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Sex-specific pathways of parental age effects on offspring lifetime reproductive success in a long-lived seabird

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The conditions under which individuals are reared vary and sensitivity of offspring to such variation is often sex-dependent. Parental age is one important natal condition with consequences for aspects of offspring fitness, but reports are mostly limited to short-term fitness consequences and do not take into account offspring sex. Here we used individual-based data from a large colony of a long-lived seabird, the common tern *Sterna hirundo*, to investigate longitudinal long-term fitness consequences of parental age in relation to both offspring and parental sex. We found that recruited daughters from older mothers suffered from reduced annual reproductive success. Recruited sons from older fathers were found to suffer from reduced life span. Both effects translated to reductions in offspring lifetime reproductive success. Besides revealing novel sex-specific pathways of transgenerational parental age effects on offspring fitness, which inspire studies of potential underlying mechanisms, our analyses show that reproductive senescence is only observed in the common tern when including transgenerational age effects. In general, our study shows that estimates of selective pressures underlying the evolution of senescence, as well as processes such as age-dependent mate choice and sex allocation, will depend on whether causal transgenerational effects exist and are taken into account.

KEY WORDS: Ageing, fitness, Lansing effect, life-history evolution, sexual dimorphism, transgenerational effects.

Parental effects occur when the phenotype of one or both parent(s) affects the phenotype of offspring beyond direct effects of genetic inheritance (e.g., Mousseau and Fox 1998). Parental effects can take many forms, such as epigenetic modification of genes in germ cells, transfer of hormones or immune factors to offspring, the extent of parental care or behavioral inheritance of novel traditions or behavior, and effects can be expressed both early and late in offspring ontogeny (Badyaev and Uller 2009). Such parental effects can influence the direction and rate of phenotypic and genetic change (Badyaev and Uller 2009; Bonduriansky and Day 2009; Jablonka and Raz 2009) and therefore have the ability to affect processes of population persistence and adaptation (e.g., Bonduriansky et al. 2012).

Parental age is one aspect of the parental phenotype known to have consequences for aspects of offspring phenotype and fitness.

Offspring from old parents, for example, have, on the short term, been found to be of reduced birth weight (e.g., Nussey et al. 2006; Hoffman et al. 2010) and/or to suffer from a reduced probability of survival (e.g., Bouwhuis et al. 2009; Hoffman et al. 2010; Schroeder et al. 2011). Such effects are believed to be manifestations of parental senescence, evolved because the strength of natural selection declines with age (Hamilton 1966), and caused by the accumulation of late-acting deleterious mutations over evolutionary time (Medawar 1952) and/or selection for pleiotropic alleles with beneficial effects early, but detrimental effects late in life (Williams 1957). Short-term effects of parental age on offspring phenotype and fitness can be supplemented with long-term effects. Indeed, on the long term, offspring from old parents have been found to have a reduced probability to recruit to the breeding population (Descamps et al. 2008; Bouwhuis et al. 2009,

2010b; Torres et al. 2011; but see Rödel et al. 2009), reduced annual (Schroeder et al. 2015) or altered age-specific (Bouwhuis et al. 2010aa) reproductive success, a reduced intrinsic rate of increase (Barks and Laird 2015), or a reduced life span (e.g., Priest et al. 2002; Carnes et al. 2012; Ducatez et al. 2012; but see Fox et al. 2003).

Parental effects may not affect each individual offspring equally. Evidence for the sexes to differ in their response to their rearing environment, for example, is plentiful (Jones et al. 2009; Wilkin and Sheldon 2009), and sex-specific epigenetic inheritance (e.g., if epigenetic modification of genes in germ cells occurs on Y- or W-linked alleles) may underlie such differences between the sexes (e.g., Hager et al. 2008; Vigé et al. 2008; Bonduriansky and Day 2009). So far, only a limited number of studies has reported on sex-specific effects of parental age, and all except one (Schroeder et al. 2015) of those studies have been performed in the lab, rather than in the wild, while findings obtained under artificial conditions may not easily be generalized to natural settings (e.g., Kawasaki et al. 2008). Maternal age was found to negatively affect daughters' annual reproductive performance, whereas paternal age negatively affected annual reproductive performance of sons, in-house sparrows (Schroeder et al. 2015). Similarly, paternal age was found to negatively affect the life span of sons in fruit flies (Priest et al. 2002), whereas maternal age was found to have the largest negative effect on the life span of daughters in both fruit flies and mice (Priest et al. 2002; Carnes et al. 2012). On the other hand, paternal age was found to negatively affect the life span of daughters, rather than sons, in humans (Gavrilov and Gavrilova 1997; Kemkes-Grottenthaler 2004), whereas maternal age was found to positively affect the life span of sons more strongly than that of daughters in seed beetles (Fox et al. 2003). Finally, maternal age was found to negatively affect life span of offspring in a second study on seed beetles, and the detrimental effect of maternal age declined with the mother's own life span in a sex-specific manner, such that the life span of male offspring was less affected by maternal age in long-lived mothers than that of female offspring (Lind et al. 2015).

This latter study used an elegant experimental design to show that parental effects on offspring do not only depend on parental age, but on parental life span as well, because the biological age of parents may differ at a given chronological age (Lind et al. 2015). Studies of parental age effects on offspring, as studies of ageing and senescence in general (Nussey et al. 2008), therefore benefit from adopting a longitudinal approach and separating within- and between-parental age effects. A simple statistical method to do so in a nonexperimental setting is referred to as within-subject centering (van de Pol and Wright 2009). This method involves subtracting an individual's mean trait value from each of its observed values, such that, in the case of parental age and offspring performance, the mean age values capture between-parental

effects of selective (dis)appearance on offspring performance, while within-individual parental age deviations capture the plastic offspring performance responses to parental age. Although this approach is increasingly used in studies of ageing and senescence (e.g., Bouwuis and Vedder in press), it was not adopted in the studies of sex-specific parental age effects mentioned above.

Besides studies of parental age effects on offspring generally either not investigating sex-specific effects, or not adopting a longitudinal analysis approach, the full fitness consequences of parental age effects have also relatively rarely been reported. We are aware of five studies investigating parental age effects on a complete measure of offspring fitness. The first, on European rabbits, reported that lifetime reproductive success (LRS) of daughters peaked at a maternal age of 2–3 years, before declining (Rödel et al. 2009). The second, on great tits, found that while daughters' life-history trajectories varied with maternal age, these different trajectories resulted in a similar LRS (Bouwuis et al. 2010aa). In preindustrial humans, offspring LRS showed a linear decline of 18% between the maternal ages of 21 and 43 years (Gillespie et al. 2013). Offspring LRS, as well as intrinsic rate of increase, declined curvilinearly with parental age in asexually reproducing duckweed (Barks and Laird 2015). Finally, LRS linearly declined with maternal age in female song sparrows and with paternal age in male song sparrows (Schroeder et al. 2015).

In cases where long-term parental age effects are transmitted across generations (i.e., are transgenerational), knowledge of the full fitness consequences of parental age is required if we are to understand potential effects on population dynamics and on, for example, processes underlying the evolution of ageing. As recently pointed out (Barks and Laird 2015), classical theories for the evolution of senescence implicitly assume offspring fitness to be independent of parental age (e.g., Hamilton 1966). If this is not the case, then estimates of age-specific selection pressures can be over- or underestimated, depending on whether offspring quality improves or declines with parental age, respectively, (Barks and Laird 2015), although care must be taken when assigning measures of offspring fitness to parents in evolutionary models (Wolf and Wade 2001). In cases of sex-specific effects, the potential evolutionary implications are even wider, because the optimality of life-history strategies will additionally depend on processes of age-assortative mating and adaptive sex allocation (Trivers and Willard 1973; Uller 2006). Understanding the nature and level of occurrence of long-term transgenerational effects is therefore important for understanding a wide range of evolutionary processes.

Here, we used longitudinal individual-based data from a large colony of a long-lived seabird, the common tern *Sterna hirundo*, to investigate sex-specific effects of parental age on offspring fitness. The common terns from this colony are ideal for our purpose,

because the numerous locally hatched (and therefore known-aged) birds are individually marked with rings and transponders, sexed prior to fledging and recruit with a high probability, after which they are highly philopatric, so that they can be followed throughout life using an automatic detection system that allows extremely accurate determination of individual presence and breeding status (Szostek and Becker 2012). Various performance measures of common terns in the study colony are known to be age-dependent (Ezard et al. 2007; Becker et al. 2008; Limmer and Becker 2009, 2010; Rebke et al. 2010; Zhang et al. 2015a; Zhang et al. 2015), and recent findings suggest that parental age effects differ for male and female offspring early in the offspring's development (Vedder et al. unpubl. ms). In this study, we built on these results and (1) quantified male and female offspring LRS as the lifetime number of fledglings produced and related it to parental age, (2) investigated male and female offspring life span and age-specific fledgling production in relation to parental age to investigate the origin of parental age effects on offspring fitness, and (3) separated parental age effects into between- and within-parental components. In doing so, we uniquely investigated sex-specific longitudinal transgenerational age effects on offspring fitness in the wild and revealed novel sex-specific pathways of parental age effects.

MATERIAL AND METHODS

Study population

The common tern is a Nearctic and Palearctic colonial breeding and migratory seabird (Becker and Ludwigs 2004). The data we present here come from a long-term study population located in the Banter See at Wilhelmshaven on the German North Sea coast (53°36'N, 08°06'E), where the presence and reproductive performance of individual common terns has been monitored following standard protocol since 1992. In 1992, 101 adult birds were caught and marked with individually numbered subcutaneously injected transponders (TROVAN ID 100; TROVAN, Köln, Germany), and since 1992 all locally hatched birds have similarly been marked with such a transponder shortly prior to fledging. The colony site consists of six concrete islands, each of which measures 10.7 × 4.6 m and is surrounded by a 60 cm wall. The walls support 44 platforms for terns to land on, and each platform is equipped with an antenna that reads transponder codes at a distance of ≤11 cm every 5–10 sec to automatically record the presence of transponder-marked individuals (i.e., prospectors, nonbreeders, and breeders). All transponder-marked breeders are additionally identified by placing an antenna around each clutch for at least 24 h during incubation, which is shared between partners. Three times weekly checks of each nest provide information on reproductive performance of breeders: laying date, clutch size, and brood size are recorded and chicks are individually marked with metal rings upon hatching. Once birds have established

themselves as breeders, their resighting probability is almost 100% and their return rate, not conditional of survival, is 90% (Szostek and Becker 2012). The number of breeding pairs at the colony has ranged between 90 and 530 since 1992.

DATA SELECTION

We focused our analyses on local recruits with known sex, age, and life span, whose maternal and/or paternal age at hatching was also known (268 out of 953 local recruits, see Supporting Information). Birds were considered local recruits if their local lifetime number of eggs produced exceeded 0, so that birds prospecting at the colony, but dying before reproduction or deciding to reproduce elsewhere were not taken into account. The sex of local recruits, and their parents, has been determined by standard molecular methods since 1998 (Becker and Wink 2003) and was determined by behavioral observations, after recruitment, before that. The life span of recruits was defined as the age at last observation, and considered known if the bird was not registered by our detection system in 2012–2013. Although we thus assumed death, rather than observed it, we assess the reliability of this assumption to be high, as 97% of breeders does not skip observation for more than two consecutive years after first reproduction (see Table S1, also see Zhang et al. 2015b). We defined LRS as the lifetime number of local fledglings produced. Fledging is inferred from offspring leaving the colony site alive (around 27 days of age, Becker and Wink 2003), and can reliably be measured because offspring can only cross the walls when capable of flying. Skipped observation years were relatively rare (65 bird-years out of a maximum number of 1670 bird-years between recruitment and age at last observation, i.e., 3.9%), but we cannot exclude the possibility that birds bred elsewhere in these years. There was no (sex-specific) effect of maternal age on recruited offspring probability to have skipped observation, or on the number of skipped observation years (Table S2a). The effect of paternal age on the probability of skipping and the number of skipped observation years was, however, statistically significant (Table S2b), and the average ± standard deviation of paternal age of offspring without and with skipped observation years was 6.6 ± 4.4 ($N = 170$) and 8.6 ± 2.9 ($N = 19$), respectively. Although our fitness measure therefore is unbiased with respect to sex and maternal age, it may be biased with respect to paternal age.

Our data included 104 male offspring (with 626 bird-years, Table S3) and 96 female offspring (with 587 bird-years, Table S3) hatched from 103 mothers of known age (one to seven recruited offspring per parent, Table S4; maternal age range: 2–21 years, average ± standard deviation: 7.4 ± 3.4), and 95 male offspring (with 563 bird-years, Table S3) and 94 female offspring (with 564 bird-years, Table S3) hatched from 103 fathers of known age (one to seven recruited offspring per parent, Table S4; paternal age range: 3–19 years, average ± standard deviation: 6.9 ± 3.1). For

58 male and 63 female offspring (with 335 and 400 bird-years, respectively, Table S3), the age of both parents was known, and these birds hatched from 76 fathers and 72 mothers. The year of hatching for offspring included in our analyses ranged from 1993 to 2008.

Note that while we focus our analyses on long-term transgenerational effects of parental age, we do not assume that pre fledging mortality is independent of sex and/or parental age. In fact, we know that sex and parental age effects occur in the nestling phase (Vedder et al. unpubl. ms), but cannot test them in concert with long-term effects due to the fact that while the sex of recruited offspring has been determined since the start of the individual-based study in 1992, the sex of part of all hatchlings and of all fledglings has been determined since 1998. Reducing the dataset to offspring hatched from known-aged parents breeding between 1998 and 2008 would not provide sufficient sample size in our relatively long-lived study species to study long-term fitness effects of parental age.

STATISTICAL ANALYSES

We analyzed sex and parental age effects on offspring LRS in additive cross-classified random-effect models with Poisson-distributed errors and a Markov chain Monte Carlo estimation algorithm with 100,000 iterations. These models included random effects of year of birth and parental identity to account for temporal environmental heterogeneity (Szostek and Becker 2012) and the nonindependence of offspring hatched from the same parent, respectively. Full models included the following fixed effects: year of birth, offspring sex, parental age, parental age², offspring sex × parental age, and offspring sex × parental age². The linear covariate of year of birth was added to the model to account for the fact that recruited offspring from older parents may have largely been born recently, such that the successful offspring from older parents can currently still be alive, biasing our dataset (Fig. S1). Offspring sex was added as a categorical variable with males as the reference category, and parental age was added as a covariate. Full models were simplified by backward stepwise removal of nonsignificant terms and significance ($P < 0.05$, two-tailed) was assessed using the Wald statistic, which approximates the chi-square distribution.

Models were run for maternal and paternal age separately to maximize sample size for each analysis, but effects of parental age-assortative mating (Fig. S2) and combined parental age effects were investigated as follows. We ran a model for the subset of 121 offspring for which both maternal and paternal age were known. This model included cross-classified random effects of year of birth, maternal identity and paternal identity, fixed effects of year of birth, offspring sex, maternal age and paternal age, and both the sex × maternal age and sex × paternal age interactions.

The maternal age × paternal age and the sex × maternal age × paternal age interactions were also added to the model, but were not significant and are not presented.

We also reran the two minimal adequate models of offspring LRS using a dataset of birds with no skipped observation years ($N = 185$ and 170 for maternal and paternal age analyses, respectively), and with the number of skipped observations as an extra covariate, to assess the robustness of our results to the paternal age-dependent occurrence of skipped observation years mentioned above.

To investigate the origin of parental age effects on offspring fitness (see Results), we ran models using offspring life span and age-specific fledgling production as dependent variables. For offspring life span, the models were identical to the ones described above for LRS. For offspring age-specific fledgling production, models included cross-classified random effects of year, nest identity, offspring identity, and parental identity, to account for temporal environmental heterogeneity and the nonindependence of reproductive attempts by two parents with known parental age, by the same breeder in different years, and by recruited offspring hatched from the same parent, respectively. The basic model included fixed effects of offspring year of birth, life span, age, and age², all as linear covariates. The offspring life span term was kept in the model irrespective of its statistical significance, so that the offspring age terms reflected an unbiased estimate of within-individual change (van de Pol and Verhulst 2006). To test for sex-specific parental age effects, we also added offspring sex, parental age, and the offspring sex × parental age interaction to the model.

To investigate a potential proximate mechanism underlying parental age effects on offspring fitness (see Results), we ran models using offspring fledging mass as a dependent variable, which again included random effects of year of birth and parental identity to account for temporal environmental heterogeneity, as well as year of birth as a linear covariate and offspring sex, parental age, and the offspring sex × parental age interaction as fixed effects. We then tested whether offspring fledging mass predicted future body mass during incubation, as this incubation mass is known to affect reproductive performance in our study species and population (Wendeln and Becker 1999).

Finally, we separated parental age effects into between- and within-parental components using a method referred to as within-subject centering (van de Pol and Wright 2009). This method involves subtracting an individual's mean trait value from each of its observed values, such that, in the case of parental age, the mean age values captured the between-parental effects of selective (dis)appearance on offspring performance, while the within-individual parental age deviations captured the plastic offspring performance responses to parental age. Whether

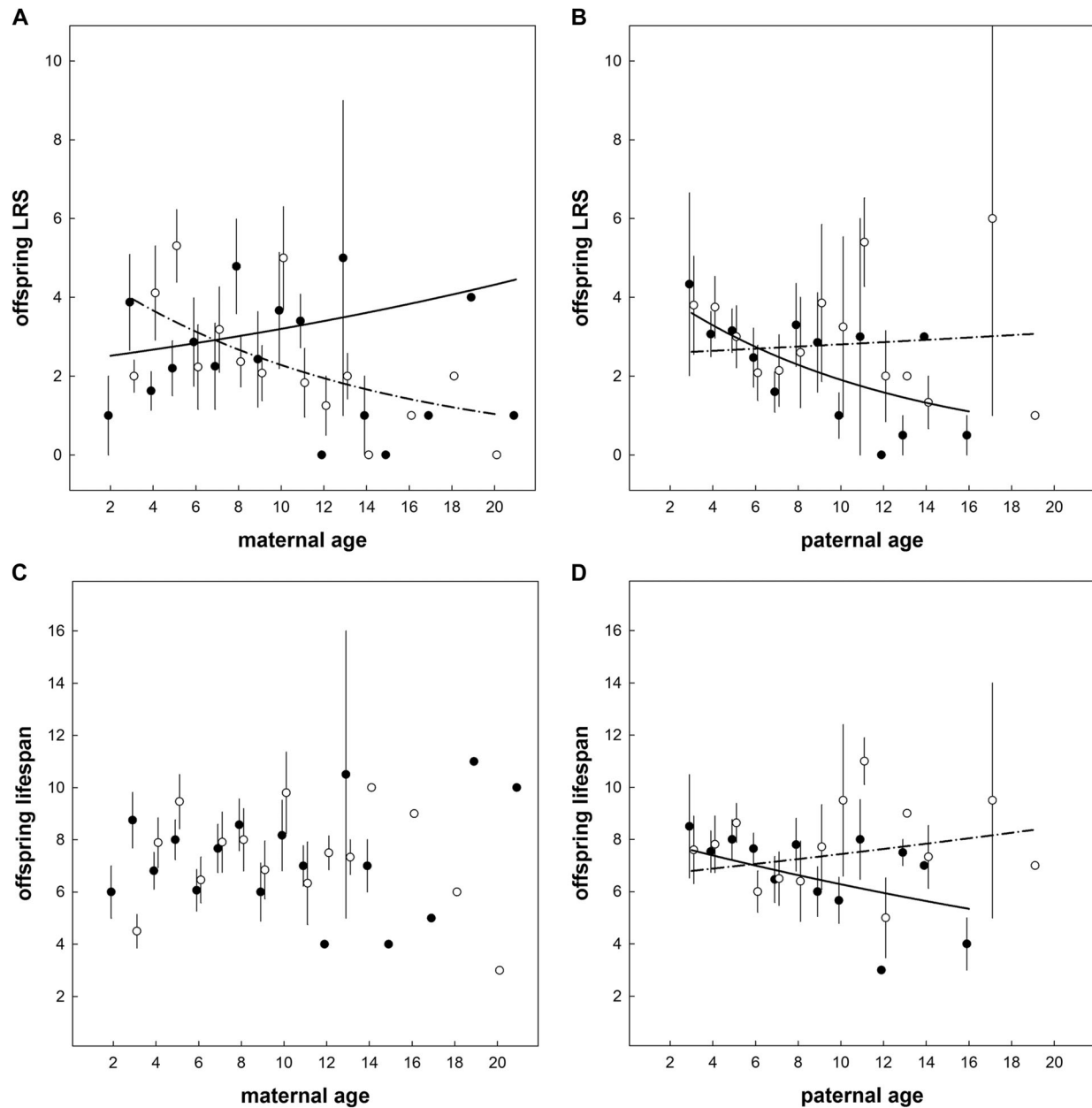


Figure 1. Offspring lifetime reproductive success (LRS, the lifetime number of fledglings produced, (A, B)) and life span (age at last observation, in years, (C, D)) in relation to maternal and paternal age (in years). Filled circles and solid lines present raw data and predicted values for male recruits, whereas open circles and dotted lines present raw data and predicted values for female recruits. Lines were only drawn in case of a significant effect.

within- and between-parental age effects were different was calculated using models in which both the initial parental age term and the average parental age term were added. In these models, the average parental age term represented the difference and was non-significant if the within- and between-parental age effects were effectively the same (van de Pol and Wright 2009). Do note that the statistical power to distinguish between- and within-parental components is relatively low, as the average number of recruited offspring per parent is (biologically unavoidably) low, at 1.9 and

1.8 for mothers and fathers, respectively (Table S4). All models were run in MLwiN version 2.26 (Rasbash et al. 2005).

Results

OFFSPRING LRS

LRS ranged from 0 to 15 fledglings for both male and female recruits, with an average \pm standard deviation of 2.8 ± 3.3 and 2.8 ± 3.1 , respectively. For 200 recruits whose maternal age at

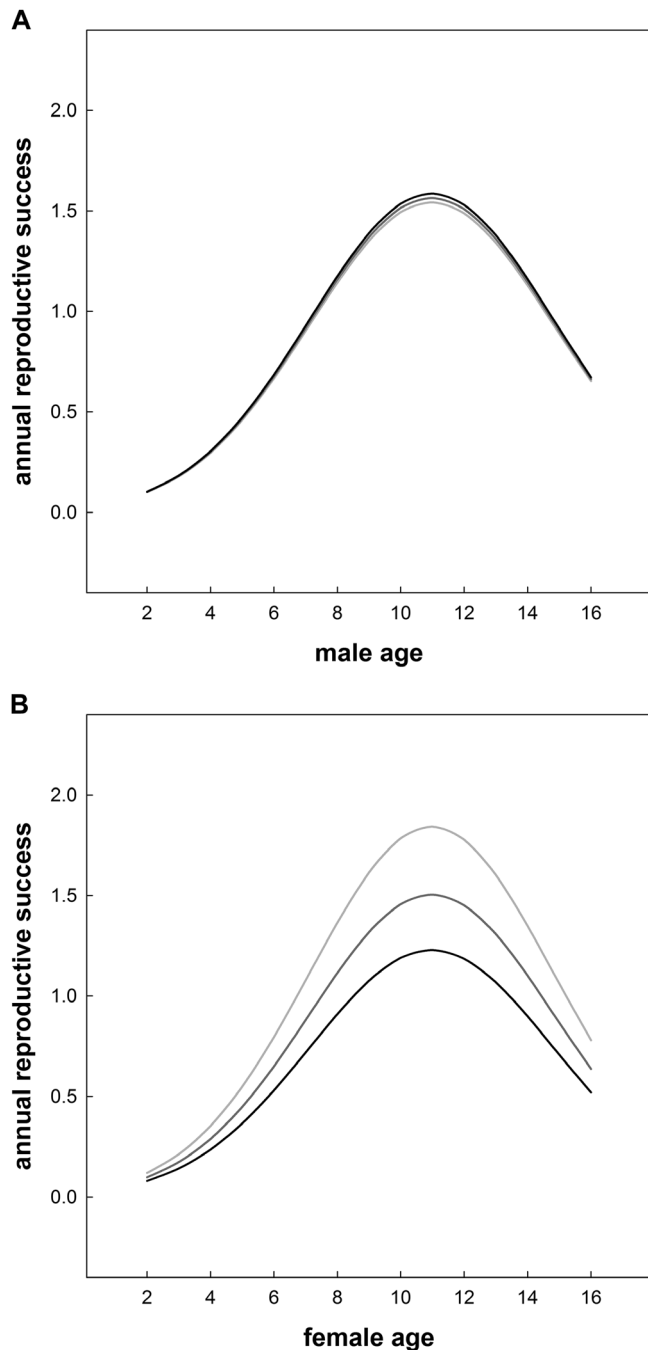


Figure 2. Offspring age-specific reproductive success (annual number of fledglings produced; A: male recruits, B: female recruits) in relation to maternal age. Lines are fitted values representing birds hatched from mothers one standard deviation younger than average (3.7 and 4.5 years for males and females, respectively; light gray), birds hatched from average-aged mothers (7.2 and 7.8 years for males and females, respectively; dark gray), and birds hatched from one standard deviation older than average-aged mothers (10.6 and 11.0 years for males and females, respectively; black).

hatching was known, LRS depended on an interaction between their own sex and the age of their mother when they hatched. This interaction showed that while recruited daughters from older mothers suffered from reduced LRS, LRS of recruited sons increased with maternal age (Fig. 1A, Table S5a left). The sex \times maternal age interaction was very robust. It remained significant when 15 recruits with skipped observation years were excluded from the dataset (Table S5a middle), or when the number of skipped observations was added as a covariate to the model (Table S5a right). It also remained significant when the dataset was reduced to include only 121 recruits whose maternal and paternal age at hatching was known and when paternal age was included in the analysis as a main effect and in interaction with offspring sex (sex \times maternal age: -0.178 ± 0.071 , $\chi^2_1 = 6.357$, $P = 0.012$).

For 189 recruits whose paternal age at hatching was known, LRS also depended on an interaction between their own sex and the age of their father when they hatched. This interaction showed that while recruited sons from older fathers suffered from reduced LRS, daughters were not affected (Fig. 1B, Table S5b left). The sex \times paternal age interaction was not as robust as the sex \times maternal age interaction. When 19 recruits with skipped observation years were excluded from the dataset, the sex \times paternal age effect became marginally nonsignificant (Table S5b middle). The interaction did remain significant when the number of skipped observations was added as a covariate to the model (Table S5b right), but when the dataset was reduced to include only 121 recruits whose maternal and paternal age at hatching was known and when maternal age was also included in the analysis, both as a main effect and in interaction with offspring sex, it again became nonsignificant (sex \times paternal age: 0.086 ± 0.057 , $\chi^2_1 = 2.315$, $P = 0.128$).

OFFSPRING LIFE SPAN

Life span of male recruits ranged from 3 to 16 years, with an average \pm standard deviation of 7.4 ± 3.2 . Among female recruits, life span ranged from 2 to 16 years, with an average \pm standard deviation of 7.4 ± 3.5 .

For 200 recruits whose maternal age at hatching was known, life span did neither depend on maternal age, nor on an interaction between offspring sex and maternal age (Fig. 1C). Adding life span as a covariate to the minimal adequate model for LRS showed that life span was a very strong predictor of LRS (life span: 0.191 ± 0.013 , $\chi^2_1 = 208.407$, $P < 0.001$), but that its addition did not cause the sex \times maternal age interaction to become nonsignificant (sex \times maternal age: -0.086 ± 0.032 , $\chi^2_1 = 7.113$, $P = 0.008$).

For 189 recruits whose paternal age at hatching was known, life span depended on an interaction between their own sex and the age of their father when they hatched. This interaction showed that while recruited sons from older fathers suffered from reduced life span, daughters were not affected (Fig. 1D). Adding life span as

a covariate to the minimal adequate model for LRS again showed that life span was a very strong predictor of LRS (life span: 0.183 ± 0.014 , $\chi^2_1 = 172.449$, $P < 0.001$), but also that its addition caused the sex \times paternal age interaction to become small and nonsignificant (sex \times paternal age: 0.022 ± 0.035 , $\chi^2_1 = 0.380$, $P = 0.538$).

OFFSPRING AGE-SPECIFIC REPRODUCTIVE SUCCESS

For 200 recruits whose maternal age at hatching was known, age-specific reproductive success depended on an interaction between their own sex and the age of their mother when they hatched (Table S6 left). This interaction showed that while recruited daughters from older mothers suffered from reduced annual reproductive success throughout life, annual reproductive success of recruited sons did not depend on maternal age (Fig. 2). For 189 recruits whose paternal age at hatching was known, age-specific reproductive success did neither depend on paternal age, nor on an interaction between offspring sex and paternal age (Table S6 right).

POTENTIAL MECHANISM: FLEDGING MASS

In a subset of 171 of 200 recruits whose maternal age at hatching was known, fledging mass was also known, and related to maternal age in a sex-specific manner. Female recruits hatched from older mothers fledged at a lower weight, whereas fledging mass of sons was unaffected by maternal age (Fig. 3A). Moreover, offspring fledging mass was a good predictor of average mass during incubation in reproductive life (Fig. S3). Offspring fledging mass was not related to paternal age in a subset of 167 of 189 recruits whose paternal age at hatching and fledging mass were both known (Fig. 3B).

BETWEEN- AND WITHIN-PARENTAL EFFECTS

Replacing the maternal age term by an average and delta maternal age term in the minimal adequate models for offspring LRS and age-specific reproductive success showed that between-mother age effects contributed 12 and three times as much to the sex-specific effect of maternal age, respectively (Table 1, left). For neither trait did between- and within-mother effects differ significantly, but there was a trend toward mothers producing recruits at an on average older age raising daughters that suffered from reduced LRS.

Replacing the paternal age term by an average and delta paternal age term in the minimal adequate models for offspring LRS and life span showed that within-father age effects contributed twice as much and three times as little to the sex-specific effect of paternal age, respectively (Table 1, right). For neither trait did between- and within-father effects differ.

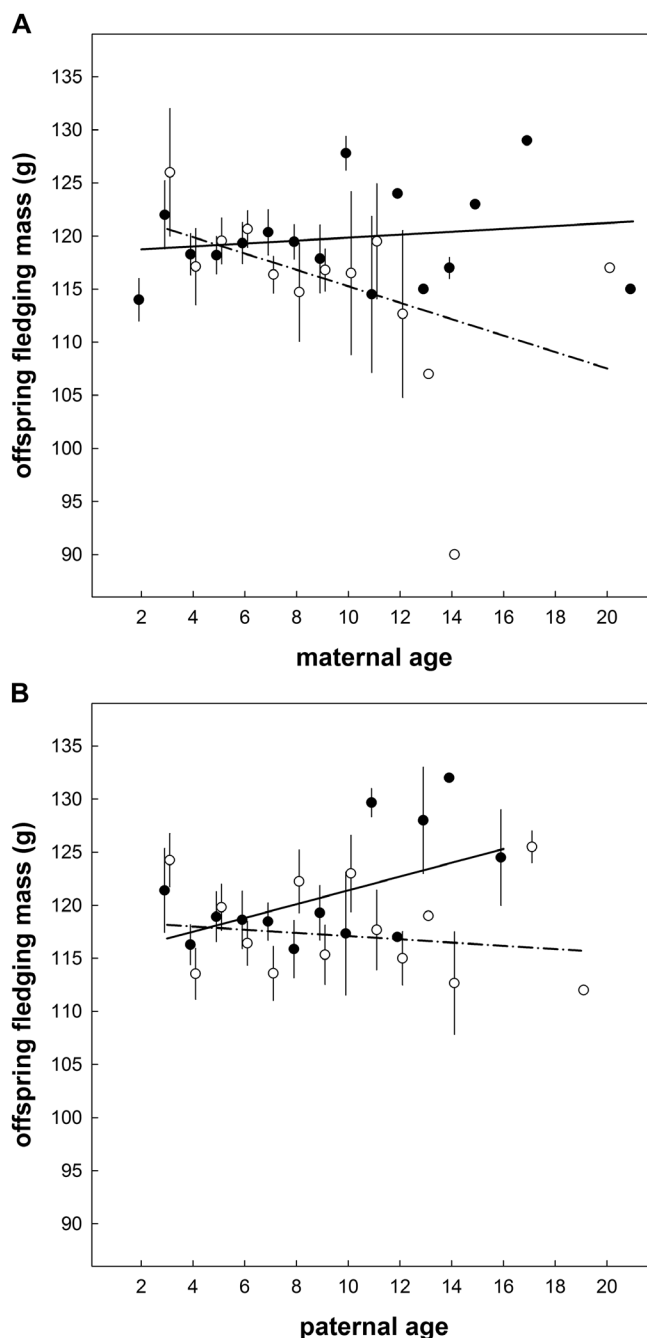


Figure 3. Offspring fledging mass (mass at last registration prior to fledging) in relation to maternal ($N = 171$ recruits, (A)) and paternal ($N = 167$ recruits, (B)) age (in years). Filled circles and solid lines present raw data and predicted values for male recruits, whereas open circles and dotted lines present raw data and predicted values for female recruits.

Discussion

Reports of short-term fitness consequences of parental age on development and fitness components of offspring are plentiful, and investigations of long-term effects are increasing as well. Here, we added to the growing body of evidence for long-term

Table 1. Results from models separating parental age (age) effects on three fitness measures into between- and within-parental components.

Fitness measure	Trait	Maternal age				Paternal age			
		est	SE	χ^2_1	<i>P</i>	est	SE	χ^2_1	<i>P</i>
LRS	Sex × age _b	-0.149	0.038	15.146	<0.001	0.080	0.043	3.448	0.063
	sex × age _w	-0.012	0.060	0.040	0.841	0.136	0.077	3.148	0.076
	Difference	-0.127	0.065	3.820	0.051	-0.060	0.082	0.541	0.462
Life span	sex × age _b	0.044	0.021	4.409	0.036
	sex × age _w	0.017	0.038	0.188	0.665
	Difference	0.021	0.043	0.247	0.619
Age-specific fledging production	sex × age _b	-0.093	0.035	7.028	0.008
	sex × age _w	-0.029	0.053	0.288	0.592
	Difference	-0.060	0.058	1.058	0.304

The offspring sex × age_b interaction captured between-parental age effects on offspring performance, whereas the offspring sex × age_w interaction captured within-parental age effects. Whether within- and between-parental age effects differed was calculated using models in which the full parental age term and the average parental age term were added. In these models, the average parental age term represented the difference and was nonsignificant if the within- and between-parental age effects were effectively the same (van de Pol and Wright 2009). Reported are estimates (est) with standard errors (SE) and their significance (two-tailed, assessed using the Wald statistic, which approximates the chi-square distribution). Note that models were fitted only for traits for which an overall parental age effect on offspring fitness was found, such that "." show that a model was not fitted.

effects of parental age on offspring phenotypes, but extended these analyses by investigating full fitness consequences in relation to offspring sex in a long-lived seabird, the common tern. Our analyses revealed sex-specific pathways of parental age effects on offspring fitness. We found that recruited daughters from older mothers suffered from reduced annual reproductive success and therefore obtained a reduced LRS. In contrast, recruited sons from older fathers suffered from a reduced life span, and this effect also translated to a reduced LRS. Both parental age effects were driven by between- and within-parent effects, but to different extents.

Our findings are partly coherent with recent findings in free-living house sparrows. In this relatively short-lived bird species, daughters from older mothers similarly suffered from a reduced LRS because they showed a reduced annual reproductive success (Schroeder et al. 2015). Sons from older fathers also suffered from a reduced LRS in the house sparrows, but in their case it was caused by a reduction in annual reproductive success (Schroeder et al. 2015) rather than a reduction in life span, as in the common terns. So while the net result is the same, the underlying mechanism differs between these species.

If a sex-specific transgenerational parental age effect generally occurs, it is interesting to investigate potential underlying physiological mechanisms. Although at present we can only speculate, there are examples of parental foraging behavior depending on age (e.g., Lecomte et al. 2010; Jaeger et al. 2014), as well as on adult and offspring sex (e.g., Beaulieu et al. 2009), and such effects could potentially cause food-induced sex-specific differences in condition in relation to parental sex and age.

Interestingly, in the subset of common tern recruits whose maternal age at hatching and fledging mass were known, fledging mass was related to maternal age in a sex-specific manner (Fig. 3A). Female recruits hatched from older mothers fledged at a lower weight, whereas fledging mass of sons was unaffected by maternal age. Moreover, offspring fledging mass was a good predictor of average mass during incubation in reproductive life (Fig. S3), and body mass measured during incubation is known to positively affect reproductive performance in our study species and population (Wendeln and Becker 1999). Studies of age- and sex-specific parental provisioning behavior in relation to offspring sex are required to further investigate this option.

The negative effect of paternal age we found on the life span of sons, cannot be explained by effects of paternal age on male fledging mass (Fig. 3B). Perhaps rather than environmentally, this effect is (epi)genetically induced. In common terns, telomeres, specialized, and highly conserved DNA protein structures, which form the ends of eukaryotic chromosomes and protect their stability, are known to shorten with age (Bauch et al. 2013). Reproductive effort accelerated the shortening of telomeres, but this was especially pronounced in males (Bauch et al. 2013), perhaps because males take a larger share in offspring provisioning in this species (Wiggins and Morris 1987; Wendeln 1997). If the heritability of telomere length in common terns is sex-specific (as it is in lizards, Olsson et al. 2011), sons of older fathers may start life with shorter telomeres. Because telomere length predicted survival in the common tern (Bauch et al. 2014), as well as in other bird species (e.g., Haussmann et al. 2005; Salomons et al. 2009), this may cause sons hatched from older fathers to live less long.

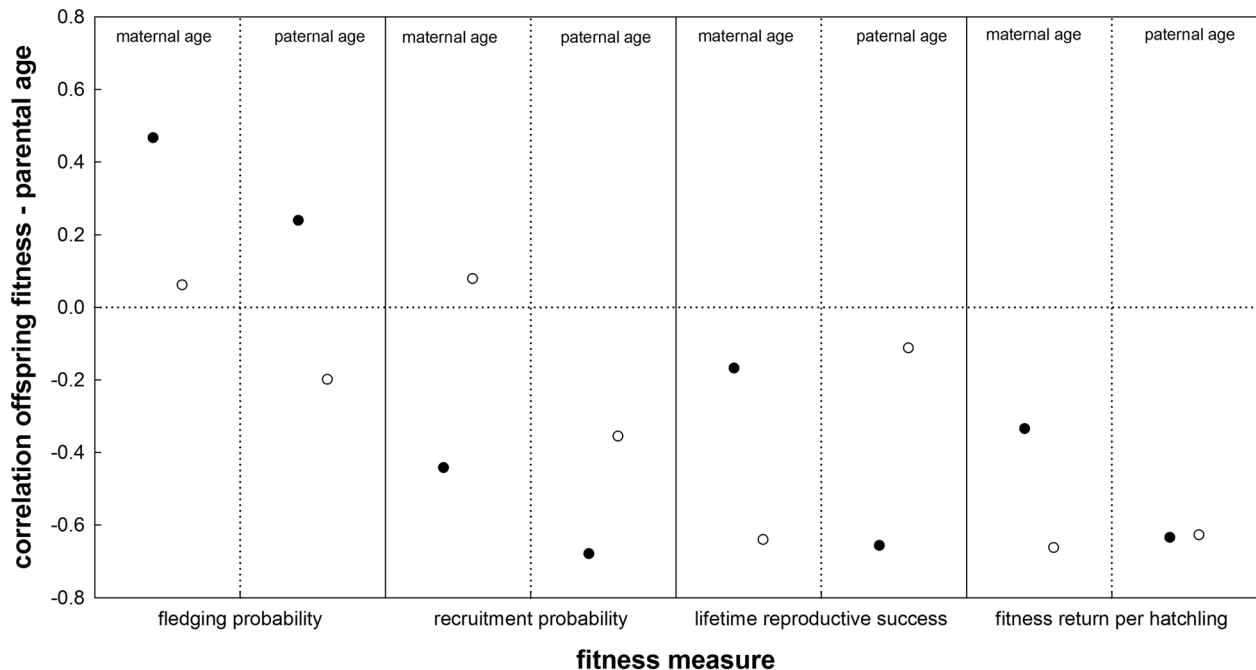


Figure 4. Coefficients of the correlation between sex-specific offspring fitness and sex-specific parental age for four measures of fitness: fledgling probability (raw data, analyzed further in Vedder et al. unpubl. ms), recruitment probability (Fig. S4), lifetime reproductive success (Fig. 1A, B) and the product of these three measures, termed fitness return per hatchling. Filled circles present estimates for male offspring, whereas open circles present estimates for female offspring.

Studies of age- and sex-specific inheritance of telomere length are currently in progress to evaluate this hypothesis.

Irrespective of potential mechanisms, our finding that offspring LRS decreased with parental age has important consequences for our interpretation of the senescence process. Previous work in the Banter See study population had shown that many phenological and reproductive traits, including fledgling production, improved with age, before leveling off (Zhang et al. 2015), providing little evidence for senescence. Indeed, the only evidence for senescence came from findings of age-specific changes in breeding and survival probability, with only the latter underlying a decline in reproductive value with age (Zhang et al. 2015a). If negative parental age effects, however, are manifested after fledging of the offspring, common terns may suffer from reproductive senescence after all, depending on the balance between improved fledgling production and reduced fledgling quality. To investigate the extent to which a conclusion regarding reproductive senescence would depend on the fitness measure used, we performed additional analyses that allowed us to plot the coefficients of the offspring fitness parental age correlation for consecutive life-history stages. Analyses of offspring sex-specific recruitment probability in relation to sex-specific parental age showed that the recruitment probability of sons and daughters declined with paternal, but not maternal age (Fig. S4). Although the slopes of the offspring fitness—parental age correlations were mostly positive

when considering fledgling probability as the fitness measure, they therefore became negative when considering recruitment probability as the fitness measure (Fig. 4). As presented here, the slopes of the fitness—parental age correlation were negative when considering offspring LRS as the fitness measure as well (Figs. 1A, B, 4), and, when combining all three estimates to obtain sex-specific offspring fitness returns as a fitness measure, the slopes remained convincingly negative (Fig. 4). We can therefore conclude that reproductive senescence was wrongly considered absent by quantifying reproductive performance using only fledgling production. This finding corroborates previous findings by Bouwhuis et al. (2009), who also found senescence to largely originate in the postfledging period in another bird species, the short-lived great tit, although in that species the LRS of recruits did not depend on parental age, such that the number of recruits was a suitable fitness measure (Bouwhuis et al. 2010a). In general, this finding underlines that, if we are to understand the evolution of senescence, we will need to use fitness measures that incorporate transgenerational age effects (also see Gillespie et al. 2013; Schroeder et al. 2015; Barks and Laird 2015).

The found sex-specific parental age effects on offspring fitness are expected to not only affect the evolution of senescence in the common tern, but selection pressures on age-assortative mating and on adaptive primary sex ratio adjustment as well, if costs of parental senescence are not outweighed by positive

effects of increased pair bond duration and if sex ratio adjustment is unconstrained by mechanistic limitations or unmeasured costs. Interestingly, age-assortative mating as found in our population (Fig. S2) is itself age dependent, and declines after the age of 8 (Ludwig and Becker 2008), when parental age effects on offspring fitness start to diverge (Fig. 1A, B). Whether this is an adaptive behavioral strategy (i.e., divorce, González-Solís et al. 1999) or a consequence of an increased occurrence of widowhood as a result of survival senescence (Zhang et al. 2015a) is, however, unclear and remains to be investigated. With respect to adaptive sex-ratio adjustment, a hatchling sex ratio bias has not been found in relation to parental age in our species (Vedder et al. unpubl. ms), whereas older mothers would benefit from producing sons rather than daughters if they were to minimize senescence effects (Fig. 4) and if an altered sex allocation would not come at new costs that would offset the benefit suggested by our study. Whether females can actually adaptively manipulate offspring sex ratio is still unknown, although mechanisms of sex determination do not necessarily constrain the evolution of sex ratio adjustment (e.g., West and Sheldon 2002), and perhaps the improved fledging probability of sons with maternal age (Fig. 4) in itself is a form of adaptive sex allocation instead.

It is worth noting that while there was no strong statistical support for a difference in between- and within-parental sex-specific age effects on offspring fitness, the sex \times maternal age interaction was 12 times stronger on the between- than within-mother level. This trend suggests that while daughters produced by the same mother, but at different maternal ages, may differ in their quality, daughters produced by mothers who on average produce recruits late in life do even worse. A high average age for mothers with respect to recruit production can arise through two nonmutually exclusive processes. First, those mothers could have required a long improvement phase before finally producing local recruits and thus be of relatively poor quality. Alternatively, these mothers could have produced recruits throughout life, but have done so over a long reproductive life span, and thus be of relatively high quality. Because not all of the mothers in our dataset are currently assumed dead, we can only provisionally investigate these two options by quantifying the relationship between average maternal age and maternal age range and number of recruits produced in the dataset. Both relationships are significantly positive (age range: 0.507 ± 0.094 , $\chi^2_1 = 28.818$, $P < 0.001$; and number of recruits: 0.729 ± 0.194 , $\chi^2_1 = 14.192$, $P < 0.001$), which suggests that mothers with a high average age are of high phenotypic quality. Poor performance in their female offspring may thus constitute a cost of reproduction, but studies of sex-specific antagonistic genetic variation for LRS (e.g., Foerster et al. 2007) will be required to investigate its underlying basis.

Overall, our study revealed novel sex-specific pathways of parental age effects on offspring fitness, which inspire studies of

potential mechanisms and studies assessing their generality, of which we require knowledge if we are to understand the selective pressures underlying the evolution of senescence, as well as processes such as mate choice and sex allocation.

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DATA ARCHIVING

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Distribution of the number of consecutively skipped observation years after recruitment for the offspring included in our dataset.

Table S2. Results from models testing the effects of offspring sex and parental age on whether offspring had skipped observation years and on the number of skipped observation years.

Table S3. Distribution of the number of bird-years for male and female offspring (in number of males and females as well as overall percentage) hatched from mothers of known age, fathers of known age, and two parents of known age.

Table S4. Distribution of the number of recruits included in the analyses and produced by mothers and fathers of known age.

Table S5. Results from models testing the effects of offspring sex and parental age on offspring lifetime reproductive success.

Table S6. Results from models testing the effects of offspring sex and parental age on offspring age-specific fledgling production.

Figure S1. The proportion of recruits that was assumed dead in relation to parental age.

Figure S2. The association between maternal and paternal age for the recruits for which the age of both parents was known.

Figure S3. The association between offspring fledging mass and average incubation mass during reproductive life for a subset recruits for which both values were recorded.

Figure S4. The proportion of recruited offspring in relation to maternal and paternal age (in years).