

Spatial and temporal variation in the generation time of a bird metapopulation: density regulation and the evolutionary potential of a pace-of-life measure

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Abstract (150/150 words)

Generation time determines the pace of key demographic and evolutionary processes. Quantified as the weighted mean age at reproduction, it can be studied as a trait that varies within and among populations and may evolve in response to ecological conditions. We combined quantitative genetic analyses with age- and density-dependent models to study generation time variation in a bird metapopulation. Generation time was heritable, and males had longer generation times compared with females. Individuals with longer generation times had a higher lifetime reproductive success but not a higher expected population growth rate. Density regulation acted on recruit production, suggesting that longer generation times should be favored when populations are closer to carrying capacity. Furthermore, generation times were shorter when populations were growing, and longer when populations were closer to equilibrium or declining. These results support classic theory predicting that density regulation is an important driver of the pace of life-history strategies.

Introduction

Generation time describes the pace of key biological processes. It is related to mutation rates (Lehtonen & Lanfear 2014) and the time a population needs to replace itself (Bienvenu & Legendre 2015). In age-structured populations, generation time is determined by age-specific survival and reproduction (Cochran & Ellner 1992) and reflects how organisms resolve the trade-off between current and future reproduction. Generation time is in allometric relation with key phenotypic characteristics of an organism, such as its body size and metabolic rate (Brown *et al.* 2004), while the responses to selection of a trait per unit time depend upon a population's generation time (Lande 1982). Generation time is thus a measure connecting the demographic and phenotypic characteristics of a population with the rate of evolutionary change. Furthermore, generation time is related to the susceptibility of organisms to stochastic fluctuations in the environment (Sæther *et al.* 2005) and it is a key component of evolutionary rescue models (Chevin *et al.* 2010). Understanding the ecological processes affecting generation time is therefore essential for predicting how organisms will respond to environmental change.

Among-species comparisons have shown that generation time predicts an organism's position in the fast-slow continuum of pace of life history strategies (Gaillard *et al.* 2005, 2016). At the fast end are species with high reproductive rates, short lifespans and short generation times. At the slow end are organisms characterized by high survival rates, low reproduction rates and long generation times (Saether & Bakke 2000). Despite being generally defined as a population attribute, there are several definitions of generation time for age-structured populations, which can be used to study the factors driving variation in the timing of reproduction within populations (Cochran & Ellner 1992; Bienvenu & Legendre 2015). These definitions relate to the weighted mean age at reproduction (Charlesworth 1994). For instance, it is possible to study within population variation in generation time as the "mean age of the parents of offspring produced in a particular time period" (Cochran & Ellner 1992), such as per cohort (Caswell 2001), year, or generation (Steiner *et al.* 2014). Furthermore, the weighted mean age at reproduction for an individual, estimated from its age dependent reproduction, can be used as a measure of an individual's generation time (McGraw & Caswell 1996; Araya-Ajoy *et al.* 2018). Studies quantifying multi-level variation in generation time can provide insights into the evolutionary potential of the pace of life history strategies and how they are shaped by ecological conditions (Wright *et al.* 2019).

Life-history theory is largely based on optimality models, where the evolutionary end points are the life-history strategies that maximize a measure of fitness given a set of resource allocation trade-offs (Roff 1993). The role of density dependence as an environmental driver determining optimal life-history strategies has been a long-standing research topic in evolutionary ecology (Boyce 1984; Stearns 1992; Reznick *et al.* 2002). Density dependence was introduced as a driver of

life-history strategies in the context of r - versus K -selection after island colonization (MacArthur & Wilson 1967). The general idea was that when populations are growing, density-independent selection will favor fast life-history strategies, but as populations approached their carrying capacity, density-dependent selection will favor slower life-history strategies (Reznick *et al.* 2019). Hence, r - versus K -selection was suggested as the general explanation of among-species variation in life histories (Pianka 1970). This slowly lost favor and was replaced by density-independent but age-dependent variation in extrinsic mortality as the favored explanation for differences in the pace of life history strategies (Stearns 1976; Boyce 1984). More recently, age-structured models of density-dependent evolution have shown to provide general predictions concerning the role of density dependence in determining the optimal life history strategies (Engen & Sæther 2016; Wright *et al.* 2020). Despite early models of life-history evolution also predicting an important role of density regulation in shaping age-dependent reproductive effort (Charlesworth & Leon 1976; Michod 1979), very few empirical studies have focused on understanding the role of population dynamics in shaping spatial and temporal variation in generation times (Nilsen *et al.* 2009; Kentie *et al.* 2020).

We assessed the role of population dynamics and density regulation in shaping the pace of life history strategies, by studying spatial, temporal and genetic sources of variation in the weighted mean age at reproduction of a house sparrow (*Passer domesticus*) metapopulation. We first estimated individual generation time, measured as the weighted mean age of successful contribution of an individual to the breeding population, and decomposed its variation into genetic and environmental sources. We then proceeded to quantify how age- and density-dependent survival and reproduction shape the mean age at reproduction in the whole metapopulation. Classic models of optimal allocation of resources predict that the distribution of survival across ages and the point of the life cycle of an organism where density dependence acts will influence the optimal age-dependent investment in reproduction (Charlesworth 1994). Optimality models also state that the pattern of density regulation will determine whether evolution will maximize a measure of fitness that favors early reproduction (e.g. ‘population growth rate of the individual’, *sensu* McGraw & Caswell 1996) or other fitness measures (Mylius & Diekmann 1995; Engen & Sæther 2017). We thus studied the relationship between an individual’s generation time, lifetime reproductive success and an individual’s expected population growth rate. Finally, we studied how fluctuations in population growth affected the mean age at reproduction to test the prediction that when populations are expanding, the mean age at reproduction should be younger, whereas when populations are decreasing or near their carrying capacity, the mean age at reproduction should be older.

Methods

Study system

We focused on eight populations in a metapopulation of house sparrows inhabiting eighteen islands in northern Norway (66°N 13°E). Each time a bird was handled as a nestling, fledged juvenile or adult, we took a blood sample for genetic analyses. A pedigree based on 605 highly polymorphic and independent single nucleotide polymorphisms (SNPs; Niskanen *et al.* 2020) was generated and then used for estimating the number of recruits produced per individual. The extensive sampling effort combined with the genetic analyses, allows close monitoring of the life histories of most individuals inhabiting these islands. We used specific data sets for the different analyses, but in general this metapopulation has been monitored continuously since 1993 (Ringsby *et al.* 2002). However, systematic SNP genotyping of all adults started in 1998 in some islands and in 2003 for others. Therefore, the maximum possible time period of data included in these analyses differed between populations (Table S1).

Estimates of generation time

We studied generation time at different levels of biological organization. We started by quantifying the generation time of the whole metapopulation, separately for males and females. The metapopulation generation time (T) was calculated as the mean age of the mother or father of recruits in the population (Charlesworth 1994). This estimate was calculated from the age of the parents of 1706 recruits. We formulated this as:

$$T = \frac{\sum_{h=1}^n a_h}{n},$$

where a is the age of the parent of recruiting offspring h and n is the number of recruiting offspring in the whole metapopulation. We also did this for each island of the metapopulation separately. A population's generation time was thus estimated as the mean age of offspring parents on population j (T_j). In a similar manner, we estimated the mean age of offspring parents (T_{jk}) for each year k for each island j (Cochran & Ellner 1992). Finally, we estimated an individual's generation time (T_i) as its weighted mean age at reproduction (McGraw & Caswell 1996; Araya-Ajoy *et al.* 2018) where a is the age of individual i in year k where it produced f number of recruits:

$$T_i = \frac{\sum_{i=1}^{d_i} (af)_{ik}}{\sum_{i=1}^{d_i} f_{ik}}.$$

Where d is the lifespan of individual i and the sum in the denominator reflects the lifetime reproductive success of individual i . Estimates of individual generation times included only individuals that produced at least one recruit during their lifetime, resulting in a total of 1052 individuals (see Table S1 for more details). Using the number of recruits produced by each individual in each year, we also calculated all the elements of individual projection matrices and derived an individual's expected population growth rate (λ_i) as the dominant eigen value of the individual's projection matrix (see eq. S1 for formulas). This can be interpreted as the growth rate of a population of individuals with the same characteristics as individual i . From these data we also estimated the total number of recruits produced during an individual's life – i.e. lifetime reproductive success. In these analyzes we included only individuals that were assumed dead before the breeding season of 2013, as they were never recaptured in any of the following years.

Sources of variation in individual generation time

We used univariate linear mixed-effect models to quantify the sources of variation in the individual estimates of generation time (T_i). First, we modelled the untransformed estimates of individual generation time with sex as fixed effect and random intercepts for population identity ($n =$ eight populations) and birth year ($n = 15$ cohorts). We also included pedigree information to decompose individual differences in generation time into additive genetic variation versus environmental variation. The pedigree consisted of 3116 individuals with a mean of 4.6 ancestral generations. We also modelled log-transformed generation time with the same random and fixed effects but included as fixed effect log-transformed body mass. We also fitted the same animal models but only included sex as a fixed effect in order to estimate unadjusted additive genetic variances, heritabilities and evolvabilities (Table S2).

We also used univariate mixed models to study the relationships between individual generation time, lifetime reproductive success and the expected population growth rate of an individual (λ_i). These models had sex and individual generation times as fixed effects and random intercepts for population identity and birth year. We present the analyses assuming normally distributed errors, because parameter estimates are easier to interpret biologically and mixed models are generally robust to violations of the distributional assumptions (Schielzeth *et al.* 2020). Nevertheless, we corroborated these results using different link functions (see Table S2).

Age and density dependent reproduction and survival

For the age- and density-dependent models, we utilized annual data on reproduction and survival for all individuals present within the studied time periods, regardless of whether they had produced a recruit or not (Table S1). In total, there were 5247 records of 2729 individuals. Annual number of recruits was modelled using generalized linear mixed-effect models assuming a negative binomial

error distribution. Variation in survival probability was modelled as a binomial process using a mark-recapture framework. We used a the Cormack–Jolly–Seber Model to jointly estimate the factors affecting survival, while accounting for island-specific yearly variation in recapture probabilities (Kéry & Schaub 2011). We included in both models sex as fixed effects, and age as both linear and quadratic fixed effects. We also fitted an interaction between sex and the linear and quadratic effects of age, because we were expecting sex-specific patterns of age-dependent reproduction and survival (Stubberud et al. 2017). In addition, these models included mean population size and annual deviations from the mean population size (relative density) as fixed effects. This within-subject centering approach (van de Pol & Wright 2009) allowed us to model density regulation accounting for spatial and temporal effects of population size in recruitment and survival. We also fitted year, population and individual as random intercepts in all models.

Effects of population dynamics on mean age at reproduction

To explore how population dynamics affected the mean age of parents of recruits each year in each population, we utilized annual data on reproduction and survival for all adult individuals within the studied time periods (Table S1). From these data, we estimated the weighted mean age of sires and dams reproducing in each year for each population. This was estimated as the mean age of the successfully reproducing parents weighted by the number of recruits they produced (T_{jk}). We then fitted a mixed-effect model that had as the response variable the weighted mean age of reproducing individuals in a given year in a given population (T_{jk}), and as fixed effects sex plus the mean and annual deviations of population size to distinguish between effects of spatial versus temporal fluctuations in population size on the mean age at reproduction of a population.

To further examine how the weighted mean age at reproduction (T_{jk}) was related to ecological factors determining population growth, we fitted another mixed-effect model where the mean age at reproduction was also fitted as a response variable and the mean fitness of the population in each year and sex as fixed effects. We estimated the fitness of each individual in a given years as its own survival plus half the number of recruits it contributed to the next year (see Supplementary material C), because, in the absence of dispersal, this metric of fitness directly connects to local population dynamics (Sæther & Engen 2015). This measure of fitness will determine the changes in population size across years that are not caused by immigration and emigration. Importantly, the mean fitness in the population in a given year directly connects to the expected population growth and should reflect current levels of competition in the population (Sæther & Engen 2015), either because of variation in environmental conditions and/or due to variation in population density relative to the amount of resources. To control for the effects of age structure in determining the mean age at reproduction, we also fitted the two above-mentioned

models including the mean age of all the adults breeding in the population as an additional fixed effect (Table S3). We further corroborated that results were robust to the choice of link function (Table S3).

General modelling procedures

We fitted linear mixed-effect models in a Bayesian framework using Stan (Carpenter *et al.* 2017) implemented in RStan (Stan Development Team 2018) and brms (Bürkner 2018) in Rv3.6 (R Core Team 2019). We ran models for 3000 iterations for 3 chains with warm up period of 1000 iterations. We assessed chain convergence based on the \hat{R} statistic (Gelman *et al.* 2013b). Posterior means and 95% credible intervals were estimated across samples for the fixed and random effects. For most of the models we used improper flat priors for fixed-effect priors and for the standard deviations of the random effects half student-t priors with 3 degrees of freedom plus a scale parameter that depends on the standard deviation of the response after applying the link function (Bürkner 2018). For the mark-recapture models, we used diffused normally distributed priors with mean of zero and large variance for the fixed effects and for the standard deviations of the random effects uniformly distributed priors of positive values with a maximum of 10 (Gelman *et al.* 2013a).

Results

Mean age at reproduction (generation time) at different levels

The average age of the fathers of all the recruits produced in this house sparrow metapopulation (T) was 2.24 years, while the average age (T) of the mothers was 2.06 years. Island average generation times for fathers ranged from 1.5 to 2.4 years, while for mothers ranged from 1.6 to 2.7 years.

While mean age at reproduction for each year within each island (T_{jk}), ranged between 1 and 5 years for males, and 1 to 3.9 years for females. Finally, average individual generation time (T_i) for males was 1.84 years (ranging from 1 to 5.6 years), while for females it was 1.67 years (ranging from 1 to 5.7 years). The general trend was that males had longer generation times compared to females, and that there was more variation in generation time among years within islands (T_{jk}) than among islands (T_j). Importantly, the average age of the parents of recruits (T) is older than the average individual generation time (T_i), implying that individuals that reproduced when they are older were the ones who contributed more recruits to the population.

Individual generation time (T_i)

When we studied the sources of variation in individual measures of generation time (T_i), we found that individual generation time was longer for males than females, and that larger individuals also

had longer generation times (Table 1). Among-population differences explained around 3.02% (CI=0.01, 10) of the variance in individual estimates of generation time, while birth year explained around 11.74% (CI=4.23, 25.23). We also found support for a non-zero standard deviation associated with the additive genetic effects (0.15, CI= 0.01, 0.42). The proportion of the variance explained by additive genetic variance was around 4.08% (CI=0.09, 11.2), which translates into an evolvability of 1.43 % (CI=0.03, 3.60). Larger individuals had longer generation times and individuals with longer generation times had higher lifetime reproductive success. However, there was no relationship between individual generation time and an individual's expected population growth rate (λ_i).

Age-dependent survival and reproduction

We found that individuals produced fewer recruits in their first year of breeding (Table 2), but the distribution of reproduction with age was different for males and females. For both sexes, the number of recruits per individual increased with age, and there was a slight decrease at older ages, especially for males (Figure 1A and 1C). However, a higher proportion of the total number of recruits were still produced by one-year old parents (Figure 1B and 1E), because at any given time the fraction of one-year old individuals was larger than any other age class (Figure 1C and 1F). Males produced, on average, fewer recruits in their first breeding year than females. However, from their second year onwards, males produced more recruits than females per breeding season. Males also had a higher survival probability than females on average (Table 3). Thus, males had longer generation times, both because they lived longer and because they were more successful at reproducing when they were older.

We also found strong evidence for negative effects of density regulation in recruit production and some evidence for density regulation in adult survival (Table 2). In years when population size was relatively high compared to the average population size, recruit production was lower and there was a tendency that adult survival was also lower.

Mean age at reproduction and population growth

In years when the mean fitness of the population was lower, the mean age of successfully reproducing individuals was older (Table 3, Figure 2), specially for males. This suggests that in years when competition was high and/or environmental conditions were poor, resulting in low average individual fitness, the successfully reproducing males were amongst the older males. In contrast, when the mean fitness of the population was high, and thus populations are expected to grow, the average age of reproducing males was younger. These effects cannot be solely attributed to differences in age structure, because even after correcting for the mean age of all the adults present, there was evidence that these effects were still different from zero (Table S3). Supporting

these findings, we also found a trend suggesting that in years when population size was higher than average, the mean age of reproducing males was older (Table 3).

Discussion

The fast-slow axis is one of the most general and taxon-wide patterns of life-history (co)variation (Saether & Bakke 2000; Oli 2004; Salguero-Gómez *et al.* 2016). The position of an organism in this axis is tightly linked to its generation time (Gaillard *et al.* 2005). Quantifying the factors underpinning variation in generation time at different levels is thus essential to understand life-history evolution. Using a combination of quantitative genetic and demographic analyses on a unique data set from a house sparrow metapopulation, we found support for classic theories of life-history evolution (Charlesworth 1994) stating that density regulation through competitive regimes is a key selective pressure that can determine the evolutionary trajectories of the pace of life-history strategies.

Life-history theory predicts that the observed population differences in generation time, partly reflect the optimal values provided the ecological conditions of the studied islands. Accordingly, temporal fluctuations in the mean age at reproduction within islands might also reflect adaptive responses to temporal changes in environmental conditions. We indeed found that temporal variation in the mean age at reproduction was associated with local fluctuations in demographic competitive regimes. The evolution of generation time in response to these competitive regimes, hinges upon there being genetic variation underpinning the traits determining the age specific patterns of survival and reproduction. We found that evolutionary potential or evolvability of generation time in this metapopulations was within the range of values estimated for other life-history traits (Hansen *et al.* 2011). Therefore, spatial and temporal variation in competitive regimes could have shaped the observed variation in mean age at reproduction in this metapopulation. Whilst it might be possible to estimate additive genetic variance in the age-specific survival and reproduction patterns (Nussey *et al.* 2007), for a relatively short-lived species like the house sparrow, we think that the weighted mean age at reproduction summarizes the distribution of reproduction with age. Furthermore, it allows measuring among population, among year and among individual variation in a key theoretical quantity, generation time. Our analyzes thus suggest that the observed patterns of variation in generation time are the result of a combination of evolutionary responses to selection, stochasticity and plastic responses to the environmental.

Density regulated pace-of-life

The early formulation of life-history theory in the form of *r*- and *K*-selection integrated density regulation and evolutionary ecology through density-dependent selection (MacArthur 1962; MacArthur & Wilson 1967) suggesting that population dynamics are a key determinant of equilibrium life-history strategies observed in nature (Pianka 1970; Boyce 1984). Around the same time, models based on an age-specific allocation of limited resources suggested the importance of density regulation in life-history evolution (Charlesworth & Leon 1976; Michod 1979). For instance, Charlesworth and Leon (1976) predicted that when density regulation acts through juvenile survival, reproductive effort should increase with age. We found that density regulation in this metapopulation indeed acted on recruit production. In agreement with the prediction of this model, we find that recruit production increases after the first adult year (Table 2). Importantly, higher investment in reproduction with age should result in longer generation times.

When we analyzed how generation time was affected by population dynamics across years and populations, our results further suggest that local population dynamics affects the mean age at reproduction, because density-dependent competition constrains the reproductive output of younger individuals. When the mean fitness of the population was low and population size was expected to decrease, individuals that managed to reproduce were older (Table 4, model 1A). In contrast, when mean fitness was high and populations were expected to grow, all individuals, even the young ones, managed to reproduce. These results are consistent with classic density-dependent selection theory predicting that when populations are growing, individuals that invest more in current reproduction are favored, but when populations are close to or above their carrying capacity, the favored individuals will be the ones that allocate more in traits enhancing survival and competitive ability.

In our analyses of patterns of recruitment, we cannot distinguish whether density regulation acts through parental investment in reproduction or juvenile survival, or both. Thus, in years when population sizes were greater than average parents fledged fewer offspring and/or juvenile survival was lower. However, comparative analyses suggest that a common density regulation pattern in birds is that in high-density years increased competition decreases survival probabilities, whereas when populations are growing (e.g. after environmentally driven population declines) it is an increase in recruit production which brings population size back to its equilibrium size (Sæther *et al.* 2016). Therefore, a plausible explanation for the patterns of density regulation of this metapopulation is that when local populations size is increasing, all individuals manage to reproduce (even first breeding year individuals), while in years where competition is high and populations are around their carrying capacity, only individuals with high competitive ability able to reach the old age classes are able to successfully fledge offspring that manage to survive to the next breeding season.

Generation time, fitness and constraints

The patterns of covariation between generation time, lifetime reproductive success and individual expected population growth rates (λ_i) also support our interpretation that density-dependent competition influences generation time. We found that individuals with longer generation times had greater lifetime reproductive success, but not necessarily a greater λ_i . Theoretical models show that, depending on the form of density regulation, evolution is expected to maximize the total number of recruits or individual population growth rates (Mylius & Diekmann 1995). In a hypothetical scenario where individuals produce the same number of recruits during their lifetime, individuals that reproduce earlier in life and thus have shorter generation times will be selected for, because early reproduction results in higher individual population growth rates (McGraw & Caswell 1996). However, in the presence of density regulation in recruit production, evolution is instead expected to maximize lifetime reproductive success. Investing more in reproduction in one breeding event early in life should increase an individual's expected population growth rate (λ_i), but this will be counteracted by density-regulated juvenile mortality when populations are closer to or above their equilibrium density, because then only a few individuals will manage to recruit each year. This will favor parents allocating more resources to survival enabling them to reproduce later and have longer generation times, because they will be able to contribute to population growth in several breeding seasons. This is consistent with recent models of density-dependent evolution showing that evolution maximizes a function that includes the density-independent growth rate of a phenotype and also its sensitivity to density regulation (Lande *et al.* 2017). Longer generation times will thus be favored if the degree to which they buffer individuals against density-dependent competition is greater than their negative effect on density-independent population growth rates.

Our results suggest that evolutionary responses to selection will result in longer generation times over time as populations approach their equilibrium densities. However, several processes are expected to constrain the evolution of longer generation times: (i) extrinsic sources of mortality; (ii) stochastic fluctuations in population size; and (iii) life-history trade-offs. The role of extrinsic sources of mortality, such as predation or adverse weather conditions, dominated the study of adaptive life histories in the early 1990s, when they were seen as the main driver of life-history variation (Stearns 1992). If adult mortality is very high, then natural selection should favor individuals that allocate energy towards reproduction earlier in life. Whereas if juvenile mortality is high, natural selection should favor individuals that invest more in self-maintenance so that they have the chance to reproduce later in life. Interestingly, we did not find that adult survival changed with age (but see Holand *et al.* 2016). Extrinsic sources of mortality therefore seem to be the main drivers constraining the evolution of longer life spans and thus longer generation times in this

metapopulation. The observed patterns of age-specific reproduction would thus appear to be the result of an interaction between density regulation and external environmental factors affecting survival probabilities.

Another factor constraining the evolution of longer generation times can arise when there are stochastic environmentally driven fluctuations in population size (Engen & Sæther 2016). When stochastic population fluctuations are large selection should favor fast life-history strategies and short generation times, but when population fluctuations are small and limited at and around the carrying capacity then selection should favor slower life-history strategies and long generation times (Engen *et al.* 2013). Thus, density-dependent selection favoring longer generation times may be counterbalanced by density-independent selection induced by stochastic fluctuations in population size favoring shorter generation times. The observed fluctuations in population size in this metapopulation are thus expected to affect the optimal mean age at reproduction.

All optimal life-history models assume that there is a resource allocation trade-off that constrains evolution to a sub-set of possible life-history strategies (Stearns 1989). Such trade-offs include those between reproduction and survival, current versus future reproduction, and density-independent versus density-dependent reproduction. Such trade-offs are difficult to detect without experimental manipulations, because variation in resource acquisition is expected to mask life-history trade-offs in observational studies (van Noordwijk & de Jong 1986). Such an effect is perhaps reflected in our results when recruit production increases with age (Figure 1) and when older individuals were the ones that managed to reproduce when competition was high or the environment was harsh (Figure 2). It could be that individuals acquiring more resources are the ones that managed to grow old and also reproduce under strong density-dependent competition.

Sex differences in mean age at reproduction

Sex differences in generation time also support the idea that competitive regimes have a strong influence on the pace of life history strategies. We found that males contributed more to population growth when they were older, and thus males had longer generation times compared to females (Table 1). These differences can be explained by competition for nest sites and/or mates being stronger for males. Another potential cause of sex differences in the mean age at reproduction could also be associated to extra-pair reproduction. If older males increased their reproductive output through competitive access to extra-pair fertilizations (Cleasby & Nakagawa 2012), then this might explain why the mean age at reproduction was older for our male sparrows. The observed sex differences in generation time seem to be caused by stronger intra-specific competition in males, but the specific mechanisms underpinning these effects certainly deserve further study.

Conclusions

Density regulation is a ubiquitous process in natural populations and has been a key component of early life-history models. However, few empirical studies of life-history evolution have attempted to test evolutionary theory about the timing of reproduction that incorporates density regulation. By combining multi-level analyses of the mean age at reproduction along with models of age- and density-dependent survival and reproduction, we provide various lines of evidence supporting classic life-history theory predicting that density dependence is a key determinant in shaping the pace of life history strategies. Because generation time determines the speed of evolutionary responses to selection, detailed understanding of the eco-evolutionary dynamics of the mean age at reproduction is key for predicting whether organisms will be able to adapt to the current pace of environmental change.

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Table 1. Univariate mixed-effect model results on the sources of variation in life-history traits measuring the timing of reproduction of 1052 individual house sparrows. Only individuals that produced at least one recruit were included in the analyses. We present point estimates and 95% credible intervals in parenthesis.

Parameter	Generation Time	Generation time (log)	Lifetime rep success	Individual growth rate
<u>Fixed effects (β)</u>				
Intercept	1.68 (1.46, 1.91)	-1.36 (-2.93, 0.18)	0.76 (0.32, 1.18)	1.80 (1.64, 1.98)
Sex (male)	0.16 (0.06, 0.26)	0.09 (0.03, 0.14)	-0.08 (-0.32, 0.16)	-0.05 (-0.09, 0.03)
Generation time	-	-	1.08 (0.95, 1.22)	-0.05 (-0.16, 0.05)
Body mass (log)		0.52 (0.08, 0.97)		
<u>Random effects (σ^2)</u>				
Additive genetic	0.14 (0.01, 0.29)		-	-
Population	0.17 (0.06, 0.38)	0.07 (0.03, 0.17)	0.39 (0.14, 0.83)	0.13 (0.02, 0.33)
Year	0.32 (0.19, 0.51)	0.16 (0.10, 0.28)	0.15 (0.01, 0.37)	0.19 (0.10, 0.29)
Residual	0.84 (0.80, 0.89)	0.44 (0.42, 0.46)	1.95 (1.87, 2.04)	0.86 (0.82, 0.90)

Table 2 Results for the age- and density-dependent mixed-effect models on reproduction (number of recruits produced per year, negative binomial) and survival (binomial), based upon 5247 individual breeding attempts for 2729 individual house sparrows. Age effects are modelled as a quadratic function. Survival analysis was carried out in a mark-recapture framework. The average recapture probability was 0.80 (95% CI=0.76, 0.84) with a standard deviation among years within populations in the latent scale of 0.76 (95% CI=0.56, 0.84).

Parameter	Reproduction	Survival
<u>Fixed effects (β)</u>		
Intercept	-0.85 (-1.42, -0.83)	0.03 (-0.32, 0.40)
Age	0.23 (0.13, 0.34)	0.02 (-0.06, 0.11)
Age ²	-0.04 (-0.06, -0.01)	0.00 (-0.01, 0.01)
Sex (male)	-0.17 (-0.29, -0.05)	0.31 (0.12, 0.50)
Age: sex	0.22 (0.07, 0.37)	-0.01 (-0.11, 0.09)
Age ² : sex	-0.05 (-0.08, -0.01)	-0.01 (-0.01, 0.01)
Mean pop size	0.12 (-0.05, 0.30)	-0.03 (-0.34, 0.31)
Relative pop size	-0.20 (-0.28, -0.14)	-0.11 (-0.24, 0.02)
<u>Random effects (σ)</u>		
Individual	0.62 (0.54, 0.70)	0.20 (0.11, 0.40)
Population	0.18 (0.06, 0.40)	0.36 (0.17, 0.76)
Year	0.33 (0.21, 0.51)	0.33 (0.11, 0.40)
Shape	2.41 (1.81, 3.26)	-

Table 3. Mixed-effect model results explaining variation in the age of successfully reproducing parents of house sparrows. Model 1 focuses on the effects of mean fitness, and model 2 focuses on the effect of population size. Point estimates are given with 95% credible intervals in parenthesis.

Parameter	Model 1	Model 2
<u>Fixed effects</u>		
Intercept	2.45 (2.03, 2.88)	2.09 (1.82, 2.37)
Sex (male)	0.45 (-0.07, 0.97)	0.12 (-0.07, 0.31)
\bar{w}	-0.41 (-0.76, -0.06)	
$\bar{w} : \text{sex}$	-0.36 (-0.90, 0.18)	
Mean pop size		-0.06 (-0.31, 0.21)
Relative pop size		0.03 (-0.18, 0.23)
Relative pop size: sex		0.09 (-0.19, 0.37)
<u>Random effects</u>		
Population	0.30 (0.11, 0.62)	0.26 (0.05, 0.59)
Year	0.15 (0.02, 0.31)	0.13 (0.01, 0.30)
Residual	0.65 (0.59, 0.73)	0.68 (0.62, 0.76)

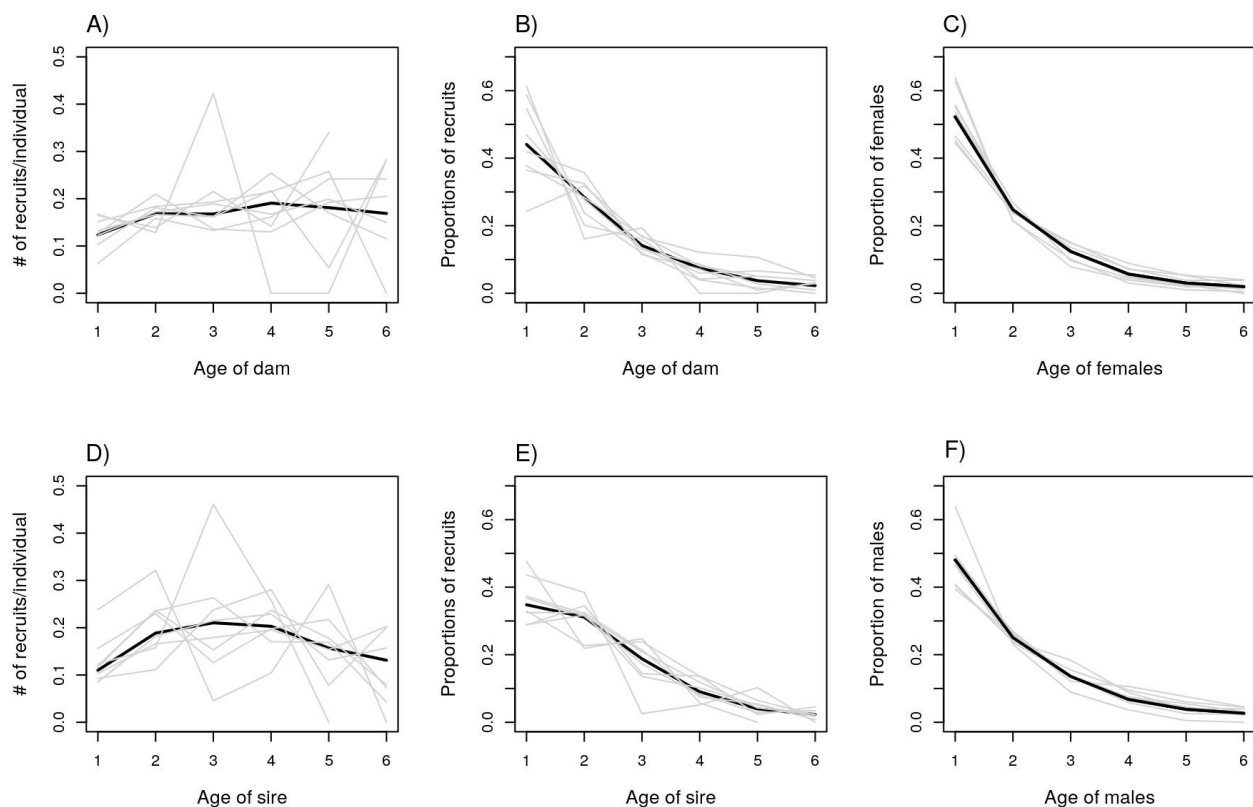


Figure 1. Average number of recruits per individual female (A) or male (D) house sparrows in relation to age. The age-specific variation in the proportion of recruits of mothers (B) and fathers (E) on the metapopulation whereas age-distribution age distribution of adults in the population is shown in C and F, respectively. Thick black lines represent the average in the metapopulation as a whole and gray lines represent each island population.

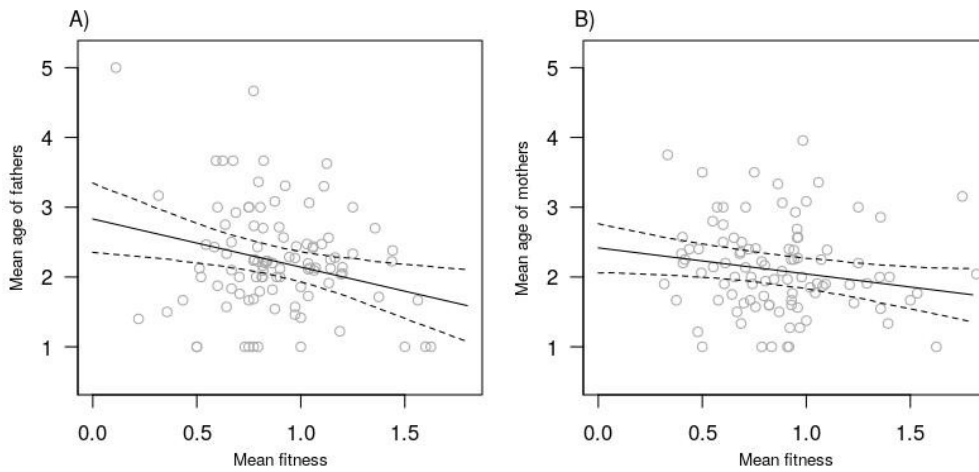


Figure 2. The relationship between mean age of successful reproduction for (A) males and (B) females in relation to mean fitness in the house sparrow population. Each dot represents a population in a given year. Lines are the predicted mean values and dotted lines the 95% credible intervals.

Supplementary material

A) Sample sizes

Table S1. Sample sizes of unique adult individuals and time periods for each of the studied populations. For the time period of data on individual life histories, the first year refers to the earliest cohort year included in the analyses (i.e. born that year and recruits into the adult breeding population the year after), and we included only individuals that were known to be dead after the last year (i.e. not recorded in the next two breeding seasons). For age and density dependent analyses, the sample sizes refer to all unique adult individuals present during the years included in the given time period.

Population	Individual life-histories		Age- and density-dependence models	
	Time period	Individuals	Time period	Individuals
Inner-farm				
Nesøy	1997-2012	40	1998-2012	122
Gjerøy	1997-2012	184	1998-2012	529
Hestmannøy	1997-2012	432	1998-2012	1014
Indre Kvarøy	1997-2012	134	1998-2012	344
Aldra	1997-2012	83	1998-2012	181
Outer-non-farm				
Myken	2003-2012	16	2004-2012	68
Selvær	2002-2012	77	2003-2012	223
Træna	2002-2012	86	2003-2012	248
Total		1052		2729

B) Estimates of individual life-history traits

Based on the pedigree, we used the number of recruits produced by each individual in each year to calculate all the elements of the individual projection matrices and derive some key life-history traits, such as individual expected growth rate and generation time (McGraw & Caswell 1996). To calculate an individual's generation time, it must have produced a recruit. Thus, only individuals that produced at least one recruit during their lifetime were considered in these analyses of individual life histories, resulting in a total of 1052 individuals (552 females and 500 males, see Table S1 for more details).

To estimate the projection matrix $A^{(i)}$ of individual i we need to know the number of successful recruits it produced ($F_a^{(i)}$) at each age a and the age when it died d (McGraw & Caswell 1996). In the main text the notations is slightly different most notably we denote F as f . Where survival ($S_a^{(i)}$) will be equal to one until the age it died:

$$A^{(i)} = \begin{bmatrix} F_1^{(i)} & F_2^{(i)} & \cdots & F_d^{(i)} \\ S_1^{(i)} & 0 & \cdots & 0 \\ \vdots & \textcolor{red}{\lambda} & 0 & \textcolor{red}{\lambda} \end{bmatrix} . \quad (\text{eq. S1a})$$

Once an individual's transition matrix $A^{(i)}$ is formed, the dominant eigenvalue $\lambda^{(i)}$ of this matrix estimates the asymptotic population growth rate for a collection of individuals with the propensities to survive and reproduce equal to individual i (McGraw & Caswell 1996). That is, it is an estimate of the expected growth rate of a population consisting of individuals with the characteristics of individual i (i.e. individual expected population growth rate):

$$1 = \sum_{a=1}^{d^{(i)}} F_a^{(i)} (\lambda^{(i)})^{-a} . \quad (\text{eq. S1b})$$

The lifetime reproductive success $R^{(i)}$ of individual i can be estimated as the sum of the fecundities at each age a :

$$R^{(i)} = \sum_{h=1}^{d^{(i)}} F_a^{(i)} . \quad (\text{eq. S3})$$

From these data we can also estimate an individual measure of generation time $T^{(i)}$ as the weighted mean age of an individual when it reproduced as:

$$T^{(i)} = \frac{\sum_{a=1}^{d^{(i)}} a F_a^{(i)}}{\sum_{a=1}^{d^{(i)}} F_a^{(i)}} . \quad (\text{eq. S4})$$

Table S2. Complementary univariate mixed-effect model results on the sources of variation in life history traits measuring the timing of reproduction of 1052 individual house sparrows. Only individuals that produced at least one recruit were included in the analyses. We present point estimates and 95% credible intervals in parenthesis.

Parameter	Generation Time	Generation time (log transformed)	Generation time (log normal link)	Lifetime rep success (Poisson link)	Individual growth rate (log normal link)
<u>Fixed effects (β)</u>					
Intercept	1.64 (1.56, 1.73)	-1.35 (-2.94, 0.17)	0.40 (0.27, 0.52)	0.31 (0.14, 0.48)	0.42 (0.32, 0.52)
Sex (male)	0.18 (0.07, 0.29)	0.08 (0.03, 0.14)	0.08 (0.03, 0.14)	-0.02 (-0.09, 0.06)	-0.03 (-0.08, 0.02)
Generation time	-	-	-	0.34 (0.30, 0.37)	0.02 (-0.01, 0.05)
<u>Random effects (σ^2)</u>					
Additive genetic	0.19 (0.05, 0.31)	0.14 (0.01, 0.29)	0.09 (0.01, 0.17)	-	-
Population			0.09 (0.03, 0.20)	0.16 (0.07, 0.34)	0.08 (0.03, 0.19)
Year			0.17 (0.11, 0.29)	0.09 (0.03, 0.17)	0.03 (0.00, 0.08)
Residual	0.88 (0.84, 0.93)	0.43 (0.40, 0.45)	0.43 (0.40, 0.45)	-	0.43 (0.41, 0.45)

C) Effects of population dynamics on the mean age of reproduction

To explore how population dynamics affected the mean age of parents of recruits each year in each population (T_{jk}), we utilized annual data on reproduction and survival for all adult individuals i present within the studied time periods (Table S1). From this data we estimated the weighted mean age of the parents reproducing in year j and population k as:

$$T_{jk} = \frac{\sum_{i=1}^{N_{jk}} a F^{(ijk)}}{\sum_{i=1}^{N_{jk}} F^{(ijk)}} , \quad (\text{eq. S4})$$

where a is the age and F is the number of recruiting offspring produced by individual i in population j in year k . The sum is taken for all individuals breeding in year j in population k (N_{jk}). We estimated the mean age at reproduction in a population each year for males and females separately. We then fitted a mixed-effect model that had as the response variable the mean age of reproducing individuals in a given year in a given population (T_{jk}), and as fixed effects sex and the

mean and annual deviations of population size to distinguish between effects of spatial versus temporal fluctuations in population size on the mean age at reproduction of a population.

To further examine how T_{jk} was related to the ecological factors determining population growth, we fitted another mixed-effect model where the mean age at reproduction (T_{jk}) was fitted as a response variable and the mean fitness of the population in each year and sex as fixed effects. We estimated the fitness of individual i in year j as survival plus half the number of recruits to the next year, because, in the absence of dispersal, this metric of fitness accounts for sexual reproduction and directly connects to local population dynamics (Sæther & Engen 2015):

$$w_{ijk} = S_{ijk} + \frac{1}{2} F_{ijk} \quad . \quad (\text{eq. S5})$$

The average fitness of a population each year was thus estimated as the mean fitness of all individuals breeding in a year in a population:

$$\bar{w}_{jk} = \frac{1}{N_{jk}} \sum_{i=1}^{N_{jk}} w_{ijk} \quad , \quad (\text{eq. S6})$$

where the sum is taken for all individuals breeding in year k in population j . Here, N is the number of adults breeding in year j in population k . Importantly, \bar{w}_{jk} will determine the changes in population size across years that are not caused by immigration and emigration.

Table S3. Mixed-effect model results explaining variation in the age of successfully reproducing parents. Model 1A focuses on the effects of mean fitness, and model 2A focuses on the effect of population size. B The same models but the results are after correcting for the age structure of the population. We present the mean and the 95% credible intervals.

Parameter	Model 1A log-normal link	Model 2A log -normal link	Model 1B	Model 2B
<u>Fixed effects</u>				
Intercept	1.01 (0.77, 1.25)	2.09 (1.82, 2.37)	0.43 (-0.04, -0.88)	0.07 (-0.26, 0.39)
Sex (females)	-0.14 (-0.40, 0.11)	0.12 (-0.07, 0.31)	-0.24 (-0.64, 0.18)	0.02 (-0.12, 0.16)
\bar{w}	-0.32 (-0.55, -0.10)		-0.35 (-0.69, -0.01)	
$\bar{w} : \text{sex}$	0.11 (-0.17, 0.38)		0.28 (-0.15, 0.68)	
Mean adult age			1.05 (0.90, 1.19)	1.06 (0.96, 1.21)
Mean pop size		-0.06 (-0.31, 0.21)		-0.01 (-0.11, 0.09)
Relative pop size		0.03 (-0.18, 0.23)		0.09 (-0.07, 0.23)
Relative pop size: sex		0.09 (-0.19, 0.37)		-0.08 (-0.29, 0.13)
<u>Random effects</u>				
Population	0.16 (0.07, 0.33)	0.26 (0.05, 0.29)	0.05 (0.00, 0.16)	0.05 (0.00, 0.17)

Year	0.07 (0.01, 0.15)	0.13 (0.01, 0.30)	0.07 (0.00, 0.19)	0.07 (0.00, 0.17)
Residual	0.31 (0.28, 0.34)	0.68 (0.62, 0.76)	0.49 (0.44, 0.54)	0.49 (0.45, 0.54)
