

University of Groningen

The impact of reproductive investment and early-life environmental conditions on senescence

Hammers, M.; Richardson, D. S.; Burke, T.; Komdeur, J.

Published in:
Journal of Evolutionary Biology

DOI:
[10.1111/jeb.12204](https://doi.org/10.1111/jeb.12204)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2013

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Hammers, M., Richardson, D. S., Burke, T., & Komdeur, J. (2013). The impact of reproductive investment and early-life environmental conditions on senescence: Support for the disposable soma hypothesis. *Journal of Evolutionary Biology*, 26(9), 1999-2007. <https://doi.org/10.1111/jeb.12204>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

The impact of reproductive investment and early-life environmental conditions on senescence: support for the disposable soma hypothesis

M. HAMMERS*†, D. S. RICHARDSON†‡, T. BURKE§ & J. KOMDEUR*

*Behavioural Ecology and Self-Organization, Centre for Ecological and Evolutionary Studies, University of Groningen, Groningen, The Netherlands

†Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich, UK

‡Nature Seychelles, Victoria, Mahé, Seychelles

§Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK

Keywords:

Acrocephalus sechellensis;
ageing;
antagonistic pleiotropy;
disposable soma;
early-life investment;
life-history trade-off;
Seychelles warbler;
survival senescence.

Abstract

Several hypotheses have been put forward to explain the evolution of senescence. One of the leading hypotheses, the disposable soma hypothesis, predicts a trade-off, whereby early-life investment in reproduction leads to late-life declines in survival (survival senescence). Testing this hypothesis in natural populations is challenging, but important for understanding the evolution of senescence. We used the long-term data set from a contained, predator-free population of individually marked Seychelles warblers (*Acrocephalus sechellensis*) to investigate how age-related declines in survival are affected by early-life investment in reproduction and early-life environmental conditions. The disposable soma hypothesis predicts that higher investment in reproduction, or experiencing harsh conditions during early life, will lead to an earlier onset, and an increased rate, of senescence. We found that both sexes showed similar age-related declines in late-life survival consistent with senescence. Individuals that started breeding at a later age showed a delay in survival senescence, but this later onset of breeding did not result in a less rapid decline in late-life survival. Although survival senescence was not directly related to early-life environmental conditions, age of first breeding increased with natal food availability. Therefore, early-life food availability may affect senescence by influencing age of first breeding. The disposable soma hypothesis of senescence is supported by delayed senescence in individuals that started breeding at a later age and therefore invested less in reproduction.

Introduction

Lifespan is one of the most important determinants of fitness in many vertebrates in which lifetime reproductive success increases with lifespan (Clutton-Brock, 1988; Newton, 1989). Therefore, to understand the evolution of life histories, it is important to identify the factors and trade-offs that influence survival (Stearns, 1992). Senescence is defined as the decline in

performance with advancing age and is caused by a progressive decline in an individual's physiological and cellular functions (Kirkwood & Austad, 2000). Individuals may show senescent declines in performance across a wide range of traits, such as foraging (Lecomte *et al.*, 2010), immune function (Hayward *et al.*, 2009) and body mass (Nussey *et al.*, 2011). This reduced performance may ultimately lead to a progressive decrease in survival with age.

Senescence occurs in many taxa in the wild (Jones *et al.*, 2008; Ricklefs, 2008; Nussey *et al.*, 2013), but how and why individuals age remains poorly understood. Several hypotheses have been proposed to explain the evolution of senescence (Kirkwood & Austad, 2000), all of which assume that the force of

Correspondence: Martijn Hammers, Behavioural Ecology and Self-Organization, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 11103, 9700 CC, Groningen, The Netherlands. Tel.: +31 50 363 5928; e-mail: m.hammers@rug.nl

natural selection becomes weaker on older age classes. The effect of selection diminishes because it is proportional to the number of individuals alive in each age class, which diminishes with age because of extrinsic mortality. The ‘antagonistic pleiotropy’ hypothesis proposes that senescence may be caused by weakened selection against late-acting deleterious mutations, leading to greater selection on genes that are beneficial during early life, but that have deleterious effects later on (Williams, 1957). A related hypothesis, the ‘disposable soma’ hypothesis, suggests that an individual should only invest in maintenance of the soma for as long as it has a realistic chance of survival (Kirkwood, 1977; Kirkwood & Holliday, 1979; Kirkwood & Austad, 2000). Higher investment in reproduction is expected at younger ages at the cost of investment into maintenance and repair, even though this may lead to higher levels of damage to cells and tissues and, therefore, senescence (Kirkwood & Rose, 1991). The accumulation of this damage during early life may then be manifested in a late-life decline in survival. Thus, the antagonistic pleiotropy and disposable soma hypotheses predict a trade-off between investment during early life and late-life survival (Kirkwood & Rose, 1991). The main difference between these two hypotheses is that the antagonistic pleiotropy hypothesis focuses on the effects of genes with pleiotropic effects, whereas the disposable soma hypothesis focuses on the optimal allocation of resources to reproduction, self-maintenance and repair (Kirkwood & Austad, 2000).

Clearly, to understand the evolution of senescence, it is important to investigate how early-life environmental conditions and reproductive investment influence survival senescence (the progressive age-dependent decline of survival probability). Several studies have shown that survival senescence occurs in a wide variety of taxa, including birds and mammals (Jones *et al.*, 2008; Péron *et al.*, 2010), insects (Bonduriansky & Bransil, 2002) and fish (Reznick *et al.*, 2004). However, few studies have investigated which factors contribute to differences in senescent declines in survival probability between individuals within a population. Factors that are predicted to affect the onset and the rate of survival senescence include early-life reproductive investment and early-life environmental conditions. Several studies have shown that individuals that allocate more resources to reproduction during early life (e.g. produce more offspring) suffer from increased survival senescence later in life (Luckinbill *et al.*, 1984; McCleery *et al.*, 1996; Orell & Belda, 2002; Reid *et al.*, 2003; Pettay *et al.*, 2005; Reed *et al.*, 2008), but see Gaillard *et al.* (2003). One way to invest less in reproduction during early life is to delay breeding until well into adulthood. Hence, individuals that start breeding at a later age are expected to show delayed senescence and/or a less rapid decline in late-life survival compared with individuals that start breeding at a younger age.

Furthermore, the environmental conditions experienced during early life are predicted to influence senescence. For example, animals experiencing poor conditions during early life (e.g. low food availability or high local breeding density) may show steeper declines in late-life survival (Nussey *et al.*, 2007), but see Millon *et al.* (2011).

The effective study of survival senescence in the wild requires long-term, longitudinal data sets of individually marked animals living in closed populations with low levels of extrinsic mortality (Monaghan *et al.*, 2008). Here, we use the long-term data set (1981–2011) on the Cousin Island (29 ha, 4°20’S, 55°40’E) population of the Seychelles warbler (*Acrocephalus sechellensis*). In this population, the majority (> 96%; Richardson *et al.*, 2001) of individuals have been individually colour-marked, and there is virtually no inter-island dispersal (Komdeur *et al.*, 2004). This lack of dispersal provides a rare opportunity to follow nearly all individuals within a single population from birth to death. Importantly, predation on adults is absent, thus individuals have relatively long lives (life expectancy at fledging = 5.5 years (Komdeur, 1991), maximum life-span = 17 years (Barrett *et al.*, 2013)). Food availability is an important determinant of environmental conditions, with survival declining with lower food abundance in territories (Komdeur, 1991) and with higher local breeding density (Brouwer *et al.*, 2006). Although survival senescence has not yet been investigated, previous studies have indicated that reproductive senescence occurs in this species, with reproductive output in females declining beyond 6 years of age (Komdeur, 1996c; Hammers *et al.*, 2012). Although Seychelles warblers can breed successfully in socially monogamous pairs, cooperative breeding occurs frequently (Komdeur, 1992; Richardson *et al.*, 2001) and is primarily driven by the shortage of high-quality breeding vacancies (Komdeur, 1992; Komdeur *et al.*, 1995). Not all mature offspring start independent breeding at the same age. Mature offspring often become subordinates within a territory until a breeding position becomes vacant. These individuals often gain both direct and indirect benefits from being a subordinate within a territory (Richardson *et al.*, 2002). Komdeur (1992) showed that 1-year-old Seychelles warblers may produce more offspring over their lifetimes by remaining in a high-quality territory for several years as a subordinate helper than when they would by starting breeding immediately in a lower quality territory. Indeed, individuals that were born in high-quality territories were more likely to stay as subordinate helpers rather than filling breeding vacancies on lower quality territories than individuals born in lower quality territories (Komdeur, 1992). An individual’s eventual acquisition of a dominant breeding position within a territory may occur between 1 and 8 years of age (this study), although some adult individuals will die without ever

acquiring a territory (Komdeur, 1992). Individuals that have acquired a breeding position typically remain on and defend the same stable territory until their death (99.1%, Komdeur & Edelaar, 2001), but see (Richardson *et al.*, 2007).

In this study, we present a test of the disposable soma hypothesis of senescence. This hypothesis predicts a trade-off between investment during early-life and late-life survival, consequently, we predict that individuals that started breeding at a later age will show gentler declines in age-dependent survival probabilities and/or a delay in survival senescence because of reduced investment in early-life reproduction. In addition, we test the prediction that individuals that spent the first years of their lives in poor-quality territories with low food availability, or lived with many other individuals in a territory (so experiencing high local competition) will show lower late-life survival.

Materials and methods

Study population and data collection

The Cousin Island population of Seychelles warblers is at carrying capacity and comprises *ca.* 320 colour-banded adults of known age in *ca.* 115 territories (Brouwer *et al.*, 2009). The population has been monitored since 1981 as part of a long-term study (Komdeur, 1992; Brouwer *et al.*, 2012). The warbler's life history is characterized by high annual adult survival (84%), predominantly single-egg clutches (87% of clutches) and extended periods of parental care (3–6 months) (Komdeur, 1991, 1994b; Brouwer *et al.*, 2006). The presence and dominance status of all individuals in each territory was determined during each main breeding season (June–September) from 1982 to 2011 (except in 1992 when no fieldwork was conducted, and 1982–1984 and 1991–1994, when only 68% of the territories were monitored; Brouwer *et al.*, 2009). The 'dominant' male and female were defined (based on behavioural observations) as the primary, pair-bonded male and female in a territory, whereas the term 'subordinate' includes all other mature birds (> 8 months old) resident in the territory (Richardson *et al.*, 2007). Typically, dominant individuals remain together in the same territory until one of the partners dies. The dead partner is then rapidly replaced by a subordinate, providing a rare opportunity for a subordinate to acquire a territory and a dominant breeding position. We recorded the birth year and the death year for each individual. As the resighting probability of breeding individuals is virtually one (0.98 ± 0.01 SE; Brouwer *et al.*, 2010), and the probability of dispersal from the island is extremely low (0.10%; Komdeur *et al.*, 2004), we assumed that all individuals that were not seen during the subsequent year, or thereafter, died in the first year they were missing. The sex of each individual that was sampled

since 1994 was established using molecular sexing methods (Griffiths *et al.*, 1998). Before 1994, the sex of individuals was established using a combination of body size and behaviour, which corresponds with molecular sexing (Komdeur, 1996a).

Territory quality, group size and age of first breeding

Seychelles warblers are purely insectivorous, taking insect food from the undersides of leaves and territory quality – measured in terms of insect prey availability in a territory – is important for reproductive success (Komdeur, 1991). To estimate local food availability, a territory quality index was calculated following Komdeur (1992) and van de Crommenacker *et al.* (2011), using the formula $a \cdot \sum(c_x \cdot i_x)$, where a is the territory size in hectares, c_x is the total foliage cover for broad-leaved tree species x (sum of foliage score, see below) and i_x is the mean monthly insect count for tree species x per unit leaf area (dm^2). Territory size was determined by mapping observations of foraging and territorial defence behaviour at the territory borders. Foliage cover was scored by determining the presence of each tree species at 20 random points in every territory, in the following height bands: 0–0.75 m, 0.75–2 m and at 2 m intervals thereafter. Insect counts were estimated by monthly counting of the total number of insects on the undersides of 50 leaves for each tree species present in 14 different regions across the island, reflecting the regional variation in insect abundance. Because territory quality was not measured every year (measured in 1987, 1990, 1996–1999, 2003, 2004, 2006–2011), and because of fluctuations in overall territory quality between years, we calculated one index of territory quality for each territory, rather than extrapolating territory quality for the missing years. To this end, we calculated the standardized territory quality for each territory in each year (mean-centred by year and divided by the standard deviation) and averaged these values to obtain one value of quality for each territory for all years combined (Hammers *et al.*, 2012). Because reproductive output increases with food availability, and food availability differs markedly between years (Komdeur, 1991, 1996b), population-level food availability was estimated based on the total number of birds that fledged in a certain year. Group size was the number of adult individuals (dominants and subordinates) resident in a territory and reflects the local competition for food (Brouwer *et al.*, 2006). The age of first breeding (defined as when an individual became a dominant territory owner) provides a measure of early-life investment, as it reflects abrupt increased investment in reproduction and territorial defence. Although subordinates sometimes participate in aspects of reproductive behaviour (e.g. incubation, feeding dependent offspring, co-breeding) and territorial

defence (Komdeur, 1994b; Richardson *et al.*, 2001), the costs of territory ownership and reproduction can be assumed to be much greater for dominants compared to subordinates. For example, it was shown experimentally that dominant males, but not subordinate males, invest in energetically costly mate-guarding (Komdeur, 2001). Because vacant territories are extremely limited in this saturated population (only 16% of adults die each year; Brouwer *et al.*, 2006), and because the loss of a territory typically means the end of the individual's reproductive career (c.f. Richardson *et al.*, 2007), dominant individuals are expected to invest much more in territory defence compared to subordinates. In addition, almost all dominant individuals attempt to breed each year (average 98.2%; Komdeur & Daan, 2005), whereas only a proportion of subordinates contribute to nest care and territorial defence in each breeding attempt and, if so, to a lesser extent than dominants (Komdeur, 1991).

Data analyses

We used generalized linear mixed models with a binomial error distribution and logit link function to investigate age-dependent survival using R (2.13.0, R Development Core Team, 2011) in the package LME4 (0.999375, Bates *et al.*, 2011). We recorded whether each individual was alive or not in each year. To control for differences in survival probabilities between years (Brouwer *et al.*, 2006), we included year as a random effect in the analyses. The 116 birds that had been translocated from Cousin to neighbouring islands as part of the conservation programme (29 individuals in 1988, 29 individuals in 1990 and 58 individuals in 2004 (Komdeur, 1994a; Richardson *et al.*, 2006)) were excluded from all analyses. Population-level food availability could not be established for individuals born before 1992 and so was included only for birds born after 1991. Furthermore, because the year of death could not be established precisely for birds that died in 1992, birds that were not observed in 1993 were assigned 1991 as their death year. Repeating all analyses using only individuals that were born after 1991 did not change the results of these analyses (analyses not shown).

To investigate late-life declines in survival, we restricted the data set to include only dominant individuals older than 6 years of age. We did so for two reasons: (i) 6 years demarks the mean onset of reproductive senescence in Seychelles warblers (Komdeur, 1996c; Hammers *et al.*, 2012); (ii) all individuals that eventually became dominant breeders had acquired a territory when 7 years old, except for one individual that gained dominance at 8 years of age. We used territory quality ('early-life territory quality'), population-level food availability ('early-life population-level food availability') and group size ('early-life group size'),

averaged over the first 3 years of an individual's life, as measures of early-life conditions. Along with age, the starting model (143 females and 127 males older than 6 years) contained sex, the age at which an individual became a dominant breeder, early-life territory quality, early-life population-level food availability and early-life group size. A significant main effect, along with a significant decline in survival with age, would indicate that senescence is advanced (left-shifted) or delayed (right-shifted). All two-way interactions with age were included to investigate whether the rate of decline in survival with age was associated with gender, age of first breeding or early-life conditions. Nonsignificant terms ($P > 0.05$) were then – in order of least significance and starting with the interaction terms – removed until a model was retained with only significant terms. Repeating the model including all (significant and nonsignificant) fixed effects, but excluding nonsignificant interactions, gave similar results.

Because early-life environmental conditions may affect senescence through their effects on age of first breeding (Nussey *et al.*, 2007), we used generalized linear models with a quasi-Poisson error distribution and log link function to investigate how age of first breeding is related to natal (first year of life) conditions. In these models, we included cohort (birth year) and sex as factors, and natal territory quality, natal population-level food availability and natal group size as covariates. These data were available for 124 individuals.

We related reproductive lifespan (number of years from the start until the end of the reproductive career) to age of first breeding (*sensu* Hawn *et al.* 2007) using parametric survival models (time to event models) with a Weibull distribution using the package Survival (2.36-5, Therneau 2011). In this analysis, we included all dominant individuals (irrespective of age). Sex was included as a covariate and individuals that were still alive in 2011 ($n = 228$ of 942 individuals, 24%) were censored in the analyses.

Results

Annual survival decreased sharply and progressively with age in individuals older than 6 years (Table 1, Fig. 1). Males and females showed similar declines in survival with age (Table 1). The annual survival probabilities predicted by the statistical model declined by 46% from age seven (0.85) to age 17 (0.46) (Fig. 1). Age of first breeding ranged from 1 to 8 years, with 48% (129/270) of individuals starting breeding as 1-year-olds, 35% (95/270) starting at 2 years and 17% (46/270) after 2 years of age. The age-dependent decline in survival was delayed (right-shifted) in individuals that started breeding at a later age (Table 1, Fig. 1). The coefficients of the model were almost identical, but opposite, for age and age of first breeding, suggesting that starting independent breeding 1 year

Table 1 The relationship between age-dependent annual survival in Seychelles warblers and age at first breeding and early-life conditions. The analyses included 143 females and 127 males older than 6 years. One hundred and 29 individuals started breeding at 1 year of age, 95 individuals at 2 years of age and 46 after 2 years of age.

	β	SE	Z	P
Intercept	3.12	0.39	8.03	<0.01
Age	-0.21	0.04	-5.91	<0.01
Age of first breeding	0.21	0.07	3.13	<0.01
Sex	0.08	0.16	0.50	0.62
Early-life group size	-0.02	0.13	-0.16	0.87
Early-life territory quality	0.01	0.21	0.05	0.96
Early-life year quality	0.00	0.01	0.01	0.99
Age \times Age first breeding	0.01	0.03	0.47	0.63
Age \times Sex	0.08	0.09	0.90	0.36
Age \times Early-life group size	0.05	0.06	0.83	0.40
Age \times Early-life territory quality	-0.07	0.10	-0.67	0.50
Age \times Early-life year quality	0.00	0.00	-0.54	0.58
	Variance		SD	
Year (random)	0.07		0.27	

Summaries were derived from binomial response, linear mixed models with survival to the next year as dependent variable (see Methods for details). Variables included in the final models are indicated in bold.

later also delays the age-dependent decline in late-life survival probability for 1 year. At 7 years of age, the average survival probabilities for individuals that started breeding at 1 year of age, 2 years of age or when they were older than 2 years of age, were 0.83, 0.86 and 0.92, respectively. The trajectory of the age-dependent decline in survival (rate of survival senescence) did not differ for individuals that started breeding at different ages (no interaction between age and age of first breeding: Table 1, Fig. 1).

There was considerable variation between individuals in the conditions encountered during the first 3 years of their life (territory-level food availability (mean \pm SD = 0.08 ± 0.46 , range = -0.73 – 1.66), population-level food availability (mean \pm SD = 78.84 ± 10.16 , range = 54.5 – 115.0) and group size (mean \pm SD = 2.78 ± 0.63 , range = 2.00 – 5.33). The onset of survival senescence was not associated with early-life territory quality, early-life population-level food availability and early-life group size (Table 1). Also, the rate of the age-dependent decline in survival was not related to any of the three measures of early-life condition, as indicated by the absence of significant interaction effects with age (Table 1).

Age of first breeding increased with natal territory quality (mean \pm SE = 0.14 ± 0.05 , $t = 2.82$, $P < 0.01$), tended to increase with natal population-level food availability (mean \pm SE = 0.004 ± 0.002 , $t = 1.93$, $P = 0.06$),

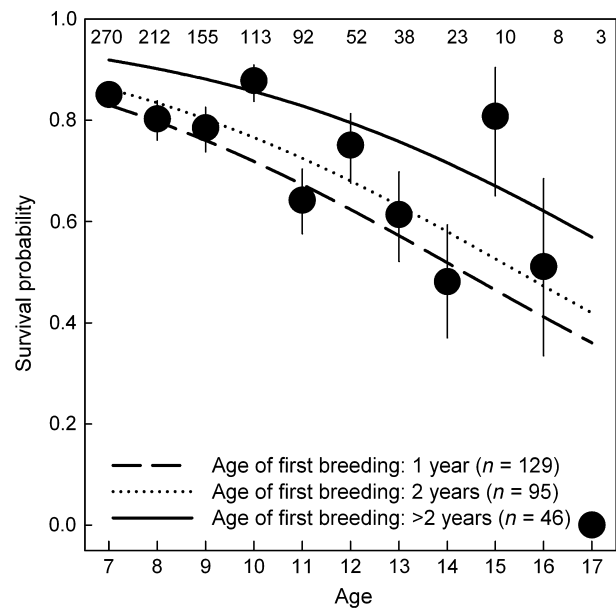


Fig. 1 Annual survival probabilities in relation to age, and age of first breeding, in Seychelles warblers older than 6 years. The survival probabilities are means and standard errors from a generalized linear model with age as a factor and year as a random effect. These survival probabilities are for all individuals combined, regardless of the age of first breeding. Numbers are sample sizes for each age class. The same individuals may occur several times in subsequent age classes. The lines are the model-predicted age-dependent declines in survival probability for individuals that started breeding at different ages.

but was not related to natal group size (mean \pm SE = -0.05 ± 0.05 , $t = -1.18$, $P = 0.24$). Age of first breeding did not differ between males and females (mean \pm SE = 0.03 ± 0.07 , $t = 0.34$, $P = 0.73$), but differed between cohorts ($\chi^2_{12} = 13.45$, $P < 0.01$).

When considering dominant individuals of all ages, reproductive lifespan was similar for individuals with different ages of first reproduction ($\beta = 0.01$, SE = 0.03 , $z = 0.11$, $P = 0.78$). Males and females showed similar lifespans ($\beta = -0.08$, SE = 0.05 , $z = -1.58$, $P = 0.11$). The model-predicted reproductive lifespans for individuals that first bred at 1, 2 or after 2 years of age were 6.08, 6.12 and 6.25 years, respectively.

Discussion

Late-life annual survival probabilities declined progressively with age in Seychelles warblers, thus providing clear evidence for survival senescence in this natural population. That similar declines in survival were observed in males and females is consistent with predictions about sex-specific senescence. Evolutionary hypotheses of senescence predict higher rates of survival senescence in the sex with higher annual mortality (Williams, 1957; Charlesworth, 1994; Ricklefs,

1998), and similar rates of senescence when sexes have similar annual mortality and adopt similar strategies to maximize fitness (Promislow, 2003; Clutton-Brock & Isvaran, 2007). The latter is the case in the Seychelles warbler, where individuals have similar annual mortality (Brouwer *et al.*, 2006), form long-term pair-bonds, defend stable territories over many years, and both sexes invest extensively in most aspects of parental care (Komdeur, 1991, 1994b).

The disposable soma hypothesis predicts that individuals that start breeding at a later age should show reduced survival senescence because lower reproductive investment during early life has allowed them to allocate more resources to somatic maintenance and long-term survival (Kirkwood & Rose, 1991). That a higher age of first breeding was associated with delayed senescence in the Seychelles warbler supports this hypothesis. For example, a 13-year-old individual that became a breeder when it was 5 years old, and therefore invested less in reproduction and territorial defence during early life, had a similar survival probability to a nine-year-old individual that started reproducing when it was 1 year of age.

Although the disposable soma and antagonistic pleiotropy hypotheses predict similar trade-offs between early-life reproductive effort and senescence, these trade-offs are caused by different mechanisms. In this study, disposable soma is the most likely mechanism to explain the delay in senescence for individuals that first bred independently at a later age because in the Seychelles warbler a delayed onset of independent breeding, and the associated reduction in resources allocated to reproduction during early-life, is most probably due to the limited availability of high-quality independent breeding opportunities, rather than a genetic mechanism (Komdeur, 1992). To confirm this, it would be informative to explore the physiological mechanisms that are affected by early-life reproductive effort and predict mortality. One mechanism that may contribute to this pattern might be the build-up of senescent cells within organs as a result of telomere shortening because of oxidative stress; previous work has shown that telomere dynamics predict mortality in the Seychelles warbler (Barrett *et al.*, 2013). Future studies might profitably investigate how age of first breeding, early-life reproductive investment, early-life conditions and survival senescence are related to telomere dynamics. In contrast, the antagonistic pleiotropy hypothesis could be tested formally by looking at genetic correlations between early-life reproductive effort and late-life survival. A negative genetic correlation between early-life reproductive effort and late-life survival would support the antagonistic pleiotropy hypothesis. Alternatively, antagonistic pleiotropy might be investigated by identifying specific loci that have opposite effects on early- and late-life fitness by mapping quantitative trait loci.

Several other studies in wild populations have also shown that increased survival senescence was associated with investment in early reproduction, or an earlier age of first breeding, (McCleery *et al.*, 1996; Orell & Belda, 2002; Reid *et al.*, 2003; Reed *et al.*, 2008). However, these studies were conducted in open populations, in which individuals could move freely in and out of the study area, and so emigration and death could not be distinguished; therefore, they were measuring apparent, rather than actual, survival. In our study, survival estimates reflect true survival as individuals remain in the study population until they die (Komdeur *et al.*, 2004). In addition, because adult predation is absent on Seychelles warblers, it is likely that most individuals succumbed to intrinsic, senescence-related mortality, rather than dying from extrinsic causes unrelated to senescence. Comparative studies across species also found longer lifespans or a later onset of survival senescence in species with a higher age of first breeding (Blumstein & Møller, 2008; Péron *et al.*, 2010). However, other studies found no relationship between survival senescence and early-life reproductive effort (Gaillard *et al.*, 2003), or that lower late-life survival was associated with higher age of first reproduction (Nussey *et al.*, 2007; Aubry *et al.*, 2011). Potential explanations for these contrasting results include the possibilities that individuals may have started breeding at a higher age because they experienced harsh environmental conditions during early life (e.g. Nussey *et al.*, 2007), or that they were of inferior phenotypic quality (e.g. Aubry *et al.*, 2011). There is some evidence that in the Seychelles warbler a later onset of independent breeding is related to individual quality; Richardson *et al.* (2007) found that individuals that had been a subordinate previously (and thus had a later onset of independent breeding) had a higher chance to be deposed from their dominant breeding position. Alternatively, investment in early-life reproduction might be state-dependent, such that individuals in better physiological condition are able to produce more offspring, at the same cost, as individuals in worse physiological condition that produce fewer offspring (McNamara & Houston, 1996).

Intriguingly, the reproductive lifespans of individuals started breeding at different ages were similar. Apart from reducing the costs of reproduction and territory defence, and thereby delaying survival senescence, a later onset of independent breeding in the Seychelles warbler has other fitness benefits. For example, subordinates have been shown to benefit through the accumulation of breeding experience, which is subsequently associated with increased reproductive output during the individual's first independent breeding attempt (Komdeur, 1996d). In addition, male subordinates may increase their lifetime reproductive success by budding off part of their resident territory (Komdeur & Edelaar, 2001). Finally, female subordinates may gain indirect

(kin-selected) benefits from helping (Richardson *et al.*, 2003), or direct benefits (maternity) by laying eggs within the dominant's nest (Richardson *et al.*, 2002). Therefore, because reproductive lifespans were similar for individuals with a different age of first breeding, other sources of benefit may lead to higher fitness of individuals with a later onset of independent breeding in this species. A previous study suggested that this may be the case in the Seychelles warbler as 1-year-old Seychelles warblers may achieve greater lifetime reproductive success when they remain as a subordinate helper in a territory for several years than when they would acquire an independent breeding position immediately (Komdeur, 1992). However, to compare the fitness of individuals with different ages of first reproduction as a dominant territory holder, genetic data on lifetime reproductive success is required for each individual (including shared breeding before the onset of independent reproduction, and extra-pair offspring). Because this data is not yet available, we were not able to estimate lifetime reproductive success for the individuals included in this study. A genetic pedigree is currently under construction which may be used to investigate fitness of individuals with different ages of first reproduction as dominants.

The lack of a direct relationship between late-life survival and early-life conditions in our study is contrary to what we expected based on the disposable soma hypothesis. Other recent studies of early-life conditions and survival senescence in wild populations also failed to detect a correlation between these two factors (Descamps *et al.*, 2008; Millon *et al.*, 2011). One other study showed an indirect relationship between the rate of survival senescence and poor conditions during early life, which occurred through their mutual linkage with age of first breeding (Nussey *et al.*, 2007). Individuals that experienced poor conditions during early life started breeding at a later age, and subsequently showed increased rates of survival senescence (Nussey *et al.*, 2007). Although in our study, survival senescence was not directly related to early-life conditions, age of first breeding increased with natal food availability (see also Komdeur, 1992), and survival senescence was delayed in individuals that started independent breeding at a later age. Our results therefore also suggest an indirect association between survival senescence and early-life food conditions through age at first breeding. A possible explanation for the absence of a direct relationship between survival senescence and early-life conditions might be that Seychelles warblers adopt a conservative reproductive tactic, in which survival is favoured over reproduction. In long-lived species, a long remaining reproductive life is more valuable than high current reproductive investment that might result in the death of an individual. This is especially so in species that experience low adult extrinsic mortality, variable juvenile survival and

prolonged periods of parental care, in which parents cannot predict the survival of their offspring (Hirshfield & Tinkle, 1975). Indeed, the life history of the relatively long-lived Seychelles warbler is characterized by low extrinsic mortality and considerable variation in juvenile survival across years (Brouwer *et al.*, 2006). In addition, adults may not be able to predict adequately the conditions that promote offspring survival, as the optimal timing for nest initiation that will result in the highest juvenile survival is 2 months before the peak in food availability (Komdeur, 1996b). Consequently, individuals should reduce their reproductive effort under harsh conditions in order to maintain their survival (e.g. Hamel *et al.*, 2010; Martin & Festa-Bianchet, 2010). Such a scenario might mask a direct relationship between late-life survival and early-life conditions. Conversely, it is possible that periods of lower food availability (dietary restriction) decelerate senescence, which is well established in laboratory organisms (e.g. Weindruch & Walford, 1982; Nakagawa *et al.*, 2012), but has not yet been investigated in wild vertebrate populations.

Acknowledgments

Nature Seychelles kindly allowed us to work on Cousin Island Nature Reserve, and we thank them and the Cousin Island staff for providing accommodation and facilities during our visits. The Department of Environment and the Seychelles Bureau of Standards gave permission for fieldwork and sampling. We thank Karl Phillips, Joost van den Heuvel and an anonymous reviewer for helpful comments on the manuscript. This study would not have been possible without the help of countless fieldworkers during the whole study period, supported by grants from the UK Natural Environment Research Council and the Netherlands Organisation for Scientific Research. MH was supported by a grant to JK, DSR and TB from the Netherlands Organisation for Scientific Research (NWO-ALW1PJ/07080).

References

- Aubry, L.M., Cam, E., Koons, D.N., Monnat, J.Y. & Pavard, S. 2011. Drivers of age-specific survival in a long-lived seabird: contributions of observed and hidden sources of heterogeneity. *J. Anim. Ecol.* **80**: 375–383.
- Barrett, E.L.B., Burke, T., Hammers, M., Komdeur, J. & Richardson, D.S. 2013. Telomere length and dynamics predict mortality in a wild longitudinal study. *Mol. Ecol.* **22**: 249–259.
- Bates, D., Maechler, M. & Bolker, B. 2011. lme4: Linear mixed-effects models using Eigen and S4 classes.
- Blumstein, D.T. & Møller, A.P. 2008. Is sociality associated with high longevity in North American birds? *Biol. Lett.* **4**: 146–148.
- Bonduriansky, R. & Brassil, C.E. 2002. Rapid and costly ageing in wild male flies. *Nature* **420**: 377.

- Brouwer, L., Richardson, D.S., Eikenaar, C. & Komdeur, J. 2006. The role of group size and environmental factors on survival in a cooperatively breeding tropical passerine. *J. Anim. Ecol.* **75**: 1321–1329.
- Brouwer, L., Tinbergen, J.M., Both, C., Bristol, R., Richardson, D.S. & Komdeur, J. 2009. Experimental evidence for density-dependent reproduction in a cooperatively breeding passerine. *Ecology* **90**: 729–741.
- Brouwer, L., Barr, I., van de Pol, M., Burke, T., Komdeur, J. & Richardson, D.S. 2010. MHC-dependent survival in a wild population: evidence for hidden genetic benefits gained through extra-pair fertilizations. *Mol. Ecol.* **19**: 3444–3455.
- Brouwer, L., Richardson, D.S. & Komdeur, J. 2012. Helpers at the nest improve late-life offspring performance: evidence from a long-term study and a cross-foster experiment. *PLoS ONE* **7**: e33167.
- Charlesworth, B. 1994. *Evolution in Age-Structured Populations*. Cambridge University Press, Cambridge.
- Clutton-Brock, T.H. 1988. *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*. University of Chicago Press, Chicago.
- Clutton-Brock, T.H. & Isvaran, K. 2007. Sex differences in ageing in natural populations of vertebrates. *Proc. R. Soc. Lond. B* **274**: 3097–3104.
- van de Crommenacker, J., Komdeur, J., Burke, T. & Richardson, D.S. 2011. Spatio-temporal variation in territory quality and oxidative status: a natural experiment in the Seychelles warbler (*Acrocephalus sechellensis*). *J. Anim. Ecol.* **80**: 668–680.
- Descamps, S., Boutin, S., Berteaux, D. & Gaillard, J.M. 2008. Age-specific variation in survival, reproductive success and offspring quality in red squirrels: evidence of senescence. *Oikos* **117**: 1406–1416.
- Gaillard, J.M., Loison, A., Festa-Bianchet, M., Yoccoz, N.G. & Solberg, E. 2003. Ecological correlates of life span in populations of large herbivorous mammals. *Popul. Dev. Rev.* **29**: 39–56.
- Griffiths, R., Double, M.C., Orr, K. & Dawson, R.J.G. 1998. A DNA test to sex most birds. *Mol. Ecol.* **7**: 1071–1075.
- Hamel, S., Côté, S.D. & Festa-Bianchet, M. 2010. Maternal characteristics and environment affect the costs of reproduction in female mountain goats. *Ecology* **91**: 2034–2043.
- Hammers, M., Richardson, D.S., Burke, T. & Komdeur, J. 2012. Age-dependent terminal declines in reproductive output in a wild bird. *PLoS ONE* **7**: e40413.
- Hawn, A.T., Radford, A.N. & du Plessis, M.A. 2007. Delayed breeding affects lifetime reproductive success differently in male and female green woodhoopoes. *Curr. Biol.* **17**: 844–849.
- Hayward, A.D., Wilson, A.J., Pilkington, J.G., Pemberton, J.M. & Kruuk, L.E.B. 2009. Ageing in a variable habitat: environmental stress affects senescence in parasite resistance in St Kilda Soay sheep. *Proc. R. Soc. Lond. B* **276**: 3477–3485.
- Hirshfield, M.F. & Tinkle, D.W. 1975. Natural selection and the evolution of reproductive effort. *Proc. Natl Acad. Sci. USA* **72**: 2227–2231.
- Jones, O.R., Gaillard, J.-M., Tuljapurkar, S., Alho, J.S., Armitage, K.B., Becker, P.H. *et al.* 2008. Senescence rates are determined by ranking on the fast-slow life-history continuum. *Ecol. Lett.* **11**: 664–673.
- Kirkwood, T.B.L. 1977. Evolution of ageing. *Nature* **270**: 301–304.
- Kirkwood, T.B.L. & Austad, S.N. 2000. Why do we age? *Nature* **408**: 233–238.
- Kirkwood, T.B.L. & Holliday, R. 1979. The evolution of ageing and longevity. *Proc. R. Soc. Lond. B* **205**: 531–546.
- Kirkwood, T.B.L. & Rose, M.R. 1991. Evolution of senescence: late survival sacrificed for reproduction. *Proc. R. Soc. Lond. B* **332**: 15–24.
- Komdeur, J. 1991. *Cooperative Breeding in the Seychelles Warbler*. Ph.D. Thesis. University of Cambridge, Cambridge.
- Komdeur, J. 1992. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature* **358**: 493–495.
- Komdeur, J. 1994a. Conserving the Seychelles warbler *Acrocephalus sechellensis* by translocation from Cousin Island to the islands of Aride and Cousine. *Biol. Conserv.* **67**: 143–152.
- Komdeur, J. 1994b. Experimental evidence for helping and hindering by previous offspring in the cooperative-breeding Seychelles warbler *Acrocephalus sechellensis*. *Behav. Ecol. Sociobiol.* **34**: 175–186.
- Komdeur, J. 1996a. Facultative sex ratio bias in the offspring of Seychelles warblers. *Proc. R. Soc. Lond. B* **263**: 661–666.
- Komdeur, J. 1996b. Seasonal timing of reproduction in a tropical bird, the Seychelles warbler: a field experiment using translocation. *J. Biol. Rhythms* **11**: 333–346.
- Komdeur, J. 1996c. Influence of age on reproductive performance in the Seychelles warbler. *Behav. Ecol.* **7**: 417–425.
- Komdeur, J. 1996d. Influence of helping and breeding experience on reproductive performance in the Seychelles warbler: a translocation experiment. *Behav. Ecol.* **7**: 326–333.
- Komdeur, J. 2001. Mate guarding in the Seychelles warbler is energetically costly and adjusted to paternity risk. *Proc. R. Soc. Lond. B* **268**: 2103–2111.
- Komdeur, J. & Daan, S. 2005. Breeding in the monsoon: semi-annual reproduction in the Seychelles warbler (*Acrocephalus sechellensis*). *J. Ornithol.* **146**: 305–313.
- Komdeur, J. & Edelaar, P. 2001. Male Seychelles warblers use territory budding to maximize lifetime fitness in a saturated environment. *Behav. Ecol.* **12**: 706–715.
- Komdeur, J., Huffstadt, A., Prast, W., Castle, G., Mileto, R. & Wattel, J. 1995. Transfer experiments of Seychelles warblers to new islands: changes in dispersal and helping behaviour. *Anim. Behav.* **49**: 695–708.
- Komdeur, J., Piersma, T., Kraaijeveld, K., Kraaijeveld Smit, F. & Richardson, D.S. 2004. Why Seychelles Warblers fail to recolonize nearby islands: unwilling or unable to fly there? *Ibis* **146**: 298–302.
- Lecomte, V.J., Sorci, G., Cornet, S., Jaeger, A., Faivre, B., Arnoux, E. *et al.* 2010. Patterns of aging in the long-lived wandering albatross. *Proc. Natl. Acad. Sci. USA* **107**: 6370–6375.
- Luckinbill, L.S., Arking, R., Clare, M.J., Cirocco, W.C. & Buck, S.A. 1984. Selection for delayed senescence in *Drosophila melanogaster*. *Evolution* **38**: 996–1003.
- Martin, J.G.A. & Festa-Bianchet, M. 2010. Bighorn ewes transfer the costs of reproduction to their lambs. *Am. Nat.* **176**: 414–423.
- McCleery, R.H., Clobert, J., Julliard, R. & Perrins, C.M. 1996. Nest predation and delayed cost of reproduction in the great tit. *J. Anim. Ecol.* **65**: 96–104.
- McNamara, J.M. & Houston, A.I. 1996. State-dependent life histories. *Nature* **380**: 215–221.

- Millon, A., Petty, S.J., Little, B. & Lambin, X. 2011. Natal conditions alter age-specific reproduction but not survival or senescence in a long-lived bird of prey. *J. Anim. Ecol.* **80**: 968–975.
- Monaghan, P., Charmantier, A., Nussey, D.H. & Ricklefs, R.E. 2008. The evolutionary ecology of senescence. *Funct. Ecol.* **22**: 371–378.
- Nakagawa, S., Lagisz, M., Hector, K.L. & Spencer, H.G. 2012. Comparative and meta-analytic insights into life extension via dietary restriction. *Aging Cell* **11**: 401–409.
- Newton, I. 1989 *Lifetime reproductive success in birds*. Academic, San Diego.
- Nussey, D.H., Kruuk, L.E.B., Morris, A. & Clutton-Brock, T.H. 2007. Environmental conditions in early life influence ageing rates in a wild population of red deer. *Curr. Biol.* **17**: R1000–R1001.
- Nussey, D.H., Coulson, T., Delorme, D., Clutton-Brock, T.H., Pemberton, J.M., Festa-Bianchet, M. *et al.* 2011. Patterns of body mass senescence and selective disappearance differ among three species of free-living ungulates. *Ecology* **92**: 1936–1947.
- Nussey, D.H., Froy, H., Lemaitre, J.F., Gaillard, J.M. & Austad, S.N. 2013. Senescence in natural populations of animals: widespread evidence and its implications for bio-gerontology. *Ageing Res. Rev.* **12**: 214–225.
- Orell, M. & Belda, E.J. 2002. Delayed cost of reproduction and senescence in the willow tit *Parus montanus*. *J. Anim. Ecol.* **71**: 55–64.
- Péron, G., Gimenez, O., Charmantier, A., Gaillard, J.M. & Crochet, P.A. 2010. Age at the onset of senescence in birds and mammals is predicted by early-life performance. *Proc. R. Soc. Lond. B* **277**: 2849–2856.
- Pettay, J.E., Kruuk, L.E.B., Jokela, J. & Lummaa, V. 2005. Heritability and genetic constraints of life-history trait evolution in preindustrial humans. *Proc. Natl. Acad. Sci. USA* **102**: 2838–2843.
- Promislow, D. 2003. Mate choice, sexual conflict, and evolution of senescence. *Behav. Genet.* **33**: 191–201.
- R Development Core Team 2011. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reed, T.E., Kruuk, L.E.B., Wanless, S., Frederiksen, M., Cunningham, E.J.A. & Harris, M.P. 2008. Reproductive senescence in a long-lived seabird: rates of decline in late-life performance are associated with varying costs of early reproduction. *Am. Nat.* **171**: E89–E101.
- Reid, J.M., Bignal, E.M., Bignal, S., McCracken, D.I. & Monaghan, P. 2003. Age specific reproductive performance in red billed choughs *Pyrrhonorax pyrrhonorax*: patterns and processes in a natural population. *J. Anim. Ecol.* **72**: 765–776.
- Reznick, D.N., Bryant, M.J., Roff, D., Ghalambor, C.K. & Ghalambor, D.E. 2004. Effect of extrinsic mortality on the evolution of senescence in guppies. *Nature* **431**: 1095–1099.
- Richardson, D.S., Jury, F.L., Blaakmeer, K., Komdeur, J. & Burke, T. 2001. Parentage assignment and extra group paternity in a cooperative breeder: the Seychelles warbler (*Acrocephalus sechellensis*). *Mol. Ecol.* **10**: 2263–2273.
- Richardson, D.S., Burke, T. & Komdeur, J. 2002. Direct benefits and the evolution of female biased cooperative breeding in Seychelles warblers. *Evolution* **56**: 2313–2321.
- Richardson, D.S., Komdeur, J. & Burke, T. 2003. Altruism and infidelity among warblers. *Nature* **422**: 580.
- Richardson, D.S., Bristol, R. & Shah, N.J. 2006. Translocation of the Seychelles warbler *Acrocephalus sechellensis* to establish a new population on Denis Island, Seychelles. *Conserv. Evid.* **3**: 54–57.
- Richardson, D.S., Burke, T. & Komdeur, J. 2007. Grandparent helpers: the adaptive significance of older, postdominant helpers in the Seychelles warbler. *Evolution* **61**: 2790–2800.
- Ricklefs, R.E. 1998. Evolutionary theories of aging: confirmation of a fundamental prediction, with implications for the genetic basis and evolution of life span. *Am. Nat.* **152**: 24–44.
- Ricklefs, R.E. 2008. The evolution of senescence from a comparative perspective. *Funct. Ecol.* **22**: 379–392.
- Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford University Press, New York.
- Therneau, T.M. 2011. *A Package for Survival Analysis in S*. <http://CRAN.R-project.org/package=survival>.
- Weindruch, R. & Walford, R.L. 1982. Dietary restriction in mice beginning at one year of age: effect on life-span and spontaneous cancer incidence. *Science* **215**: 1415–1418.
- Williams, G.C. 1957. Pleiotropy, natural selection, and the evolution of senescence. *Evolution* **11**: 398–411.

Received 16 February 2013; revised 17 May 2013; accepted 21 May 2013