University of Groningen

No effect of partner age and lifespan on female age-specific reproductive performance in blue tits

Amininasab, Seyed Mehdi; Hammers, Martijn; Vedder, Oscar; Komdeur, Jan; Korsten, Peter

Published in:
Journal of Avian Biology

DOI:
[10.1111/jav.00970](https://doi.org/10.1111/jav.00970)

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:
2017

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

Citation for published version (APA):

Amininasab, S. M., Hammers, M., Vedder, O., Komdeur, J., & Korsten, P. (2017). No effect of partner age and lifespan on female age-specific reproductive performance in blue tits. *Journal of Avian Biology*, 48(4), 544-551. <https://doi.org/10.1111/jav.00970>

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.

No effect of partner age and lifespan on female age-specific reproductive performance in blue tits

Seyed Mehdi Amininasab, Martijn Hammers, Oscar Vedder, Jan Komdeur* and Peter Korsten*

S. M. Amininasab (s.m.amini.nasab@rug.nl), M. Hammers, O. Vedder and J. Komdeur, Groningen Inst. for Evolutionary Life Sciences, Univ. of Groningen, the Netherlands. SMA also at: Dept of Environmental Science, Behbahan Khatam Alanbia Univ. of Technology, Iran. OV also at: Inst. of Avian Research, Wilhelmshaven, Germany. – P. Korsten, Dept of Animal Behaviour, Bielefeld Univ., Germany.

Studies of age-specific reproductive performance are fundamental to our understanding of population dynamics and the evolution of life-history strategies. In species with bi-parental care, reproductive ageing trajectories of either parent may be influenced by their partner's age, but this has rarely been investigated. We investigated within-individual age-specific performance (laying date and number of eggs laid) in wild female blue tits *Cyanistes caeruleus* and evaluated how the age and longevity of their male partner indirectly influenced the females' reproductive performance. Females showed clear age-dependence in both laying date and number of eggs laid. We found that female reproductive performance improved in early life, before showing a decline. Longer-lived females had an earlier laying date throughout their lives than shorter-lived females, but there was no difference in number of eggs laid between longer- and shorter-lived females. Within breeding pairs, the female's (age-specific) reproductive performance was not dependent on the age and longevity of the male partner. We conclude that the age and quality of the male partner may be of little importance for traits that are under direct female control.

Studies of age-specific reproductive performance and reproductive lifespan are fundamental to our understanding of population dynamics and the evolution of life-history strategies (Stearns 1992). In vertebrates, reproductive performance typically improves with age because of changes in physiology or reproductive allocation (Curio 1983), or accumulation of breeding experience (Forslund and Pärt 1995, Cichon 2003), before declining as a result of senescence (Clutton-Brock 1988, Jones et al. 2008). To accurately describe and understand these within-individual processes, it is crucial to separate within-individual changes from changes in age composition that occur at the population level. For example, differences in intrinsic quality between individuals may be manifested by the occurrence of poor-quality individuals with low reproductive performance that die relatively early compared to high-quality individuals with high reproductive performance (Blas et al. 2009). Failure to correct for such selective disappearance may obscure within-individual patterns of senescence, or may even lead to wrong interpretation of the patterns of age-specific reproduction (van de Pol and Verhulst 2006, Bouwhuis et al. 2009). Longitudinal data on the breeding performance of marked individuals followed throughout their lives are essential for separating these within- and between-individual effects (Nussey et al. 2008, Bouwhuis and Vedder 2017).

There is an increasing number of studies that have quantified patterns of reproductive ageing as a within-individual process in birds (Nussey et al. 2013, Bouwhuis and Vedder 2017). Although most of those studies have focused on age-specific female reproductive performance, several recent studies have investigated age-specific reproductive performance as a within-individual process in both males and females. Generally, studies that considered both males and females have focused on traits that are directly influenced by the performance of both parents, such as the number of offspring that reach independence in species with bi-parental care (Millon et al. 2011, Torres et al. 2011, Balbontín et al. 2012), but some have also included traits that are usually regarded as under mechanistic control by the female, such as clutch size (Schroeder et al. 2012, Zhang et al. 2015). Studies which have investigated how ageing patterns of female reproductive traits are influenced by the age or lifespan of the male partner remain scarce (but see Balbontín et al. 2007, Brown and Roth 2009, Auld and Charmantier 2011, Auld et al. 2013). Given that mating patterns are often not random with respect to age (e.g. age-assortative mating; Black and Owen 1995, Auld and Charmantier 2011) and investment in reproduction may be influenced by (age-dependent) characteristics of the partner (e.g. attractiveness; Trivers 1972, Burley 1986), it is important to also consider the effect of the partner when investigating patterns of age-specific reproduction. Male age or lifespan may potentially affect the age-specific expression of reproductive traits

*Shared last authorship

that are typically regarded as traits that are almost entirely determined by the female, such as laying date and clutch size (Sheldon et al. 2003, Caro et al. 2009). Hence, to gain a better understanding of ageing patterns in reproductive performance in females, the influence of their partner's age and lifespan should also be studied.

In a recent study on mute swans *Cygnus olor*, it was found that female reproductive performance was influenced by the age of the male breeding partner: females breeding with middle-aged male partners started laying earlier in the season and laid larger clutches compared to females breeding with young or old partners (Auld et al. 2013). Similarly, in barn swallows *Hirundo rustica* and wood thrushes *Hylocichla mustelina* females that were paired with middle-aged males started laying earlier in the season than those paired with either young or old partners (Baltontín et al. 2007, Brown and Roth 2009). Finally, in a study on blue tits *Cyanistes caeruleus* females showed an improvement in reproductive performance (i.e. earlier laying and larger clutch size) and a reduced rate of reproductive senescence when they were mated with early-reproducing males, which were likely to be of higher quality than late-reproducing males (Auld and Charmantier 2011).

In this study we aimed to investigate whether female age-specific reproductive performance is affected by the age and reproductive lifespan of the male partner, while accounting for selective disappearance of 'lower quality' individuals. We used 12 yr of longitudinal breeding data on an individually marked blue tit population. Two measures of reproductive performance that are under direct female control were considered: laying date and clutch size; both of which are important predictors of fitness (Perrins 1965, Norris 1993, Verboven and Visser 1998, Both et al. 2000). We tested the hypothesis that females improve their reproductive performance when they are paired with older males (which may also provide more resources), or longer-lived males (which may be of higher quality).

Methods

Study area and study population

The blue tit is a widespread cavity-nesting bird. Blue tits are socially monogamous and care for the chicks is shared between both pair members. The data presented here were collected between 2001 and 2014 as part of a long-term study on the blue tit population at 'De Vosbergen' estate near Groningen in the Netherlands (53°08'N, 06°35'E). The study area covers 54 ha and is characterized by mixed deciduous and coniferous forest interspersed with areas of open grassland. In our study area, blue tits breed in nest-boxes of which a total of 188 have been available since 2001.

Data collection and definition of variables

Blue tits breeding in nest-boxes were studied following the protocols of the long-term monitoring program established for the study population since 2001 (for details see Korsten 2006). Each year, from early April onwards, the nest-boxes were checked regularly to determine the date of the first egg,

clutch size and hatching date for each nest. We attempted catching the male and female breeding at each nest box when they were feeding their nestlings (mostly at 7–8 d of age; hatching = day 0) using a 'flap-trap' inside the nest-box. Individuals that were caught were aged in the field using plumage characters (classifying them into yearlings or older) according to Svensson (1992), and sexed according to the presence or absence of a brood patch (only females develop a brood patch). Each adult was marked with an individually numbered aluminum ring. All young were ringed, mostly at 7–8 d of age.

Various experiments have been carried out on this population during the years of its study (Korsten et al. 2006, Kingma et al. 2009, Vedder et al. 2010, 2012, de Jong 2013, Schut et al. 2014; Supplementary material Appendix 1, Table A1). Some experiments were carried out before or during egg laying (before incubation started) and some of them were carried out after the incubation onset. Because these experiments may have influenced some aspects of reproductive performance, we focused on data on reproductive traits that were not influenced by experimentation (see Supplementary material Appendix 1, Table A1 for an overview of experiments for each year). We adopted a conservative approach and selected only the laying date and the number of eggs laid as focal reproductive parameters. We acknowledge that there might be potential limitations associated with our study population being subjected to experiments. However, because we only focussed on traits that were not influenced by experimental manipulations, we have no reasons to assume that the experimental manipulations altered the conclusions of our study. The laying date was defined as the date the first egg was laid (1 April was taken as day 1). The number of eggs was the total number of eggs laid by a female during a reproductive attempt. As a result of the collection of eggs without replacement with dummy eggs (Supplementary material Appendix 1, Table A1) in some years, it was not possible to determine the actual clutch size (i.e. the maximum number of eggs present in the nest during an unmanipulated reproductive attempt), as females may have partly compensated for the removal of eggs by laying additional eggs. In recognition of this potential influence, we use the term number of eggs laid instead of clutch size for all years. We excluded second clutches, which occurred only rarely, as well as replacement clutches after failed first breeding attempts, from our analyses. Due to the experiments performed in the population during the incubation and nestling provisioning stages, we were not able to incorporate other relevant parameters of a pair's reproductive performance expressed after the onset of incubation (e.g. number of fledglings, number of recruits).

The experimental manipulations influenced the laying date and the number of eggs laid in 2006–2007 (Amininasab et al. 2016a), and the number of eggs laid in 2009 (Vedder et al. 2012; for details see Supplementary material Appendix 1, Table A1). As a result, for those years and breeding parameters, we excluded the experimental nests and only included unmanipulated and control nests in our analyses. Hence, nests included in the analyses represent typical, unmanipulated, nests. We did an extra analysis that examined whether the excluded experimental nests may have had females and males of different age compared to the included nests. This

confirmed that females and males did not significantly differ in average age between excluded and included nests, in the respective years (2006: females $F_{1,61} = 0.05$, $p = 0.81$; males $F_{1,61} = 0.25$, $p = 0.62$; 2007: females $F_{1,58} = 0.01$, $p = 0.93$; males $F_{1,58} = 0.10$, $p = 0.75$; 2009: females $F_{1,65} = 0.004$, $p = 0.95$; males $F_{1,61} = 0.90$, $p = 0.35$).

The age of adults was estimated based on ringing records since 2001. In a number of cases, individuals were first caught with > 1-yr-old plumage (17.4% of females and 15.9% of males in our dataset). In these cases, we assigned them a minimum age of two years. We also calculated the recruitment rates for both females and males. 16.6% of females and 38.7% of males breeding recruited after they were ringed as nestlings in our study population. We assigned immigrant status (locally born versus immigrant) of both pair members accordingly.

Blue tits that were not caught during the breeding season for two consecutive years were assumed dead and their age of last reproduction (ALR) was defined as the age at which they were observed for the last time breeding in the population. Adult birds that were still alive in 2013 or 2014, and hence could not be assigned an ALR, were excluded from our dataset (following Bouwhuis et al. 2009). In total, following the above selection criteria, we recorded 989 breeding attempts: these included 932 breeding attempts of 633 females and 820 breeding attempts of 589 males. The percentage of breeding attempts where both female and male identity was recorded was 77.1%. Hereafter, the calculations are based on 763 breeding attempts where both female and male identity were recorded (541 females and 548 males). As the blue tit is a short-lived species (average lifespan of adults based on the individuals in our dataset is 1.86 yr in females and 1.68 yr in males), for the majority of individuals we only recorded a breeding attempt in a single year (381 females (70.4%) and 402 males (73.4%) were only recorded breeding in one year). However, a considerable number of individuals were recorded in multiple years, which allowed us to investigate longitudinal changes in reproductive performance. The number of females with repeated observations were: two times observed: 114, three times observed: 35, four times observed: 8, and five or more times observed: 3, and the number of males with repeated observations were: two times observed: 95, three times observed: 35, four times observed: 14, and five times observed: 2. There was considerable variation in ALR in both female and males. The number of females with ALR 1 until $ALR \geq 5$ were 250, 181, 67, 30, 13, respectively, and the number of males with ALR 1 until $ALR \geq 5$ were 309, 153, 53, 21, 12, respectively.

Statistical analyses

A potential issue in separating female and male contributions to reproductive performance is that the ages of the partners are highly correlated (e.g. when partners are always the same age). Therefore, before investigating the impact of male age on female age-specific reproductive performance, we investigated the degree of age-assortative mating. For this primary test, in case a pair stayed together for multiple years, only one year was selected randomly. The ages of male and female partners were significantly correlated

in our dataset ($t = 3.44$, $DF = 707$, $r = 0.13$, $p < 0.001$). However, the relatively small Pearson correlation coefficient of 0.13 between male and female age suggests that it should be possible to statistically separate the effects of the female and male partner's age using a multiple regression approach as described below.

We analyzed how egg laying onset and the number of eggs laid were predicted by female age and evaluated how the male partner's age affected the expression of these traits. We used linear mixed models (LMMs) with normally distributed errors and an identity link function using the package lme4 (ver. 1.1-7; Bates et al. 2014) in R (ver. 3.1.0; R Development Core Team).

The breeding parameters laying date and the number of eggs laid varied between years and also between different nest-boxes in each year (Amininasab et al. 2016a). Therefore, we included year and nest-box identity as random effects to statistically control for differences between years and nest-sites. We only used breeding attempts in the model for which the identity and age of both pair members were known. Linear and quadratic effects of age were tested by including both age and its squared term (age^2) as covariates. In the analyses of the number of eggs laid, a negative coefficient of the quadratic effect of age would suggest an initial increase in reproductive performance (i.e. increase in the number of eggs laid) followed by a decline. In the analyses of laying date, a positive coefficient of the quadratic effect of age would suggest an initial increase in reproductive performance (i.e. an advanced laying date) followed by a decline. We added individual identity as a random effect in the models to control for the use of repeated, non-independent observations on the same individual in consecutive years. Furthermore, for the age effect to reflect an estimate of within-individual change, we also used the age at last reproduction (ALR) for each individual as a fixed effect in the models (see van de Pol and Verhulst 2006 for a detailed explanation of this statistical method). In short, ALR accounts for potential differential disappearance from the breeding population of birds of different intrinsic quality (van de Pol and Verhulst 2006, Bouwhuis et al. 2009). We then repeated the analyses and included immigrant status of both pair members (locally born versus immigrant, a two-level factor) as a factor in the models.

We did not include the age of first reproduction in our models, because the majority of blue tits in our study population start their reproductive career at one year of age (82.6% of females and 84.1% of males). Two-way interactions between age, age^2 and ALR were included as fixed effects. Maximal models (i.e. including all explanatory variables and their two-way interactions) were simplified by backward stepwise removal of non-significant terms (starting with the least-significant interaction terms) to reach a minimal adequate model. Age, age^2 , ALR, and the random effects were always kept in the model, independent of their significance. Estimated coefficients for each term (with associated standard errors and p-values) are presented on the basis of the minimal adequate model. Following the terminology of Bouwhuis et al. (2009), Table 1 contains a brief description of all variables and interactions that are used in the models.

Table 1. Parameters used, and their interpretation, in models testing for a relationship between age and female reproductive performance.

Fixed effect	Interpretation
♀ or ♂ age	linear change in female reproductive performance with a direct effect of female age, or an indirect effect of male age
♀ or ♂ age ²	quadratic change in female reproductive performance with a direct effect of female age, or an indirect effect of male age
♀ or ♂ ALR	linear change in female reproductive performance with female (direct effect) or male (indirect effect) reproductive lifespan
♀ age × ♀ ALR	age effects on female reproductive performance differ for females (direct effect) or males (indirect effect) of different reproductive lifespan
♂ age × ♂ ALR	age effects on female reproductive performance differ quadratically for females (direct effect) or males (indirect effect) of different reproductive lifespan
♀ age ² × ♀ ALR	age effects on female reproductive performance differ quadratically for females (direct effect) or males (indirect effect) of different reproductive lifespan
♂ age ² × ♂ ALR	age effects on female reproductive performance differ quadratically for females (direct effect) or males (indirect effect) of different reproductive lifespan
♀ age × ♂ age	age-dependent reproductive performance of females is dependent on the age of the male partner
♀ age × ♂ ALR	age effects (direct for females and indirect for males) on female reproductive performance depend on the partner's reproductive lifespan
♂ age × ♀ ALR	age effects (direct for females and indirect for males) on female reproductive performance depend on the partner's reproductive lifespan
♀ age ² × ♂ ALR	age effects (direct for females and indirect for males) on female reproductive performance differ quadratically depending on the partner's reproductive lifespan
♂ age ² × ♀ ALR	age effects (direct for females and indirect for males) on female reproductive performance differ quadratically depending on the partner's reproductive lifespan

A significant quadratic effect of age does not necessarily provide evidence for senescence (Reid et al. 2003, Keller et al. 2008), as it might also reflect improvement early in life only, with performance leveling off (but not declining) at later ages. We therefore also performed a 'post-peak analysis', using the minimal adequate model resulting from the analyses described above, but excluding the quadratic effect of age, and selecting only breeding attempts that occurred after the predicted peak in reproductive performance (cf. Bouwhuis et al. 2009, Hammers et al. 2012). If the age term in such a 'post-peak model' is significantly negative for the number of eggs laid, or positive for laying date, this provides support for performance showing a senescent decline with age. p -values < 0.05 were considered significant.

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.4g099> (Amininasab et al. 2016b).

Results

Female reproductive performance: influence of own and partner age

Laying date and number of eggs laid showed clear age-dependence for females, but not for their male partners (Table 2, Fig. 1; Supplementary material Appendix 1, Table A2). Age of the male did also not explain variation in laying date and number of eggs laid when we repeated the model excluding the effects of female age (Supplementary material Appendix 1, Table A3, A4). In females, we found a clear pattern of improvement with age in both traits, until *ca.* three years of age (Fig. 1). We found no significant differences between locally born and immigrant individuals with respect to laying date and number of eggs laid (Supplementary material Appendix 1, Table A5). Post-peak analyses (i.e. restricting the analyses to females ≥ 3 yr old) of the reproductive attempts where the identity and age of both pair members were known provided no evidence for senescence for either of the two traits, but the sample sizes were rather small (Supplementary material Appendix 1, Table A6). Repeating these post-peak analyses using a larger dataset which included all females of known age (regardless of whether the identity of their partner was known) suggested that after three years of age the laying date delayed and the number of eggs laid decreased with age, but these effects

were marginally non-significant ($p = 0.051$ and $p = 0.050$, respectively; Supplementary material Appendix 1, Table A7). We found no significant interaction between female age and the age of the male partner (Table 2), indicating that the age of the male partner did not influence the female's pattern of age-dependent reproductive performance. Examination of the variances explained by the random effects in the final model (Table 2) corroborates our findings; female identity explains a considerable proportion of the variance in both laying date (27%) and number of eggs laid (39%), whereas male identity does not (6 and 7%, respectively).

Influence of male and female age-dependent selective disappearance on female reproductive performance

We found a clear pattern of age-dependent selective disappearance in females for laying date, but not for the number of eggs laid (Table 2; Supplementary material Appendix 1, Table A2). Specifically, we found that longer-lived females have an earlier age-specific laying date than shorter-lived females throughout their lives (Fig. 2). This analysis also suggests that the peak in reproductive performance occurred later in life in longer-lived females than in shorter-lived females (Fig. 2). There was no relationship between female age-specific reproductive performance and the lifespan of the male partner (Table 2; Supplementary material Appendix 1, Table A3, A4).

Discussion

In our study population, reproductive performance improved with female age in early life and tended to decline among older females. A similar pattern has been shown in many other bird species (Nussey et al. 2013, Bouwhuis and Vedder 2017). While female performance in timing (laying date) and initial effort in reproduction (number of eggs laid) was influenced by the female's own age, it was not influenced by her partner's age. This result, combined with the relatively small amount of variation in laying date and number of eggs laid that was explained by male identity, suggests that these traits are predominantly determined by the female. This corroborates the findings of several quantitative genetic studies that indicated that these traits are mainly influenced by an additive genetic effect of the female (van der Jeugd and McCleery 2002, Sheldon et al. 2003, Caro et al. 2009).

Table 2. Linear mixed models investigating the effect of female age and the age of the male partner on laying date and number of eggs laid for breeding attempts in blue tits where the identity and age of both pair members are known. Estimated effects of each term (Estimate) with associated standard errors (SE) and p-values are presented on the basis of the final model. ALR stands for age of last reproduction. Non-significant (ns) fixed effects, except the age, age² and ALR terms which were always retained in the model, were deleted by stepwise deletion, in order of least significance and starting with the interactions.

	Laying date			Number of eggs laid		
	Estimate	SE	p	Estimate	SE	p
Fixed effects						
Intercept	22.50	1.73	< 0.001	10.64	0.35	< 0.001
♀ age	−5.30	1.23	< 0.001	0.51	0.22	0.023
♀ age ²	1.17	0.32	< 0.001	−0.09	0.04	0.028
♀ ALR	−0.49	0.36	0.17	0.07	0.08	0.37
♀ age × ♀ ALR	0.49	0.27	0.07		ns	
♀ age ² × ♀ ALR	−0.14	0.05	< 0.01		ns	
♂ age	−0.36	0.61	0.56	−0.01	0.27	0.96
♂ age ²	0.10	0.12	0.40	−0.01	0.05	0.82
♂ ALR	−0.03	0.17	0.85	0.11	0.07	0.14
♂ age × ♂ ALR			ns			ns
♂ age ² × ♂ ALR			ns			ns
♀ age × ♂ age			ns			ns
♀ age × ♂ ALR			ns			ns
♀ age ² × ♂ ALR			ns			ns
♂ age × ♀ ALR			ns			ns
♂ age ² × ♀ ALR			ns			ns
Random effects						
	Variance	Proportion variance explained		Variance	Proportion variance explained	
♂ identity	2.25	0.06		0.23	0.07	
♀ identity	10.12	0.27		1.38	0.39	
Nest-box	1.72	0.05		0.13	0.04	
Year	18.12	0.48		0.28	0.08	
Residual	5.22	0.14		1.48	0.42	
Sample sizes						
Individuals ♂	548			536		
Individuals ♀	541			532		
Years	12			12		
Breeding attempts	763			736		

Males and females may allocate resources differently according to their different roles during the different stages of the reproductive cycle. These different roles can cause differences in energetic investments between the sexes (Tavecchia et al. 2001, Bouwhuis and Vedder 2017). For example, the energetic and nutritional costs associated with egg production and optimizing egg laying onset are probably higher for females than for their male partner (Monaghan and Nager 1997, Monaghan et al. 1998). This, in turn, may explain why we observed clear age-dependence and improvement in these traits in females, but not in males. However, this is not always the case as other studies have found age-dependent improvements in both males and females for female-specific traits such as laying date and/or clutch size (barn swallow: Balbontín et al. 2007, blue-footed booby *Sula nebouxii*: Kim et al. 2011, mute swan: Auld et al. 2013). Conversely, the reproductive performance of males may improve with age for traits which are influenced by both male and female reproductive allocation (e.g. number of fledglings in species with bi-parental care; Brown and Roth 2009, Millon et al. 2011).

For the two reproductive traits that we investigated, the model-predicted maximum female reproductive performance was reached around three years of age. Post-peak analyses on females partly suggested a delay in laying date and a decrease

in the number of eggs laid in older females, but not in older males. This is in line with the observed lack of an overall male influence on these two reproductive traits. These results are also broadly consistent with some studies where reproductive senescence was only reported for females (barn swallow: Balbontín et al. 2012, collared flycatcher *Ficedula albicollis*: Evans et al. 2011), but differ from other studies where laying onset and/or clutch size were found to deteriorate both with female and the male partner's age (barn swallow: Balbontín et al. 2007, blue tit: Auld and Charmantier 2011, blue-footed booby: Kim et al. 2011, house sparrow *Passer domesticus*: Schroeder et al. 2012). Hence, it is clear that sex-specific patterns of age-dependence in reproductive traits can differ between populations and species. However, currently there are too few studies that have assessed both sexes simultaneously to reach general conclusions regarding the causes of these differences.

For females, but not for males, we found a clear pattern of age-dependent selective disappearance with respect to laying date. Our analyses suggest that longer-lived females have an earlier age-specific laying date than shorter-lived females throughout their lives, and that the difference in laying date between individuals with different lifespans increases with age. An earlier laying onset in longer-lived females has also been shown in several other species (McCleery et al. 2008,

Figure 1. Overall pattern of (a) laying date and (b) number of eggs laid in relation to female age (direct effect) and the age of the male partner (indirect effect) in blue tits. Relative reproductive performance is the observed value (of laying date or number of eggs) minus the mean value in a given year. Data plotted are the means and standard errors for breeding attempts where the identity and age of both pair members are known. For each age class, sample sizes are given above the data points. The solid lines are the model predicted within-individual regression slopes from the final model (Table 2).

Evans et al. 2011, Auld et al. 2013; but see Balbontín et al. 2007, 2012, Kim et al. 2011). Potentially, shorter-lived females are in poorer condition throughout their lives, causing short-lived females to be more constrained than

long-lived females to lay early (Torres et al. 2011). Similar to many other studies (Bouwhuis et al. 2009, Balbontín et al. 2012, Potti et al. 2013; but see McCleery et al. 2008, Evans et al. 2011) we found no evidence for female selective disappearance with respect to clutch size.

In species with bi-parental care, reproductive performance in females may improve when they are mated to preferred (high quality) males (Horváthová et al. 2012). For example, in another study on blue tits, females that were paired with males that started their breeding career at a younger age (an indication of high quality) showed a slower rate of senescence in laying date and clutch size (Auld and Charmanier 2011). Because most individuals in our population start breeding in their first year, we were not able to test whether male age of first reproduction explained female ageing trajectories in our population. However, we did not find a relationship between the female's age-specific reproductive performance and the lifespan (also a measure of quality) of the partner. Several studies found similar results as ours. For example, Kim et al. (2011) and Auld et al. (2013) found no association between male lifespan and female laying date in the blue-footed booby, and clutch size in the mute swan, respectively. In contrast to our study, female mute swans started laying earlier when paired with relatively long-lived males (Auld et al. 2013). One explanation for why the patterns of covariation between male lifespan and the female partner's reproductive performance

Figure 2. Age-specific laying date of female blue tits subdivided in groups of different age of last reproduction (ALR). Relative reproductive performance is the observed value of laying date minus the mean value in a given year. For each age class, sample sizes are given above the data points. The data points and error bars (connected with solid lines) represent means with standard errors at each age for individuals with different ALR.

vary among species may be that males may invest more in maintaining a territory across years in longer-lived species (such as the mute swan), than in shorter-lived species (such as the blue tit). Therefore, males may exert a greater influence on female reproductive decisions early in the breeding cycle (e.g. laying date and clutch size) in longer-lived species (Auld et al. 2013).

In conclusion, our study suggests that the age and quality of the male may be of little importance for reproductive traits that are under direct female control. However, more studies are needed to seek for generality in between-trait and species differences in the role of male age and longevity in female reproductive performance.

Acknowledgements – We thank the Kraus-Groeneveld Stichting for permission to work on De Vosbergen estate. We thank Frank Groenewoud, Michele Busana, Maaike Versteegh and Lei Lv for their help and advice with the graphs. We also thank Michael Magrath, Berber de Jong, Elske Schut and numerous BSc and MSc Students for their indispensable help in the field from 2001–2014. Permission for all procedures involving handling of blue tits was granted by the Animal Experiments Committee (DEC) of the Univ. of Groningen. The research was financially supported by grant numbers 028696 (European Community's Sixth Framework Programme) and 821.01.008 (ALW-NWO) which were allocated to JK. PK was financially supported by the European Union's Seventh Framework Programme (PCIG10-GA-2011-304280). MH was supported by a NWO VENI-fellowship (863.15.020).

References

- Amininasab, S. M., Vedder, O., Schut, E., de Jong, B., Magrath, M. J. L., Korsten, P. and Komdeur, J. 2016a. Influence of fine-scale habitat structure on nest-site occupancy, laying date and clutch size in blue tits *Cyanistes caeruleus*. – *Acta Oecol.* 70: 37–44.
- Amininasab, S. M., Hammers, M., Vedder, O., Komdeur, J. and Korsten, P. 2016b. Data from: No effect of partner age and lifespan on female age-specific reproductive performance in blue tits. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.4g099>>.
- Auld, J. R. and Charmantier, A. 2011. Life history of breeding partners alters age-related changes of reproductive traits in a natural population of blue tits. – *Oikos* 120: 1129–1138.
- Auld, J. R., Perrins, C. M. and Charmantier, A. 2013. Who wears the pants in a mute swan pair? Deciphering the effects of male and female age and identity on breeding success. – *J. Anim. Ecol.* 82: 826–835.
- Balbontín, J., Hermosell, I. G., Marzal, A., Reviriego, M., de Lope, F. and Møller, A. P. 2007. Age-related change in breeding performance in early life is associated with an increase in competence in the migratory barn swallow *Hirundo rustica*. – *J. Anim. Ecol.* 76: 915–925.
- Balbontín, J., Møller, A. P., Hermosell, I. G., Marzal, A., Reviriego, M. and de Lope, F. 2012. Geographical variation in reproductive ageing patterns and life-history strategy of a short-lived passerine bird. – *J. Evol. Biol.* 25: 2298–2309.
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H. and Dai, B. 2014. lme4: linear mixed-effects models using Eigen and S4. – R package ver. 1.1-7.
- Black, J. M. and Owen, M. 1995. Reproductive performance and assortative pairing in relation to age in barnacle geese. – *J. Anim. Ecol.* 64: 234–244.
- Blas, J., Sergio, F. and Hiraldo, F. 2009. Age-related improvement in reproductive performance in a long-lived raptor: a cross-sectional and longitudinal study. – *Ecography* 32: 647–657.
- Both, C., Tinbergen, J. M. and Visser, M. E. 2000. Adaptive density dependence of avian clutch size. – *Ecology* 81: 3391–3403.
- Bouwhuis, S. and Vedder, O. 2017. Avian escape artists? Patterns, processes and costs of senescence in wild birds. – In: Shefferson, R. P., Jones, O. R. and Salguero-Gomez, R. (ed.), *The evolution of senescence in the tree of life*. Cambridge Univ. Press, pp. 156–174.
- Bouwhuis, S., Sheldon, B. C., Verhulst, S. and Charmantier, A. 2009. Great tits growing old: selective disappearance and the partitioning of senescence to stages within the breeding cycle. – *Proc. R. Soc. B* 276: 2769–2777.
- Brown, W. P. and Roth, R. R. 2009. Age-specific reproduction and survival of individually marked wood thrushes, *Hylocichla mustelina*. – *Ecology* 90: 218–229.
- Burley, N. 1986. Sexual selection for aesthetic traits in species with biparental care. – *Am. Nat.* 127: 415–445.
- Caro, S. P., Charmantier, A., Lambrechts, M. M., Blondel, J., Balthazart, J. and Williams, T. D. 2009. Local adaptation of timing of reproduction: females are in the driver's seat. – *Funct. Ecol.* 23: 172–179.
- Cichoń, M. 2003. Does prior breeding experience improve reproductive success in collared flycatcher females? – *Oecologia* 134: 78–81.
- Clutton-Brock, T. H. 1988. Reproductive success. – In: Clutton-Brock, T. H. (ed.), *Reproductive success: studies of individual variation in contrasting breeding systems*. Univ. of Chicago Press, pp. 472–485.
- Curio, E. 1983. Why do young birds reproduce less well? – *Ibis* 125: 400–404.
- de Jong, B. 2013. Testosterone a female hormone: testing the function and evolution of testosterone in female birds. – PhD thesis, Univ. of Groningen, Groningen, the Netherlands.
- Evans, S. R., Gustafsson, L. and Sheldon, B. C. 2011. Divergent patterns of age-dependence in ornamental and reproductive traits in the collared flycatcher. – *Evolution* 65: 1623–1636.
- Forslund, P. and Pärt, T. 1995. Age and reproduction in birds – hypotheses and tests. – *Trends Ecol. Evol.* 10: 374–378.
- Hammers, M., Richardson, D. S., Burke, T. and Komdeur, J. 2012. Age-dependent terminal declines in reproductive output in a wild bird. – *PLoS One* 7: e40413.
- Horváthová, T., Nakagawa, S. and Uller, T. 2012. Strategic female reproductive investment in response to male attractiveness in birds. – *Proc. R. Soc. B* 279: 163–170.
- Jones, O. R., Gaillard, J. M., Tuljapourkar, S., Alho, J. S., Armitage, K. B., Becker, P. H., Bize, P., Brommer, J., Charmantier, A., Charpentier, M., Clutton-Brock, T., Dobson, F. S., Festa-Bianchet, M., Gustafsson, L., Jensen, H., Jones, C. G., Lillandt, B. G., McCleery, R., Merilä, J., Neuhaus, P., Nicoll, M. A., Norris, K., Oli, M. K., Pemberton, J., Pietiäinen, H., Ringsby, T. H., Roulin, A., Saether, B. E., Setchell, J. M., Sheldon, B. C., Thompson, P. M., Weimerskirch, H., Jean Wickings, E. and Coulson, T. 2008. Senescence rates are determined by ranking on the fast–slow life-history continuum. – *Ecol. Lett.* 11: 664–673.
- Keller, L. F., Reid, J. M. and Arcese, P. 2008. Testing evolutionary models of senescence in a natural population: age and inbreeding effects on fitness components in song sparrows. – *Proc. R. Soc. B* 275: 597–604.
- Kim, S. Y., Velando, A., Torres, R. and Drummond, H. 2011. Effects of recruiting age on senescence, lifespan and lifetime reproductive success in a long-lived seabird. – *Oecologia* 166: 615–626.
- Kingma, S. A., Komdeur, J., Vedder, O., von Engelhardt, N., Korsten, P. and Groothuis, T. G. G. 2009. Manipulation of

- male attractiveness induces rapid changes in avian maternal yolk androgen deposition. – *Behav. Ecol.* 20: 172–179.
- Korsten, P. 2006. Avian sex allocation and ornamental coloration: a study on blue tits. – PhD thesis, Univ. of Groningen, Groningen, the Netherlands.
- Korsten, P., Lessells, C. M., Mateman, A. C., van der Velde, M. and Komdeur, J. 2006. Primary sex ratio adjustment to experimentally reduced male UV attractiveness in blue tits. – *Behav. Ecol.* 17: 539–546.
- McCleery, R. H., Perrins, C. M., Sheldon, B. C. and Charmantier, A. 2008. Age-specific reproduction in a long-lived species: the combined effects of senescence and individual quality. – *Proc. R. Soc. B* 275: 963–970.
- Millon, A., Petty, S. J., Little, B. and 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. and Nager, R. G. 1997. Why don't birds lay more eggs? – *Trends Ecol. Evol.* 12: 270–274.
- Monaghan, P., Nager, R. G. and Houston, D. C. 1998. The price of eggs: increased investment in egg production reduces the offspring rearing capacity of parents. – *Proc. R. Soc. B* 265: 1731–1735.
- Norris, K. 1993. Seasonal variation in the reproductive success of blue tits: an experimental study. – *J. Anim. Ecol.* 62: 287–294.
- Nussey, D. H., Coulson, T., Festa-Bianchet, M. and Gaillard, J. M. 2008. Measuring senescence in wild animal populations: towards a longitudinal approach. – *Funct. Ecol.* 22: 393–406.
- Nussey, D. H., Froy, H., Lemaître, J. F., Gaillard, J. M. and Austad, S. N. 2013. Senescence in natural populations of animals: widespread evidence and its implications for bio-gerontology. – *Ageing Res. Rev.* 12: 214–225.
- Perrins, C. M. 1965. Population fluctuations and clutch-size in the great tit, *Parus major*. – *J. Anim. Ecol.* 34: 601–647.
- Potti, J., Canal, D. and Serrano, D. 2013. Lifetime fitness and age-related female ornament signalling: evidence for survival and fecundity selection in the pied flycatcher. – *J. Evol. Biol.* 26: 1445–1457.
- Reid, J. M., Bignal, E. M., Bignal, S., McCracken, D. I. and Monaghan, P. 2003. Age-specific reproductive performance in red-billed choughs *Pyrrhocorax pyrrhocorax*: patterns and processes in a natural population. – *J. Anim. Ecol.* 72: 765–776.
- Schroeder, J., Burke, T., Mannarelli, M. E., Dawson, D. A. and Nakagawa, S. 2012. Maternal effects and heritability of annual productivity. – *J. Evol. Biol.* 25: 149–156.
- Schut, E., Vedder, O., Komdeur, J. and Magrath, M. J. L. 2014. Sperm depletion does not account for undeveloped eggs in blue tits *Cyanistes caeruleus*. – *Ibis* 156: 366–373.
- Sheldon, B. C., Kruuk, L. E. B. and Merila, J. 2003. Natural selection and inheritance of breeding time and clutch size in the collared flycatcher. – *Evolution* 57: 406–420.
- Stearns, S. C. 1992. The evolution of life histories. – Oxford Univ. Press.
- Svensson, L. 1992. Identification guide to European passerines, 4nd ed. – Stockholm.
- Tavecchia, G., Pradel, R., Boy, V., Johnson, A. R. and Cezilly, F. 2001. Sex- and age-related variation in survival and cost of first reproduction in greater flamingos. – *Ecology* 82: 165–174.
- Torres, R., Drummond, H. and Velando, A. 2011. Parental age and lifespan influence offspring recruitment: a long-term study in a seabird. – *PLoS One* 6: e27245.
- Trivers, R. L. 1972. Parental investment and sexual selection. – In: Campbell, B. (ed.), *Sexual selection and the descent of man 1871–1971*. Aldine Publishing Company, pp. 136–179.
- van de Pol, M. and Verhulst, S. 2006. Age-dependent traits: a new statistical model to separate within- and between-individual effects. – *Am. Nat.* 167: 766–773.
- van der Jeugd, H. P. and McCleery, R. 2002. Effects of spatial autocorrelation, natal philopatry and phenotypic plasticity on the heritability of laying date. – *J. Evol. Biol.* 15: 380–387.
- Vedder, O., Magrath, M. J. L., Harts, A. M. F., Schut, E., van der Velde, M. and Komdeur, J. 2010. Reduced extrapair paternity in response to experimental stimulation of earlier incubation onset in blue tits. – *Behav. Ecol.* 21: 9–15.
- Vedder, O., Magrath, M. J. L., Niehoff, D. L., van der Velde, M. and Komdeur, J. 2012. Declining extra-pair paternity with laying order associated with initial incubation behavior, but independent of final clutch size in the blue tit. – *Behav. Ecol. Sociobiol.* 66: 603–612.
- Verboven, N. and Visser, M. E. 1998. Seasonal variation in local recruitment of great tits: the importance of being early. – *Oikos* 81: 511–524.
- Zhang, H., Vedder, O., Becker, P. H. and Bouwhuis, S. 2015. Age-dependent trait variation: the relative contribution of within-individual change, selective appearance and disappearance in a long-lived seabird. – *J. Anim. Ecol.* 84: 797–798.

Supplementary material (Appendix JAV-00970 at <www.avianbiology.org/appendix/jav-00970>). Appendix 1.