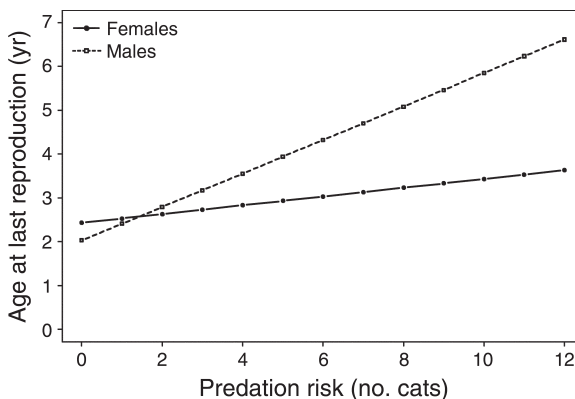

FIG. 4. Effects of the interaction term of predation risk (number of cats) and sex on ALR in Barn Swallows. The lines represent the predicted values for different levels of predation risk for male and female Barn Swallows. These predictions were obtained from a final linear mixed-effect model presented in Table 5. The list of top models is provided in Appendix B.

TABLE 5. Summary results after model averaging of the effects of early life environmental conditions (predation risk and colony size) on annual number of eggs and annual number of fledglings raised by old Barn Swallows (age ≥ 4 years) in Denmark.

Parameter	Estimate†	SE	95% CI	RI
No. eggs				
Intercept	8.446	0.365	(7.729, 9.162)	
Age	**−1.824**	**0.633**	**(−3.066, −0.582)**	**1.00**
ALR	1.193	0.905	(−0.580, 2.967)	0.35
Cats	−0.442	0.630	(−1.677, 0.792)	0.89
CS	−1.106	0.733	(−2.544, 0.332)	1.00
Age × Cats	−0.790	1.225	(−3.192, 1.610)	0.24
Age × CS	**−1.886**	**0.931**	**(−3.712, −0.061)**	**0.35**
Cats × CS	**−3.394**	**1.135**	**(−5.620, −1.168)**	**0.83**
No. fledglings				
Intercept	7.126	0.359	(6.420, 7.831)	
Age	**−1.655**	**0.350**	**(−2.342, −0.969)**	**1.00**
Sex	−0.616	0.463	(−1.524, 0.292)	0.42
ALR	−0.203	0.590	(−1.360, 0.956)	0.22
Cats	0.031	0.494	(−0.938, 1.001)	0.49
CS	**−2.503**	**0.629**	**(−3.737, −1.269)**	**1.00**
Age × Cats	−0.906	0.650	(−2.180, 0.368)	0.22
Age × CS	−1.366	0.709	(−2.756, 0.023)	0.63
Cats × CS	−1.056	0.845	(−2.712, 0.600)	0.19

Notes: Sample sizes are 128 observations taken from 93 individuals for number of eggs and 136 observations taken from 96 individuals for the number of fledglings. Parameters estimated for predictors with confidence intervals that do not include zero are highlighted in bold. Abbreviations are as in Table 1.

† Effect sizes were standardized with 2 SD following Gelman (2008).

predation pressure as density increased (Fig. 6). None of the other predictors included in the global model affected the annual number of fledglings among the subset of individuals reaching an age of at least four years (Table 5). The list of top models for clutch size and number of fledglings and the estimated variance for random effects are provided in Appendix C: Tables C1–C4.

DISCUSSION

We found for the first time in this species evidence of actuarial senescence in Barn Swallows. Survival rate increased with age until reaching a plateau at middle age and then decreased in late life. Survival rate was higher for males than females, although patterns of change across life did not differ between the two sexes. Furthermore, survival rates decreased as density increased, as expected under a density-dependent scenario, although this effect was present only in sites without cats. Interestingly, the situation was reversed in sites exposed to a higher predation pressure, with survival rate increasing as density increased. The effect of predation pressure was most likely caused by nonlethal effects of predation, given the low rate of cat predation on adult Barn Swallows.

Our long-term study of Barn Swallows differing in the extent of exposure to a predator and intraspecific competence helped us to evaluate predictions proposed by life history theories of aging. In contrast to theory, we did not find trade-offs between early-life investment in reproduction and life span. Nor did we find that more stressful early environmental conditions mea-

sured as different levels of predation risk and density predicted life span, as life history of aging suggested. However, the analyses related to reproductive senescence indicated that environmental conditions during early life accelerated the rate of reproductive senescence, which supports one of the predictions made by
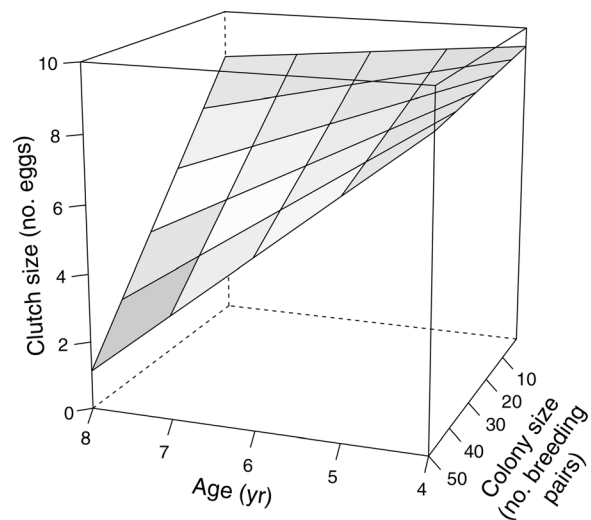

FIG. 5. Annual number of eggs produced by Barn Swallows in relation to colony size and age (years). Values are the predicted values for the effect of the interaction term between age and colony size on annual number of eggs, with other predictors included in the final model at average values (final model in Table 6 and top models in Appendix C). The sample size is 136 observations of 96 individuals.
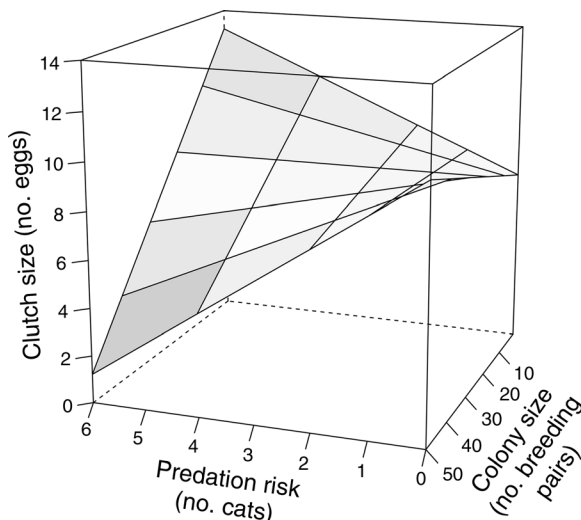
FIG. 6. Annual number of eggs produced by female Barn Swallows during senescence in relation to colony size and predation risk (number of cats). Values are the predicted values for the effect of the interaction term between number of cats and colony size on clutch size, with other predictors included in the final model at average values (final model in Table 6 and top models in Appendix C). The sample size is 58 observations of 44 individuals.

the life history theory of aging. For instance, annual clutch size decreased more steeply in late life at breeding sites where there was a larger number of breeding pairs. Furthermore, the rate of reproductive senescence increased with predation pressure, being more evident at sites with a large number of breeding pairs. Therefore, breeding density and predation pressure experienced early in life interacted to accelerate the rate of reproductive senescence.

Actuarial senescence was present in both male and female Barn Swallows. Survival senescence occurs in a wide range of free-ranging animals, including many taxa of invertebrates and vertebrates (Bonduriansky and Brassil 2002, Reznick et al. 2004, Jones et al. 2008, Peron et al. 2010, Nussey et al. 2013). Here, we showed survival senescence in a short-lived species and showed that annual survival rates differed between the sexes. In this study, survival estimates reflect true rather than apparent survival because adult Barn Swallows remain in the breeding sites where they first recruited until they die (for details, see Møller 1992, Møller et al. 2005, Balbontín et al. 2009). In many animals, male survival is lower than female survival (Promislow 1992, Promislow et al. 1992, Christe et al. 2006). Male-biased survival is commonly found in polygynous species because males suffer more from mate competition than do females (Promislow 2003, Clutton-Brock and Isvaran 2007). However, a difference in annual survival rates between males and females has rarely been reported in monogamous species (Clutton-Brock and Isvaran 2007, Bonduriansky et al. 2008). The majority

of field studies on survival senescence have focused on females, and detailed comparisons of aging pattern between sexes are rare (but see Hammers et al. 2013). Interestingly, male annual survival rate was higher than that of females in the Barn Swallow. This could only be explained as females suffering more than males from the presence of predators or other causes of extrinsic mortality. Usually, male birds are exposed to a higher predation risk than females, because competition for mates makes males more vulnerable to predators. Thus, males usually undertake risky behavior, such as singing from high perches, or they develop costly secondary sexual characters such as long tails or colorful plumage that make them more vulnerable to predators (e.g., Zahavi 1975, Møller et al. 2010). However, our results did not seem to support this reasoning because we did not find an effect of the interaction term between sex and the number of cats on age-related survival rate. Therefore, further studies are needed to understand the cause of female-biased survival in this species. Early environmental conditions also affected annual survival rate in an interactive manner. We found negative density dependence in survival in sites with low predation pressure and positive density dependence in sites with high predation pressure. As expected, intraspecific competition might be the cause of a decrease in survival rate in sites with low predation pressure. It is possible that in such sites subject to high levels of predation pressure, an increase in density increases the probability of survival due to protection provided by conspecifics.

There is evidence in favor of the evolutionary theory of senescence in studies of the fruit fly (*Drosophila melanogaster*) under laboratory conditions (e.g., Rose and Charlesworth 1981, Luckinbill et al. 1984, Stearns et al. 2000) and in simulation studies (Ricklefs 1998). Under field conditions, empirical evidence exists for a trade-offs between investment in reproduction and survival (Luckinbill et al. 1984, McCleery et al. 1996, Orell and Belda 2002, Reid et al. 2003, Pettay et al. 2005, Reed et al. 2008, Hammers et al. 2013), although there are also studies showing opposite results (Berubé et al. 1999, McElligott et al. 2002, Beauplet et al. 2006, Moyes et al. 2006). This result contradicts the life history theory of aging, and particularly the concept of trade-offs between survival and reproduction. In these analyses, we also investigated the effect of early-life environmental condition on life span. As expected, we found that predation risk and density affected life span in the same way that they affected survival. Probably, the increase in life span in high-density sites could be attributed to an effect of protection against predators. We did not find a main effect of density or the number of cats on life span, which did not support prediction (3). The interactive effect between predation risk and density probably could influence the lack of support for prediction (3) in our study system. Therefore, we highlight the importance of studying more than just

one factor related to environmental conditions in early life because these could interact in such a way that predictions from the life history of aging would be more difficult to test adequately. Furthermore, we found a positive, rather than a negative, effect of predation risk (i.e., number of cats) on ALR in males, which is the opposite of prediction (3) from the life history theory of aging. Specifically, males that lived at sites with many cats increased the duration of their life span compared with males that lived at sites with few cats. The tendency was the same for females, although it was much weaker.

To our knowledge, few studies have documented an effect of density on senescence patterns, although density has been shown to affect senescence patterns in red deer (*Cervus elaphus*) (e.g., Nussey et al. 2007). However, there is some evidence of an increase in the rate of aging related to predation risk for morphological, physiological, and behavioral traits. Thus, opossums (*Didelphis virginianus*) living on predator-free islands delayed age at first reproduction and aged more slowly compared to those living on the more hazardous mainland (Austad 1993). In guppies (*Poecilia reticulata*), individuals exposed to a higher extrinsic mortality rate reproduced at an earlier age and invested more in reproduction, but opposite to predictions, they did not show an early onset of reproductive senescence or a shorter life span, as expected from theory (Reznick et al. 2004). Likewise, natal conditions at birth measured as prey abundance did not affect senescence rates in Tawny Owls (*Strix aluco*) (Millon et al. 2011). Here, we found that the rate of reproductive senescence was faster for individuals experiencing harsh environmental conditions. Thus, the rate of reproductive senescence increased with high breeding density (e.g., colony size $\geq$ 30 breeding pairs; Fig. 6) and the number of cats. At breeding sites with 10 pairs, the slope of clutch size on the abundance of cats increased rather than decreased. Therefore, the risk of predation affected reproductive senescence differently depending on local population density. The effect of predators on their prey could be a direct effect, when predators kill their prey, or, alternatively, an indirect effect, as when predators impose stress on their prey. For instance, female Barn Swallows that were presented with a stuffed domestic cat during the egg-laying period produced eggs with higher level of corticosterone than did control females. Moreover, eggs with experimentally injected high levels of corticosterone produced offspring in poorer physical condition than did low-level corticosterone eggs receiving a control treatment (Saino et al. 2005). Here we found that the direct effect of predation caused by cats is negligible because only 34 Barn Swallows were killed by cats. During 1988 to 2011, we monitored 3651 adult Barn Swallows throughout their lives, and found a predation rate by domestic cats of only 0.93%. These findings suggest that the effect of domestic cats on Barn Swallows is indirect rather than direct. These results

support one of the predictions of the life history theory of aging, because females that experience a high level of competition and high predation pressure in early life also senesce faster. In contrast, Reznick et al. (2004) did not find an earlier onset or a faster rate of reproductive senescence in sites where guppies were exposed to a higher predation risk, but they found a decrease in swimming performance associated with high extrinsic mortality caused by an increase in predation risk. The study of guppies suggested that predators could reduce the amount of resources available under a density-dependent situation, thereby favoring individuals exposed to predators over those free of predators. In addition, a study of sockeye salmon (*Oncorhynchus nerka*) showed that condition-dependent susceptibility to predation by brown bears (*Ursus arctos*) was the main factor explaining the rate of actuarial senescence in this predator–prey system (Carlson et al. 2007). Therefore, predators could affect individuals of different ages or condition differently, or predators could interact differently, with density depending on the study system, making predictions concerning the association between extrinsic mortality and senescence controversial due to a mixture of multiple factors (review in Bronikowski and Promislow 2005).

In conclusion, we found evidence consistent with the life history theory of aging concerning predictions related to the rate of reproductive senescence, but did not find evidence for predictions related to the existence of trade-offs between reproduction and survival in this long-term field study of Barn Swallows. The rate of reproductive senescence was faster among individuals inhabiting breeding sites exposed to a high local population density and also to a high risk of predation, but only in sites experiencing high levels of competition due to high breeding density. We did not find support for the existence of trade-offs between reproduction and survival when investment in reproduction was measured in early life. Survival senescence was present and survival rate was higher in males than in females. We documented intricate patterns of senescence because we were able to statistically control for variance caused by conspecific density and abundance of predators, factors that are rarely quantified in studies of senescence and reproductive trade-offs under field conditions.

Literature Cited

Abrams, P. A. 1984. Foraging time optimization and interactions in food webs. American Naturalist 124:80–96.

Austad, S. N. 1993. Retarded senescence in an insular population of Virginia opossums *Didelphis virginiana*. Journal of Zoology 229:695–708.

Balbontín, J., I. G. Hermosell, A. Marzal, M. Reviriego, F. de Lope, and A. P. Møller. 2007. Age-related change in breeding performance in early life is associated with an increase in competence in the migratory barn swallow *Hirundo rustica*. Journal of Animal Ecology 76:915–925.

Balbontín, J., A. P. Møller, I. G. Hermosell, A. Marzal, M. Reviriego, and F. de Lope. 2009. Individual responses in spring arrival date to ecological conditions during winter and migration in a migratory bird. Journal of Animal Ecology 78: 981–989.

Balbontín, J., A. P. Møller, I. G. Hermosell, A. Marzal, M. Reviriego, and F. de Lope. 2012. Geographical variation in reproductive ageing patterns and life history strategy in a short-lived passerine bird. Journal of Evolutionary Biology 25:2298–2309.

Bartón, K. 2009. MuMIn: multi-model inference. R package version 0.12.2. http://r-forge.r-project.org/projects/mumin/

Bates, D., and M. Maechler. 2009. lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-31. http://cran.r-project.org/package=lme4

Beauplet, G., C. Barbraud, W. Dabin, C. Kussener, and C. Guinet. 2006. Age-specific survival and reproductive performances in fur seals: evidence of senescence and individual quality. Oikos 112:430–441.

Bérubé, 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.

Bonduriansky, R., A. Maklakov, F. Zjitschek, and R. Brooks. 2008. Sexual selection, sexual conflict and the evolution of ageing and lifespan. Functional Ecology 22:443–453.

Bouwhuis, S., B. C. Sheldon, S. Verhulst, and A. Charmantier. 2009. Great tits growing old: selective disappearance and the partitioning of senescence to stages within the breeding cycle. Proceedings of the Royal Society B 276:2769–2777.

Bronikowski, A. M., and D. E. L. Promislow. 2005. Testing evolutionary theories of ageing in wild populations. Trends in Ecology and Evolution 20:271–273.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Carlson, S. M., R. Hilborn, A. P. Hendry, and T. P. Quinn. 2007. Predation by bears drives senescence in natural populations of salmon. PLoS ONE 212:e1286.

Cartwright, S. J., M. A. C. Nicoll, C. G. Jones, V. Tatayah, and K. Norris. 2014. Anthropogenic natal environmental effects on life histories in a wild bird population. Current Biology 24:536–540.

Charmantier, A., C. Perrins, R. H. McCleery, and B. C. Sheldon. 2006. Quantitative genetics of age at reproduction in wild swans: support for antagonistic pleiotropymodels of senescence. Proceedings of the National Academy of Sciences USA 103:6587–6592.

Chen, J. J., D. Senturk, J. L. Wang, H. G. Muller, J. R. Carey, H. Caswell, and E. P. Caswell-Chen. 2007. A demographic analysis of the fitness cost of extended longevity in *Caenorhabditis elegans*. Journals of Gerontology Series A: Biological Sciences and Medical Sciences 62:126–135.

Christe, P., L. Keller, and A. Roulin. 2006. The predation cost of being a male: implications for sex-specific rates of ageing. Oikos 114:381–384.

Clutton-Brock, T. H., and K. Isvaran. 2007. Sex differences in ageing in natural populations of vertebrates. Proceedings of the Royal Society B 274:3097–3104.

Descamps, S., S. Boutin, D. Berteaux, and J. M. Gaillard. 2006. Best squirrels trade a long life for an early reproduction. Proceedings of the Royal Society B 273:2369–2374.

Ewer, R. F. 1973. The carnivores. Weidenfeld and Nicholson, London, UK.

Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine 27:2865–2873.

Grueber, C. E., S. Nakagawa, R. J. Laws, and I. G. Jamieson. 2011. Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology 24:699–711.

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

Hammers, M., D. Richardson, T. Burke, and J. Komdeur. 2013. The impact of reproductive investment and early-life environmental conditions on senescence: support for the disposable soma hypothesis. Journal of Evolutionary Biology 26:1999–2007.

Jenkins, N. L., G. McColl, and G. J. Lithgow. 2004. Fitness cost of extended lifespan in *Caenorhabditis elegans*. Proceedings of the Royal Society B 271:2523–3252.

Jones, O. R., et al. 2008. Senescence rates are determined by ranking on the fast–slow life-history continuum. Ecology Letters 11:664–673.

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

Lima, S. L. 1998. Nonlethal effects in the ecology of predator–prey interactions: What are the ecological effects of anti-predator decision-making? BioScience 48:25–34.

Lima, S. L., and L. M. Dill. 1990. Behavioural decisions made under the risk of predation: A review and prospectus. Canadian Journal of Zoology 68:619–640.

Loss, S. R., T. Will, and P. P. Marra. 2013. Impact of free-ranging domestic cats on wildlife of the United States. Nature Communications 4:1396.

Luckinbill, L. S., R. Arking, M. J. Clare, W. C. Cirocco, and S. A. Buck. 1984. Selection for delayed senescence in *Drosophila melanogaster*. Evolution 38:996–1003.

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.

McElligott, A. G., R. Altwegg, and T. J. Hayden. 2002. Age-specific survival and reproductive probabilities: evidence for senescence in male fallow deer (*Dama dama*). Proceedings of the Royal Society B 269:1129–1137.

Millon, A., S. J. Petty, B. Little, and X. Lambin. 2011. Natal conditions alter age-specific reproduction but not survival or senescence in a long-lived bird of prey. Journal of Animal Ecology 80:968–975.

Møller, A. P. 1992. Sexual selection in the monogamous swallow *Hirundo rustica*. II. Mechanisms of intersexual selection. Journal of Evolutionary Biology 5:603–624.

Møller, A. P. 1994. Phenotype-dependent arrival time and its consequence in a migratory bird. Behavioral Ecology and Sociobiology 35:115–122.

Møller, A. P., and F. de Lope. 1999. Senescence in a short-lived migratory bird: age-dependent morphology, migration, reproduction and parasitism. Journal of Animal Ecology 68:163–171.

Møller, A. P., F. de Lope, and N. Saino. 2005. Reproduction and migration in relation to senescence in the barn swallow

Hirundo rustica: a study of avian 'centenarians'. Age 27:307–318.

Møller, A. P., J. Erritzøe, and J. T. Nielsen. 2010. Causes of interspecific variation in susceptibility to cat predation in birds. Chinese Birds 1:97–111.

Møller, A. P., and T. Szép. 2002. Survival rate of adult Barn Swallows *Hirundo rustica* in relation to sexual selection and reproduction. Ecology 83:2220–2228.

Monaghan, P., A. Charmantier, D. H. Nussey, and R. E. Ricklefs. 2008. The evolutionary ecology of senescence. Functional Ecology 22:371–378.

Moyes, K., T. Coulson, B. J. T. Morgan, A. Donald, S. J. Morris, and T. H. Clutton-Brock. 2006. Cumulative reproduction and survival costs in female red deer. Oikos 115:241–252.

Newton, I. 1989. Lifetime reproduction in birds. Academic Press, London, UK.

Nussey, D. H., T. Coulson, M. Festa-Bianchet, and J. M. Gaillard. 2008. Measuring senescence in wild animal populations: towards a longitudinal approach. Functional Ecology 22:393–406.

Nussey, D. H., H. Froy, J. F. Lemaitre, J. M. Gaillard, and S. N. Austad. 2013. Senescence in natural populations of animals: widespread evidence and its implications for bio-gerontology. Ageing Research Reviews 12:214–225.

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.

Nussey, D. H., L. E. B. Kruuk, A. Morris, and T. H. Clutton-Brock. 2007. Environmental conditions in early life influence ageing rates in a wild population of red deer. Current Biology 17:R1000–R1001.

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.

Oro, D., N. Hernández, L. Jover, and M. Genovart. 2014. From recruitment to senescence: food shapes the age-dependent pattern of breeding performance in a long-lived bird. Ecology 95:446–457.

Pardo, D., C. Barbraud, M. Authier, and H. Weimerskirch. 2013. Evidence for an age-dependent influence of environmental variations on a long-lived seabird's life-history traits. Ecology 94:208–220.

Peron, G., O. Gimenez, A. Charmantier, J. M. Gaillard, and P. A. Crochet. 2010. Age at the onset of senescence in birds and mammals is predicted by early-life performance. Proceedings of the Royal Society B 277:2849–2856.

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 USA 102:2838–2843.

Promislow, D. E. L. 1992. Cost of sexual selection in natural populations of mammals. Proceedings of the Royal Society B 247:203–210.

Promislow, D. 2003. Mate choice, sexual conflict, and evolution of senescence. Behavior Genetics 33:191–201.

Promislow, D. E. L., R. Montgomerie, and T. E. Martin. 1992. Mortality costs of sexual dimorphism in birds. Proceedings of the Royal Society B 250:143–150.

R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reed, T. E., L. E. B. Kruuk, S. Wanless, M. Frederiksen, E. J. A. Cunningham, and M. P. Harris. 2008. Reproductive senescence in a long-lived seabird: rates of decline in late-life performance are associated with varying costs of early reproduction. American Naturalist 171:E89–E101.

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. 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.

Richards, S. A. 2008. Dealing with overdispersed count data in applied ecology. Journal of Applied Ecology 45:218–227.

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.

Rose, M., and B. Charlesworth. 1981. Genetics of life history in *Drosophila melanogaster*. II. Exploratory selection experiments. Genetics 97:187–196.

Saino, N., M. Romano, F. P. Ferrari, R. Martinelli, and A. P. Møller. 2005. Stressed mothers lay eggs with high corticosterone levels which produced low-quality offspring. Journal of Experimental Zoology 303A:998–1006.

Sharp, S. P., and T. H. Clutton-Brock. 2011. Competition, breeding success and ageing rates in female meerkats. Journal of Evolutionary Biology 24:1756–1762.

Stearns, S. C. 1989. Trade-offs in life-history evolution. Functional Ecology 3:259–268.

Stearns, S. C., M. Ackermann, M. Doebeli, and M. Kaiser. 2000. Experimental evolution of aging, growth, and reproduction in fruitflies. Proceedings of the National Academy of Sciences USA 97:3309–3313.

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.

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

Zahavi, A. 1975. Mate selection—a selection for a handicap. Journal of Theoretical Biology 53:205–214.

SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–C are available online: http://dx.doi.org/10.1890/14-1274.1.sm