ECOLOGY LETTERS cnrs WILEY

Variation in generation time reveals density regulation as an important driver of pace of life in a bird metapopulation

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Funding information
Norges Forskningsråd, Grant/Award Number: 223257

Editor: Jean-Michel Gaillard

Abstract

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 life-history 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 than females. Individuals with longer generation times had greater lifetime reproductive success but not a higher expected population growth rate. Density regulation acted on recruit production, suggesting that longer generation times should be favoured 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.

KEYWORDS
age dependence, density dependence, fast–slow axis, life-history theory, pace-of-life syndromes, trade-offs

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 characterised by high survival rates, low reproduction rates and long generation times (Sæther & 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 age-dependent reproduction within populations (Bienvenu & Legendre, 2015; Cochran & Ellner, 1992). 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 (Araya-Ajoy et al., 2018; McGraw & Caswell, 1996). 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 has been strongly influenced by optimality models, where the evolutionary end points are the life-history strategies that maximise a measure of fitness, given a set of resource allocation trade-offs (Roff, 1993). The role of density dependence in determining optimal life-history strategies has been a longstanding topic in evolutionary ecology (Boyce, 1984; Reznick et al., 2002; Stearns, 1992). Density dependence was introduced as a driver of life-history strategies in the context of *r*- versus *K*-selection after island colonisation (MacArthur & Wilson, 1967). The general idea is that when populations are growing, density-independent selection will favour fast life-history strategies, but as populations approach their carrying capacity, selection will favour traits that increase the ability of individuals to monopolise resources, resulting in slower life-history strategies (Reznick et al., 2019). Hence, *r*- versus *K*-selection was suggested as the general explanation of among-species variation life histories (Pianka, 1970). This idea slowly lost favour and was replaced by density-independent but age-dependent variation in mortality as the favoured explanation for differences in the pace of life-history strategies (Boyce, 1984; Stearns, 1976). More recently, age-structured models of density-dependent evolution have provided general predictions concerning the role of density dependence in determining the optimal life-history strategies (Engen & Sæther, 2016; Lande

et al., 2017; Wright et al., 2020). Despite early models of life-history evolution, showing that density regulation should shape age-dependent reproductive effort (Charlesworth & Leon, 1976; Michod, 1979), very few empirical studies have focused on clarifying the role of population dynamics in shaping spatial and temporal variation in generation times (Kentie et al., 2020; Nilsen et al., 2009).

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 in a house sparrow (*Passer domesticus*) metapopulation. We first estimated an individual's 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. 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 age-dependent allocation in reproduction (Charlesworth & Leon, 1976; Michod, 1979). We therefore proceeded to study how the patterns of age- and density-dependent survival and reproduction affect the generation time of the population. Optimality models also state that the pattern of density regulation will determine whether evolution will maximise a measure of fitness that favours early reproduction (e.g. 'population growth rate of the individual', *sensu* McGraw & Caswell, 1996) or other fitness measures that not include the timing of reproduction such as lifetime reproductive success (Engen & Sæther, 2017; Mylius & Diekmann, 1995). We thus studied the relationship between generation time, lifetime reproductive success and the expected population growth rate of an individual. 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.

MATERIALS AND METHODS

Study system

We focused on eight island populations in a metapopulation of house sparrows 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 metapopulation level 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 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 organisation. 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 the 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 follows:

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

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 population separately. A population's generation time was thus estimated as the mean age of offspring parents in population j (T_j). Similarly, we estimated the mean age of parents (T_{jk}) for each year k for each population j (Cochran & Ellner, 1992). Finally, we estimated an individual's generation time (T_i) as its weighted mean age at reproduction (Araya-Ajoy et al., 2018; McGraw & Caswell, 1996), where a is the age of individual i in year k when it produced f number of recruits

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

Here d is the lifespan of individual i, and the sum in the denominator reflects the lifetime reproductive success of individual i. Estimates of individual's generation time included only individuals 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's projection matrices and derived an individual's expected population growth rate (λ_i) as the dominant eigenvalue of the individual's projection matrix (see eq. S1 for formulae). This can be interpreted as the growth rate of a population of individuals with the same characteristics as individual i. We also calculated the total number of recruits produced during an individual's life, that

is lifetime reproductive success. The average recapture rate was 0.80, with an among-year and among-island variance of 0.76, potentially biasing lifetime reproductive success estimates. However, we could detect the presence of additional non-captured individuals using the genetic analyses if they produced a recruit. This additional information increased the recapture probability (0.88) and reduced the variance in recapture rates (0.34), increasing the accuracy of lifetime reproductive success estimates. These analyses thus included individuals that were assumed to be dead before the breeding season of 2013 (i.e. never recaptured in any of the following years) even if it was not captured in all the years it was assumed to be alive.

Sources of variation in individual's 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 a fixed effect and random intercepts for population identity (n = eight populations) and birth year (n = 15 cohorts). We then included pedigree information in an animal model to decompose individual differences into additive genetic variation versus environmental variation (Lynch & Walsh, 1998). 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 then fitted the same animal models but only included sex as a fixed effect in order to estimate unadjusted additive genetic variances, heritabilities and evolvabilities (*sensu* Hansen et al., 2011).

We used univariate mixed models to study the relationships between individual's 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 corroborate our results using alternative generalised mixed-effect model structures (see Table S2).

Age- and density-dependent reproduction and survival

For the age- and density-dependent models, we used 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 generalised 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 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 fixed effects, sex and the linear and quadratic effects of age, in both models. We also fitted an interaction between the 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 used 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 fathers and mothers 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 each year in a given population (T_{jk}). As fixed effects, we fitted 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. We also fitted year and island identities as random intercepts.

To further examine how the weighted mean age at reproduction (T_{jk}) was related to factors determining population growth, we fitted another mixed-effect model where the mean age at reproduction was included as a response variable and the mean fitness of the population in each year and sex were included as fixed effects. We estimated the fitness of each individual in a given year 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 relates to the expected population growth

rate (Sæther & Engen, 2015). Therefore, the mean fitness in the population in a given year should partly reflect the 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 these results were robust to the choice of error distribution (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 three chains and adjusted the number of iterations per model until convergence based on the $\hat{R}$ statistic (Gelman et al., 2013). Warm-up periods were set to halve the number of iterations. 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 effects, and for the standard deviations of the random effects half student-t priors (see Bürkner (2018) for details). For the mark-recapture models, we used diffused normally distributed priors with a 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., 2013).

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 population average generation times (T_j) for fathers ranged from 1.5 to 2.4 years and for mother ranged from 1.6 to 2.7 years. Mean age at reproduction for each year within each island population (T_{jk}) ranged between 1 and 5 years for males and between 1 and 3.9 years for females. Finally, the average individual generation time (T_i) for males was 1.84 years (ranging from 1 to 5.6 years), whereas 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 with 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) was older

than the average individual's generation time (T_i), implying that individuals that reproduced when they were older were the ones contributing more recruits to the population.

Individual's generation time (T_i)

When we studied 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 adult 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, whereas 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 (0.14, CI = 0.01, 0.29). 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). Individuals with longer generation times obtained greater lifetime reproductive success. However, there was no evidence for a relationship between individual's 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 after their first breeding year, and there was a slight decrease at older ages, especially for males (Figure 1a and c). However, a higher proportion of the total number of recruits was still produced by 1-year old parents (Figure 1b and e), because at any given time, the fraction of 1-year old individuals was larger than any other age class (Figure 1c and f). 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 of the same age and there was some evidence suggesting that males also had a higher survival probability than females in their first breeding year (Table 2, S4). Thus, males had longer generation times, because they were more successful at reproducing when they were older and were more likely to survive their first breeding year than females. While the quadratic model did not reveal age-related changes in survival (Table 2), analyses treating age as a categorical variable suggests that there are non-linear changes in survival with age (Table S4).

We also found strong evidence for negative effects of density regulation on recruit production and some evidence for density regulation of adult survival (Table 2, S4). In years, when local population density was relatively high compared with average population sizes, recruit production was lower and there was a tendency for adult survival to also be 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

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

Parameter	Generation time	Generation time (log)	Lifetime reproductive success	Individual's growth rate
Fixed effects (β)				
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)	–	–
Random effects (σ)				
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)

Only individuals produced at least one recruit were included in the analyses. We present point estimates and 95% credible intervals in parenthesis.

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 on 5247 individual breeding attempts for 2729 individual house sparrows

Parameter	Reproduction	Survival
Fixed effects (β)		
Intercept	−0.85 (−1.42, −0.83)	0.25 (−0.28, 0.79)
Age	0.23 (0.13, 0.34)	−0.17 (−0.44, 0.14)
Age^2	−0.04 (−0.06, −0.01)	−0.01 (−0.05, 0.03)
Sex (male)	−0.17 (−0.29, −0.05)	0.27 (−0.20, 0.75)
Age: sex	0.22 (0.07, 0.37)	−0.01 (−0.11, 0.09)
Age^2: sex	−0.05 (−0.08, −0.01)	−0.02 (−0.07, 0.03)
Mean pop size	0.12 (−0.05, 0.30)	−0.04 (−0.34, 0.31)
Relative pop size	−0.20 (−0.28, −0.14)	−0.12 (−0.25, 0.03)
Random effects (σ)		
Individual	0.62 (0.54, 0.70)	0.78 (0.17, 0.93)
Population	0.18 (0.06, 0.40)	0.46 (0.21, 0.86)
Year	0.33 (0.21, 0.51)	0.36 (0.10, 0.42)
Shape	2.41 (1.81, 3.26)	–

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 on the latent scale of 0.76 (95% CI = 0.56, 0.84).

individuals was older (Table 3, Figure 2), especially for males. This suggests that in years, when the competition was strong and/or environmental conditions were poor, resulting in low average individual fitness, the successfully reproducing males tended to be older males. In contrast, when the mean fitness of the population was high, and thus populations were 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). In line with these results, the point estimate of the effect of adult population size on the mean age at reproduction suggests that in years, when population size was higher than average, the mean age of reproducing males was older (Table 3), however, the credible intervals are wide and overlapping zero.

DISCUSSION

The fast–slow axis is one of the most general and taxon-wide patterns of life-history (co)variation (Oli, 2004; Sæther & Bakke, 2000). The position of an organism along 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 our understanding of 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 models of life-history evolution stating that density regulation through intra-specific competition is a key factor shaping the pace of life-history strategies (Charlesworth & Leon, 1976; Engen & Sæther, 2016; Mylius & Diekmann, 1995).

The contemporary evolution of generation time hinges upon there being genetic variation in the traits determining the age-specific patterns of survival and reproduction. The estimated mean-scaled additive genetic variance (evolvability) of individual generation time in this metapopulation was within the range of values estimated for other life-history traits (Hansen et al., 2011), suggesting that it may change in response to selection. However, most variation in individual generation time was caused by adaptive and/or non-adaptive plasticity. While we could have quantified individual variation in age-specific survival and reproduction using a reaction norm approach (Nussey et al., 2007), the weighted mean age at reproduction summarises the distribution of reproduction across age in a single metric. Importantly, using such a metric allows the measurement of among-population, among-year and among-individual variation in a key theoretical quantity, generation time.

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 is a key determinant of the equilibrium life-history strategies observed in nature (Boyce, 1984; Pianka, 1970). Around the same time, models based on the age-specific allocation of limited resources showed that how and when density regulation affected population dynamics will affect life-history evolution (Charlesworth & Leon, 1976; Michod, 1979). For instance, models presented in Charlesworth and Leon (1976) imply that if density regulation acts through recruit production, then reproductive effort should vary with age. In agreement with the prediction of this model, we found that density regulation in this metapopulation acts on recruitment and that recruit production increases after the first adult year (Table 2). Importantly, higher allocation in reproduction with age should result in longer generation times.

When we analysed how generation time was affected by population dynamics, our results further suggest that local population dynamics affect 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. In contrast, when
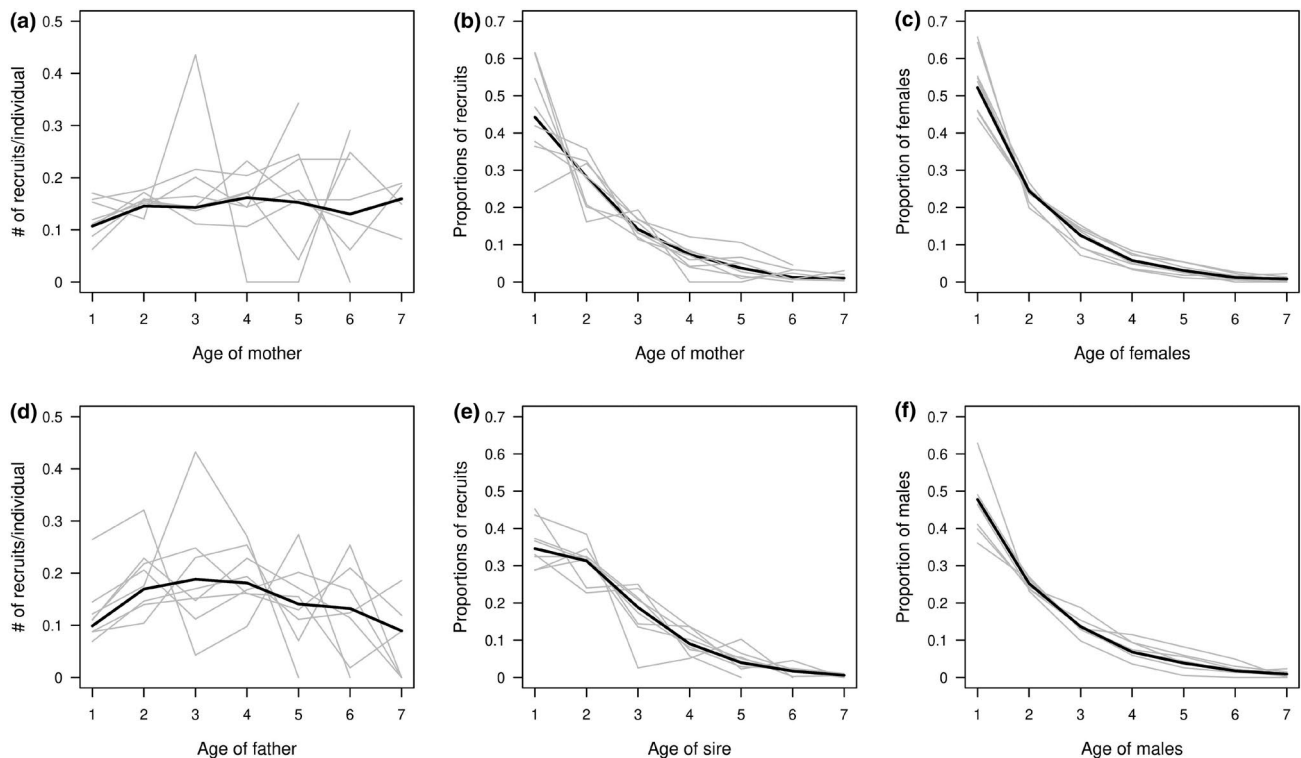
FIGURE 1 Average number of recruits per individual female (a) and male (d) house sparrows in relation to age. The age-specific variation in the proportion of recruits of mothers (b) and fathers (e) in the metapopulation. The age distribution of females and males in the metapopulation is shown in (c) and (f), respectively. Thick black lines represent the average in the metapopulation as a whole and grey lines represent each island population

TABLE 3 Mixed-effect model results explaining variation in the age of successfully reproducing parents of house sparrows

Parameter	Model 1	Model 2
Fixed effects		
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)
Mean fitness	−0.41 (−0.76, −0.06)	
Mean fitness: 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)
Random effects		
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)

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.

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 investing more in current reproduction are favoured, but when populations are close to or above their carrying capacity, the favoured individuals will be the ones that allocate more into traits enhancing survival and competitive ability (see Engen et al., 2013, Wright et al., 2020 and Sæther et al., 2016b, 2021 for empirical evidence).

In our analyses of patterns of recruitment, we cannot distinguish whether density regulation acts through parental allocation in reproduction or juvenile survival. 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 that brings populations back to their equilibrium size (Sæther et al., 2016a). Therefore, a plausible explanation for the patterns of density regulation in this metapopulation is that when local population sizes were increasing then all individuals managed to reproduce (even first-year breeding individuals), while in years when competition was high and populations were around their carrying capacity only individuals with high competitive abilities that were able to reach the older age classes managed to fledge offspring that recruited into the breeding population.
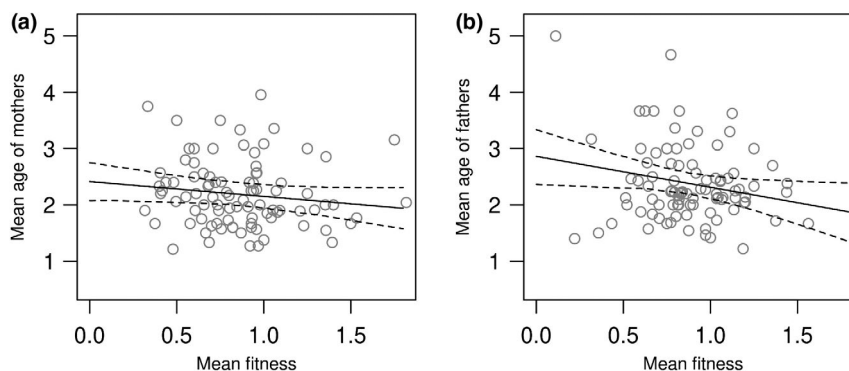
FIGURE 2 The relationship between mean age of successful reproduction and mean fitness for females (a) and males (b) in the house sparrow metapopulation. Each dot represents an island population in a given year. Lines represent the predicted mean values and dotted lines the 95% credible intervals

Generation time, fitness and constraints

The patterns of covariation between generation time, lifetime reproductive success and individual's 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 maximise 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 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 maximise lifetime reproductive success. Selection will favour 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 maximises a function that includes the density-independent growth rate of a phenotype and also its sensitivity to density regulation (Lande et al., 2017).

Our results suggest that stronger competitive regimes will result in longer generation times over time as local populations approach their equilibrium size in this metapopulation. However, they also imply that the effects of competition on life-history strategies depend on the stage in the life history where density regulation acts, and thus on the demographic characteristics of the species (e.g. Kentie et al., 2020). Furthermore, several processes are expected to constrain the evolution of longer generation times: (1) environmental sources of mortality, (2) stochastic fluctuations

in population size, and (3) life-history trade-offs. The role of environmental sources of mortality, such as predation or adverse weather conditions, dominated life-history studies in the early 1990s (Stearns, 1992). If adult mortality is very high, then natural selection should favour individuals that allocate energy towards reproduction earlier in life (Michod, 1979). In contrast, if juvenile mortality is high, natural selection should favour individuals allocate more in self-maintenance so that they have the chance to reproduce in several breeding seasons. We did not find strong evidence that adult survival decreases linearly (Table S5) with age or that it follows a quadratic relationship (Table 2); however, survival was not totally independent of age (Figure S1, Table S4) and the patterns varied between islands (Holand et al., 2016). Environmental sources of mortality therefore seem to be critical drivers constraining the evolution of longer lifespans and thus longer generation times in this metapopulation. The observed patterns of age-specific reproduction appear to be the result of an interaction between density regulation and environmental factors affecting survival.

Another factor constraining the evolution of longer generation times is environmentally driven fluctuations in population size (Engen & Sæther, 2016). When environmental stochasticity in population growth rates are large, fast life-history strategies and short generation times are favoured, but when population fluctuations are small and around the carrying capacity, then selection should favour slower life-history strategies and long generation times (Engen et al., 2013). Thus, density-dependent selection favouring longer generation times may be counterbalanced by density-independent selection induced by stochastic fluctuations in population size favouring shorter generation times. The observed fluctuations in population size in this metapopulation (Baalsrud et al., 2014, Niskanen et al., 2020) are thus expected to affect the mean age at reproduction.

Life-history models assume that there is a resource allocation trade-off that constrains evolution to a subset 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 and/or survival. 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 suggested by our results showing an increase in production of recruits with age (Figure 1) and that older individuals were the ones that managed to reproduce when the competition was high or the environment was harsh (Figure 2). It could therefore be that individuals that acquired more resources were the ones that managed to grow old and 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 with 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 with extra-pair reproduction. If older males increased their reproductive output through competitive access to extra-pair fertilisations (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 this effect certainly deserve further study.

CONCLUSION

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 variation have focused on density-dependent effects on the mean age of reproduction. 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, a detailed understanding of the eco-evolutionary dynamics of the mean age at reproduction may provide important insights for predicting whether organisms will be able to adapt to current rates of environmental change.

AUTHORSHIP
YAA wrote the first draft of the manuscript, and all authors contributed substantially to revisions. YAA and JW designed the study. The study population was established by BES, THR and HJ. HJ, THR, TK, PSR and BR conducted fieldwork. AN and HJ developed the pedigree. YAA performed the analyses with input from all co-authors.

PEER REVIEW
The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13835.

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