Effects of ambient temperatures on evolutionary potential of reproductive timing in boreal passerines

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Abstract

1. Many populations need to adapt to changing environmental conditions, such as warming climate. Changing conditions generate directional selection for traits critical for fitness. For evolutionary responses to occur, these traits need to be heritable. However, changes in environmental conditions can alter the amount of heritable variation a population expresses, making predictions about expected responses difficult.
2. The aim of this study was to evaluate the effects of ambient temperatures on evolutionary potential and strength of natural selection on the timing of reproduction in two passerine birds breeding in boreal forests.
3. Long-term data on individually marked Willow Tits (*Poecile montanus*, 1975–2018) and Great Tits (*Parus major*, 1969–2018) were analysed with random regression animal models to assess if spring temperatures affect the expressed amount of additive genetic variation (V_A) and heritability (h^2) in the timing of breeding. We assessed if ambient temperatures of different seasons influenced the direction and strength of selection on breeding time. We also evaluated if the strength of selection co-varied with evolutionary potential.
4. Levels of V_A or h^2 expressed in laying date were unaffected by spring temperatures in both study species. Selection for earlier breeding was found in the Willow Tit, but not in the Great Tit. In the Willow Tit, selection for earlier breeding was more intense when the temperatures of following autumns and winters were low. Different measures of evolutionary potential did not co-vary strongly with the strength of selection in either species.
5. We conclude that there is no or little evidence that climate warming would either constrain or promote evolutionary potential in timing of breeding through changes in amount of genetic variance expressed in boreal Willow and Great Tits. However, selection on the timing of breeding, a life-history event taking place in springtime, is regulated by

temperatures of autumns and winters. Rapid warming of these periods have thus potential to reduce the rate of expected evolutionary response in reproductive timing.

Keywords: breeding time, climate change, heritability, natural selection, quantitative genetics

Introduction

Many populations are facing a need to adapt to changing environmental conditions, such as to those brought along by the ongoing anthropogenically driven climate change. An evolutionary response is possible, if a trait is subject to directional natural selection, and there is heritable variation in the trait in question (Lynch & Walsh, 1998). However, changes in environmental conditions not only influence the strength of selection, but they can also affect traits' evolutionary potential through changing the amount of heritable variation a population expresses (e.g. Wilson et al., 2006).

The amount of genetic variation a population expresses in given trait is not constant, but it may vary according to environmental conditions that prevail (Hoffmann & Merilä, 1999). Phenotypic plasticity refers to genotype's ability to produce different phenotypes in different environmental conditions (Pigliucci, 2001), and inter-individual variation in the amount of phenotypic plasticity can make population to express different amounts of genetic variation in different environmental conditions. Unfavourable conditions may either decrease or increase the amount of genetic variation a population expresses (Hoffmann & Merilä, 1999). For example, poor nutrition often results in lowered heritability of body size in birds (Gebhardt-Henrich & van Noordwijk, 1991; Hoffmann & Merilä, 1999, Merilä & Sheldon, 2000). It is also possible that harsh conditions lead to increased heritability, as often has been observed in insect studies (Hoffmann & Merilä, 1999).

The narrow-sense heritability (h^2) of a trait is defined as the proportion of the phenotypic variance (V_P) ascribable to additive genetic variance (V_A) ($h^2 = V_A/V_P$). It indicates the extent to which a trait can be expected to evolve in response to directional selection. However, variation in heritability can be induced either by changes in additive genetic or residual variance (e.g. Merilä & Sheldon, 1999, Wheelwright et al., 2014). Thus, heritability may not be a practical measure to compare evolutionary potential between traits or between populations. Hansen, Pélabon, and Houle (2011) suggest that heritability is not a suitable stand-alone measure of evolutionary potential in the wild, especially when comparing populations or species. However, comparisons of heritabilities of the same trait in different environmental conditions are valid.

Changes in the amount of expressed heritable variation may or may not be coupled with the same environmental factors that determine the strength of natural selection. Heritability values can correlate with the strength of natural selection (Merilä, 1997, Wilson et al., 2006), but this is not a universal phenomenon (Ramakers, Culina, Visser, & Gienapp, 2018a). Climate warming has affected phenologies of different organisms in both terrestrial and aquatic environments (e.g. Walther et al., 2002, Parmesan & Yohe, 2003, Root et al., 2003). Different rates of phenological shifts among interacting species can lead to temporal mismatches between e.g. a predator and its prey (Visser & Both, 2005), which can give rise to novel selection pressures. In the temperate zone Dutch Great Tit (*Parus major*) population, availability of caterpillar food during the nestling period that affects natural selection on breeding time is linked with spring temperature (Ramakers, Gienapp, & Visser, 2018b). However, in the boreal zone, the strength of natural selection may be more strongly affected by winter than spring temperatures. For instance, unfavourable spring conditions do not necessarily result in high mortality rates in the following winter if winter conditions are favourable. In fact, winter temperatures in Northern Europe are rising more rapidly than temperatures during other seasons (Ruosteenoja, Jylhä, & Kämäräinen, 2016).

The aim of this study was to evaluate the effects of ambient temperatures on evolutionary potential and strength of natural selection on the timing of breeding in two passerine birds breeding in boreal zone forests. We analysed long-term data on individually marked and pedigreed Willow Tit (*Poecile montanus*, 1975–2018) and Great Tit (1969–2018) populations to address the following two questions: First, do spring temperatures affect the expressed amount of additive genetic variation (V_A) and heritability (h^2) in breeding time in two species? Second, how do ambient temperatures of different seasons affect the direction and strength of selection on breeding time, and does the strength of selection co-vary with levels of expressed additive genetic variance and heritability?

Material and Methods

Study species

Willow Tits and Great Tits are small hole-nesting passerine birds. The Willow Tit is a boreal forest specialist with a declining population size (Hyvärinen, Juslén, Kemppainen, Uddström, & Liukko, 2019), whereas the Great Tit has relatively recently expanded its range to the boreal zone and the population size is growing (Valkama, Vepsäläinen, & Lehikoinen, 2011). Willow Tits breed in cavities they have excavated in decaying stumps, whereas Great Tits accept nest boxes. The timing of breeding is affected by spring temperatures both in the Willow Tit (Vatka, Orell, & Rytkönen, 2011) and in the Great Tit (Vatka, Rytkönen, & Orell, 2014) – both populations show advancing long-term trends in reproductive timing. Annual median egg-laying dates of Willow Tits are strongly correlated with the mean ambient temperature of the period March 27–May 6 ($R^2 = 0.717$; Vatka et al., 2011). For the Great Tit, the corresponding period is 29 March–15 May ($R^2 = 0.721$; Vatka et al., 2014). Spring temperatures also determine the timing of the main food source for nestling provisioning: caterpillars of moths and sawflies that forage in tree canopies (Vatka et al., 2011, 2014). Warming of springs has not yet led to a temporal mismatch between the caterpillar availability and nestlings' food demands in the study populations – in fact, the match with the food peak has improved in the Willow Tit (Vatka et al., 2011, 2014).

Willow Tits spend their winters in territorial flocks whose social hierarchy is influenced by prior residency (Koivula, Lahti, Orell, & Rytkönen, 1993). Willow Tits hoard food for winter (Brodin, Lahti, Lens & Suhonen, 1996) and young from early broods have more time to prepare for the upcoming winter. Because of these, Willow Tit young from relatively early broods have higher recruitment rates than young from late broods, whereas for the Great Tit, recruitment rates are better explained by synchrony with the caterpillar food availability (Pakanen, Orell, Vatka, Rytkönen, &

Broggi, 2016). Winter survival of boreal Great Tits depends primarily on food supplied by humans (Orell, 1989).

Study area

The Oulu study area in Northern Finland (ca. 65°05’N, 25°33′E) consists of coniferous, deciduous and mixed forests and swamps of varying ages (Orell & Ojanen, 1983a, b; Rytkönen & Orell, 2001). Similar forest habitats continue outside the study area, and thus the study populations are open. The Willow Tit study area has expanded in size, starting from ca. 2 km^2 in 1975 (Orell & Ojanen, 1983c) and gradually increasing to ca. 25 km^2 in 1996. From 1969 onwards, 100–400 wooden nest boxes were provided for Great Tits in separate sub-areas of 2–4 km^2 total in 1969–1997, and since 1998, in four neighbouring sub-areas in total of 8 km^2 (Orell & Ojanen, 1983a, b; Rytkönen & Orell, 2001; Karvonen, Orell, Rytkönen, Broggi, & Belda, 2012, Vatka et al., 2014, Pakanen et al., 2016).

Data collection

Long-term monitoring of nesting attempts of Willow Tits (1975–2018) and Great Tits (1969–2018) followed routine procedures (Orell & Ojanen, 1983a, Orell & Koivula, 1988, Orell, Lahti, Koivula, Rytkönen, & Welling, 1999). Nests were visited at least weekly and their contents were recorded. The Willow Tit nests were checked through the entrance hole with the aid of a small mirror and a torch, or through a small peak hole cut at the level of the nest, covered afterwards with birch bark. The laying date of the first egg was as a rule calculated from the observed number of eggs in an incomplete clutch (i.e., incubation had not yet started) under the assumption that one egg is laid per day. The data consisted of 3331 and 3903 laying date records of first broods for the Willow Tit and the Great Tit, respectively.

Both the parents and young were marked with individually coded aluminium leg rings and parents with unique combinations of plastic colour rings, enabling pedigree construction and identification of individuals that recruited to the study populations. Birds were ringed under a license provided by the Finnish Natural History Museum, University of Helsinki. Parental birds were aged as yearlings or older either by calculating from the ringing date of recruits, or based on the tail feather shape in Willow Tits (Laaksonen & Lehikoinen, 1976) or on plumage coloration in Great Tits (Svensson, 1992).

Pruned Willow Tit pedigree consisted of 1950 individuals and reached up to eight generations in depth. It contained the following pair-wise relatedness categories: 0.025 (N=554), 0.05 (460), 0.075 (3), 0.1 (1), 0.125 (638), 0.15 (4), 0.175 (4), 0.25 (793), 0.275 (2), 0.3 (5), 0.375 (1), 0.5 (907), 0.525 (2), 0.55 (1) and 0.625 (2). The relatedness category 0.5 signifies parent-offspring and full sib pairs, 0.25 grandparent-grandchild and half sib pairs, and 0.125 first cousins *et cetera*. Pruned Great Tit pedigree contained 3187 individuals, with a pedigree depth up to nine generations, with the following pair-wise relatedness categories: 0.025 (N=85), 0.05 (103), 0.125 (196), 0.175 (4), 0.25 (303), 0.275 (5), 0.375 (4), 0.5 (589), 0.525 (5), 0.55 (2), 0.625 (1) and 0.75 (2).

Data of daily mean ambient temperatures for 1969–2018 were retrieved from the Finnish Meteorological Institute, Oulunsalo observatory that is situated ca. 20 km south from the study area.

Quantitative genetic analyses

Random regression animal models were used to estimate how additive genetic variances and heritabilities were related to spring temperatures. The function ‘MCMCglmm’ (library ‘MCMCglmm’; Hadfield, 2010) was used to fit models in R 3.6.2 (R Core Team, 2019). Laying date (y) of the individual i in year j was modelled as:

$$y_{ij} = \alpha_y + \beta_1 age_{ij} + \beta_2 T_j + year_j + a_i + b_i T_j + A_i + B_i T_j + e_{y,ijl}, \tag{1}$$

where α_y is the intercept and β_1 and β_2 are regression coefficients for fixed effects female's age (age_{ij}) and spring temperature (T_j), respectively. Spring temperature was the mean temperature of periods 27 March–6 May or 29 March–15 May for the Willow and the Great Tits, respectively. Spring temperature was mean centered. Year ($year_j$) was used as a block random factor with estimated variance of $year_j \sim N(0, \sigma^2_{year})$. a_i and b_i are female specific random intercepts and slopes of permanent environmental effect, and A_i and B_i are random intercepts and slopes of the additive genetic component. Permanent environmental and additive genetic variances were estimated using two 2×2 variance-covariance matrices:

$$P = \begin{bmatrix} \sigma_a^2 & \sigma_{a,b} \\ \sigma_{a,b} & \sigma_b^2 \end{bmatrix} \tag{2}$$

$$G = \begin{bmatrix} \sigma_A^2 & \sigma_{A,B} \\ \sigma_{A,B} & \sigma_B^2 \end{bmatrix} \tag{3}$$

$e_{y,ijl}$ (eqn. 1) is the residual term. Possible heteroscedasticity of residual variance across spring temperatures was considered by estimating the residual variance for each equal-interval group *l* of spring temperatures as $e_{y,ijl} \sim N(0, \sigma^2_{e,l})$ (Ramakers et al. 2018a). The number of groups *n* was decided upon from four alternatives (*n* = 4, 6, 8 or 10) based on model comparison using DIC values (Ramakers, Visser, & Gienapp, 2020). For both species, *n* = 10 was selected.

We used a wide normal distribution as a prior for fixed factors as a default. For the residual variance, we used inverse-Wishart prior with V = diag(*n*) and nu = 0.002. For other variance components, parameter-expanded priors (V = diag(*x*), nu = *x*, alpha.mu = 0, alpha.V = diag(*x*)*1000) were used. A total of 10 100 000 MCMC iterations were run for each species, including a burn-in period of 100 000 iterations. The remaining 10 000 000 iterations were sampled with a thinning interval of 10 000, leading to sample sizes of 1000 saved iterations.

Additive genetic variances (V_A) and heritabilities (h^2) were estimated for each documented spring temperature value for both species. The method described in the Appendix of Hadfield, Wilson, Garant, Sheldon, and Kruuk (2010) was applied to create confidence intervals for these estimates. This involved calculation of the above-mentioned estimates for each of the saved 1000 iterations to create distributions of estimated values, of which median values are reported along with 95% HPD intervals using function 'HPDinterval' in library 'coda' (Plummer, Best, Cowles, & Vines 2006). V_A for each spring temperature value T_j were derived using the **G** matrix as

$$V_{A_j} = \sigma_A^2 + 2\sigma_{A,B}T_j + \sigma_B^2 T_j^2 \qquad (4)$$

and V_{PE} similarly using the **P** matrix. Temperature-dependent heritability was calculated as

$$h_j^2 = \frac{V_{A_j}}{V_{A_j}+V_{PE_j}+\sigma_{year}^2+\sigma_{e,l}^2}, \qquad (5)$$

where $\sigma_{e,l}^2$ is the error variance component in the corresponding temperature group *l*. Temperature-dependent V_A and h^2 values were plotted against spring temperatures.

Selection on the breeding time

We studied which temperature periods (*viz*. spring, autumn and winter) affect selection on breeding time. These periods were selected *a priori* to present different potential mechanisms of selection. Spring temperatures (the mean temperature of periods March 27–May 6 or 29 March–15 May for the Willow and the Great Tit, respectively) may affect the temporal match-mismatch with food availability during the nestling period (Vatka et al., 2011), which in turn may affect breeding success and thus selection on the timing of breeding. Temperatures of the following autumn (the mean temperature of August–October) coincide with the period of intensive food hoarding in the

Willow Tit (Haftorn, 1956), and winter temperatures (the mean temperature of December–February) represent the coldest time of the year. These may affect survival, and thus, recruitment rates of the young.

We used generalized linear mixed effect models fit with function 'glmer' in library 'lme4' (Bates, Mächler, Bolker, & Walker, 2015) with Poisson error structure. In these models, the response variable was annual proxy of individual fitness, measured as the number of recruits a female produced annually, including recruits from the first brood and a potential re-nesting attempt or second brood. The number of recruits (rather than the number of fledglings or eggs produced) was used as a proxy of fitness, because the definition of fitness refers to the relative contribution of a phenotype to the future generations (e.g. Krebs, 2009) and thus, only offspring that make it to express the trait (the timing of breeding) count. However, for comparison we present an analysis with the number of fledglings as a proxy of individual fitness in Appendix 1. Annual proxy of individual fitness was regressed against the annually centered timing of breeding of the female's first brood in interaction with temperature (centered temperatures of the three periods were tested one at a time). A significant interaction term would tell that ambient temperatures affect selection on the timing of breeding. Female identity and year were used as block random factors.

These analyses were restricted to years 1991–2017 and 1999–2017 for the Willow and the Great Tit, respectively. These restrictions were applied because the Willow Tit study area was small and fragmented before 1991 (Lampila, Orell, Belda, & Koivula, 2006), and the Great Tit study area reached its current extent in 1998. Thus, early years were omitted in order to acquire selection gradients that are comparable between years. In 1998, a large number of Great Tit nests were experimentally destroyed during the incubation stage, and therefore this year was also excluded from the analysis.

Covariance of measures of evolutionary potential and selection

To estimate annual selection gradients, we used models with Poisson error structure fit by 'MCMCglmm'. Annual proxy of individual fitness (measured as the number of recruits a female produced annually) was regressed against the standardized timing of breeding (centered to a mean of zero and scaled to a variance of one) in annual subsets of data. Standardisation was done before creating annual subsets. Regression coefficients β_j were interpreted as directional selection gradients (Morrissey & Goudie, 2016).

We examined covariance of different measures of evolutionary potential (i.e., expressed additive genetic variation and heritability) and selection. As explained above, V_{A_j} and h_j^2 were calculated and β_j were retrieved for each of the 1000 saved iterations. We calculated Pearson's correlation coefficients *r* between each k^{th} set of values of V_{A_j} or h_j^2 and β_j, reporting their mean and HPD intervals. In similar fashion, we calculated Pearson's correlation coefficients *r* between measures of evolutionary potential and $|\beta_j|$ to infer the covariance between evolutionary potential and the strength of selection (regardless of its direction).

Results

Effects of spring temperatures on additive genetic variance and heritability

The amount of additive genetic variance (V_A) expressed in laying date tended to be higher for Great Tits than for Willow Tits (Fig. 1a, b), but in both species V_A was independent of spring temperatures (Fig. 1a, b). In fact, the variance attributable to random slopes of the additive genetic component σ_B^2 was low in both species (Table S1, Table S2).

Heritability estimates (h^2) of laying date were somewhat low both in the Willow Tit (h^2 range = 0.134–0.238; Table S3) and the Great Tit (h^2 range = 0.237–0.425; Table S4), and independent of spring temperatures (Fig. 1c, d). There was some variability in heritability estimates especially in the Great Tit (Fig. 1d), owing to variation in estimated error variances between different temperature groups (Table S2).

Effects of ambient temperatures on the strength of selection

Early broods produced more recruits than late broods and thus, there was a significant selection pressure for earlier breeding in the Willow Tit (Table 1). However, for the Great Tit, the main effect of the timing of breeding on recruitment rate was nonsignificant and thus no significant overall selection for earlier breeding was found (Table 2). The strength of directional selection on the timing of breeding was independent of spring temperatures in both species (Table 1, Table 2). In the Willow Tit, selection for earlier breeding was more intense when the temperatures of the following autumn or winter were cold, indicated by significant interaction terms Timing*Temperature (Table 1). Winter temperatures had also a significantly negative main effect, meaning that recruitment rates are lower in warm winters (Table 1). In the Great Tit, autumn or winter temperatures did not affect the strength of directional selection on reproductive timing (Table 2).

Covariance of measures of evolutionary potential and selection

There was year-to-year variation in the selection gradients β on breeding time, ranging from -1.208 to 0.246 in the Willow Tit ($\bar{\beta} =$ -0.408) and from -0.634 to 1.497 in the Great Tit ($\bar{\beta} =$ 0.006; Table S5). Neither the levels of expressed additive genetic variance nor heritability were correlated with annual selection gradients, or with the strength of selection in either species (Table 3).

Discussion

We did not detect any significant changes in the expression of additive genetic variance or heritability with warming spring temperatures. As in the case of our results, V_A in timing of breeding did not change with warming springs in a UK Great Tit population (Husby et al., 2010). Similarly, Ramakers, Gienapp, and Visser (2018) found little genotype-by-environment interaction in the timing of breeding related to spring temperatures in a Dutch Great Tit population. However, inconsistent effects of environmental conditions on expression of additive genetic variance have been reported in other traits (Hoffmann & Merilä, 1999).

Heritability values of breeding time were rather low, which is typical of avian life-history traits (e.g. Merilä & Sheldon, 2000, McCleery et al., 2004). The observed variation in heritability estimates was mostly due to variation in residual variance estimates between different temperature groups, rather than due to variation in the additive genetic variance component. Studies from other Great Tit populations have reported heritability values on breeding time that are somewhat lower than the values we report here (h^2 range: 0.237–0.425; an overall average = 0.332, Table S4). McCleery et al. (2004) reported a heritability of 0.159 (SE=0.059) for Wytham Woods population, whereas Gienapp, Calus, Laine, and Visser (2019) estimated heritability of 0.24 (SE=0.07) based on a social pedigree and 0.17 (SE=0.06) based on kinships inferred from genetic markers for Hoge Veluwe population. To our knowledge, no other heritability estimates of the timing of breeding are available for the Willow Tit. That the additive genetic variance and heritability were lower in the Willow than in the Great Tit makes sense in the light that the timing of breeding in Willow Tits seem to be a subject for directional selection more often than in Great Tits, and because directional selection is expected to erode genetic variation. Whatever the ultimate reason for the low heritability, low heritabilites translate to low rates of expected evolutionary change for given intensity of selection (Falconer & Mackay, 1996). As the heritabilities in both species did not show any trend in relation to spring temperatures, warming of springs are not expected to neither accelerate nor slow down evolutionary responses as far as the effect of heritability values is concerned.

As noted also in earlier studies (e.g. Sheldon, Kruuk, & Merilä, 2003, Husby, Visser, & Kruuk, 2011, Visser et al., 2015), the strength of directional selection on breeding time was quite variable among years. However, in spite of the fact that boreal Willow and Great Tits show advancing long-term trends in their timing of breeding (Vatka et al., 2011, 2014), we did not detect statistically significant directional selection for earlier breeding in the Oulu Great Tit population. This indicates that the observed change in the timing of breeding in the Great Tit results most likely from phenotypic plasticity, and hence, is not a genetically based evolutionary response (cf. Charmantier, & Gienapp, 2014). In contrast, we found significant selection for earlier breeding in the Willow Tit, which in combination with low but significant heritability of breeding time should promote evolutionary response towards earlier breeding. However, to what degree the advanced breeding time in the Willow Tit reflects genetic *vs*. plastic changes remains to be investigated.

Spring temperatures do not seem to influence selection on the timing of breeding in either of the two study species. Yet, spring temperatures affect the synchrony between the breeding time and the timing of caterpillar food availability in the Willow Tit: synchrony is better in warm years (Vatka et al., 2011). In contrast, Great Tits advance their breeding time at the same rate as the timing of the caterpillar food peak advances with rising spring temperatures, and thus, spring temperatures do not affect the level of synchrony in the Oulu Great Tit population (Vatka et al., 2014). Hence, one would expect that spring temperatures would influence selection on the timing of breeding in the Willow Tit. However, a previous study suggests that the synchrony with the caterpillar food peak is not the most relevant selection mechanism in the Willow Tit – instead, timing of breeding in relation to conspecifics affected recruitment rate (Pakanen et al., 2016). Visser et al. (2015) also found a similar lack of association between the level of synchrony with the food availability and selection on the timing of breeding in migratory Pied Flycatchers (*Ficedula hypoleuca*).

Autumn and winter temperatures were found to affect the strength of selection on the timing of breeding in the Willow Tit. This is an understandable outcome when considering the species' ecology. Willow Tits spend their winters in flocks whose social hierarchy is affected by prior residency (Koivula et al., 1993). They hoard food in autumn (Brodin et al., 1996) and young from early broods have more time to prepare for the winter. Thus, young from early broods are in a better position to survive than young from late broods. This seems to be particularly so when autumns and winters are cold. Autumn temperatures likely affect food hoarding, inducing a selection pressure on breeding time. Cold winters are associated with higher overall recruitment rate, but selection for earlier breeding is more intense when winters are cold. Rapid warming of autumns and winters appear to reduce the strength of directional selection for earlier breeding. This in turn can reduce the rate of expected evolutionary change, unless some other important ultimate factor(s) comes into play.

That warm winters are associated with lower recruit production in the Willow Tit can be explained by several mechanisms, yet they are so far only speculative explanations. Temperatures fluctuating above and below the freezing point can first melt the snow and then create an ice shield covering the food hoards. Warm winters can cause food hoards to decay (Sechley, Strickland, & Norris, 2015), and thus food availability can decrease drastically. It is also possible that wet weathers (rain coming down as water instead of snow) affect the thermoregulation of birds when plumage gets wet. Winter rain can decrease foraging efficiency during short days, followed by cold and long nights. These mechanisms would likely affect all birds similarly, regardless of their social status or birth date.

In order to understand how environmental changes affect natural selection, one needs to identify the life stage when selection kicks in. In the boreal zone, (pre-)winter conditions seem to play an important role for the selection on breeding time. The situation may be different in temperate zone populations where winters are not equally harsh. Visser et al. (2015) found that in a long-distance migratory bird, temperatures at the time of arrival to the breeding grounds affected selection on timing of reproduction. They suggested that environmental conditions with a lag of up to two years can affect selection on a phenological trait (Visser et al., 2015). We also found that environmental conditions affect selection on timing of breeding with a temporal lag, although in our case the lag was not more than about six months. It is important to recognize that evolution of the timing of breeding, a life history event that takes place in spring, can be regulated by environmental conditions outside this period. In other words, one needs to consider the whole lifespan of individuals when trying to assess factors influencing a certain life-history trait.

Environmental coupling of heritability and selection appears to be rare in wild populations (Ramakers et al., 2018, but see Merilä, 1997, Wilson et al., 2006, Husby et al., 2011). In accordance with this, we did not find any strong correlations between the different measures of evolutionary potential and the selection or its strength. This corresponds with the finding of little changes in evolutionary potential with the environment. In this perspective, it might be worth emphasizing that it may be relevant to consider separately on the one hand factors that affect the expressed amount of heritable variation, and on the other hand factors that affect selection on the trait in question – these might be totally distinct factors, influenced differently by changes in environmental conditions. If this is a common, or a general pattern, it will be difficult to predict how populations respond to selection brought by, for instance, changing climatic conditions.

Conclusions

The results suggest that climate warming will neither constrain nor promote evolutionary potential in boreal populations of Willow and Great Tits. However, environmental conditions can affect selection on breeding time with a temporal lag: evolution of a life history event that takes place in springtime appears to be regulated by conditions prevailing in following autumns and winters in the

Willow Tit. Hence, in the light of the findings of this study, rapid warming of these periods can be expected to reduce the strength of directional selection for earlier breeding, and thereby also the expected evolutionary response to selection.

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Authors' contributions

EV, JM and MO conceived the ideas; MO, SR and EV collected the data; EV analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability Statement

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.s1rn8pk5w (Vatka et al., 2020).

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Figure legends

Figure 1. Additive genetic variances (A-B) and heritabilities (C-D) of breeding time in relation to spring temperatures in the Willow Tit (A, C) and the Great Tit (B, D).

Tables

Table 1. Parameters of generalized linear mixed effect models explaining annual proxy of individual fitness (measured as the number of recruits produced) in the Willow Tit. Explanatory variables are centered. A significant interaction term (Timing*Temperature) indicates that selection on the timing of breeding is influenced by ambient temperatures. Statistically significant ($p < 0.050$) parameter estimates are depicted in boldface.

Model	Fixed effects	Estimate	SE	z value	p
Spring temperature	Intercept	**-1.534**	0.112	-13.686	< 0.001
	Timing of breeding	**-0.067**	0.010	-6.510	< 0.001
	Temperature	-0.042	0.079	-0.534	0.594
	Timing*Temperature	0.003	0.007	0.470	0.638
Autumn temperature	Intercept	**-1.544**	0.113	-13.657	< 0.001
	Timing of breeding	**-0.071**	0.010	-6.861	< 0.001
	Temperature	-0.040	0.108	-0.373	0.709
	Timing*Temperature	**0.026**	0.012	2.159	0.031
Winter temperature	Intercept	**-1.550**	0.102	-15.130	< 0.001
	Timing of breeding	**-0.066**	0.010	-6.434	< 0.001
	Temperature	**-0.086**	0.036	-2.351	0.019
	Timing*Temperature	**0.009**	0.004	2.169	0.030

Table 2. Parameters of generalized linear mixed effect models explaining annual proxy of individual fitness (measured as the number of recruits produced) in the Great Tit. Explanatory variables are centered. A significant interaction term (Timing*Temperature) would indicate that selection on the timing of breeding is influenced by ambient temperatures. Statistically significant (p < 0.050) parameter estimates are depicted in boldface.

Model	Fixed effects	Estimate	SE	z value	p
Spring temperature	Intercept	**-1.927**	0.125	-15.414	< 0.001
	Timing of breeding	-0.008	0.012	-0.654	0.513
	Temperature	0.026	0.086	0.306	0.760
	Timing*Temperature	0.015	0.010	1.507	0.132
Autumn temperature	Intercept	**-1.933**	0.123	-15.691	< 0.001
	Timing of breeding	-0.004	0.012	-0.350	0.726
	Temperature	0.140	0.135	1.033	0.302
	Timing*Temperature	0.020	0.016	1.287	0.198
Winter temperature	Intercept	**-1.947**	0.122	-16.000	< 0.001
	Timing of breeding	-0.004	0.012	-0.370	0.712
	Temperature	-0.063	0.036	-1.740	0.082
	Timing*Temperature	0.007	0.005	1.410	0.159

Table 3. Pearson’s correlation coefficients r (and their 95% HPD intervals) between different measures of evolutionary potential and selection in the Willow Tit and the Great Tit.

Species	Measure of evolutionary potential	Annual selection gradients		Strength of selection	
		r	95% HPD interval	r	95% HPD interval
The Willow Tit	Additive genetic variance V_A	-0.090	[-0.395, 0.211]	0.058	[-0.271, 0.366]
	Heritability h^2	-0.157	[-0.446, 0.153]	0.095	[-0.245, 0.443]
The Great Tit	Additive genetic variance V_A	0.065	[-0.342, 0.360]	-0.145	[-0.493, 0.255]
	Heritability h^2	-0.026	[-0.297, 0.245]	-0.128	[-0.460, 0.148]