Individual variation in rates of senescence: natal origin effects and disposable soma in a wild bird population

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Summary

1. Longitudinal studies of various vertebrate populations have recently demonstrated senescent declines in reproductive performance and/or survival probability with age to be almost ubiquitous in nature. Little is known, however, about the extent to which rates of senescence vary between individuals, and about causes or consequences of such variation. Quantifying these links in natural populations is important for understanding the constraints and adaptive processes underlying the evolution of senescence.

2. Here, we analyse breeding data from 1029 female great tits Parus major to quantify the effect of natal conditions and early life reproduction on rates of reproductive senescence, reproductive life span and lifetime reproductive success.

3. Although for locally born females we find no evidence that natal conditions influence rates of reproductive senescence, we show that immigrant females suffer from faster rates of senescence than locally born females, and that this difference contributes to immigrants having a lower lifetime reproductive success.

4. Additionally, and independently, we find rates of reproductive senescence to increase with rates of early life reproduction, as predicted by the disposable soma hypothesis. Despite accelerated senescence late in life, high early life reproduction is, however, positively associated with lifetime reproductive success across individuals.

5. Female immigrant status and early life reproduction do not relate to reproductive life span.

6. We thus show that both immigration into our population, and high levels of early life reproduction, are associated with reduced late life reproductive performance in female great tits, but that fitness can be increased by high levels of early life reproduction at the expense of accelerated reproductive senescence. These results suggest disposable soma to be a likely mechanism underlying senescence in these birds, and encourage further study of the genetic basis (i.e. antagonistic pleiotropy) of such an early vs. late life trade-off.

Key-words: ageing, cost of reproduction, disposable soma, great tit, immigrant status, life-history, Parus major, senescence, trade-off

Introduction

Senescent declines in reproductive performance and survival probability with age are increasingly recognized to be an important part of the life history of individuals of many species (Jones et al. 2008; Nussey et al. 2008a). Mechanistically, such age-specific fitness declines are thought to result from the progressive loss of somatic functioning, in turn caused by the accumulation of unrepairable damage from metabolism over time (Harman 1956; Finkel & Holbrook 2000). From an evolutionary perspective, processes leading to the loss of somatic function are thought to be able to evolve because successful life histories require resources to be allocated from maintenance and repair to growth and reproduction (the disposable soma hypothesis of senescence; Kirkwood 1977). If so, rates of senescence are expected to vary with factors influencing the ability to prevent or repair somatic damage, such as natal conditions (Metcalfe & Monaghan 2003; Monaghan et al. 2008) or the investment in early life reproductive activity (Kirkwood & Rose 1991).

The conditions under which individuals are reared vary because of parental decisions and quality, and as a result of differences in the natal environment. That variation in natal conditions can have fitness consequences is well known, a
classical example being the trade-off between number and quality of offspring (Stearns 1992). Offspring born in large broods generally suffer from increased mortality before reaching independence (e.g. Tinbergen & Boerlijst 1990; Pettifor, Perrins & McCleery 2001; Koivula et al. 2003), and this short-term effect on mortality can be compounded by long-term effects such as reduced reproductive performance or impaired survival after the age of first reproduction (Gustafsson & Sutherland 1988; de Kogel 1997). Additionally, natal brood size has been shown to affect physiological factors that may reflect the capacity for long-term somatic maintenance, including metabolic rate (Verhulst, Holveck & Riebel 2006) and resistance to oxidative stress (Alonso-Alvarez et al. 2006). These findings are consistent with predictions of the disposable soma hypothesis of senescence, although whether offspring reared in large broods suffer from increased rates of senescence is presently an unexplored facet of the trade-off between number and quality of offspring.

Similarly, whereas long-term fitness effects of various other natal conditions, such as maternal age, birth date, environmental quality or natal density, have received considerable empirical attention (e.g. Visser & Verboven 1999; Roulin 2002; Cam, Monnat & Hines 2003; Reid et al. 2003; van de Pol et al. 2006; Oksanen et al. 2007; Descamps et al. 2008b; Hamel et al. 2009; Wilkin & Sheldon 2009; Bouwhuis et al. 2010), we are aware of only two studies that have tested for associations between natal conditions and rates of senescence in wild populations. In female red deer Cervus elaphus, age-specific reproduction and survival show significant associations with natal breeding density, such that females born in high density years suffer from increased rates of senescence (Nussey et al. 2007). In red squirrels Tamiasciurus hudsonicus, cohort effects associated with food abundance were found to relate to age-specific declines in female litter size, although they were unrelated to age trajectories of other reproductive traits, or survival (Descamps et al. 2008a). The generality of cohort effects through natal density or food availability, and the question of whether rates of senescence are also associated with maternal or other cohort effects, therefore remain important areas of research (also see Wilkin & Sheldon 2009).

Besides being influenced by natal conditions, life histories can also be shaped by the trade-off between current and future reproduction (Stearns 1992). Short-term costs of reproduction, such as impaired parental survival to, or reproductive output at, the next breeding attempt are thought to be ubiquitous (reviewed by Dijkstra et al. 1990; Koivula et al. 2003). Additional long-term effects may appear if costs of reproduction accumulate (Moyes et al. 2006), or have delayed fitness consequences (McCleery et al. 1996; Orell & Belda 2002). Moreover, long-term effects may not only appear in the level of late life performance, but also in its rate of change. Correlative support for this prediction comes from natural populations of long-lived red deer (Nussey et al. 2006) and common guillemots Uria aalge (Reed et al. 2008), where the rate (or timing) of senescence is higher (or advanced) for individuals with high reproductive output early in life. Similar analyses for short-lived species are currently lacking, and information on additional costs of reproduction through adverse early life environmental conditions (Reed et al. 2008) is scarce.

Here, we present what is to our knowledge the first study of the effect of both natal conditions and early life reproduction on rates of senescence in a natural population of a short-lived income breeder, the great tit Parus major. We focus on female reproductive senescence, recently shown to occur in our population (Bouwhuis et al. 2009), and test the age-specific effects of individual and environmental parameters on two reproductive fitness measures: the number of fledglings and number of recruits produced. Moreover, we quantify the fitness consequences of the effects we find, in terms of lifetime reproductive success, and calculate selection differentials in view of predicting the potential for evolution of senescence rates.

Materials and methods

STUDY POPULATION AND DATA COLLECTION

This study is part of a long-term study of a nest box breeding population of great tits in the c. 380 ha mixed deciduous woodland of Wytham Woods, Oxfordshire, UK. The first nest boxes were put up in 1947, and their numbers have been kept constant at 1020 from 1960 onwards. Every breeding season, all nest boxes are checked weekly to ascertain laying date, clutch size (i.e. number of eggs laid), hatching date, brood size (i.e. number of chicks hatched) and number of fledglings. Chicks are ringed with individually numbered metal rings at 15 days of age. Parents are trapped at the nest whilst feeding their chicks, and identified by their ring number, or ringed if they are newly immigrated birds. Parental age is based on known birth year for locally born birds (recruits), or inferred birth year based on plumage moult contrasts (relative colour of the primary coverts; Svensson 1984) at first catching for immigrants. Immigration rates are high (47%; McCleery et al. 2004), but as most immigrants enter the population as yearlings, exact age is known for 91% of birds. Immigrants first caught with adult plumage are assigned a minimal age of 2. Birds that are not found breeding for two consecutive years are assumed to have died and their age at last reproduction (ALR) is taken as an approximation for their reproductive life span (also see Bouwhuis et al. 2009).

DATA SELECTION

Previous analyses of reproductive senescence in our population (Bouwhuis et al. 2009) focused on first broods by females of known reproductive life span only, as Wytham great tits rarely produce a second brood within years (0-2% of all breeding attempts), data on male reproductive performance are less complete and confounded by extra pair paternity, and reproductive life span is an important factor to separate within-individual from between-individual effects when analysing longitudinal data (van de Pol & Verhulst 2006). Breeding attempts which were subject to experimental manipulation were included for assessment of ALR, but excluded from analyses of reproductive performance, whilst assuming no carry-over effects to the next breeding season (see Doligez et al. 2002). Here, we used the same data selection criteria, but furthermore selected only breeding attempts at ages 3–9, which resulted in a data set of 1505 breeding attempts by 1029 females. As, on average, reproductive senescence starts at the age of 3 in our population (and thereby affects on aver-
age 20% of breeding females each year; see Table S1 and Bouwhuis et al. 2009), using only breeding attempts between the age of 3 and 9 allowed us to model rates of reproductive senescence specifically, unconfounded statistically by performance changes early in life.

As fitness measures, we used the number of young from a breeding attempt that fledged and the number that recruited into (i.e. subsequently bred in) the breeding population. The number of fledglings was calculated as the difference between the number of offspring ringed at 15 days of age and the number of offspring found dead in the nest box after fledging at around 20 days of age. The number of recruits captures local survival of these fledglings, and reflects female fitness if emigration of chicks is independent of maternal age (suggested by the absence of a relationship between female age and offspring dispersal distance; Bouwhuis et al. 2009).

**Statistical Analyses**

**Natal conditions**

We analysed the effect of natal condition parameters on female fledgling and recruit production using a mixed-effects model approach on longitudinal data (Nussey et al. 2008a), following the senescence models reported in Bouwhuis et al. (2009). In short, these models included fixed effects of female age, female ALR, year quality estimated as the population-level average fledgling number and local breeding density in breeding pairs per hectare. Cross-classified random effects included female identity, year and sector of the wood to account for repeated, non-independent observations on the same bird and spatiotemporal environmental heterogeneity, respectively. To these models, we added six natal condition parameters, measured for locally born females only: (i) *hatching date*: female’s date of birth; Z-transformed by subtracting the annual population average hatch date and dividing by the year-specific SD (e.g. Visser & Verboven 1999); (ii) *sibling number*: number of siblings among which a female was reared, Z-transformed by subtracting the annual population mean and dividing by the year-specific SD (e.g. Gustafsson & Sutherland 1988); (iii) *maternal age*: age of a female’s mother when she was born (Bouwhuis et al. 2010); (iv) *natal year quality*: quality of the year in which a female was born, defined as the average fledgling production (Szulkin & Sheldon 2007); (v) *natal density*: breeding density in the area in which a female was born in breeding pairs per hectare (Wilkin et al. 2006); and (vi) *natal beech mast*: two-level class variable describing the amount of beech mast crop available for a female as food in the winter after breeding at ages 1 and 2 (twice little or once little and once much; the periodicity of large beech mast crops during our study period was on average 3-4 years, with a range of 2-6 years).

Of the 1029 females with breeding attempts between ages 3 and 9, 559 (54%) were initially omitted from our data set, such that minimal adequate models were run on 709 breeding attempts by 470 females. Of these 559 omitted females, 163 (29%) were excluded because information on their hatching date (N = 8), sibling number (N = 1) or maternal age (N = 48) was missing. Both minimal adequate models were therefore run on 702 breeding attempts by 488 locally born females.

One final natal condition, which could not be included in the models described before, but is known to affect reproductive traits in various bird species (e.g. Newton & Marquiss 1983; Part 1990; Julliard, Perret & Blondel 1996), including the great tits in our study population (McCleery & Clobert 1990), is female immigrant status, that is, immigrant vs. locally born. Wytham is a continuous block of woodland surrounded by farmland, which is unsuitable as breeding habitat for great tits. Hence, assuming that all locally born offspring are reared as nestlings, immigrants represent a class of birds that have moved between habitat patches. We analysed the effect of immigrant status on fledgling and recruit production by adding immigrant status and its interaction with female age as fixed effects to the basic senescence models described before. As immigrant status was known for all females, the models were run on 1504 breeding attempts by 1029 females. However, as for 13.8% of immigrants in our data set we had to assume a minimal age of 2 at first capture, we repeated the analyses excluding these birds to ensure that that our results were not driven by underestimating the age of immigrants. Here, the models were run on 1304 breeding attempts by 887 females of exactly known age.

**Early life reproduction**

The effects of early life reproduction on female age-specific fledgling and recruit production were analysed in models similar to the ones described before, but with the natal condition parameters replaced by the following four early life reproduction parameters: (i) *fledging production*: sum of the numbers of fledglings (Z-transformed by subtracting the annual population mean and dividing by the year-specific SD) produced at ages 1 and 2; (ii) *early year quality*: sum of the overall year quality at ages 1 and 2; (iii) *early density*: sum of the density in the areas of breeding at ages 1 and 2; and (iv) *early beech mast*: two-level class variable describing the amount of beech mast crop available as food in the winter after breeding at ages 1 and 2 (twice little or once little and once much; the periodicity of large beech mast crops during our study period was on average 3-4 years, with a range of 2-6 years).

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Table 1. Results from models testing the effects of selected natal condition parameters on rates of late life age-specific change in number of fledglings and number of recruits per female per year (702 breeding attempts by 488 locally born females) for great tits. Estimates for random effects are marked by (r). Shown are parameter estimates with standard errors and significance (*P < 0.05, **P < 0.01, ***P < 0.001). Values for significant terms are in bold, and values for non-significant terms are presented as estimated when re-added to the minimal adequate model.
Table 2. Results from models testing the effect of immigrant status on rates of late life age-specific change in number of fledglings and number of recruits per female per year (1504 breeding attempts by 1029 females). Estimates for random effects are marked by r. Shown are parameter estimates with standard errors and significance (*P < 0.05, **P < 0.01, ***P < 0.001). Values for significant terms are in bold, and values for non-significant terms are presented as estimated when re-added to the minimal adequate model.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>No. of fledglings</th>
<th>No. of recruits</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimated SE</td>
<td>χ² (d.f. = 1)</td>
</tr>
<tr>
<td>Year quality</td>
<td>0.94 ±0.07</td>
<td>184.39**</td>
</tr>
<tr>
<td>Local density</td>
<td>−0.31 ±0.15</td>
<td>4.24*</td>
</tr>
<tr>
<td>Age</td>
<td>−0.57 ±0.11</td>
<td>25.44**</td>
</tr>
<tr>
<td>Age at last reproduction</td>
<td>0.24 ±0.08</td>
<td>9.22**</td>
</tr>
<tr>
<td>Status</td>
<td>1.43 ±0.54</td>
<td>7.05**</td>
</tr>
<tr>
<td>Status × age</td>
<td>0.44 ±0.15</td>
<td>8.86**</td>
</tr>
<tr>
<td>Female (r)</td>
<td>1.70 ±0.38</td>
<td>–</td>
</tr>
<tr>
<td>Year (r)</td>
<td>0.02 ±0.03</td>
<td>–</td>
</tr>
<tr>
<td>Area (r)</td>
<td>5.58 ±0.37</td>
<td>–</td>
</tr>
</tbody>
</table>

χ²₁ = 7.18, P = 0.01 for the number of fledglings, and 0.08 ± 0.08, χ²₁ = 0.88, P = 0.35 for the number of recruits, showing that the female immigrant status effect is not driven by the 13.8% of immigrants that are assumed to be of age 2 at first capture.

**EARLY LIFE REPRODUCTION**

Of the four parameters we used to characterize early life reproduction – fledgling production, early year quality, early density and beech mast – only fledgling production interacted with female age to explain variation in rates of senescence in females with complete life histories (Table 3). The negative interaction was significant for fledgling production, showing that high levels of early life reproduction are associated with increased rates of reproductive senescence (Fig. 2a, black lines). A broadly similar interaction was found for recruit production (Fig. 2b, black lines), but failed to reach statistical significance, such that only a significantly positive main effect of early life fledgling production remained. As well as no interaction effects with age, there were no main effects of environmental conditions during early life reproduction on late life performance (Fig. S2).

Adding 559 females with experimental or missing breeding attempts in early life to the data set by assuming missing attempts to have resulted in no fledglings, and re-running the minimal adequate models described in Table 3, we found no evidence for an early life fledgling production × age interaction for the number of fledglings (fledgling production × age: −0.03 ± 0.04, χ²₁ = 0.77, P = 0.38) or the number of recruits (fledgling production × age: −0.01 ± 0.02, χ²₁ = 0.57, P = 0.45) produced. For the number of fledglings produced, a three-way interaction between female group (complete life history, missing breeding attempts, experimental breeding attempts), early life fledgling production and age, however, proved significant (group × fledgling production × age: χ²₂ = 10.24, P = 0.01). This revealed that high levels of early life reproduction are associated with increased rates of reproductive senescence in females with complete or manipulated life histories, but not in females with missing breeding attempts in early life (Fig. 2a). For the number of recruits produced, the interaction was statistically insignificant (group × fledgling production × age: χ²₂ = 1.49, P = 0.48; Fig. 2b).

The effect of early life fledgling production on rates of reproductive senescence could, in theory, be linked to the female immigrant status effect found to be associated with late life performance. Within the restricted data set, we therefore tested whether Z-transformed early life fledgling production differed between immigrant and locally born females,
Table 3. Results from models testing the effects of selected early life (EL) reproduction parameters on rates of late life age-specific change in number of fledglings and number of recruits per female per year (709 breeding attempts by 470 females). Estimates for random effects are marked by (r). Shown are parameter estimates with standard errors and significance (*P < 0.05, **P < 0.01, ***P < 0.001). Values for significant terms are in bold, and values for insignificant terms are presented as estimated when re-added to the minimal adequate model

<table>
<thead>
<tr>
<th>Parameter</th>
<th>No. of fledglings</th>
<th>No. of recruits</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimated</td>
<td>SE</td>
</tr>
<tr>
<td>Year quality</td>
<td>0.98</td>
<td>0.10</td>
</tr>
<tr>
<td>Local density</td>
<td>−0.38</td>
<td>0.22</td>
</tr>
<tr>
<td>Age</td>
<td>−0.32</td>
<td>0.14</td>
</tr>
<tr>
<td>Age at last reproduction</td>
<td>0.25</td>
<td>0.12</td>
</tr>
<tr>
<td>EL fledglings</td>
<td>1.00</td>
<td>0.29</td>
</tr>
<tr>
<td>EL fledglings × age</td>
<td>−0.18</td>
<td>0.08</td>
</tr>
<tr>
<td>EL year quality × age</td>
<td>−0.15</td>
<td>0.28</td>
</tr>
<tr>
<td>EL year quality × age × age</td>
<td>0.01</td>
<td>0.08</td>
</tr>
<tr>
<td>EL density</td>
<td>0.15</td>
<td>0.49</td>
</tr>
<tr>
<td>EL density × age</td>
<td>0.02</td>
<td>0.13</td>
</tr>
<tr>
<td>EL beech crop × age</td>
<td>−0.53</td>
<td>0.85</td>
</tr>
<tr>
<td>Female (r)</td>
<td>1.38</td>
<td>0.53</td>
</tr>
<tr>
<td>Year (r)</td>
<td>0.04</td>
<td>0.05</td>
</tr>
<tr>
<td>Area (r)</td>
<td>5.14</td>
<td>0.54</td>
</tr>
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</table>

Fig. 2. Rates of age-specific change in number of fledglings (a) and number of recruits (b) produced per female per year in relation to levels of standardized early life reproductive output in females with complete early life histories (black lines), females with experimental manipulations in early life (dark grey lines) and females with missing breeding attempts in early life (light grey lines). Lines are fitted curves calculated from models including a female group × early life fledgling production × age interaction, and represent great tits which produced the average standardized early life output above (dotted lines) or below (solid lines) the median value.

but found no evidence that this was the case (average ± SD: immigrants: 0.12 ± 1.52, locally born birds: −0.03 ± 1.47, χ²₁ = 1.11, P = 0.292, N = 470). Similarly, Z-transformed early life recruit production was not significantly higher in locally born birds compared with immigrants (average ± SD: immigrants: 0.16 ± 1.52, locally born birds: 0.25 ± 1.51, χ²₁ = 0.48, P = 0.49, N = 470).

REPRODUCTIVE LIFE SPAN AND LIFETIME REPRODUCTIVE SUCCESS

Female immigrant status had no effect on reproductive life span measured as ALR (average ± SD: immigrants: 3.80 ± 1.05, locally born birds: 3.74 ± 0.94, χ²₁ = 0.26, P = 0.61, N = 1029), but lifetime reproductive success differed between immigrants and locally born birds, such that locally born birds, which senesce more slowly, have a 15% higher LRS (average ± SD: immigrants: 1.92 ± 1.89, locally born birds: 2.27 ± 2.07, χ²₁ = 15.25, P < 0.001, N = 1029; Fig. 3a). This effect is at least partly because of lower production of offspring by immigrants, as an additional analysis showed that immigrants produce 6% fewer fledglings over their lifetime (average ± SD: immigrants: 18.27 ± 9.40, locally born birds: 19.49 ± 9.76, χ²₁ = 4.14, P = 0.041, N = 1029), and that both lifetime fledgling production (0.05 ± 0.00, χ²₁ = 665.05, P < 0.001) and immigrant status (0.10 ± 0.04, χ²₁ = 5.09, P = 0.024) explained variation in LRS.

Female early life fledgling production also had no effect on ALR (fledgling production: 0.00 ± 0.02, χ²₁ = 0.02,
Our results show that female great tits immigrating into Wytham Woods achieve similar reproductive output as locally born females in the first two years of life, but subsequently suffer from elevated rates of reproductive senescence. As local knowledge is expected to increase with breeding experience and age, such a pattern seems unlikely to result from late expressed differences in local adaptation. Increased costs of reproduction for the same level of early life reproductive output, perhaps because of poorer initial local knowledge, seems a more likely candidate mechanism underlying this observation. Alternatively, as some of these birds are known to originate from low-quality areas surrounding Wytham Woods (Riddington & Gosler 1995; Verhulst, Perrins & Riddington 1997), immigrants might suffer from long-term effects of natal conditions that were not captured in our measures of natal conditions for locally born females. Finally, immigrants could have come from areas in which rates of senescence have evolved to be higher, for example, because of higher levels of extrinsic mortality (Medawar 1952; Williams 1957). However, genetic differentiation to this extent seems implausible (especially because of the high level of immigration reported in this study), and at present too little is known about the genetic basis of senescence in passerines (Brommer, Wilson & Gustafsson 2007), or about variation in rates of senescence between populations of the same species (Reznick et al. 2004), to evaluate the likelihood of this option.

As well as accelerated reproductive senescence, immigrants also show a reduction in lifetime reproductive success of 15% in our sample of birds (Fig. 3a; also see McCleery & Clobert 1990). In contrast to the situation in a Dutch population of great tits (Verhulst & van Eck 1996), this difference cannot be attributed to a shorter reproductive life span of immigrants, as previous analyses in this population have shown similar survival rates for immigrant and locally born females (0.41 and 0.40, respectively; Clobert et al. 1988), and we also found no difference in average ALR between them in this study. Recapture probability of immigrants in our population is, however, lower than that of locally born birds (0.77 and 0.84, respectively; Clobert et al. 1988), and indeed an analysis of the number of missing breeding attempts over all ages in the 1029 females reveals this number to be higher for immigrants than locally born birds (average: immigrants: 0.31, locally born birds: 0.27, χ² = 6.37, P = 0.011). Missing breeding attempts include failed attempts (6% of all attempts), successful attempts within the study area for which the female was not caught (4% of all attempts), skipped attempts and perhaps breeding attempts in natural cavities or outside the study area, although the frequency of these last two is thought to be low (Harvey, Greenwood & Perrins 1979; Perrins 1979). As the extent to which each type of breeding attempt contributes to the number of missing attempts in relation to female immigrant status, and therefore the extent to which they might bias our estimates of LRS, is presently unknown, we should be cautious in interpreting the difference. But, assuming a difference in LRS exists, our findings of accelerated reproductive senescence
and lower lifetime fledgling production in immigrants suggest it to be at least partly because of reduced reproductive performance. The remaining status effect could originate from both reduced survival of fledglings of immigrant females, and a higher probability for offspring of immigrant females to leave the study area if natal dispersal is heritable (Doligez & Partre 2008).

Besides female immigrant status (which could be regarded as an indirect natal effect), we found no evidence that direct effects of natal environmental conditions (density, year quality, beech mast crop), or natal brood characteristics (maternal age, hatching date, sibling number) were associated with rates of reproductive senescence within Wytham-born females. This result supplements recent analyses of other life-history traits in locally born females in this population, which also showed that natal environmental variation has at most very weak effects on post-recruitment fitness components in females (Wilkin & Sheldon 2009). These findings contrast with previous studies of senescence in populations of red deer and red squirrels, which reported associations between natal density (Nussey et al. 2007) and food abundance (Descamps et al. 2008a) and rates of reproductive senescence, respectively. With respect to natal density, the absence of a relationship with rates of senescence in our population might perhaps be explained by birds escaping resource competition effects by dispersal or emigration; no such behavioural response was possible for the red deer born on the Isle of Rum. Indeed, local recruitment is known to be inversely related to natal density in Wytham (Wilkin et al. 2006), although it is unknown whether emigration or mortality underlies this pattern. But if natal density drives emigration, late acting costs of natal density in terms of accelerated reproductive senescence may be apparent only in immigrants, as found here. Studies in which fledglings are followed until recruitment over larger spatial scales are required to test this hypothesis.

With respect to food abundance in the year of fledging, we found no effect on rates of reproductive senescence, but we did find a positive correlation with average late life reproductive performance. Beech mast crop has previously been shown to be important for subsequent reproductive success of female great tits in adult life (Verhulst 1998), and the long-term effect reported here raises the question of the proximate mechanism by which high quantities of beech mast in the first winter of life affect female reproductive output in the long run. As with beech mast crop, sibling number did not relate to rates of reproductive senescence, but correlated positively with average late life reproductive performance. This is in contrast to experimental evidence for a negative effect of natal brood size on offspring future reproduction in collared flycatchers Ficedula albicollis (Gustafsson & Sutherland 1988), and perhaps suggests positive effects because of the heritability of clutch size (McCleery et al. 2004) to outweigh negative effects of being reared in a larger brood; experiments are probably needed to disentangle these effects.

Previous analyses of maternal age on offspring age-specific reproductive performance in our population showed that offspring born from older mothers perform better early in life, but suffer from an earlier onset, and stronger rate, of reproductive senescence later in life (Bouwhuis et al. 2010). A negative interaction between maternal age and female age to explain late life fledgling and recruit production was therefore expected. Parameter estimates for these interactions were indeed negative, but failed to reach statistical significance (Table 1 and Fig. S1e,f). Apparently, the effect of maternal age on their daughter’s life-history trajectory works over the entire age range, and is not just driven by the senescent phase of life.

EARLY LIFE REPRODUCTION

In addition to an effect of female immigrant status, we found individual rates of reproductive senescence to be associated with early life fledgling production. Birds with high early life reproductive performance maintained a high level at the start of the senescent phase, but then suffered from accelerated deterioration, whereas birds with low early life reproductive performance showed a less pronounced senescent decline from their lower starting point. Such a late life cost of reproduction, not in the level of late life performance but in its rate of change, and apparent only in a subset of individuals, may explain why a previous study of the cost of reproduction in our population failed to find one (Doligez et al. 2002). It, however, supplements an earlier finding of a delayed survival cost of reproduction in the female great tits in our study area (McCleery et al. 1996). In addition, the pattern found here matches recent findings in long-lived red deer (Nussey et al. 2006) and common guillemots (Reed et al. 2008), and supports the assumption of the disposable soma hypothesis of senescence of a trade-off between early life and late life performance (Kirkwood & Rose 1991). Furthermore, our results support the idea that a disposable soma mechanism can promote the evolution of senescence, as birds adopting a strategy of high early life reproductive performance and high rates of reproductive senescence enjoyed the highest lifetime reproductive success. In fact, a selection analysis revealed strong positive directional selection on early life fledgling production, such that an evolutionary response towards higher levels of early life reproduction and stronger rates of senescence is expected if the trade-off between early life and late life reproduction has a genetic basis and is unconstrained by other genetic correlations. Quantitative genetic analyses of age-specific reproduction (e.g. Charmantier et al. 2006a,b; Brommer, Wilson & Gustafsson 2007; Wilson et al. 2007; Nussey et al. 2008b; Wilson, Charmantier & Hadfield 2008) are required to address this issue.

Note that the previous discussion is based on a subset of females in our data set for which we had complete early life histories. This subset only included about half of the entire set of females reaching a minimum age of 3, the other half of which was subject to experiments in early life, or had missing breeding attempts. Adding these females to the data set, assuming missing attempts to have resulted in no fledglings, showed that, encouragingly, females who had undergone

experimental manipulation in early life showed a qualitatively similar trade-off between early life and late life reproduction as females with complete life histories. This was not the case for females with missing breeding attempts in early life. Because, as mentioned before, missing breeding attempts can be the result of a heterogeneous set of causes, it is difficult at present to interpret the discrepancy. Earlier identification of breeding females, as well as improved opportunities to track individuals over time are required to investigate this, but given the life history differences among these groups this is generally advisable. Indeed, greater attention to the problem of missing data seems advisable for a wide range of studies that estimate fitness and selection in wild populations (also see Nakagawa & Freckleton 2008).

Finally, we found no associations between environmental conditions during early life reproduction and rates of late life performance declines. Surprisingly, such effects were found in a long-lived seabird, the common guillemot (Reed et al. 2008), even though long-lived organisms might be expected to adjust reproductive effort to environmental conditions to a greater extent than shorter-lived ones, and therefore to suffer less repercussion of early life conditions (Williams 1966). Perhaps the magnitude of environmental variation was larger for common guillemots compared with great tits, or the damage done was of a different type. Study of physiological correlates of reproductive senescence and early life environmental conditions may shed light on this matter.

Conclusions
Our investigation of correlates of rates of reproductive senescence in a population of wild great tits revealed that few measures of the natal and early life reproductive environment explain variation in late life performance declines. For female great tits, only natal origin (i.e. immigrant status) and early life fledgling production were found to be related to senescence rates. Whereas accelerated senescence in immigrant females contributes to immigrants having lower lifetime reproductive success, increased rates of senescence related to high early life reproductive performance seem part of an adaptive disposable soma process optimizing lifetime reproductive success. Disposable soma could therefore underlie the evolution of senescence if trade-offs found on the phenotypic level also have a genetic basis, in the form of antagonistic pleiotropy (Williams 1957), a question we hope will soon receive more empirical research.

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References


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**Supporting Information**

Additional Supporting Information may be found in the online version of this article:

Table S1. Age-distribution (in %) of breeding female great tits between 1960 and 2006.

| Fig. S1. Rates of age-specific change in number of fledglings (a, c, e, g, i, k) and number of recruits (b, d, f, h, j, l) produced in relation to female hatching date (a, b), sibling number (c, d), maternal age (e, f), natal year quality (g, h), natal density (i, j) and natal beech mast crop (k, l). Lines are fitted curves calculated from significant terms re-added to the minimal adequate models. Solid lines represent high values (average + SD, or much beech mast), short dashed lines |

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represent low values (average – SD, or little beech mast) and long dashes represent the average condition, where it exists.

**Fig. S2.** Rates of age-specific change in number of fledglings (a, c, e) and number of recruits (b, d, f) produced in relation to early year quality (a, b), early density (c, d) and early beech mast crop (e, f). Lines are fitted curves calculated from insignificant terms re-added to the minimal adequate models. Solid lines represent high values (average + SD, or much beech mast), short dashed lines represent low values (average – SD, or little beech mast) and long dashes represent the average condition, where it exists.

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