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

3

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14

15 **Abstract**

- 16 1. Many populations need to adapt to changing environmental conditions, such as warming
17 climate. Changing conditions generate directional selection for traits critical for fitness. For
18 evolutionary responses to occur, these traits need to be heritable. However, changes in
19 environmental conditions can alter the amount of heritable variation a population expresses,
20 making predictions about expected responses difficult.
- 21 2. The aim of this study was to evaluate the effects of ambient temperatures on evolutionary
22 potential and strength of natural selection on the timing of reproduction in two passerine
23 birds breeding in boreal forests.
- 24 3. Long-term data on individually marked Willow Tits (*Poecile montanus*, 1975–2018) and
25 Great Tits (*Parus major*, 1969–2018) were analysed with random regression animal models
26 to assess if spring temperatures affect the expressed amount of additive genetic variation
27 (V_A) and heritability (h^2) in the timing of breeding. We assessed if ambient temperatures of
28 different seasons influenced the direction and strength of selection on breeding time. We
29 also evaluated if the strength of selection co-varied with evolutionary potential.
- 30 4. Levels of V_A or h^2 expressed in laying date were unaffected by spring temperatures in both
31 study species. Selection for earlier breeding was found in the Willow Tit, but not in the
32 Great Tit. In the Willow Tit, selection for earlier breeding was more intense when the
33 temperatures of following autumns and winters were low. Different measures of
34 evolutionary potential did not co-vary strongly with the strength of selection in either
35 species.
- 36 5. We conclude that there is no or little evidence that climate warming would either constrain
37 or promote evolutionary potential in timing of breeding through changes in amount of
38 genetic variance expressed in boreal Willow and Great Tits. However, selection on the
39 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

47 **Introduction**

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

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

64 The narrow-sense heritability (h^2) of a trait is defined as the proportion of the phenotypic variance
65 (V_P) ascribable to additive genetic variance (V_A) ($h^2 = V_A/V_P$). It indicates the extent to which a
66 trait can be expected to evolve in response to directional selection. However, variation in
67 heritability can be induced either by changes in additive genetic or residual variance (e.g. Merilä &
68 Sheldon, 1999, Wheelwright et al., 2014). Thus, heritability may not be a practical measure to
69 compare evolutionary potential between traits or between populations. Hansen, Pélabon, and Houle
70 (2011) suggest that heritability is not a suitable stand-alone measure of evolutionary potential in the

71 wild, especially when comparing populations or species. However, comparisons of heritabilities of
 72 the same trait in different environmental conditions are valid.

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

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

95 does the strength of selection co-vary with levels of expressed additive genetic variance and
96 heritability?

97 **Material and Methods**

98

99 Study species

100 Willow Tits and Great Tits are small hole-nesting passerine birds. The Willow Tit is a boreal forest
101 specialist with a declining population size (Hyvärinen, Juslén, Kemppainen, Uddström, & Liukko,
102 2019), whereas the Great Tit has relatively recently expanded its range to the boreal zone and the
103 population size is growing (Valkama, Vepsäläinen, & Lehikoinen, 2011). Willow Tits breed in
104 cavities they have excavated in decaying stumps, whereas Great Tits accept nest boxes. The timing
105 of breeding is affected by spring temperatures both in the Willow Tit (Vatka, Orell, & Rytönen,
106 2011) and in the Great Tit (Vatka, Rytönen, & Orell, 2014) – both populations show advancing
107 long-term trends in reproductive timing. Annual median egg-laying dates of Willow Tits are
108 strongly correlated with the mean ambient temperature of the period March 27–May 6 ($R^2 = 0.717$;
109 Vatka et al., 2011). For the Great Tit, the corresponding period is 29 March–15 May ($R^2 = 0.721$;
110 Vatka et al., 2014). Spring temperatures also determine the timing of the main food source for
111 nestling provisioning: caterpillars of moths and sawflies that forage in tree canopies (Vatka et al.,
112 2011, 2014). Warming of springs has not yet led to a temporal mismatch between the caterpillar
113 availability and nestlings' food demands in the study populations – in fact, the match with the food
114 peak has improved in the Willow Tit (Vatka et al., 2011, 2014).

115

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

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

124

125 Study area

126 The Oulu study area in Northern Finland (ca. 65°05'N, 25°33'E) consists of coniferous, deciduous
127 and mixed forests and swamps of varying ages (Orell & Ojanen, 1983a, b; Rytkönen & Orell,
128 2001). Similar forest habitats continue outside the study area, and thus the study populations are
129 open. The Willow Tit study area has expanded in size, starting from ca. 2 km² in 1975 (Orell &
130 Ojanen, 1983c) and gradually increasing to ca. 25 km² in 1996. From 1969 onwards, 100–400
131 wooden nest boxes were provided for Great Tits in separate sub-areas of 2–4 km² total in 1969–
132 1997, and since 1998, in four neighbouring sub-areas in total of 8 km² (Orell & Ojanen, 1983a, b;
133 Rytkönen & Orell, 2001; Karvonen, Orell, Rytkönen, Broggi, & Belda, 2012, Vatka et al., 2014,
134 Pakanen et al., 2016).

135

136 Data collection

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

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

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 $year_j \sim N(0, \sigma_{year}^2)$. 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:

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

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

$e_{y,ijl}$ (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 $e_{y,ijl} \sim N(0, \sigma_{e,l}^2)$ (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 $V = \text{diag}(n)$ and $\text{nu} = 0.002$. For other variance components, parameter-expanded priors ($V = \text{diag}(x)$, $\text{nu} = x$, $\text{alpha.mu} = 0$, $\text{alpha.V} = \text{diag}(x) * 1000$) were used. A total of 10 100 000 MCMC iterations were run for each species,

189 including a burn-in period of 100 000 iterations. The remaining 10 000 000 iterations were sampled
190 with a thinning interval of 10 000, leading to sample sizes of 1000 saved iterations.

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

$$198 \quad V_{A_j} = \sigma_A^2 + 2\sigma_{A,B}T_j + \sigma_B^2T_j^2 \quad (4)$$

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

$$200 \quad h_j^2 = \frac{V_{A_j}}{V_{A_j} + V_{PE_j} + \sigma_{year}^2 + \sigma_{e,l}^2}, \quad (5)$$

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

203

204 Selection on the breeding time

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

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

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

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

235

236 Covariance of measures of evolutionary potential and selection

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

243 We examined covariance of different measures of evolutionary potential (i.e., expressed additive
244 genetic variation and heritability) and selection. As explained above, V_{A_j} and h_j^2 were calculated
245 and β_j were retrieved for each of the 1000 saved iterations. We calculated Pearson’s correlation
246 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
247 intervals. In similar fashion, we calculated Pearson’s correlation coefficients r between measures of
248 evolutionary potential and $|\beta_j|$ to infer the covariance between evolutionary potential and the
249 strength of selection (regardless of its direction).

250

251 **Results**

252

253 Effects of spring temperatures on additive genetic variance and heritability

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

258 Heritability estimates (h^2) of laying date were somewhat low both in the Willow Tit (h^2 range =
259 0.134–0.238; Table S3) and the Great Tit (h^2 range = 0.237–0.425; Table S4), and independent of
260 spring temperatures (Fig. 1c, d). There was some variability in heritability estimates especially in
261 the Great Tit (Fig. 1d), owing to variation in estimated error variances between different
262 temperature groups (Table S2).

263

264 Effects of ambient temperatures on the strength of selection

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

275

276 Covariance of measures of evolutionary potential and selection

277 There was year-to-year variation in the selection gradients β on breeding time, ranging from -1.208
278 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
279 S5). Neither the levels of expressed additive genetic variance nor heritability were correlated with
280 annual selection gradients, or with the strength of selection in either species (Table 3).

281 **Discussion**

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

289 Heritability values of breeding time were rather low, which is typical of avian life-history traits (e.g.
290 Merilä & Sheldon, 2000, McCleery et al., 2004). The observed variation in heritability estimates
291 was mostly due to variation in residual variance estimates between different temperature groups,
292 rather than due to variation in the additive genetic variance component. Studies from other Great Tit
293 populations have reported heritability values on breeding time that are somewhat lower than the
294 values we report here (h^2 range: 0.237–0.425; an overall average = 0.332, Table S4). McCleery et
295 al. (2004) reported a heritability of 0.159 (SE=0.059) for Wytham Woods population, whereas
296 Gienapp, Calus, Laine, and Visser (2019) estimated heritability of 0.24 (SE=0.07) based on a social
297 pedigree and 0.17 (SE=0.06) based on kinships inferred from genetic markers for Hoge Veluwe
298 population. To our knowledge, no other heritability estimates of the timing of breeding are available
299 for the Willow Tit. That the additive genetic variance and heritability were lower in the Willow than
300 in the Great Tit makes sense in the light that the timing of breeding in Willow Tits seem to be a
301 subject for directional selection more often than in Great Tits, and because directional selection is
302 expected to erode genetic variation. Whatever the ultimate reason for the low heritability, low
303 heritabilities translate to low rates of expected evolutionary change for given intensity of selection
304 (Falconer & Mackay, 1996). As the heritabilities in both species did not show any trend in relation

305 to spring temperatures, warming of springs are not expected to neither accelerate nor slow down
306 evolutionary responses as far as the effect of heritability values is concerned.

307 As noted also in earlier studies (e.g. Sheldon, Kruuk, & Merilä, 2003, Husby, Visser, & Kruuk,
308 2011, Visser et al., 2015), the strength of directional selection on breeding time was quite variable
309 among years. However, in spite of the fact that boreal Willow and Great Tits show advancing long-
310 term trends in their timing of breeding (Vatka et al., 2011, 2014), we did not detect statistically
311 significant directional selection for earlier breeding in the Oulu Great Tit population. This indicates
312 that the observed change in the timing of breeding in the Great Tit results most likely from
313 phenotypic plasticity, and hence, is not a genetically based evolutionary response (cf. Charmantier,
314 & Gienapp, 2014). In contrast, we found significant selection for earlier breeding in the Willow Tit,
315 which in combination with low but significant heritability of breeding time should promote
316 evolutionary response towards earlier breeding. However, to what degree the advanced breeding
317 time in the Willow Tit reflects genetic vs. plastic changes remains to be investigated.

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

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

342 That warm winters are associated with lower recruit production in the Willow Tit can be explained
343 by several mechanisms, yet they are so far only speculative explanations. Temperatures fluctuating
344 above and below the freezing point can first melt the snow and then create an ice shield covering
345 the food hoards. Warm winters can cause food hoards to decay (Sechley, Strickland, & Norris,
346 2015), and thus food availability can decrease drastically. It is also possible that wet weathers (rain
347 coming down as water instead of snow) affect the thermoregulation of birds when plumage gets
348 wet. Winter rain can decrease foraging efficiency during short days, followed by cold and long
349 nights. These mechanisms would likely affect all birds similarly, regardless of their social status or
350 birth date.

351 In order to understand how environmental changes affect natural selection, one needs to identify the
352 life stage when selection kicks in. In the boreal zone, (pre-)winter conditions seem to play an
353 important role for the selection on breeding time. The situation may be different in temperate zone
354 populations where winters are not equally harsh. Visser et al. (2015) found that in a long-distance

355 migratory bird, temperatures at the time of arrival to the breeding grounds affected selection on
356 timing of reproduction. They suggested that environmental conditions with a lag of up to two years
357 can affect selection on a phenological trait (Visser et al., 2015). We also found that environmental
358 conditions affect selection on timing of breeding with a temporal lag, although in our case the lag
359 was not more than about six months. It is important to recognize that evolution of the timing of
360 breeding, a life history event that takes place in spring, can be regulated by environmental
361 conditions outside this period. In other words, one needs to consider the whole lifespan of
362 individuals when trying to assess factors influencing a certain life-history trait.

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

373

374 Conclusions

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

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

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391

392 **Authors' contributions**

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

396

397 **Data Availability Statement**

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

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529 **Figure legends**

530

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

533

534 **Tables**

535

536 Table 1. Parameters of generalized linear mixed effect models explaining annual proxy of
 537 individual fitness (measured as the number of recruits produced) in the Willow Tit. Explanatory
 538 variables are centered. A significant interaction term (Timing*Temperature) indicates that selection
 539 on the timing of breeding is influenced by ambient temperatures. Statistically significant ($p < 0.050$)
 540 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

541

542

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

548

549

550

551 Table 3. Pearson’s correlation coefficients r (and their 95% HPD intervals) between different
 552 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]

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554