Life span and reproductive cost explain interspecific variation in the optimal onset of reproduction

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Fitness can be profoundly influenced by the age at first reproduction (AFR), but to date the AFR–fitness relationship only has been investigated intraspecifically. Here, we investigated the relationship between AFR and average lifetime reproductive success (LRS) across 34 bird species. We assessed differences in the deviation of the Optimal AFR (i.e., the species-specific AFR associated with the highest LRS) from the age at sexual maturity, considering potential effects of life history as well as social and ecological factors. Most individuals adopted the species-specific Optimal AFR and both the mean and Optimal AFR of species correlated positively with life span. Interspecific deviations of the Optimal AFR were associated with indices reflecting a change in LRS or survival as a function of AFR: a delayed AFR was beneficial in species where early AFR was associated with a decrease in subsequent survival or reproductive output. Overall, our results suggest that a delayed onset of reproduction beyond maturity is an optimal strategy explained by a long life span and costs of early reproduction. By providing the first empirical confirmations of key predictions of life-history theory across species, this study contributes to a better understanding of life-history evolution.

KEY WORDS: Age at first reproduction, comparative method, cost of reproduction, family formation theory, life-history theory.

Life-history theory predicts that the timing of reproductive events during an individual's life affects its fitness (Cole 1954; Caswell 1982). An early age at first reproduction (hereafter AFR) can increase the number of lifetime reproductive events and shorten generation time, which, in a stable or growing population, should be favored by natural selection (Cole 1954; Bell 1980; Roff 1992; Charlesworth 1994). However, an early AFR may also be costly and reduce future survival or reproductive investment (Lack 1968; Roff 1992; Stearns 1992). Additionally, individuals could benefit from deferring breeding beyond sexual maturity if this enhances parenting skills ("constraint hypothesis": Curio 1983), secures access to higher quality territories or mates ("queuing hypothesis": Zack and Stutchbury 1992; van de Pol et al. 2007), increases reproductive output with age ("restraint hypothesis": Williams 1966; Forslund and Pärt 1995), or decreases reproductive senescence ("senescence hypothesis": Charmantier et al. 2006). If AFR is shaped by natural selection, then individuals should adopt the AFR that is associated with the highest fitness return, which may depend on individual quality and annual variation in environmental conditions.

Individuals of some species express no variation in AFR, whereas there is a large range in AFR in other species. In the latter case, only certain AFRs are associated with a high lifetime reproductive success (hereafter LRS), but the exact association appears to vary among species (Clutton-Brock 1988; Newton 1989; Oli et al. 2002; Krüger 2005; Charmantier et al. 2006; Millon et al. 2010; Kim et al. 2011; Tettamanti et al. 2012; Zhang et al. 2015). Moreover, the relationship between the species-specific AFR that is associated with the highest LRS (hereafter termed Optimal AFR) and age of sexual maturity can vary across species (Komdeur 1996; Pyle et al. 1997; Oli et al. 2002; Krüger 2005). Yet, the reasons underlying this among-species variation remain unclear, as we currently lack comparative studies that investigate the evolution of AFR and deviation in the timing of Optimal AFR during reproductive life span across species. Such a study could contribute to our understanding of the general patterns of variation in this crucial life-history trait.

Whether species-specific Optimal AFR either approximates or is shifted beyond the age of sexual maturity of the species may depend on interspecific variation in life-history or ecological factors. Across species, the pace of life (i.e., slow or fast life history) is likely to be a major factor influencing variation in AFR and timing of the species-specific Optimal AFR relative to the age of sexual maturity (Roff 1992; Stearns 1992; Charlesworth 1994). A short life span should be associated with little or no variation in AFR, and with an Optimal AFR that is close to the species'

age of maturity, as any postponement would increase the risk of death before reproduction. In contrast, a long life span allows for a larger range in AFR and increases the likelihood of a delayed Optimal AFR, an outcome that is supported by field studies (Pyle et al. 1997; Tettamanti et al. 2012). In addition to life span, other life-history, ecological, or social traits may influence the deviation from the age of sexual maturity in the species-specific Optimal AFR. Species could benefit from delayed AFR when there is a high level of parental care (e.g., altricial species), or when requiring time to learn specialized skills to survive or reproduce successfully. Conversely, a prolonged association of juveniles with their parents (i.e., family-living; Drobniak et al. 2015) may facilitate skill learning and lead to an earlier species-specific Optimal AFR ("skill hypothesis": Skutch 1961; Langen 1996). An earlier Optimal AFR may also be found in cooperatively breeding species, because helpers may buffer the reproductive costs of early AFR ("load-lightening hypothesis": Khan and Walters 2002; Santos and Macedo 2011).

Here, we use data from 34 bird species to investigate the extent of variation in reproductive strategies, and to assess the potential benefits some species may gain from delaying AFR beyond sexual maturity. We examine interspecific variation in the fitness consequences of AFR using within-species relationships between AFR and a fitness proxy averaged over all individuals within a specific AFR-class. For each of the 34 species, we identified the species- and sex-specific Optimal AFR and several derived metrics, summarized in Table 1, to assess changes in LRS or survival as a function of AFR. Information on species-specific Optimal AFR was previously unavailable for typical meta-analysis approaches due to the substantial challenge of obtaining fitness estimates of populations from several species. Its investigation allows us to make inferences about the selection pressures on AFR that could not be achieved via a simple analysis of interspecific variation in AFR. As a fitness proxy, we used the most commonly provided measure of an individual's productivity, the lifetime number of fledglings or recruits produced (LRS; Clutton-Brock 1988; Newton 1989; and other references in Table S1). Although it depends on population dynamics, while rate-sensitive fitness estimates (e.g., lambda, λ_{ind}) theoretically are more accurate proxies than LRS (Cole 1954; Lewontin 1965; Caswell and Hastings 1980), a number of studies have shown that LRS is a reliable estimate of fitness (Brommer et al. 2002; Link et al. 2002; Dugdale et al. 2010).

Specifically, we addressed the following three questions: (1) How does AFR vary within and among species? (2) Is variation in AFR associated with differences in LRS, and is the typical AFR of a species the one associated with the highest LRS? (3) Which life-history (chick developmental mode, LRS, and survival change with AFR, life span), social (family-living, helper presence), and ecological (latitude, nest predation) factors are as-

sociated with among-species variation in deviation of the Optimal AFR from age at maturity? We used a generalized linear mixed model approach in a model selection framework for the analyses, with further control for similarity in phenotype among taxa due to a shared phylogenetic history.

Materials and Methods
DATA COLLECTION

We used data from published ($N = 15$) and unpublished ($N = 21$) studies on the AFR and LRS for 34 avian species (Table S1). To find published data, we searched online databases (ISI Web of Science, Scopus) using the terms "age at first reproduction," "age at first breeding," or "age at maturity" in combination with "lifetime reproductive success," "lifetime reproductive output," or "fitness" and "avian" or "bird." We included data from long-term studies (years of monitoring exceeding the mean life span) in which individuals were followed for a sufficient period to accurately measure LRS (mean duration of study: 20.75 years; range: 8–48 years) and where LRS (including its mean, SD, and sample size) was reported separately for each category of AFR. We used GetData Graph Digitizer 2.25 (http://www.getdata-graph-digitizer.com/) to extract values from published data that were only presented in figures. Unpublished data were requested from researchers who coordinated long-term monitoring studies.

We collected species-specific data on key life-history, ecological and social lifestyle factors that might influence the effect of AFR on LRS (italicized words represents variable names used in the models), including *chick development mode* (altricial or precocial), *mean life span*, *mean body mass*, *latitude*, *nest predation risk*, *family-living,* and *helper presence*. We also collected data on the age of maturity for the estimation of an index used as variables in the model (see Section "Indices and Estimates"). Age of maturity corresponded to the age at which an individual is physiologically able to reproduce, or the minimum age recorded for breeders. Among ecological factors that can contribute to nest predation risk, nest location is well known and important (Martin and Li 1992; Martin 1993). Based on this information, we ordinally ranked the nest predation risk as high risk, ground nesters; medium risk, nests in shrubs; low risk, nests in trees; or very low risk, cavity breeders or species that build their nest floating on water and thus difficult for nest predators to access. We considered species to be family-living when offspring remain with the parents beyond independence and nonfamily-living when juveniles disperse soon after becoming independent (Drobniak et al. 2015). Species were categorized with helper when offspring regularly engage in cooperative breeding and without helper when offspring do not engage in cooperative breeding. Variables not provided for the populations studied were obtained from the Animal Ageing and

Table 1. Definitions and descriptions of the parameters and indices estimated for each sex (when possible) and each species followed by a graph illustrating the description based on the case of the Eurasian sparrowhawk (*Accipiter nisus*). See also Section "Indices and Estimates" in "Materials and Methods.".

Species parameter	Definition	Biological description	Technical description
Optimal AFR	AFR that results in the highest LRS	Reflects the species average optimum strategy of onset of reproduction	AFR that maximizes mean LRS excluding AFR categories with <10% individuals; extracted visually
Optimal AFR Range	Range of optimal AFR(s)	Reflects the range of the species average optimum strategy of onset of reproduction	Number of AFR(s) adjacent to the Optimal AFR with mean LRS values overlapped by the SE bars of the Optimal AFR; extracted visually; range from 1 to 15
Before Variation Index	LRS cost of initiating reproduction before the Optimal AFR Range	Reflects the LRS cost of adopting a reproductive strategy that is earlier than the range of species average optimum strategy of onset of reproduction	Slope before the Optimal AFR Range (center of the range) between mean LRS and AFR; average of slopes obtained when all individuals were included, when excluding AFR categories with <5 and <10% individuals (mean SE slope = 0.21); a large positive value indicates a strong negative fitness impact of reproducing before the Optimal AFR Range
After Variation Index	LRS cost of initiating reproduction after the Optimal AFR Range	Reflects the LRS cost of adopting a reproductive strategy that is later than the range of species average optimum strategy of onset of reproduction	Slope after the Optimal AFR Range (center of the range) between mean LRS and AFR; average of slopes obtained when all individuals were included, when excluding AFR categories with <5 and <10% individuals (mean SE slope = 0.18); a large negative value indicates a strong negative fitness impact of reproducing after the Optimal AFR Range
Delay Index	Relative position of the Optimal AFR during the reproductive life span	Reflects when during the average reproductive life span of a species, individuals from a species benefit the most from initiating their reproduction	Varies between 0 and 1; Delay Index 0: the optimal strategy is to start reproduction at physiological maturity; Delay Index 1: the optimal strategy is to delay the onset of reproduction to maximum AFR
Choice Index	Range of optimal AFR(s) relative to the number of AFR observed	Reflects the species average span of "beneficial choice" in AFR (i.e., AFRs leading to higher LRS)	Varies between 0 and 1. Choice Index of 0: species has only one optimal AFR; Choice Index of 1: all AFR are optimal

(Continued)

Table 1. Continued.

Species parameter	Definition	Biological description	Technical description
Life span Effect Index	Effect of AFR on the mean reproductive life span (for each AFR category: see Fig. S2)	Reflects the species-specific average effect of the onset of reproduction on survival	Correlation coefficient between mean reproductive life span and AFR (Fisher's z transformed; Koricheva et al. 2013); positive values suggest a cost of early onset of reproduction, whereas negative values suggest a cost of late onset
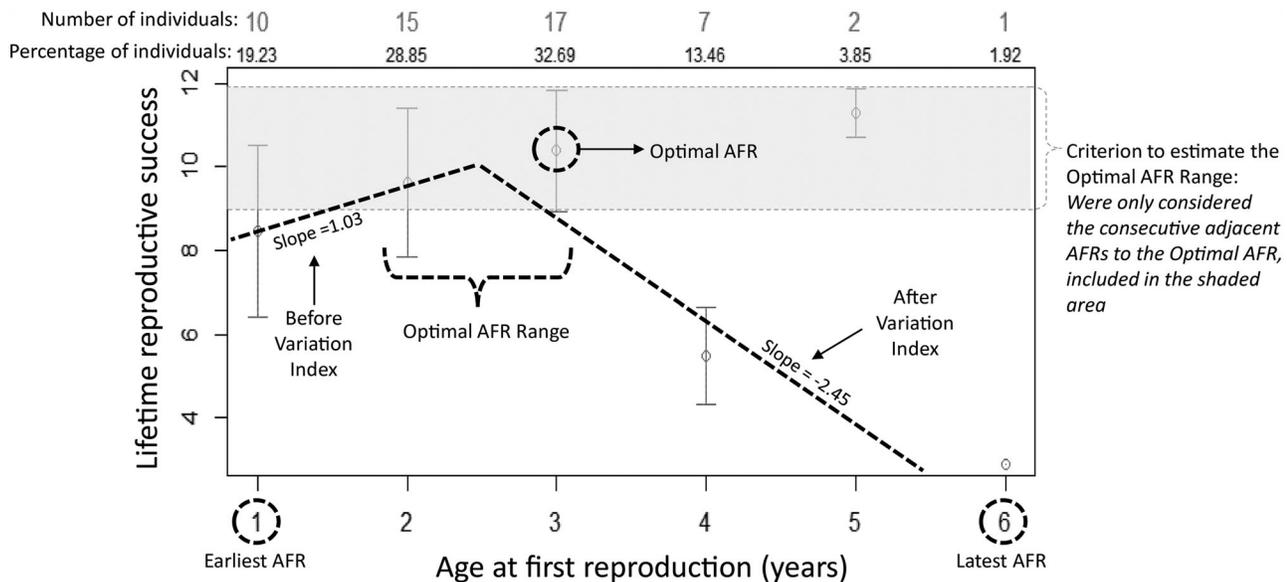
DATA COMPOSITION

The 34 species included in our study (Fig. S1) comprise 10 taxonomic orders and 22 families, with mean life span ranging from 1.4 to 18.5 years and mean LRS ranging from 0.67 to 21.16 fledglings produced over the lifetime, or from 0.54 to 2.53 recruits. For blue tits (*Cyanistes caeruleus*) and western gulls (*Larus occidentalis*), we included data from two different populations that were analyzed separately. Although AFR might be influenced by individual quality (Forslund and Pärt 1995; Kim et al. 2011), only few studies provide such information, limiting our ability to include this factor in our analyses. Data collected consisted of average values per species (i.e., body mass) or per AFR age–class category, combining data from all cohorts and years. Therefore, annual or cohort variation could not be addressed here, but we hope to do so in future work. Note that not controlling for intraspecific individual quality and combining data across cohorts and years is conservative as it reduces the chance of observing

biological patterns. Values of mean LRS ($N = 34$ species) and life span ($N = 21$ species), as well as their SD and sample size (number of individuals), were determined for each AFR age–class category (e.g., from all individuals starting to reproduce at AFR = 1-year-old, at AFR = 2, at AFR = 3, and so on), and for each sex if possible. Although it would have been more appropriate to use the geometric rather than the arithmetic mean, as it takes into account variability in fitness (see Liou et al. 1993), such data were unavailable. AFR was defined as the age at which an individual first reproduced during its life. In most species, this value corresponds to the age when a female laid at least one egg, although in some species the value reflects when a female laid a full clutch. For males, AFR corresponds to the age where its mate laid eggs, and, accordingly, reproductively competent males that failed to acquire a mate were not considered as reproductive at that time. The LRS data were based on the number of fledglings or recruits produced over the lifetime of an individual (Table S1). All LRS values were centered and scaled within species and sexes to convert the original units to those of SDs and make them comparable (Schielzeth 2010). For species with only one AFR age–class category, only a single datapoint was available. Thus, we could not

estimate the SD necessary for scaling. Instead, we used the SD of the same sex of a species with a similar value of unscaled LRS to calculate the scaled LRS. Accurate estimation of AFR and fitness proxies is challenging as it requires known-aged individuals and intensive individual-based monitoring of reproductive output throughout the life span of a representative sample of individuals, as well as data on the survival and reproduction of descendants. AFR and fitness proxies may be biased due to extra-pair paternity, or because not all reproductive events of individuals are followed due to emigration from or immigration into the study population. Consequently, AFR might be overestimated and LRS underestimated for males and overestimated for females. Such biases affect the interpretation of the relationship between AFR and fitness components, and add noise to the data. However, because a relation between AFR and extra-pair paternity and or migration has never been documented, we do not know how and to what extent such a bias would affect our interpretation.

INDICES AND ESTIMATES

Interspecific variation in deviations of the Optimal AFR from the age at sexual maturity might be explained by the association of an early or a late AFR with an increase or a decrease in subsequent survival or reproductive output. However, given the heterogeneity of the data distribution between species and sexes, conventional methods are unable to estimate changes in reproductive output or survival with a changing AFR. Thus, we calculated five derived metrics from the raw data per AFR age–class category to investigate this hypothesis (i.e., average values over all individuals from a specific AFR age–class, combining cohorts and years, for each species and where possible split by sex). These included the Delay Index, which assessed the deviations of the Optimal AFR from the age at sexual maturity, and four indices, which assessed the relationship between AFR and LRS or survival: the Before Variation Index and the After Variation Index, the Choice Index, and the Life span Effect Index (see Table 1).

We visually determined the species-specific AFR that maximized LRS (Optimal AFR; Table 1). The use of a single statistical optimization method was not feasible due to the large diversity of patterns in the relationship between AFR and LRS.

Based on the Optimal AFR, the age at sexual maturity, and the latest AFR observed within focal species and sex, we assessed the "Delay Index" representing the timing of the Optimal AFR in relation to the reproductive life span (illustrated in Table 1):

$$\text{Delay Index} = \frac{\text{Optimal AFR} - \text{maturity age}}{\text{latest AFR} - \text{maturity age}}.$$

A Delay Index equal to zero always resulted from the Optimal AFR being the age of maturity.

For 35 of 62 cases, several AFR categories had mean LRS values near that of the Optimal AFR. Hence, we determined the range of the species-specific optimum ages for the onset of reproduction, referred as the "Optimal AFR Range." The Optimal AFR Range included the AFR categories adjacent to the Optimal AFR, with mean LRS values included in the calculation of the SE bar for the mean LRS of the Optimal AFR (Table 1). The AFR categories forming the Optimal AFR Range are therefore assumed to be similarly beneficial in terms of LRS than the Optimal AFR.

Based on the Optimal AFR Range, we estimated the Before Variation Index and the After Variation Index. These indices correspond to the slope of the relationship between LRS and AFR from the earliest and the latest AFR to the center of the Optimal AFR Range. The slopes were estimated in the whole dataset with all AFR age–class categories, and in a dataset only including categories with more than 5 or 10% of the individuals (Table 1). Before and After Variation Indices represent the average of the three estimated slopes. We assumed that a delayed AFR should be favored if an early AFR is associated with a lower LRS, whereas an earlier AFR should be favored if a late AFR is associated with a lower LRS. Therefore, we expected the Delay Index to be positively correlated with the Before Variation Index, but negatively with the After Variation Index.

Based on the Optimal AFR Range and the actual value observed for the AFR, we calculated the Choice Index (Table 1), which represented the probability that individuals adopt AFR(s) with highest fitness return:

$$\text{Choice Index} = \frac{\text{Optimal AFR Range}}{\text{number of AFR categories}}.$$

In cases with only one AFR category ($N = 6$ of 62 cases), the Choice Index was assigned a zero, as in such cases there is no variation in AFR. We assumed that species with a large Optimal AFR Range relative to the number of AFR categories (i.e., with a large Choice Index) would have a lower probability of suffering a LRS cost when initiating reproduction earlier or later than the Optimal AFR. Consequently, such species may have a higher likelihood of benefiting from delayed reproduction than species with only a low number of beneficial AFR. Therefore, we expected the Delay Index to be positively correlated with the Choice Index.

The association between AFR and subsequent survival was calculated via the Life span Effect Index, that is, the correlation coefficient of the reproductive life span plotted against AFR per age–class category. We were able to estimate the Life span Effect Index for 21 of 34 species only, due to missing data for mean life span for the different AFR age–class categories for 13 species. As causes and consequences cannot be disentangled from a correlation, negative values could indicate a reproductive cost in terms of survival for individuals with a late AFR or an early AFR favored by high intrinsic mortality. By contrast, positive values could indicate a survival cost of early AFR or a late AFR favored by low intrinsic mortality (Table 1; Fig. S2). We assumed a survival cost

of early AFR to be associated with a late Optimal AFR. Therefore, we expected the Delay Index to be positively correlated with the Life span Effect Index.

We verified the robustness of our results based on the indices involving the Optimal AFR Range by considering a second method to estimate it. In this second method, the Optimal AFR Range included AFR(s) adjacent to the Optimal AFR with their 90% CIs overlapping those of the Optimal AFR. The first method (method used in the manuscript above-mentioned) represents the logic of a null hypothesis like test, which assumes an error distribution around the hypothesis (the Optimal AFR's LRS mean), and if our statistics (the other AFRs' LRS mean) do or do not fall within this range. We also considered this first method to be more straightforward, while the use of the second method is more conservative. This is because the use of 90% confidence interval (CI) indicates that the LRS population's mean of the focal AFR will fail in 90% of the time, while for the use of the SE it would do so in around 68% of the time. However, we preferred to present the results from the first method in the manuscript for two reasons. First, most of our data comes from studies with intensive monitoring of a population (Table 1, some of which pretty much sample all individuals in the population) and thus, the LRS means approach the population mean with little error. Second, for some AFRs, the LRS estimates were based on a single individual (thus without CI). Note that one could prefer to consider one or the other method depending on their data characteristics and questions.

Statistical Analysis
GENERAL PROCEDURE

All statistical analyses were carried out in R version 3.0.2 (R Core Team 2013; http://www.R-project.org/) using linear mixed-effects models (lmer function, lme4 package: Bates et al. 2014) that allow for the nonindependence of data from a single species by including species as a random factor in the model. To account for differences in sample size (N, Table S1) and decrease noise by giving greater emphasis to the more reliable species-specific estimates, all models were weighted (Garamszegi and Møller 2011) by incorporating $N - 1$ in the "weights" argument of the lmer function (Hansen and Bartoszek 2012). Note that removing the weighting did not change the results (Table S2–S7). To compare coefficients, all continuous predictors were centered (around the mean) and scaled (by the SD) before incorporation in the models (Schielzeth 2010), but we present raw data in the figures. Model assumptions of normality and homogeneity of residuals were checked by visually inspecting histograms and qq plots of the residuals as well as by plotting residuals against fitted values. For each analysis, we used a model selection process to identify the predictors that best explained variation in the response variable. Model selection was based on minimization of

the corrected Akaike's information criterion (AICc; Burnham and Anderson 2011). Support for an effect of an explanatory variable on the response variable was based on comparison of AICc values between the full model with the effect of interest included versus excluded, and when ΔAICc (AICc$_{included}$ − AICc$_{excluded}$) was less than or equal to minus five (Burnham and Anderson 2011). The 95% CI of the predictor estimates was obtained using the confint function (stats package: R Core Team 2013).

The influence of phylogenetic similarity among species was tested in the "best model" obtained during the lmer model selection process (model including only explanatory variables with ΔAICc ≤ −5). This was done by running a phylogenetically controlled mixed-effects model in ASReml-R (VSN International, Hempstead, U.K.; www.vsn-intl.com) with the same set of predictors as the lmer "best model" for each analysis. The phylogeny was included as a random effect in the form of a correlation matrix of distances from the root of the tree to the most recent common ancestor between two species. The phylogenetic effect was tested by performing an REML likelihood ratio test (LRT; comparing the REML likelihood of the same ASReml model with and without phylogeny; the log-LRT statistic was assessed against a χ^2 distribution with one degree of freedom). The phylogenetic tree used in this comparative study was adapted from a recent species-level molecular phylogenetic assessment (Jetz et al. 2012; Ericson backbone phylogeny; Fig. S1).

VARIATION IN AFR

To determine how AFR varied within and among species, we noted how often an AFR was the most frequently observed AFR within a species (mode; Fig. S3A) and considered the frequency of a specific AFR age–class across all species (Fig. S3B). Then, mean AFR and its SD were calculated for each of the 34 species. We tested the influence of sex, mean life span, and social lifestyle (family-living and presence of helpers) on variation in mean AFR across the 24 species for which we had data for both sexes (Table S1). We used a weighted linear mixed-effect model with population mean AFR as the unit of analysis, and included species as a random effect. Because AFR cannot exceed the mean life span, AFR and mean life span should be correlated positively. Therefore, we tested whether the estimated correlation between AFR and mean life span differed significantly from the null expectation. To do so, we performed a conservative permutation analysis (following Charmantier et al. 2006; Lane et al. 2011). For each mean life span, a mean AFR value was randomly selected with replacement from our dataset. During resampling, we fixed the rule that AFR was smaller than mean life span. Data were resampled 500 times and analyzed using the same weighted linear mixed-effect model as described above. We estimated the average estimates and 95% CIs over the 500 model outputs and compared them to those observed.

FITNESS CONSEQUENCES OF AFR

To determine whether variation in AFR has consequences for LRS, the correlation between AFR and LRS (within-species) as well as its average influence (among-species effect) was investigated using within-subject centering (van de Pol and Wright 2009). The within-species effect was calculated for each sex and species by subtracting the species- and sex-specific mean AFR from each AFR age–class category observed within sex and species (within-species AFR effect; van de Pol and Wright 2009). The among-species effect was determined as the mean AFR within sex and species (between-species AFR effect; van de Pol and Wright 2009). To test for nonlinear effects of AFR on LRS within species, a quadratic term of the within-species AFR effect was included in the model. The AFR values were centered to reduce collinearity between the within-species AFR effect and the within-species AFR^2 effect. Centering enabled independent interpretation of the linear and the curvature effect (Schielzeth 2010). Due to apparent interspecific variation in the relationship between AFR and LRS, the ideal analytical framework would have been a random intercept and slope model that estimated separate intercepts and slopes for each species. However, our sample size did not provide sufficient power to support such a model (Martin et al. 2011; van de Pol 2012). Therefore, we ran a standard weighted linear mixed-effect model using the average LRS within AFR age–class categories, with sex and population as units of analysis. Species was included as a random effect in this analysis, along with the natural log of mean body mass as a covariate. We included life span in this model as a covariate, because reproductive performance corrected for survival estimates approximates real fitness better (Roff 1992). Although the output of the analysis with and without life span were similar, life span is strongly correlated with the between-species AFR effect. Therefore, we present the analysis without life span to avoid issues caused by collinearity (Dormann et al. 2013).

To assess whether the most frequently observed AFR within each species was an optimal strategy, the AFR mode within each species was correlated with the AFR that maximized LRS (i.e., Optimal AFR, Table 1). Then, the species-specific Optimal AFR was compared to the age at sexual maturity to identify species with optimal delayed reproduction (i.e., species with Optimal AFR > age at maturity). Finally, the Optimal AFR was correlated with life span to identify if a benefit from delaying the onset of reproduction beyond sexual maturity coincided with long life span.

## AMONG-SPECIES VARIATION IN THE RELATIVE TIMING OF OPTIMAL AFR

We used a model selection and model averaging approach (Grueber et al. 2011) to determine the factors that explain interspecific variation in deviations of the Optimal AFR from the age

of sexual maturity (i.e., Delay Index, Table 1). All life-history, social, and ecological factors listed above were included (see Section "Data Collection"), as well as indices reflecting the relationship between LRS and AFR: the Choice Index, and the Before and After Variation Indices (see above, Table 1). In a second analysis, the Life span Effect Index was included for the 21 species for which we had detailed data on life span mean for each AFR age–class category (Table 1, Fig. S2). Due to reduced statistical power of the latter (as on restricted dataset, see above), in the results section we present only the estimates and 95% CI of the analysis excluding the Life span Effect Index. Each of the before-mentioned variables, and the biologically relevant interactions (Before Variation Index × After Variation Index, Choice Index × Before Variation Index, Choice Index × After Variation Index, Choice Index × family-living, Choice Index × helper presence, mean life span × family-living, mean life span × helper presence, nest predation risk × family-living, and nest predation risk × helper presence; Table S8 lists predictions associated with these interactions) were tested against the Delay Index in a weighted linear mixed-effect models with Delay Index for each sex and population as a unit of analysis. Species was added as a random effect. Sex and the natural logarithm of body mass were included as default fixed-effects variables to control for allometry and any differences between sexes. Due to a large number of possible combinations between all predictors, we used the R package MuMIn (Barton 2013) to perform model selection. The candidate model set included models with $\Delta AICc \leq 5$, $\Delta AICc$ being the AICc of the focal model minus the AICc of the best model (see Table S9 for analysis excluding Life span Effect Index and Table S10 for analysis including Life span Effect Index). To estimate the relative importance of a factor, we summed the Akaike's weights of the models in the set of best models including the focal factor, following the method described by Symonds and Moussalli (2011).

Results
VARIATION IN AFR

Across species ($N = 34$), AFR ranged from one to 20 years. In 11 species, the modal AFR was one year (Fig. S3A). In 70% of species, AFR was aged 3 or less and only 20% of species had an AFR that was greater than 6 years of age (Fig. S3B). Within species, the number of AFR categories ranged from one to 15 (average = 4.8 years; SD = 3.1; $N = 34$) and the mean AFR and its SD varied among species (Fig. 1). Removing sex or social variables (i.e., family-living, helper presence) from the model did not influence mean AFR (Table 2). However, mean AFR correlated positively with mean life span (parameter estimate for mean life span = 0.87, 95% CI [hereafter given in brackets after all estimates]: 0.72–1.02; Table 2), and this correlation exceeded
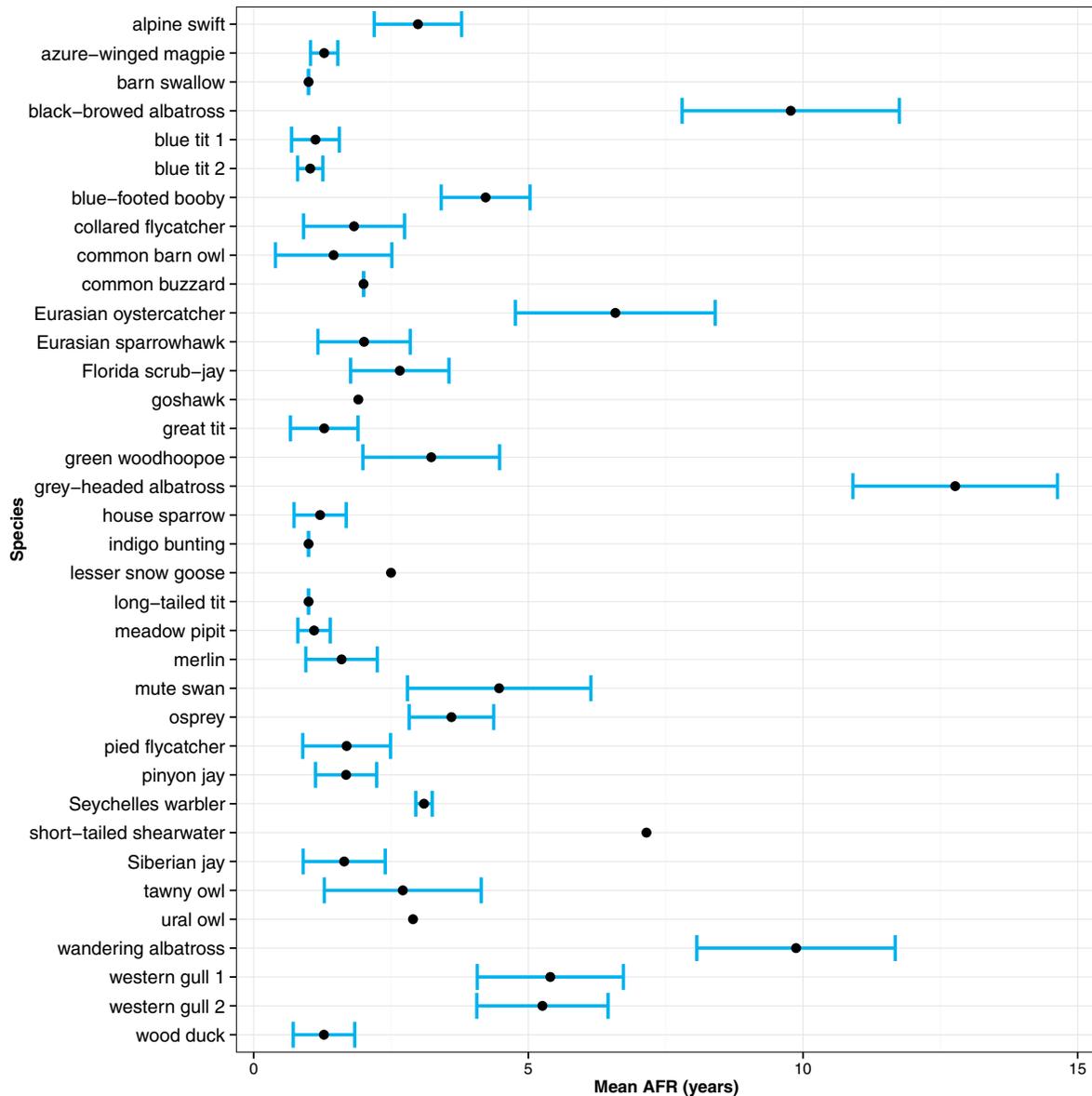
Figure 1. Mean AFR (years) and SD for all 36 populations (34 species; both sexes combined). Mean AFR ranged from 1 to 12.8 years (mean ± SD = 3.0 ± 2.6, *N* = 36), and SD from 0 to 2.31 (mean ± SD = 0.80 ± 0.58, *N* = 36). A number after the name of a species indicates different populations.

that expected from the mathematical interdependence of AFR and mean life span (estimated by the permutation test: mean of 500 simulations: 0.63 [0.87–0.79], ΔAICc = −22.24). A positive relationship between AFR and mean life span was also apparent when comparing the AFR age–class categories within each species (Fig. 2). The phylogenetic effect on mean AFR was significant (LRT = 6.99, degrees of freedom [df] = 1, *P* < 0.01).

FITNESS CONSEQUENCES OF AFR

Our within-subject centering approach revealed no among-species effect of AFR on LRS, but a within-species effect of both AFR and AFR^2 (Fig. 3). Within species, there was strong directional

selection for an early AFR (within-species AFR effect estimate= −0.54 [−0.70 to −0.39]; Table S11), as well as stabilizing selection (within-species AFR^2 effect estimate = −0.26 [−0.43 to −0.10]; Table S11; Fig. 3). The phylogenetic effect on mean LRS for the corresponding AFR was not significant (LRT: *P* = 1). Twenty-six of 34 species (76%) had an Optimal AFR delayed beyond the age at maturity, and this delay correlated positively with a longer mean life span (slope = 0.28, $r_{Spearman}$ = 0.61, *P* < 0.005; Fig. 4). Both the most-observed AFR and mean AFR correlated with the AFR with the highest LRS (Optimal AFR vs. modal AFR: slope = 0.98, $r_{Spearman}$ = 0.80, *P* < 0.0001; Optimal AFR vs. mean AFR: slope = 0.95, $r_{Spearman}$ = 0.84, *P* < 0.0001).

Table 2. Effect of sex, mean life span of species, family-living, and presence of helpers on mean AFR within a species (*N* = 26 populations, 24 species for which data were available for both sexes).

	SD	Estimate	95% CI	ΔAIC$_c$
Fixed effects				
Intercept		0.10	(−0.14, 0.34)	–
Sex: female		0.00	na	−2.51
Sex: male		0.03	(0.01, 0.05)	
Mean life span$_{species}$[1]		0.87	(0.72, 1.02)	−61.65[2]
Family-living: no		0.00	na	2.58
Family-living: yes		−0.12	(−0.89, 0.64)	
Helper presence: no		0.00	na	2.08
Helper presence: yes		−0.33	(−1.16, 0.50)	
Random effects				
Species	0.52		(0.40, 0.70)	
Residuals	0.93		(0.72, 1.26)	

Estimates and 95% CI are presented. ΔAIC$_c$ corresponds to the change in AIC$_c$ when the specific parameter was included versus excluded from the full model.
[1]Factor centered and scaled.
[2]Support for inclusion of the factor.
na = not applicable.

The latter was true even when only looking at species with a large number of observed AFR age–class categories (Table S12).

AMONG-SPECIES VARIATION IN THE RELATIVE TIMING OF OPTIMAL AFR

Although the Delay Index was associated with indices that reflect a change in LRS and survival as a function of AFR (i.e., Choice, Before Variation, and Life span Effect Indices; Table 1, all predictor weights ≥ 0.45), it was only marginally related to social (predictor weights < 0.45) or ecological factors (predictor weights ≤ 0.30; Tables 3 and 4). A delayed optimal onset of reproduction (i.e., large Delay Index) was found in species with a large range of optimal AFR relative to reproductive life span (Choice Index: estimate = 0.44 [0.15–0.72]; Table 3). Moreover, a large Delay Index was found in species in which early AFR was associated with a decreased LRS (Before Variation Index estimate = 0.30 [0.07–0.54], Table 3 and Fig. 3) and a reduced reproductive life span (Life span Effect Index estimate = 0.54 [0.37–0.72], Table 4). Finally, larger species showed later optimal onset of reproduction than smaller species (ln[body mass] estimate: 0.35 [0.01–0.69], Table 3). These results remained quantitatively similar when using indices estimated with the Optimal AFR Range determined under the criterion where AFR categories included in the Optimal AFR range were AFR(s) adjacent to the Optimal

AFR with their 90% CIs overlapping those of the Optimal AFR (Tables S13–S16).

Discussion

AFR is a key life-history parameter with consequences for individual reproductive output, and hence its effect on fitness has been studied in a number of intraspecific studies (see references in Table S1). Here, we provide a first comparative analysis using a representative amount of averaged within-species information to examine interspecific variation in the relationship between AFR and LRS. Identifying the species-specific AFR that results in the highest LRS (i.e., Optimal AFR) allowed us to investigate not only within- and among-species variation in the relationship between AFR and LRS, but also differences in the benefits and costs associated with variable timing in the onset of reproduction among species. Our results demonstrated that the most commonly observed AFR within a species corresponds to the species-specific Optimal AFR. Among species, Optimal AFR varied considerably. This study showed that life span was a major predictor of the relative timing of the Optimal AFR within the reproductive life span and that they correlated positively. Additionally, our analyses revealed that Optimal AFR beyond the age of maturity was associated with a decrease in fitness and survival that arose from starting to reproduce at earlier ages than the Optimal AFR.

AFR varied considerably both within and among species (Fig. 1). Some species displayed no variation in AFR (e.g., long-tailed tit, *Aegithalos caudatus*; indigo bunting, *Passerina cyanea*; common buzzard, *Buteo buteo*), whereas others exhibited large variation (e.g., mute swan, *Cygnus olor*; wandering albatross, *Diomedea exulans*, Eurasian oystercatcher, *Haematopus ostralegus*). Most species that expressed variation in AFR experienced negative consequences for LRS from initiating reproduction either too early or too late in life (e.g., the Optimal AFR was at an intermediate point in the reproductive life span: between the age of sexual maturity and the oldest AFR observed within a population), whereas for others the earliest or latest observed AFR resulted in the highest LRS (Fig. 3). This suggests simultaneous directional and stabilizing selection. If the pattern observed is a footprint of selection acting at the individual level, this should lead to a decrease in average AFR and a reduction in its evolvability. However, a comparative study directly investigating individual variance would be needed to assess this hypothesis.

Although there was no overall interspecific relationship between AFR and LRS, a within-species relationship between AFR and LRS (Table S11) indicates that evolutionary processes operate at different scales. On the one hand, large-scale evolution acts on all individuals within a population, which might confound
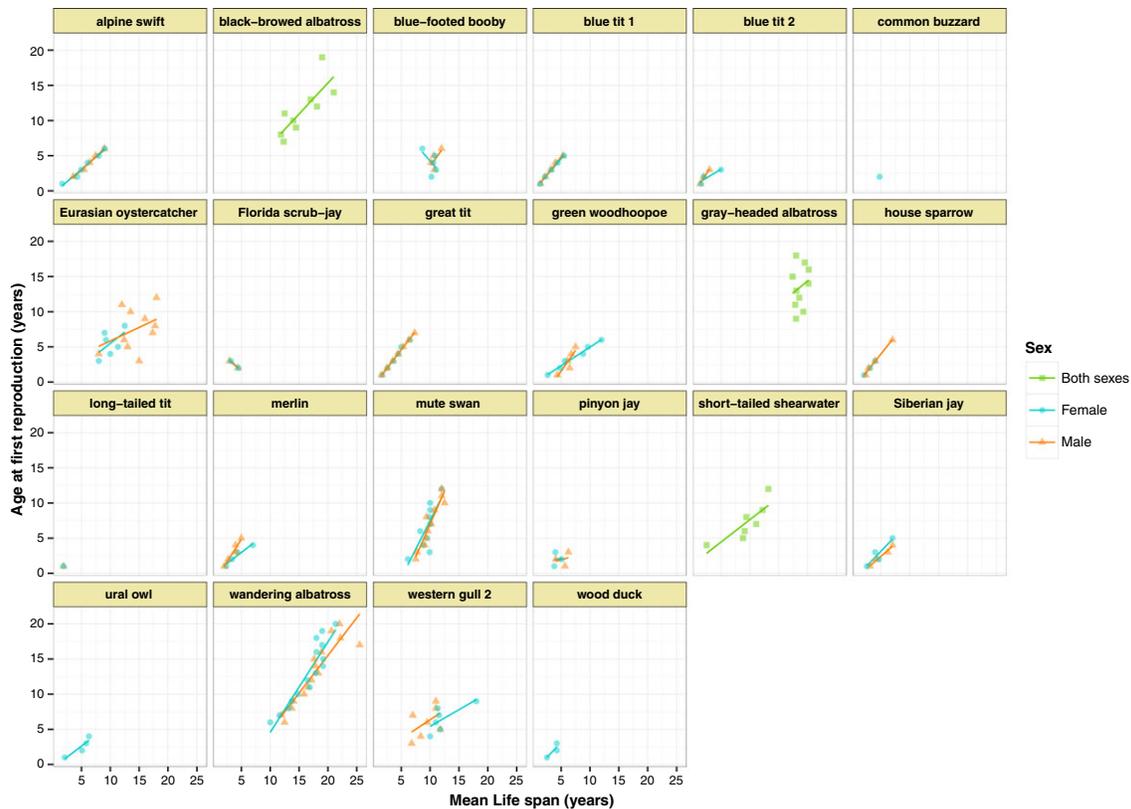
Figure 2. Relationship between AFR (years) and the associated mean life span within species and sexes (years, *N* = 22 populations [21 species] for which detailed data on mean life span per AFR category were available). Each point is the mean life span of individuals within each AFR category. A number after the name of a species indicates different populations. Regression lines are based on the raw data and were drawn for all cases independent of whether the correlation was significant or not.

the detection of a relationship between AFR and LRS. On the other hand, local-scale evolution acts on individuals, such as on variation in individual quality (Van Noordwijk and De Jong 1986; Kim et al. 2011), food availability (Brommer et al. 1998), territory quality (Krüger 2005), population density (Krüger 2005), or climatic conditions (Gibbs and Grant 1987; Kim et al. 2011), which also might drive the relationship between AFR and LRS. Differences among cohorts in the relationship between AFR and LRS (Brommer et al. 1998; Kim et al. 2011) might additionally explain the absence of a between-species effect of AFR on LRS, but our data did not allow us to take potential differences in individual or cohort quality into account.

Among-species variation in mean AFR correlated positively with life span (Table 2), supporting the life-history paradigm that the pace of life fundamentally affects reproductive timing (Roff 1992; Stearns 1992; Charlesworth 1994). Furthermore, the species-specific optimal reproductive strategy varied among species, where species with a mean life span of up to six years (median mean life span: 1.9 years) had an Optimal AFR of one year, providing a quantitative benchmark to differentiate between short- and long-lived bird species. At the other extreme, species

with a longer life span had a later mean AFR (Table 2) and a later Optimal AFR (Fig. 4).

When relating the position of the Optimal AFR to the age of sexual maturity of a species, our results revealed that the Optimal AFR was beyond the age of maturity in 26 of 34 species. Thus, individuals in these species appear to benefit from delaying their onset of reproduction (e.g., female tawny owl, *Strix aluco* (Millon et al. 2010); female goshawk, *Accipiter gentilis* (Krüger 2005); sexes combined short-tailed shearwater *Puffinus tenuirostris* (Wooller et al. 1989)). The association of an Optimal AFR beyond the age of sexual maturity with a long mean life span suggests that the positive effect of life span on mean AFR is not caused by physiological constraints associated with maturity. Indeed, longer lived species mature later and still adopt an AFR after their age of maturity, and they experienced a larger LRS as a consequence (Fig. 4). Such a benefit from delayed AFR until after the age of sexual maturity was found not only in long-lived species, but also in six of 11 short-lived species with a mean life span of less than three years (Fig. 4).

When controlling for reproductive life span, we found that interspecific variation in deviation of the Optimal AFR from the
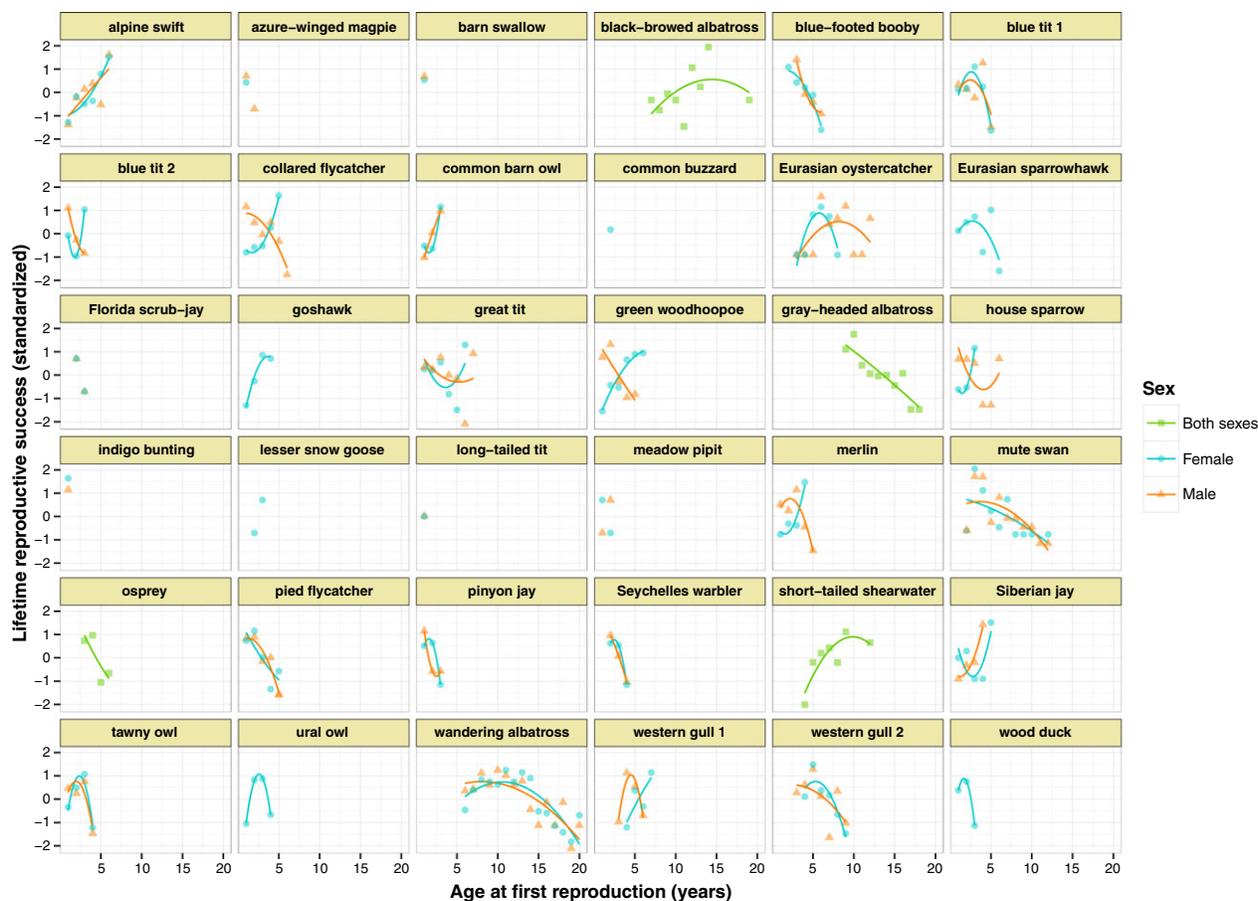
Figure 3. Variation in AFR and consequences on fitness. Relationship between standardized LRS and AFR for the 36 populations of the 34 species, separated by sex where possible (a point is the mean LRS (centered and scaled) over all individuals that started to reproduce at a specific AFR). Curves represent quadratic fit of the relationship between standardized LRS and AFR independent of whether the relationship was significant or not.

age at maturity was primarily associated with a change in survival and fitness with AFR (Tables 3 and 4). Moreover, our results confirmed that an early AFR might be favored by a short reproductive life span and vice versa (Roff 1992; Stearns 1992; Charlesworth 1994; Table 4 and Fig. 2). Species in which an early onset of reproduction was associated with a reduced reproductive life span benefited from delaying AFR (Table 4 and Fig. S2), which supports the restraint hypothesis (Williams 1966; Forslund and Pärt 1995). Moreover, the cost of early reproduction, measured as a decrease in LRS relative to the optimum, correlated positively with the optimal delayed reproductive onset (Table 3). An early reproductive onset might be costly because of differences in individual competitive ability, if this early onset leads to unequal probabilities of acquiring a high-quality territory (Ens et al. 1995; Ekman et al. 2001; Prevot-Julliard et al. 2001; Cooper et al. 2009) or to high physiological costs (Hawn et al. 2007). This pattern suggests that different factors affect the evolution of sexual maturity and the onset of reproduction. Interestingly, in species where there was limited change in LRS relative to AFR, postponing the

onset of reproduction beyond sexual maturity was chosen over other earlier AFR leading to similar fitness. Therefore, not reproducing as soon as physiologically capable might provide further benefits. Our results provide empirical support for the hypothesis that costs of reproduction shape the onset of reproduction (Lack 1968; Roff 1992; Stearns 1992).

It has been argued that variation in AFR might be suboptimal, reflecting constraints on early breeding, such as limited access to high-quality mates or to high-quality breeding sites (Lack 1968; Emlen 1982; Stearns 1989; Koenig et al. 1992). However, our results suggest that the onset of reproduction most likely is an optimal strategy, because the most commonly observed AFR coincides with the Optimal AFR. A number of theories developed to explain the evolution of cooperative breeding depicts the decision of offspring to remain with their parents beyond sexual maturity as a "best of a bad job" strategy that reflects dispersal constraints (Emlen 1982; Koenig et al. 1992; Arnold and Owens 1998; Hatchwell and Komdeur 2000). The lack of a strong correlation between the Delay Index and the different social lifestyles
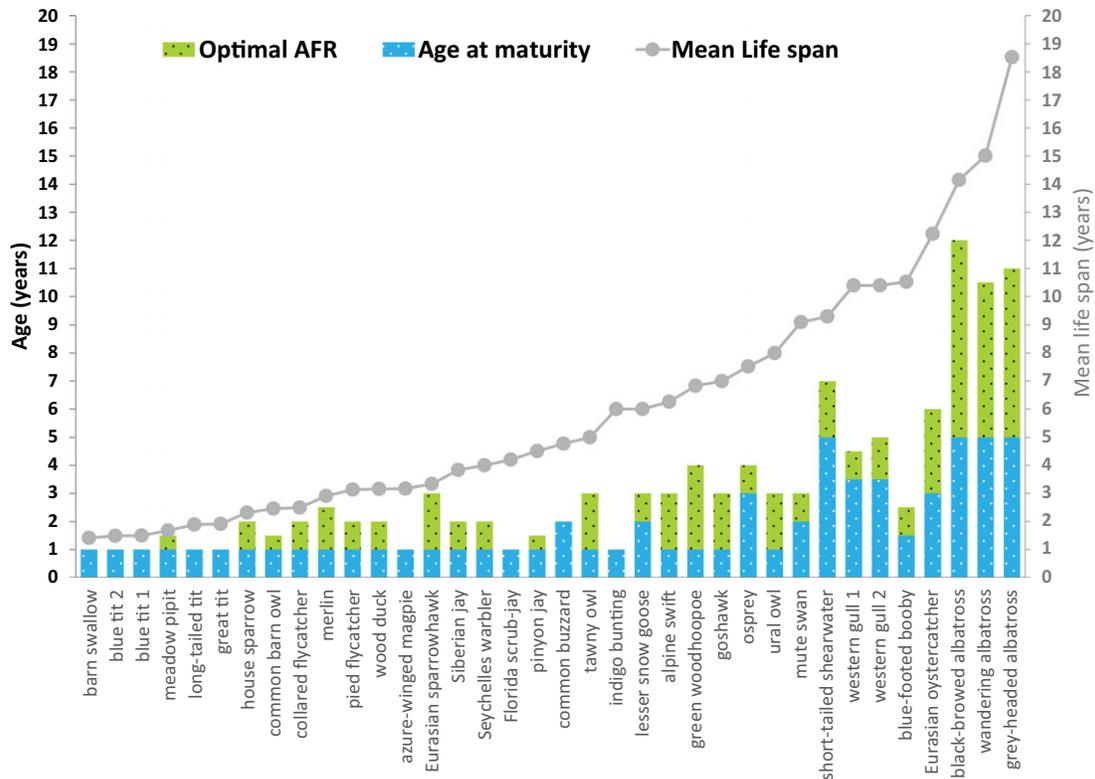
Figure 4. Species-specific Optimal AFR presented relative to the species age at maturity (left *y*-axis) with species ordered by mean life span (both sexes combined). Mean life span values are represented by the gray line and the right *y*-axis. A number after the name of a species indicates the different populations included in the study.

suggests that delayed onset of reproduction might not have evolved due to constraints (Ekman et al. 2004; Ekman 2007), but instead constitutes a beneficial life-history decision, which correlates positively with life span (Covas and Griesser 2007). Still, the lack of a correlation between social factors and variation in the optimal timing of reproduction could reflect the fact that our data are skewed toward pair-breeding, northern hemisphere species. Including more tropical and southern hemisphere species might alter our results and magnify the role of social factors in our analyses, as the latter two groups are often long-lived (Valcu et al. 2014), stay longer with their parents (Russell 2000), and are more likely to breed cooperatively (Jetz and Rubenstein 2011). The current paucity of long-term studies in these regions potentially biases our view of life-history evolution (Martin 2004).

Although we found no significant effect of sex in our study, the relationship between AFR and LRS, and the optimal timing of reproduction, sometimes differed between sexes (Figs. 3 and S4). Twelve of 24 species showed sex-specific differences in the Delay Index; females benefited more from earlier onset than males in seven species, whereas the opposite was true in five species (Fig. S4). Intraspecific studies have demonstrated sex differences in the relationship between LRS and AFR (e.g., western gull, *L. occidentalis* (Pyle et al. 1997); green woodhoopoe, *P. purpureus*

(Hawn et al. 2007); blue-footed booby, *Sula nebouxii* (Kim et al. 2011)), highlighting the need to consider sex-specific variation in life-history traits (McDonald 1993; Santos and Nakagawa 2012). The positive correlation between the relative timing of Optimal AFR and body mass concurs with findings in mammals where AFR is correlated strongly with body mass (larger mammals having later AFR; Estern 1979; Wootton 1987). Nevertheless, we additionally demonstrated that, in birds, larger species benefited more from delaying the onset of reproduction beyond sexual maturity than smaller species. Therefore, body mass seems to be an important factor associated with variation in reproductive strategy. Animals with a large body size invest substantial amounts of resources into growth. Although, in birds, growth after sexual maturity is negligible (Ricklefs 1983), postponing the onset of reproduction might counterbalance the cost endured during the development phase and increase the probability of a high lifetime reproductive output.

In conclusion, AFR varies both within and among species, and this variation is reflected in LRS. The most frequently observed AFR within a species results in the highest LRS. Where an AFR delayed beyond physiological maturity co-occurred with the highest LRS, this delay was mainly associated with a long life span and a decrease in LRS and future survival linked to early

Table 3. Relative importance of predictors included in the full model for the analysis of Delay Index variation excluding Life span Effect Index (N = 36 populations, 34 species) and model averaging estimates (based on 53 models with ΔAICc [AICc$_{\text{focal model}}$ − AICc$_{\text{best model}}$] $\leq$ 5, see Table S9).

Predictors	Predictor weight[1]	Relative importance of predictors[2]	Model averaging estimates[3,4]	95% CI
Intercept			0.14	(−0.71, 1.00)
ln (body mass)	0.49	1.00	0.35	(0.01, 0.69)
Sex	0.49	1.00	Both: 0.00	na
			Female: −0.06	(−0.94, 0.82)
			Male: −0.24	(−1.12, 0.65)
Choice Index[5]	0.49	1.00	0.44	(0.15, 0.72)
Before Variation Index[5]	0.48	0.98	0.30	(0.07, 0.54)
Family-living	0.40	0.82	No: 0.00	na
			Yes: 0.01	(−1.45, 1.48)
Helper presence	0.40	0.82	No: 0.00	na
			Yes: 0.49	(−2.12, 3.31)
Nest predation risk	0.28	0.56	0.03	(−0.34, 0.43)
Choice Index: helper presence	0.25	0.51	No: 0.00	na
			Yes: −0.67	(−2.45, −0.18)
Mean life span	0.25	0.50	0.09	(−0.26, 0.60)
Choice Index: family-living	0.23	0.46	No: 0.00	na
			Yes: 0.57	(−0.50, 3.00)
Mean life span: helper presence	0.22	0.44	No: 0.00	na
			Yes: 2.48	(2.66, 8.49)
Mean life span: family-living	0.21	0.43	No: 0.00	na
			Yes: −1.91	(−6.12, −2.72)
Nest predation risk: family-living	0.21	0.43	No: 0.00	na
			Yes: 0.91	(1.23, 2.97)
Before Variation Index: Choice Index	0.17	0.35	0.13	(−0.08, 0.82)
After Variation Index[5]	0.14	0.28	−0.04	(−0.37, 0.05)
Nest predation risk: helper presence	0.10	0.21	No: 0.00	na
			Yes: −0.41	(−3.82, −0.13)
Chick development mode	0.05	0.11	Altricial: 0.00	na
			Precocial: −0.02	(−1.20, 0.74)
Latitude	0.03	0.07	−0.01	(−0.41, 0.23)
Before Variation Index: After Variation Index	0.00	0.01	0.00	(−0.08, 0.19)

[1]Sum of model weights from Table S9 including the focal predictor.

[2]Predictor weight relative to the highest weighted predictor.

[3]Model averaging estimates according to full model averaging approach because the best AIC$_c$ model is not strongly weighted (weight = 0.05; Symonds and Moussalli 2011).

[4]Reference levels of categorical variables have an estimate of zero; estimates reflect difference in slope between the reference level and focal level.

[5]Predictors reflecting the relationship between LRS and AFR, see Table 1 and the Section "Indices and Estimates" of "Materials and Methods."

na = not applicable.

Note: The relative importance of body mass and sex is due to their inclusion by default in each model to control for allometry and sex differences. All continuous variables are centered and scaled.

reproduction. Our study is the first to provide empirical confirmation of several key predictions of life-history theory across species that life span and costs of reproduction shape reproductive timing (Lack 1968; Roff 1992; Stearns 1992; Charlesworth 1994). Moreover, the finding that, in long-lived species, postponing the onset of independent reproduction is an optimal strategy has important implications for long-held perspectives on the evolution of sociality. Hitherto, the decision of young birds to remain with their parents and become helpers has been viewed as a suboptimal response to the lack of breeding opportunities (Emlen 1982; Koenig et al. 1992; Arnold and Owens 1998). Our results clearly indicate that this decision can be a strategy to mitigate the costs of early

Table 4. Relative importance of predictors included in the full model for the analysis of Delay Index variation including Life span Effect Index (N = 22 populations, 21 species) and model averaging estimates (based on 28 models with ΔAICc [AICc$_{\text{focal model}}$ − AICc$_{\text{best model}}$] ≤ 5, see Table S10).

Predictors	Predictor weight[1]	Relative importance of predictors[2]	Model averaging estimates[3,4]	95% CI
Intercept			0.42	(−0.34, 1.18)
ln (body mass)	0.57	1.00	0.36	(−0.23, 0.95)
Sex	0.57	1.00	Both: 0.00	na
			Female: −0.67	(−1.43, 0.09)
			Male: −0.35	(−1.11, 0.42)
Choice Index[5]	0.57	1.00	0.35	(0.17, 0.52)
Life span Effect Index[5]	0.57	1.00	0.54	(0.37, 0.72)
After Variation Index[5]	0.38	0.66	−0.20	(−0.56, −0.05)
Helper presence	0.26	0.46	No: 0.00	na
			Yes: 0.56	(0.03, 2.40)
Family-living	0.24	0.42	No: 0.00	na
			Yes: −0.32	(−1.59, 0.08)
Mean life span	0.23	0.41	0.20	(−0.01, 0.98)
Chick development mode	0.10	0.17	Altricial: 0.00	na
			Precocial: −0.11	(−1.28, 0.04)
Nest predation risk	0.10	0.17	0.06	(−0.08, 0.74)
Latitude	0.07	0.13	0.02	(−0.32, 0.56)
Choice Index: family-living	0.04	0.07	No: 0.00	na
			Yes: 0.03	(−0.14, 0.87)
Choice Index: helper presence	0.04	0.07	No: 0.00	na
			Yes: 0.03	(−0.18, 1.07)
Before Variation Index[5]	0.03	0.06	0.01	(−0.16, 0.35)

[1]Sum of model weights from Table S10 including the focal predictor.
[2]Predictor weight relative to the highest weighted predictor.
[3]Model averaging estimates according to full model averaging approach because the best AIC$_c$ model is not strongly weighted (weight = 0.10; Symonds and Moussalli 2011).
[4]Reference levels of categorical variables have an estimate of zero; estimates reflect difference in slope between the reference level and focal level.
[5]Predictors reflecting relationship between LRS or survival and AFR, see Table 1 and the Section "Indices and Estimates" of "Materials and Methods."
na = not applicable.
Note: The relative importance of body mass and sex is due to their inclusion by default in each model to control for allometry and sex differences. All continuous variables are centered and scaled.

reproduction. Overall, our results are consistent with life-history theory and challenge current theories on the evolution of family formation and cooperative breeding.

EM compiled the data, performed the statistical analysis, and wrote the first draft of the manuscript. All authors contributed to revisions (especially MG) and gave final approval for publication. MG helped with data compilation and reflection on the manuscript. SMD, SN, and MG helped with the statistical methods and estimation of the indices. SMD wrote the R script to automate the estimation of two indices. The authors have no conflict of interest.

DATA ARCHIVING
The doi for our data is http://dx.doi.org/10.5061/dryad.dk8q3.

LITERATURE CITED
Arnold, K. E., and I. P. F. Owens. 1998. Cooperative breeding in birds: a comparative test of the life history hypothesis. Proc. R. Soc. B 265:739–745.

Barton, K. 2013. MuMIn: multi-model inference. R package version 2.0.0. Available at http://R-Forge.R-project.org/projects/mumin/.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-7. Available at http://CRAN.R-project.org/package=lme4.

Bell, G. 1980. The costs of reproduction and their consequences. Am. Nat. 116:45–76.

Brommer, J. E., H. Pietiainen, and H. Kolunen. 1998. The effect of age at first breeding on Ural owl lifetime reproductive success and fitness under cyclic food conditions. J. Anim. Ecol. 67:359–369.

Brommer, J. E., J. Merilä, and H. Kokko. 2002. Reproductive timing and individual fitness. Ecol. Lett. 5:802–810.

Burnham, K. P. and D. R. Anderson. 2011. AIC model selection and multi-model inference in behavioral ecology: some background, observations, and comparisons. Behav. Ecol. Sociobiol. 65:23–35.

Caswell, H. 1982. Life history strategies. Pp. 285–305 in J. M. Cherrett, ed. Ecological concepts. Blackwell Scientific Publications, Oxford, U.K.

Caswell, H., and A. Hastings. 1980. Fecundity, developmental time, and population-growth rate—an analytical solution. Theor. Popul. Biol. 17:71–79.

Charlesworth, B. 1994. Evolution in age structured populations. Cambridge Univ. Press, Cambridge, U.K.

Charmantier, A., C. Perrins, R. H. McCleery, and B. C. Sheldon. 2006. Quantitative genetics of age at reproduction in wild swans: support for antagonistic pleiotropy models of senescence. Proc. Natl. Acad. Sci. USA 103:6587–6592.

Clutton-Brock, T. H. 1988. Reproductive success. Univ. of Chicago Press, Chicago, IL.

Cole, L. C. 1954. The population consequences of life history phenomena. Q. Rev. Biol. 29:103–137.

Cooper, N. W., M. T. Murphy, L. J. Redmond, and A. C. Dolan. 2009. Density-dependent age at first reproduction in the eastern kingbird. Oikos 118:413–419.

Covas, R., and M. Griesser. 2007. Life history and the evolution of family living in birds. Proc. R. Soc. B 274:1349–1357.

Curio, E. 1983. Why do young birds reproduce less well? Ibis 125:400–404.

del Hoyo, J., A. Elliott, J. Sargatal, and D. A. Christie. 1992–2006. Handbook of the birds of the world. Lynx Edicions, Barcelona.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46.

Drobniak, M. S., G. Wagner, E. Mourocq, and M. Griesser. 2015. Family living: an overlooked but pivotal social system to understand the evolution of cooperative breeding. Behav. Ecol. 26:805–811.

Dugdale, H. L., P. Nouvellet, L. C. Pope, T. Burke, and D. W. MacDonald. 2010. Fitness measures in selection analyses: sensitivity to the overall number of offspring produced in a lifetime. J. Evol. Biol. 23:282–292.

Ekman, J. 2007. Delayed dispersal: youth costs carry lifetime gains. Curr. Biol. 17:R417–R418.

Ekman, J., S. Eggers, M. Griesser, and H. Tegelström. 2001. Queuing for preferred territories: delayed dispersal of Siberian jays. J. Anim. Ecol. 70:317–324.

Ekman, J., J. L. Dickinson, B. J. Hatchwell, and M. Griesser. 2004. Delayed dispersal. Pp. 35–47 In W. D. Koenig and J. L. Dickinson, eds. Ecology and evolution of cooperative breeding in birds. Cambridge Univ. Press, Cambridge, U.K.

Emlen, S. T. 1982. The evolution of helping. 1. An ecological constraints model. Am. Nat. 119:29–39.

Ens, B. J., F. J. Weissing, and R. H. Drent. 1995. The despotic distribution and deferred maturity—two sides of the same coin. Am. Nat. 146:625–650.

Estern, D. 1979. Size, life history and ecology in mammals. Afr. J. Ecol. 17:185–204.

Forslund, P., and T. Pärt. 1995. Age and reproduction in birds: hypothesis and tests. Trends Ecol. Evol. 10:374–378.

Garamszegi, L. Z., and A. P. Møller. 2011. Nonrandom variation in within-species sample size and missing data in phylogenetic comparative studies. Syst. Biol. 60:876–880.

Gibbs, H. L., and P. R. Grant. 1987. Ecological consequences of an exceptionally strong El-Niño event on Darwin Finches. Ecology 68:1735–1746.

Grueber, C. E., S. Nakagawa, R. J. Laws, and I. G. Jamieson. 2011. Multimodel inference in ecology and evolution: challenges and solutions. J. Evol. Biol. 24:699–711.

Hansen, T. F., and K. Bartoszek. 2012. Interpreting the evolutionary regression: the interplay between observational and biological errors in phylogenetic comparative studies. Syst. Biol. 61:413–425.

Hatchwell, B. J., and J. Komdeur. 2000. Ecological constraints, life history traits and the evolution of cooperative breeding. Anim. Behav. 59:1079–1086.

Hawn, A. T., A. N. Radford, and M. A. du Plessis. 2007. Delayed breeding affects lifetime reproductive success differently in male and female green woodhoopoes. Curr. Biol. 17:844–849.

Jetz, W., and D. R. Rubenstein. 2011. Environmental uncertainty and the global biogeography of cooperative breeding in birds. Curr. Biol. 21:72–78.

Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. The global diversity of birds in space and time. Nature 491:444–448.

Khan, M. Z. and J. R. Walters. 2002. Effects of helpers on breeder survival in the red-cockaded woodpecker (*Picoides borealis*). Behav. Ecol. Sociobiol. 51:336–344.

Kim, S. Y., A. Velando, R. Torres, and H. Drummond. 2011. Effects of recruiting age on senescence, lifespan and lifetime reproductive success in a long-lived seabird. Oecologia 166:615–626.

Koenig, W. D., F. A. Pitelka, W. J. Carmen, R. L. Mumme, and M. T. Stanback. 1992. The evolution of delayed dispersal in cooperative breeders. Q. Rev. Biol. 67:111–150.

Komdeur, J. 1996. Influence of age on reproductive performance in the Seychelles warbler. Behav. Ecol. 7:417–425.

Koricheva, J., J. Gurevitch, and K. Mengersen. 2013. Handbook of meta-analysis in ecology and evolution. Princeton Univ. Press, Princeton, NJ.

Krüger, O. 2005. Age at first breeding and fitness in goshawk *Accipiter gentilis*. J. Anim. Ecol. 74:266–273.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

Lane, J. E., L. E. B. Kruuk, A. Charmantier, J. O. Murie, D. W. Coltman, M. Buoro, S. Raveh, and F. S. Dobson. 2011. A quantitative genetic analysis of hibernation emergence date in a wild population of Columbian ground squirrels. J. Evol. Biol. 24:1949–1959.

Langen, T. A. 1996. Skill acquisition and the timing of natal dispersal in the white-throated magpie-jay, *Calocitta formosa*. Anim. Behav. 51:575–588.

Lewontin, R. C. 1965. Selection for colonizing ability. Pp. 77–91 in H. G. Baker and G. L. Stebbins, eds. The genetics of colonizing species. Academic Press, New York.

Link, W. A., E. G. Cooch, and E. Cam. 2002. Model-based estimation of individual fitness. J. Appl. Statist. 29:207–224.

Liou, L. W., T. Price, M. S. Boyce, and C. M. Perrins. 1993. Fluctuating environments and clutch size evolution in Great Tits. Am. Nat. 141:507–516.

Martin, J. G. A., D. H. Nussey, A. J. Wilson, and D. Réale. 2011. Measuring individual differences in reaction norms in field and experimental studies: a power analysis of random regression models. Methods Ecol. Evol. 2:362–374.

Martin, T. E. 1993. Nest predation and nest sites—new perspectives on old patterns. Bioscience 43:523–532.

———. 2004. Avian life-history evolution has an eminent past: does it have a bright future? Auk 121:289–301.

Martin, T. E. and P. J. Li. 1992. Life-history traits of open-nesting vs cavity-nesting birds. Ecology 73:579–592.

McDonald, D. B. 1993. Demographic consequences of sexual selection in the long-tailed manakin. Behav. Ecol. 4:297–309.

Millon, A., S. J. Petty, and X. Lambin. 2010. Pulsed resources affect the timing of first breeding and lifetime reproductive success of tawny owls. J. Anim. Ecol. 79:426–435.

Newton, I. 1989. Lifetime reproductive success. Academic Press, London.

Oli, M. K., G. R. Hepp, and R. A. Kennamer. 2002. Fitness consequences of delayed maturity in female wood ducks. Evol. Ecol. Res. 4:563–576.

Prevot-Julliard, A. C., R. Pradel, R. Julliard, V. Grosbois, and J. D. Lebreton. 2001. Hatching date influences age at first reproduction in the black-headed gull. Oecologia 127:62–68.

Pyle, P., N. Nur, W. J. Sydeman, and S. D. Emslie. 1997. Cost of reproduction and the evolution of deferred breeding in the western gull. Behav. Ecol. 8:140–147.

R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ricklefs, R. E. 1983. Comparative avian demography. Pp. 1–29 in R. F. Johnston, ed. Curr ornithol. Plenum Press, New York.

Roff, D. A. 1992. The evolution of life histories. Chapman and Hall, New York.

Russell, E. M. 2000. Avian life histories: is extended parental care the southern secret? Emu 100:377–399.

Santos, E. S. A., and R. H. Macedo. 2011. Load lightening in southern lapwings: group-living mothers lay smaller eggs than pair-living mothers. Ethology 117:547–555.

Santos, E. S. A., and S. Nakagawa. 2012. The costs of parental care: a meta-analysis of the trade-off between parental effort and survival in birds. J. Evol. Biol. 25:1911–1917.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods Ecol. Evol. 1:103–113.

Skutch, A. F. 1961. Helpers among birds. Condor 63:198–226.

Stearns, S. C. 1989. Trade-offs in life-history evolution. Funct. Ecol. 3:259–268.

———. 1992. The evolution of life histories. Oxford Univ. Press, Oxford, U.K.

Symonds, M. R. E., and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav. Ecol. Sociobiol. 65:13–21.

Tettamanti, F., W. Witvliet, and P. Bize. 2012. Selection on age at first and at last reproduction in the long-lived Alpine Swift Apus melba. Ibis 154:338–344.

Valcu, M., J. Dale, M. Griesser, S. Nakagawa, and B. Kempenaers. 2014. Global gradients of avian longevity support the classic evolutionary theory of ageing. Ecography 37:930–938.

van de Pol, M. 2012. Quantifying individual variation in reaction norms: how study design affects the accuracy, precision and power of random regression models. Methods Ecol. Evol. 3:268–280.

van de Pol, M., and J. Wright. 2009. A simple method for distinguishing within- versus between-subject effects using mixed models. Anim. Behav. 77:753–758.

van de Pol, M., I. Pen, D. Heg, and F. J. Weissing. 2007. Variation in habitat choice and delayed reproduction: Adaptive queuing strategies or individual quality differences? Am. Nat. 170:530–541.

Van Noordwijk, A. J., and G. De Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. Am. Nat. 128:137–142.

Williams, G. C. 1966. Natural selection, costs of reproduction, and a refinement of Lack's principle. Am. Nat. 100:687–690.

Wooller, R. D., J. S. Bradley, I. J. Skira, and D. L. Serventy. 1989. Short-tailed Shearwater. Pp. 405–417 in I. Newton, ed. Lifetime reproductive success. Academic Press, London.

Wootton, J. T. 1987. The effects of body-mass, phylogeny, habitat, and trophic level on mammalian age at 1st reproduction. Evolution 41:732–749.

Zack, S. and B. J. Stutchbury. 1992. Delayed breeding in avian social-systems—the role of territory quality and floater tactics. Behaviour 123:194–219.

Zhang, H., M. Rebke, P. H. Becker, and S. Bouwhuis. 2015. Fitness prospects: effects of age, sex and recruitment age on reproductive value in a long-lived seabird. J. Anim. Ecol. 84:199–207.

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