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1 **Spatial variation in senescence rates in a bird metapopulation**

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13

14 **Abstract**

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

29

30

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

33

34 **Introduction**

35 The evidence supporting the hypothesis that senescence (e.g. decline in survival and/or
36 reproduction with age) does occur in wild populations has become substantial in recent
37 decades. This has also led to an increasing interest into the underlying mechanisms that may
38 influence senescence (see Nussey et al. 2013 for a review). The fundamental evolutionary
39 mechanism(s) explaining the occurrence of actuarial senescence (a.k.a. survival senescence)
40 has been attributed to the decline of natural selection with age (Medawar 1952; Hamilton
41 1966). Williams (1957) expanded this work and provided the antagonistic pleiotropy theory
42 of aging, which states that an allele with a positive effect on reproduction early in life may be
43 selected even if it has a negative effect on survival later in life. Later, Kirkwood (1977)
44 proposed the disposable soma theory of aging. Both the antagonistic pleiotropy theory and
45 the disposable soma theory share the same prediction of a trade-off between reproduction
46 and/or growth during early life and intensity of ageing later in life (Nussey et al. 2013;
47 Lemaitre et al. 2015). Stated briefly; as the energy available to an individual is not infinite,
48 senescence may be expected to start at the age of maturity (but see Brunet-Rossinni and
49 Austad 2006) and manifest itself within the normal lifespan of the species (Nussey et al.
50 2013).

51 Rates of actuarial senescence (hereafter senescence) in wild populations may be
52 significantly influenced by the environment. Specifically, if a population is exposed to
53 environments that increase mortality, this may amplify the rate of senescence under particular
54 circumstances (Caswell 2007). For instance, it has been shown that a high level of predation
55 (e.g. Dhondt et al. 1998) or an increased competition between individuals for resources (i.e.
56 density dependence, e.g. Altwegg et al. 2003) may increase the rate of senescence (Nussey et
57 al. 2007). Predation and density may even interact with each other in affecting senescence

58 rates (e.g. Balbontin and Møller 2015). As these sources of mortality may vary between
59 populations, one may expect senescence rates to vary accordingly. For example, Kawasaki et
60 al. (2008) found that the rate of aging in stalk-legged flies (*Telostylinus angusticollis*) in wild
61 populations was significantly faster compared to laboratory populations founded from the
62 same wild population. Similarly, Austad (1993) found that an island population of Virginia
63 opossums (*Didelphis virginiana*) had a shallower senescence slope compared to the mainland
64 population. This difference coincided with a lack of predators on the island (Austad 1993).
65 Despite of this empirical foundation, there has been a lack of studies investigating
66 intraspecific spatial variation in senescence rates between different habitats/populations in the
67 wild (but see Austad 1993; Baker and Thompson 2007; also see Bouwhuis et al. 2010;
68 Balbontin et al. 2012 for studies of inter-population variation in rates of reproductive
69 senescence). The lack of studies may be caused by the requirement for long-term monitoring
70 of known-aged animals from different populations of the same species

71 The rate of senescence may vary among groups in a given population (e.g. males and
72 females). The difference in senescence rates between males and females has become a topic
73 of increased interest in evolutionary biology (Maklakov and Lummaa 2013; Regan and
74 Partridge 2013). Life-history theory predicts that the sex with the higher mortality rates
75 should be the one exhibiting the higher rates of senescence (Williams 1957). Therefore, as
76 males from polygynous and dimorphic species suffer from high mortality rates during the
77 mating season due to male-male combat for instance, they should exhibit higher senescence
78 rates than females (Bonduriansky et al. 2008; Festa-Bianchet 2012). An interspecific
79 comparison of 35 vertebrate species (Clutton-Brock and Isvaran 2007) provided an overall
80 support for that prediction, finding that, in general, males had faster rates of senescence than
81 females. As expected in socially monogamous species, such a difference in senescence rates

82 between males and females appeared to be less pronounced (Clutton-Brock and Isvaran
83 2007). However, it is noteworthy that until now, many of the studies investigating senescence
84 patterns in the wild have focused on females only (but see: Reed et al. 2008; Brown and Roth
85 2009; Nussey et al. 2009; Pardo et al. 2013; Cornwallis et al. 2014; Gamelon et al. 2014;
86 Hayward et al. 2015; Zhang et al. 2015) and evidence for sex differences in rates of
87 senescence in the wild remains somewhat scarce in the literature (Clutton-Brock and Isvaran
88 2007; Bonduriansky et al. 2008).

89 Here, we aimed at filling these gaps in our knowledge by investigating intraspecific
90 spatial variation and also sex differences in rates and onset of senescence in a wild
91 metapopulation of house sparrows (*Passer domesticus*) in a Norwegian archipelago (66.5 ° N
92 12.5 ° E). This metapopulation has been intensively monitored by annual capture, mark and
93 resight of both males and females since 1993. An important feature of this metapopulation is
94 that some islands contained farms where the birds had the option of sheltering inside cattle-
95 farm buildings whenever the weather is harsh (e.g. during winter). In contrast, other islands
96 do not have any cattle-farms and the birds have to find shelter around the human settlements.
97 Therefore, according to the current evolutionary theory of senescence, we expected: i) inter-
98 population variation in rates and onset of senescence with faster and/or earlier senescence in
99 the populations inhabiting the islands free of cattle-farms compared to the populations living
100 in more sheltered environments; ii) no sex difference in senescence rates within a given
101 population for this socially monogamous species (Anderson 2006).

102

103 **Materials and methods**

104 **Study area and habitats**

105 The study was carried out in an archipelago consisting of 18 islands covering ca. 1600 km² in
106 the Helgeland district in northern Norway (see map in Baalsrud et al. 2014). The house
107 sparrows on these islands have been systematically captured, marked and resighted several
108 times during their lifetime since 1993 (e.g. Ringsby et al. 2002; Jensen et al. 2008; Pärn et al.
109 2012). In this study, we compared two sets of islands which differed in habitat: two islands
110 with cattle farms (Gjerøy and Hestmannøy) and two islands without cattle farms (Selvær and
111 Træna). On the farm islands, house sparrows lived in association with dairy farms where they
112 reproduced, foraged and sheltered (under harsh weather conditions) inside barns and cow-
113 sheds. On these farm islands, the cattle food and seeds from cultivated crops were readily
114 available for house sparrows throughout the year. On the non-farm islands, where house
115 sparrows live in association with small human settlements, the shelter provided by the barns
116 was lacking. In addition, the main food resource on the non-farm islands was seeds from
117 birdfeeders provided by the local human inhabitants. Although we focus on 4 islands,
118 observations from the other islands were used to identify and exclude emigrants and
119 immigrants from the dataset (n = 330). This was done to ensure that the effect of
120 habitat/island on individual survival remained as constant as possible throughout the lifespan
121 of individuals. We were thus also able to separate mortality from migration in our analyses.

122

123 **Field work and datasets**

124 Field work was carried out during the summer (1 May - 15 August) and autumn (1 September
125 - 1 November). During field work, house sparrows were captured using mist nets. Upon first
126 capture, they were banded with a metal ring engraved with a unique id-number and three
127 plastic color rings (two rings on each tarsus). In addition, we visited nests (nest boxes or
128 under barn roofs) and marked fledglings (age = 8 - 14 days old). Thus, after individuals had

129 been marked, they could be resighted by capturing them, or by observing their unique
130 combination of color rings through a telescope or binoculars. For detailed description on field
131 work, see Ringsby et al. (1998), Sæther et al. (1999) and Pärn et al. (2009).

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

142 **Survival Analyses**

143 We estimated survival probabilities with capture-mark-recapture (CMR) models (Lebreton et
144 al. 1992; Kéry and Schaub 2011). Previous studies have found that resighting probabilities
145 may vary between islands and years in the metapopulation (Ringsby et al. 1999; Holand et al.
146 2014). We therefore included island, year and the interaction between islands and years in all
147 models of resighting probability. To account for temporal variation in survival estimates, we
148 included the effect of years as a random factor in all survival models. An investigation by
149 Jones et al. (2008) indicated that senescence in house sparrows at Helgeland started at the
150 mean age of first reproduction (age = 1). However, as the onset of senescence may occur later
151 than the age of first reproduction (e.g. Weimerskirch 1992; Nussey et al. 2008; Peron et al.
152 2010), we tested for linear effect of age and also non-linear (i.e. quadratic) change in survival

153 probability with increasing ages (i.e. senescence) either starting at age = 1, 2, 3 or 4 in
154 separate models. Due to low sample sizes at ages > 4 (see Fig. 2), we did not test for onsets
155 starting at later ages. In details, our analyses have been divided into three parts. First, at the
156 metapopulation level (i.e. all 4 islands pooled together), we investigated the relationship
157 between survival probability (on the logit-scale) and ages. Secondly, we investigated the
158 difference in senescence rates (i.e. difference in slopes) between the two habitats (farm- vs.
159 non-farm islands). Thirdly, we investigated if there were significant differences in senescence
160 rates between islands (Gjerøy, Hestmanøy, Selvær and Træna) in the metapopulation. The
161 rates of senescence were thus estimated separately for each habitat/island by including the
162 interaction between habitat/island and age on survival. To examine how survival probability
163 varied among age classes, we used age as a factor instead of a continuous variable (see Fig. 1
164 and 2).

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

168 We used the model fitting options provided by the programming language BUGS (Lunn
169 et al. 2000). This language offers several options for creating CMR models in a Bayesian
170 framework using MCMC simulations to obtain posterior stationary distributions of
171 parameters (Kéry and Schaub 2011). The models were run in JAGS (Version 3.2.0, Plummer
172 2003) controlled from R (Version 3.1.1, R Core Team 2014) using the package “JagsUI”
173 (Version 1.1). This package allows for easy parallel computation of multiple chains on
174 computers using a cpu with multiple cores. For all models, we used three chains each with
175 120 000 iterations and a thinning rate of six; where the first 90 000 iterations were discarded
176 (“burn-in”). Mixing and convergence of chains to a stationary distribution was evaluated by

177 visual inspection of time-series plots produced by JAGS and by the Brooks-Gelman-Rubin
178 criterion (R-hat, Brooks and Gelman 1998). Parameter estimates were obtained as the mean
179 from the respective stationary posterior distributions and lower/upper limits of the 95 %
180 Bayesian Credibility Interval (CRI). We applied vague priors for all parameters (see Kéry and
181 Schaub 2011).

182

183 **Results**

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

189 The second part of our main analysis indicated that linear senescence rates were not
190 significantly different between the two habitat types (see Table 1), starting at age = 1 ($\Delta \beta = -$
191 0.01 95% CRI: (- 0.25, 0.22)), age = 2 ($\Delta \beta = - 0.18$ 95% CRI: (- 0.61, 0.22)), age = 3 ($\Delta \beta = -$
192 0.35 95% CRI: (- 1.25, 0.414)) or age = 4 ($\Delta \beta = - 1.29$ 95% CRI: (- 2.99, 0.311)). We also
193 found no significant difference in non-linear senescence rates between habitats (Electronic
194 Supplementary Material Table 1A). In addition, we did not detect a significant difference in
195 senescence rates (linear or non-linear) between males and females either on farm islands or
196 non-farm islands (Electronic Supplementary Material Table 2A and 3A).

197 The results from third part of the main analysis indicated that there were significant
198 differences in linear senescence rates between islands (see Fig. 2 and Electronic
199 Supplementary Material Table 4A and 5A). Specifically, the senescence rates on Gjerøy and

200 Træna were found to be significantly steeper compared to Hestmannøy. There was a
201 significant linear decline in survival probability on Træna starting at age = 1 and on Gjerøy
202 starting at age = 2 (see Table 1). We found no significant difference in non-linear senescence
203 rates between islands (Electronic Supplementary Material Table 1A). We also found no
204 significant difference in senescence rates (linear or non-linear) between males and females on
205 any of the four islands (Electronic Supplementary Material Table 2A and 3A).

206

207 **Discussion**

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

218 Although the pattern found on one non-farm island fitted the expected pattern of faster
219 senescence rates and earlier onset, this was not the case on the other non-farm island (see Fig.
220 2). In addition, senescence rates on the two farm islands were significantly different (see
221 Table 1 and Electronic Supplementary Material Table 4A and 5A) even though these islands
222 are only ca. 11 km apart. A distinct difference between the two farm islands was the mean
223 survival probabilities of the first two adult age classes (see Fig. 2 and Table 1). The relatively

224 high survival probability of these age classes on the farm island of Gjerøy may point out a
225 difference in investment strategies between the two islands. Individuals that invest a
226 relatively large amount of energy in early reproduction and/or survival may also be expected
227 to suffer more pronounced senescence in later life (McCleery et al. 1996; Orell and Belda
228 2002; Reid et al. 2003; Reed et al. 2008; Hammers et al. 2013). However, the lack of
229 differences in fledgling survival probability among populations (see Fig. 2) appears to
230 exclude the possibility that the variation observed was caused by a substantial difference in
231 mortality before maturation (e.g. stronger selection for quality individuals). Alternatively,
232 differences in natal environments may have caused subsequent changes in the senescence
233 pattern between the islands that manifested in the adult age classes (Nussey et al. 2007; Reed
234 et al. 2008; Millon et al. 2011; Cartwright et al. 2014). These differences may be subtle and
235 very difficult to observe in the wild (Nussey et al. 2013).

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

245

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254

255 **Author contributions**

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

260 **Ethical approval**

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

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

264

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409 Figure legends:

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

415

416 **Fig. 2** : The change in survival probability with age in four island populations of house
417 sparrows in the Helgeland archipelago, northern Norway (1993 – 2013). The dashed line
418 indicates the predicted linear decline in survival probability starting at age = 1 (Træna) or age
419 = 2 (Gjerøy). Solid lines indicate upper and lower limit of a 95 % Bayesian credibility
420 interval of the mean value (open points). Numbers at the upper end of the figures indicate
421 observed sample sizes for each age class.