Spatial variation in senescence rates in a bird metapopulation

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Abstract

Investigations into factors that affect the rate of actuarial senescence are important in order to understand how demographic rates may vary in wild populations. Although the evidence for the occurrence of actuarial senescence in wild populations is growing, very few studies have compared actuarial senescence rates between wild populations of the same species. We used data from a long-time study of demography of house sparrows to investigate differences in rates of actuarial senescence between habitats and sub-populations. We also investigated if rates of actuarial senescence differed between males and females. We found that rates of actuarial senescence showed large spatial variation. We also found that the onset of actuarial senescence varied between sub-populations. However, these differences were not significantly explained by general difference in habitat type. We also found no significant difference in senescence rates between males and females. This study shows that senescence rates in natural populations may vary significantly between sub-populations and that failing to account for such differences may give a biased estimate of senescence rates at the metapopulation level.

Key words: Actuarial senescence, aging, capture mark recapture, habitat, house sparrow, metapopulation, senescence, spatial, survival
Introduction

The evidence supporting the hypothesis that senescence (e.g. decline in survival and/or reproduction with age) does occur in wild populations has become substantial in recent decades. This has also led to an increasing interest into the underlying mechanisms that may influence senescence (see Nussey et al. 2013 for a review). The fundamental evolutionary mechanism(s) explaining the occurrence of actuarial senescence (a.k.a. survival senescence) has been attributed to the decline of natural selection with age (Medawar 1952; Hamilton 1966). Williams (1957) expanded this work and provided the antagonistic pleiotropy theory of aging, which states that an allele with a positive effect on reproduction early in life may be selected even if it has a negative effect on survival later in life. Later, Kirkwood (1977) proposed the disposable soma theory of aging. Both the antagonistic pleiotropy theory and the disposable soma theory share the same prediction of a trade-off between reproduction and/or growth during early life and intensity of ageing later in life (Nussey et al. 2013; Lemaitre et al. 2015). Stated briefly; as the energy available to an individual is not infinite, senescence may be expected to start at the age of maturity (but see Brunet-Rossinini and Austad 2006) and manifest itself within the normal lifespan of the species (Nussey et al. 2013).

Rates of actuarial senescence (hereafter senescence) in wild populations may be significantly influenced by the environment. Specifically, if a population is exposed to environments that increase mortality, this may amplify the rate of senescence under particular circumstances (Caswell 2007). For instance, it has been shown that a high level of predation (e.g. Dhondt et al. 1998) or an increased competition between individuals for resources (i.e. density dependence, e.g. Altwegg et al. 2003) may increase the rate of senescence (Nussey et al. 2007). Predation and density may even interact with each other in affecting senescence
rates (e.g. Balbontin and Møller 2015). As these sources of mortality may vary between populations, one may expect senescence rates to vary accordingly. For example, Kawasaki et al. (2008) found that the rate of aging in stalk-legged flies (Telostylinus angusticollis) in wild populations was significantly faster compared to laboratory populations founded from the same wild population. Similarly, Austad (1993) found that an island population of Virginia opossums (Didelphis virginiana) had a shallower senescence slope compared to the mainland population. This difference coincided with a lack of predators on the island (Austad 1993). Despite of this empirical foundation, there has been a lack of studies investigating intraspecific spatial variation in senescence rates between different habitats/populations in the wild (but see Austad 1993; Baker and Thompson 2007; also see Bouwhuis et al. 2010; Balbontin et al. 2012 for studies of inter-population variation in rates of reproductive senescence). The lack of studies may be caused by the requirement for long-term monitoring of known-aged animals from different populations of the same species.

The rate of senescence may vary among groups in a given population (e.g. males and females). The difference in senescence rates between males and females has become a topic of increased interest in evolutionary biology (Maklakov and Lummaa 2013; Regan and Partridge 2013). Life-history theory predicts that the sex with the higher mortality rates should be the one exhibiting the higher rates of senescence (Williams 1957). Therefore, as males from polygynous and dimorphic species suffer from high mortality rates during the mating season due to male-male combat for instance, they should exhibit higher senescence rates than females (Bonduriansky et al. 2008; Festa-Bianchet 2012). An interspecific comparison of 35 vertebrate species (Clutton-Brock and Isvaran 2007) provided an overall support for that prediction, finding that, in general, males had faster rates of senescence than females. As expected in socially monogamous species, such a difference in senescence rates
between males and females appeared to be less pronounced (Clutton-Brock and Isvaran 2007). However, it is noteworthy that until now, many of the studies investigating senescence patterns in the wild have focused on females only (but see: Reed et al. 2008; Brown and Roth 2009; Nussey et al. 2009; Pardo et al. 2013; Cornwallis et al. 2014; Gamelon et al. 2014; Hayward et al. 2015; Zhang et al. 2015) and evidence for sex differences in rates of senescence in the wild remains somewhat scarce in the literature (Clutton-Brock and Isvaran 2007; Bonduriansky et al. 2008).

Here, we aimed at filling these gaps in our knowledge by investigating intraspecific spatial variation and also sex differences in rates and onset of senescence in a wild metapopulation of house sparrows (Passer domesticus) in a Norwegian archipelago (66.5 ° N 12.5 ° E). This metapopulation has been intensively monitored by annual capture, mark and resight of both males and females since 1993. An important feature of this metapopulation is that some islands contained farms where the birds had the option of sheltering inside cattle-farm buildings whenever the weather is harsh (e.g. during winter). In contrast, other islands do not have any cattle-farms and the birds have to find shelter around the human settlements. Therefore, according to the current evolutionary theory of senescence, we expected: i) inter-population variation in rates and onset of senescence with faster and/or earlier senescence in the populations inhabiting the islands free of cattle-farms compared to the populations living in more sheltered environments; ii) no sex difference in senescence rates within a given population for this socially monogamous species (Anderson 2006).

**Materials and methods**

**Study area and habitats**
The study was carried out in an archipelago consisting of 18 islands covering ca. 1600 km² in the Helgeland district in northern Norway (see map in Baalsrud et al. 2014). The house sparrows on these islands have been systematically captured, marked and resighted several times during their lifetime since 1993 (e.g. Ringsby et al. 2002; Jensen et al. 2008; Pärn et al. 2012). In this study, we compared two sets of islands which differed in habitat: two islands with cattle farms (Gjerøy and Hestmannøy) and two islands without cattle farms (Selvær and Træna). On the farm islands, house sparrows lived in association with dairy farms where they reproduced, foraged and sheltered (under harsh weather conditions) inside barns and cow-sheds. On these farm islands, the cattle food and seeds from cultivated crops were readily available for house sparrows throughout the year. On the non-farm islands, where house sparrows live in association with small human settlements, the shelter provided by the barns was lacking. In addition, the main food resource on the non-farm islands was seeds from birdfeeders provided by the local human inhabitants. Although we focus on 4 islands, observations from the other islands were used to identify and exclude emigrants and immigrants from the dataset (n = 330). This was done to ensure that the effect of habitat/island on individual survival remained as constant as possible throughout the lifespan of individuals. We were thus also able to separate mortality from migration in our analyses.

Field work and datasets

Field work was carried out during the summer (1 May - 15 August) and autumn (1 September - 1 November). During field work, house sparrows were captured using mist nets. Upon first capture, they were banded with a metal ring engraved with a unique id-number and three plastic color rings (two rings on each tarsus). In addition, we visited nests (nest boxes or under barn roofs) and marked fledglings (age = 8 - 14 days old). Thus, after individuals had
been marked, they could be resighted by capturing them, or by observing their unique combination of color rings through a telescope or binoculars. For detailed description on field work, see Ringsby et al. (1998), Sæther et al. (1999) and Pärn et al. (2009).

Our datasets only included individuals that had a known age (i.e. individuals marked as fledglings or juveniles during May - August). The dataset from farm islands included the years 1993 – 2013 and contained the resighting history of 3543 individuals (6574 observations). A continuous time series of observations from non-farm islands was available from 2003 – 2013 (1539 individuals, 2035 observations). Before 2003, populations on the non-farm islands had experienced a severe decline in population size (Baalsrud et al. 2014). The dataset used to compare senescence rates among males and females, contained only individuals that had been resighted and sexed as adults. The sex of individuals was determined by visual inspection of plumage characteristics. This dataset contained the resighting history of 1005 individuals (1715 observations).

**Survival Analyses**

We estimated survival probabilities with capture-mark-recapture (CMR) models (Lebreton et al. 1992; Kéry and Schaub 2011). Previous studies have found that resighting probabilities may vary between islands and years in the metapopulation (Ringsby et al. 1999; Holand et al. 2014). We therefore included island, year and the interaction between islands and years in all models of resighting probability. To account for temporal variation in survival estimates, we included the effect of years as a random factor in all survival models. An investigation by Jones et al. (2008) indicated that senescence in house sparrows at Helgeland started at the mean age of first reproduction (age = 1). However, as the onset of senescence may occur later than the age of first reproduction (e.g. Weimerskirch 1992; Nussey et al. 2008; Peron et al. 2010), we tested for linear effect of age and also non-linear (i.e. quadratic) change in survival
probability with increasing ages (i.e. senescence) either starting at age = 1, 2, 3 or 4 in
separate models. Due to low sample sizes at ages > 4 (see Fig. 2), we did not test for onsets
starting at later ages. In details, our analyses have been divided into three parts. First, at the
metapopulation level (i.e. all 4 islands pooled together), we investigated the relationship
between survival probability (on the logit-scale) and ages. Secondly, we investigated the
difference in senescence rates (i.e. difference in slopes) between the two habitats (farm- vs.
non-farm islands). Thirdly, we investigated if there were significant differences in senescence
rates between islands (Gjerøy, Hestmanøy, Selvær and Træna) in the metapopulation. The
rates of senescence were thus estimated separately for each habitat/island by including the
interaction between habitat/island and age on survival. To examine how survival probability
varied among age classes, we used age as a factor instead of a continuous variable (see Fig. 1
and 2).

To investigate sex-specific pattern of survival, we re-performed the previous analyses
at the metapopulation level, within habitats and within islands by adding “sex” as a factor
(male/female) and tested for differences in senescence rates between males and females by …

We used the model fitting options provided by the programing language BUGS (Lunn
et al. 2000). This language offers several options for creating CMR models in a Bayesian
framework using MCMC simulations to obtain posterior stationary distributions of
parameters (Kéry and Schaub 2011). The models were run in JAGS (Version 3.2.0, Plummer
2003) controlled from R (Version 3.1.1, R Core Team 2014) using the package “JagsUI”
(Version 1.1). This package allows for easy parallel computation of multiple chains on
computers using a cpu with multiple cores. For all models, we used three chains each with
120 000 iterations and a thinning rate of six; where the first 90 000 iterations were discarded
(“burn-in”). Mixing and convergence of chains to a stationary distribution was evaluated by
visual inspection of time-series plots produced by JAGS and by the Brooks-Gelman-Rubin
criterion (R-hat, Brooks and Gelman 1998). Parameter estimates were obtained as the mean
from the respective stationary posterior distributions and lower/upper limits of the 95 %
Bayesian Credibility Interval (CRI). We applied vague priors for all parameters (see Kéry and
Schaub 2011).

**Results**

The first part of our main analysis did not indicate a significant linear or non-linear decline in
survival probability with age in the metapopulation (see Fig. 1, Table 1 and Electronic
Supplementary Material Table 1A). We also found no significant difference in senescence
rates (linear or non-linear) between males and females at the metapopulation level (Electronic
Supplementary Material Table 2A and 3A).

The second part of our main analysis indicated that linear senescence rates were not
significantly different between the two habitat types (see Table 1), starting at age = 1 ($\Delta \beta = -
0.01$ 95% CRI: (- 0.25, 0.22)), age = 2 ($\Delta \beta = - 0.18$ 95% CRI: (- 0.61, 0.22)), age = 3 ($\Delta \beta =
- 0.35$ 95% CRI: (- 1.25, 0.414)) or age = 4 ($\Delta \beta = - 1.29$ 95% CRI: (- 2.99, 0.311)). We also
found no significant difference in non-linear senescence rates between habitats (Electronic
Supplementary Material Table 1A). In addition, we did not detect a significant difference in
senescence rates (linear or non-linear) between males and females either on farm islands or
non-farm islands (Electronic Supplementary Material Table 2A and 3A).

The results from third part of the main analysis indicated that there were significant
differences in linear senescence rates between islands (see Fig. 2 and Electronic
Supplementary Material Table 4A and 5A). Specifically, the senescence rates on Gjerøy and
Træna were found to be significantly steeper compared to Hestmannøy. There was a significant linear decline in survival probability on Træna starting at age = 1 and on Gjerøy starting at age = 2 (see Table 1). We found no significant difference in non-linear senescence rates between islands (Electronic Supplementary Material Table 1A). We also found no significant difference in senescence rates (linear or non-linear) between males and females on any of the four islands (Electronic Supplementary Material Table 2A and 3A).

Discussion

This study has shown that senescence rates and onset of senescence may vary spatially in a wild metapopulation. Although the lack of mean difference in senescence rates between habitats did not support our initial hypothesis, the results of this study suggest that local environmental conditions may have an important effect on the aging patterns of wild animals. Failure to account for such variation may lead to an oversimplified view of senescence rates of a species (Fig. 1 vs Fig. 2). Although the specific causes of heterogeneous senescence rates between populations may be difficult to detect, the resulting effect on local demography may influence the population dynamics of the sub-population and the metapopulation as a whole. Accounting for such heterogeneities may be important for predicting future population fluctuations of fragmented populations (i.e. metapopulations) in the wild.

Although the pattern found on one non-farm island fitted the expected pattern of faster senescence rates and earlier onset, this was not the case on the other non-farm island (see Fig. 2). In addition, senescence rates on the two farm islands were significantly different (see Table 1 and Electronic Supplementary Material Table 4A and 5A) even though these islands are only ca. 11 km apart. A distinct difference between the two farm islands was the mean survival probabilities of the first two adult age classes (see Fig. 2 and Table 1). The relatively
high survival probability of these age classes on the farm island of Gjerøy may point out a
difference in investment strategies between the two islands. Individuals that invest a
relatively large amount of energy in early reproduction and/or survival may also be expected
to suffer more pronounced senescence in later life (McCleery et al. 1996; Orell and Belda
2002; Reid et al. 2003; Reed et al. 2008; Hammers et al. 2013). However, the lack of
differences in fledgling survival probability among populations (see Fig. 2) appears to
exclude the possibility that the variation observed was caused by a substantial difference in
mortality before maturation (e.g. stronger selection for quality individuals). Alternatively,
differences in natal environments may have caused subsequent changes in the senescence
pattern between the islands that manifested in the adult age classes (Nussey et al. 2007; Reed
et al. 2008; Millon et al. 2011; Cartwright et al. 2014). These differences may be subtle and
very difficult to observe in the wild (Nussey et al. 2013).

As the house sparrow is a socially monogamous species (Anderson 2006), the lack of
difference in senescence found between adult males and adult females appears to support the
pattern found by Clutton-Brock and Isvaran (2007). Although one might expect a general
female biased mortality pattern in birds (Liker and Szekely 2005) to cause a different
senescence rate in females compared to males, this is not the case in our populations (see
Electronic Supplementary Material Table 2A and 3A). Indeed, the overall result from our
analysis did not support the notion of a general pattern of female biased mortality in house
sparrows. Previous studies on house sparrows have also not detected a general sex-bias in
adult survival probability (For review see Anderson 2006).

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Author contributions

HH, THR, BES conceived of the study. HH, TK, HJ, HP, THR contributed to field work and data collection. HH, TK, MG, JT discussed about the methods and HH (and others if any 😇) performed the analyses. HH wrote the first draft and all authors contributed to the interpretation of results and revisions of the manuscript.

Ethical approval

All applicable institutional and/or national guidelines for the care and use of animals were followed.

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

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Figure legends:

**Fig. 1** : The mean survival probability of age classes in a metapopulation of house sparrows on four islands in the Helgeland archipelago, northern Norway. Age = 0 denotes the mean survival of fledglings on the four islands. Lines indicate upper and lower limit of a 95% Bayesian credibility interval of the mean value. Numbers at the upper end of the figure indicate observed sample sizes for each age class.

**Fig. 2** : The change in survival probability with age in four island populations of house sparrows in the Helgeland archipelago, northern Norway (1993 – 2013). The dashed line indicates the predicted linear decline in survival probability starting at age = 1 (Træna) or age = 2 (Gjerøy). Solid lines indicate upper and lower limit of a 95% Bayesian credibility interval of the mean value (open points). Numbers at the upper end of the figures indicate observed sample sizes for each age class.