Are Long-Distance Migrants Constrained in Their Evolutionary Response to Environmental Change?

Causes of Variation in the Timing of Autumn Migration in a Blackcap (*S. atricapilla*) and Two Garden Warbler (*Sylvia borin*) Populations

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ABSTRACT: **Long-distance migratory birds often show little phenotypic variation in the timing of life-history events like breeding, molt, or migration. It has been hypothesized that this could result from low levels of heritable variation. If this were true, the adaptability of long-distance migratory birds would be limited, which would explain the vulnerability of this group of birds to environmental changes. The amount of phenotypic, environmental, and genetic variation in the onset of autumn migratory activity was assessed in two garden warbler (*Sylvia borin*) populations differing in breeding phenology and the length of the breeding season with the aim of investigating the effects of selection on the adaptability of long-distance migrants. High heritabilities and additive genetic variance components for the timing of autumn migration were found in both populations. Although genetic variation in the mountain population was lower than in the lowlands, this difference was not statistically significant. Moreover, no evidence was found for reduced levels of genetic variation in the garden warbler as compared to its sister species, the blackcap (*S. atricapilla*). Environmental variation, however, was markedly reduced in the garden warbler, suggesting that low levels of phenotypic variation typically found in long-distance migrants may be a consequence of environmental canalization of migratory traits. The buffering of environmental variation may be an adaptive response to strong stabilizing selection on the timing of migration. High environmental canalization of migration phenology in long-distance migrants could potentially explain low rates of immediate phenotypic change in response to environmental change.**

KEYWORDS: **heritability, zugunruhe, climate change, adaptation, canalization**

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INTRODUCTION

We are currently witnessing rapid environmental changes that are causing changes in the migratory behavior of birds.[1] These changes are characterized by an increase in the proportion of resident individuals, a shortening of migration distances, and by earlier arrival on and later departure from the breeding grounds.[2–5] Alterations of avian migration patterns, particularly in phenology, repeatedly have been reported to be more pronounced in short-distance than in long-distance migrants.[6–10] At the same time, numbers of long-distance migrants have decreased, particularly among many species breeding in Europe[11,12] and North America.[13] Habitat loss, habitat fragmentation, and deterioration have been identified as the main causes for most of these population declines.[14] Increasing competition with short-distance migrants and resident birds on the breeding grounds, and low adaptability have been proposed as additional factors favoring the decline of long-distance migrants, particularly under the prospect of recent climatic change.[2–4,15] While ecological causes for population declines in long-distance migrants have deserved much attention, the potential role of reduced rates of adaptive evolution in this group of birds has only recently become the focus of research.[4,16,17] In a compilation of recent changes and presumptive instances of lack of change in avian migration patterns, all species with suboptimal migration routes were long-distance migrants.[18] This finding suggests that migration patterns of birds migrating long distances could be more resilient to environmental change than short-distance migrants, probably as a consequence of endogenous control, and genetically transmitted migration routes.

Constraints on the response to natural selection could be imposed by reduced levels of genetic variation in migratory traits due to strong stabilizing selection,[19] and by divergent selection on migration, on the breeding, and wintering grounds.[20–22] Webster *et al.*[23] recently predicted that in populations with high migratory connectivity—as found in many long-distance migrants—genetic variation may be limited and therefore "evolutionary response to large-scale climatic change could be severely hampered." In addition, unfavorable genetic correlations of migratory traits with other life-history traits,[24,25] and the disruption of the complex life cycles of long-distance migrants could limit their adaptive response to environmental changes.[26,27] However, it is unclear whether strong selection on migratory traits affects the evolutionary response of long-distance migrants. Although most theoretical models and empirical studies predict that stabilizing selection will erode phenotypic variance due to the loss of additive genetic variation,[28,29] theoretical studies have revealed that the conditions under which stabilizing selection may deplete genetic variation may be restrictive.[30] Stabilizing selection could also result in a reduction of environmental variance as a consequence of the fitness advantage of genotypes that are insensitive to environmental variation.[31–33]

In long-distance migrants, the timing of autumn migration is expected to be under strong stabilizing selection.[22,24,34] Compared to birds migrating short distances, long-distance migrants arrive at the breeding area late in the season, and are the first to leave. This group of birds is thus characterized by rapid juvenile development, which is an adaptation to the short breeding season.[26,35] Although rapid molt and growth is associated with high energetic and other fitness costs,[36–38] these costs are offset by the advantage of leaving the breeding area before conditions deteriorate. Birds migrating late in the season are at high risk of not finding enough food to build up energy reserves to overcome large barriers like seas or deserts. Encountering inclement weather before or on migration may be particularly detrimental for insectivorous migrants. Moreover, there are a number of species that establish territories in the nonbreeding season for which early arrival on the wintering ground may be highly advantageous [e.g., for the pied flycatcher (*Ficedula hypoleuca*)[39]].

Studies investigating genetic variation and evolutionary change in the timing of migration of long-distance migrants have yielded contradictory results. While there is evidence for a lack of additive genetic variation in the timing of spring arrival in pied flycatchers breeding in Spain,[40] high heritabilities for this trait have been found in barn swallows (*Hirundo rustica*) breeding in Denmark.[41] Moreover, cliff swallows (*Petrochelidon pyrrhonota*) in North America strongly responded to natural selection on spring arrival date.[42] These results and significant among-year repeatabilities for this trait in other species[17] are in line with a number of studies demonstrating changes in spring arrival in response to global warming.[43] In contrast to spring arrival, the timing of autumn migration has been little studied, probably because it is more difficult to measure in the field.[26] Despite methodological problems, there are a few studies reporting changes in the timing of autumn migration in a number of bird species, including some long-distance migrants.[10,44–46] However, it is unclear whether these changes are just plastic responses to environmental alterations (phenotypic plasticity) or if they involve changes in the genetic composition of populations (evolutionary change).

The presence of additive genetic variation in the timing of autumn migration has hitherto only been demonstrated in a short- to middle-distance migrant, the southern German blackcap (*Sylvia atricapilla*),[22] which predominantly winters in the western Mediterranean region. The sister species of the blackcap is the garden warbler (*S. borin*), a long-distance migrant, that breeds in the western Palearctic and winters south of the Sahara in subtropical and tropical Africa.[47] This species is an excellent candidate for studying the effects of stabilizing selection on the adaptability of long-distance migrants, as results can be compared with those in the well-studied blackcap.

Here, we estimate heritabilities and variance components for the timing of autumn migration in the garden warbler with the aim of evaluating whether adaptive evolution of migratory behavior in long-distance migrants may be constrained by the lack of additive genetic variation. Moreover, we compare two garden warbler populations differing in life-history and ecology with the blackcap to study the effects of stabilizing selection on phenotypic variance and its causal components, and to assess its consequences for adaptive evolution of migratory traits.

MATERIALS AND METHODS

In 1993 and 1994, we collected a total of 89 garden warblers at an age of 4–8 days from 30 nests in two central European populations. Fifty-one nestlings were sampled in the Urseren Valley (46°36′N, 8°31′E), a population dwelling in the central Swiss Alps at 1500 m above sea level. Thirty-eight individuals were collected in the Upper Rhine Valley (47°53′N, 7°34′E), in southwest Germany, at 200-m altitude. These garden warbler populations differ markedly in their breeding biology and phenology, due to differences in climatic conditions encountered in their respective breeding areas. The arrival of spring, for instance, is about 3 weeks later in the mountain than in the lowland population. As a consequence, the breeding season in the Rhine Valley is shorter by almost 4 weeks, which may cause particularly strong selection on the timing of autumn migration and on juvenile development in this population.[48,49] For a detailed description of the habitat and biology of the populations, see Widmer.[48,50,51]

All birds were hand-raised and kept in climate chambers under identical controlled conditions (see Berthold *et al.*[52] and Widmer[49] for details on rearing, feeding, and keeping conditions). To avoid common environment effects, nest mates were separated and randomly distributed to registration cages and rooms. Artificial light–dark cycles simulated the natural photoperiodic cycle experienced by these populations. Birds were exposed to photoperiodic conditions corresponding to 47°30′N until mid-August. Thereafter, and until the end of November, day-length changes simulated conditions on migration to the wintering areas in central Africa at about 5°N.[49]

Migratory activity was quantitatively recorded in registration cages during each bird's first autumn migratory period. The onset of migratory activity was defined as the first night on which the bird was active during at least five half-hour intervals. According to this criterion, activity onset could be determined in all but two birds. Because alternative definitions of the onset of migratory activity (e.g., the beginning of the first 10-day interval with mean activity exceeding one half-hour per night[49]) yielded very similar results, here we present only the results on the onset of migratory activity assessed by the same criterion as used in the heritability study of the blackcap.[22] It has been previously shown that the onset of this night activity in hand-raised birds is a reliable measure of the timing of autumn migration in the wild.[53]

We removed the effect of hatching date on the timing of autumn migration by regressing day at the onset of migratory activity on hatching date (mountain population: $b = 0.802$, $t_{49} = 3.41$, $P < .005$; lowland population: $b = 0.676$, $t_{36} = 2.81$, $P < .01$). Residuals obtained from these regressions were used in the subsequent statistical analyses. Residual onset of migratory activity did not deviate from normality (Shapiro-Wilks' Test; mountain population: $W = 0.9675$, $P > .5$; lowland population: $W = 0.9785$, $P > .5$). We found no effects of sex, year, or their interaction on the residual onset of migratory behavior neither in the mountain [analysis of variance (ANOVA): sex: $F_{1,45} = 0.12$, $P > .5$; year: $F_{1,49} = 1.31$, $P > .2$] nor in the lowland population (ANOVA: sex: $F_{1,32} = 0.17$, $P > .5$; year: $F_{1,36} = 1.86$, $P > .1$). Therefore, we pooled data for males and females, and for both years within each population.

We estimated causal variance components and heritabilities (h^2) by computing intraclass correlations among full sibs derived from one-way ANOVA.[54] Heritability estimates derived by this method have to be cautiously interpreted, as they may include large variance components attributable to common-environment and dominance effects.[54] However, we are confident that true narrow-sense heritabilities of the onset of migratory activity do not deviate significantly from estimates obtained in this study for two reasons: (1) The experimental setup was designed to minimize common environment effects. Therefore, we expect resemblances due to correlations between genotype and environment to be minimal and random. (2) In the blackcap, there is no indication for the presence of common environment (including maternal effects) or dominance effects either in the onset of autumn migration[22] or in the amount or intensity of migratory activity.[34,55] Considering the high similarity of phenotypic covariances among migratory traits in the blackcap and the garden warbler (unpublished results), we are confident that these conclusions also hold for the garden warbler.

For the estimation of heritabilities (h^2), phenotypic (V_P), additive genetic (V_A), and residual (V_R) variances, only families with at least two nestlings were considered. Residual variance (V_R) was the component of phenotypic variance not explained by genetic variation ($V_R = V_P - V_A$). Means, standard errors, and confidence intervals for all estimates obtained by the ANOVA approach were calculated using a bootstrapping procedure.[56] Empirical bootstrap distributions were generated by resampling the original number of families 100,000 times with replacement. These bootstrap distributions were used to estimate error probabilities for the hypothesis of equality of heritabilities and coefficients of additive genetic variance among populations. Bootstrap estimates were calculated with the software package H2BOOT.[57] In addition, we computed heritabilities and their standard errors from variance component estimates obtained using a restricted maximum likelihood (REML) approach as implemented in the VARCOMP routine in SAS.[58]

For comparison of heritability estimates and variance components in the two garden warbler populations with those in a species migrating shorter distances, we used the data on the onset of autumn migratory activity in a southern German blackcap population.[22] Blackcaps from this population predominantly winter in the western Mediterranean area, and can be considered as short- to middle-distance migrants.[55] Individuals were collected, maintained, and their activity measured by the same methods as used in the garden warbler. For this interspecific comparison of genetic variation we chose not to use standardized variance components, as is generally recomended,[59] as we measured the onset of migratory activity by the same methods and on the same scale in both species. Moreover, standardization of variance components by the mean biased our results (results not shown; see also Roff[28] for a critique of standardized variance components). We considered only heritability estimates and variance components derived from the resemblances among full sibs collected in the wild (see table 1 in Pulido *et al.*[22]). This sample was complemented with the data of 145 blackcaps collected in the same population in 2000 (F. Pulido & P. Berthold, unpublished). The total blackcap sample comprised the records of migratory activity of 676 individuals belonging to 178 families hatched in 12 different years. We tested the equality of heritabilities and variance components among species by using the distribution of cohort means in the blackcap and testing them against the estimates obtained in the garden warbler with a *t*-test. Equality of phenotypic variances was tested using the complete data set by Leven's test for equality of variances. Furthermore, we tested for among-species differences in heritabilities and variance components using weighted bootstrap distributions that were generated by resampling families within each cohort. The number of bootstraps was proportional to the number of individuals studied in each cohort.

RESULTS

Intraspecific Comparison

Garden warblers from the mountain population started migration at a mean age of 50.0 ± 7.3 days on August 10. Birds collected in the lowland population, initiated

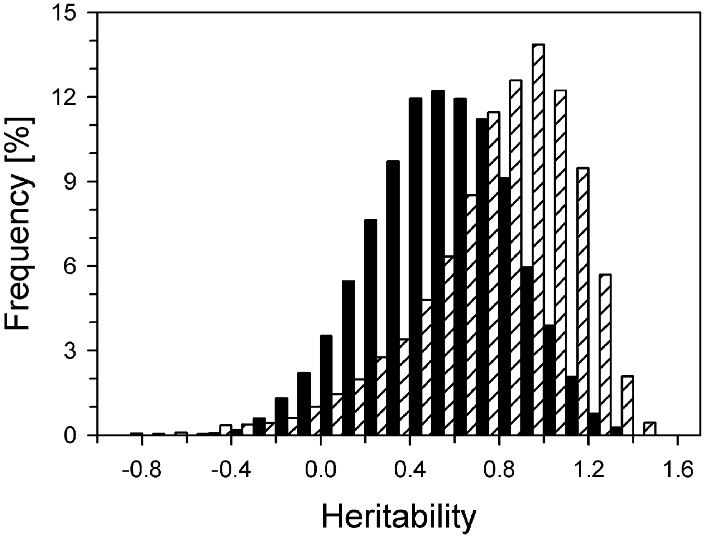

FIGURE 1. Bootstrap distribution of heritability estimates of the residual timing of autumn migratory activity in two garden warbler populations. Mean heritabilities for the mountain (*solid bars*) and the lowland population (*hatched bars*) are both significantly different from zero.

migratory activity at an age of 57.8 ± 9.6 days on August 8. While the difference in the mean age at onset of migratory activity was significant ($t_{87} = 4.3$, $P < .001$), populations did not differ in the mean date of onset of activity ($t_{87} = 1.17$, $P > .5$).

In both populations, heritability estimates obtained by bootstrapping over families were significantly different from zero (mountain: $h^2 = 0.552 \pm 0.308$, $P < .05$; lowland: $h^2 = 0.795 \pm 0.343$, $P < .05$), but not from one (FIG. 1). Estimates derived from variance components obtained by REML were in the same range, but means and standard deviations obtained by this method were a little higher than ANOVA results (mountain: $h^2 = 0.621 \pm 0.401$; lowland: $h^2 = 0.869 < .517$). Additive genetic variance was more than two times higher in garden warblers from the mountains than from the lowlands (TABLE 1). However, neither heritabilities nor additive genetic variance components differed among populations (bootstrap results: $P_{h^2} > .2$; $P_{VA} > .2$). Likewise, differences in phenotypic and residual variance (TABLE 1) were not statistically significant (V_P: $F_{1,85} = 1.64$, $P > .2$; V_R: bootstrap results: $P > .2$).

Interspecific Comparison of Variance Components

Mean phenotypic variance was significantly higher in the blackcap than in the garden warbler ($F_{1,771} = 4.96$, $P < .05$). This was due to low variance in the Urseren population, which significantly differed from the southern German blackcap population ($F_{1,735} = 5.29$, $P < .05$). Phenotypic variance in the Upper Rhine Valley population did not differ from the blackcap ($F_{1,720} = 0.64$, $P > .2$). Lower phenotypic variances in the garden warbler could, in principle, result from lower within-cohort

TABLE 1. Mean phenotypic (V_P), additive genetic (V_A), and residual (V_R) variance and standard errors (in parentheses) in two garden warbler populations and one blackcap population

Population	V_P	V_A	V_R
Mountain	51.7 (6.6)	28.9 (16.8)	22.9 (15.7)
Lowland	83.8 (21.9)	72.0 (41.2)	11.9 (23.1)
Garden warbler (mean)	67.8 (14.2)	50.4 (38.2)	17.4 (19.4)
Blackcap (mean)	119.1 (38.0)	54.6 (44.2)	64.5 (50.3)

NOTE: Means and standard errors for garden warblers were derived from bootstrap distributions. For the blackcap, weighted means and standard deviations were estimated from the distribution of the date at onset of migratory activity of 12 cohorts hatched in the wild from 1988 to 2000.

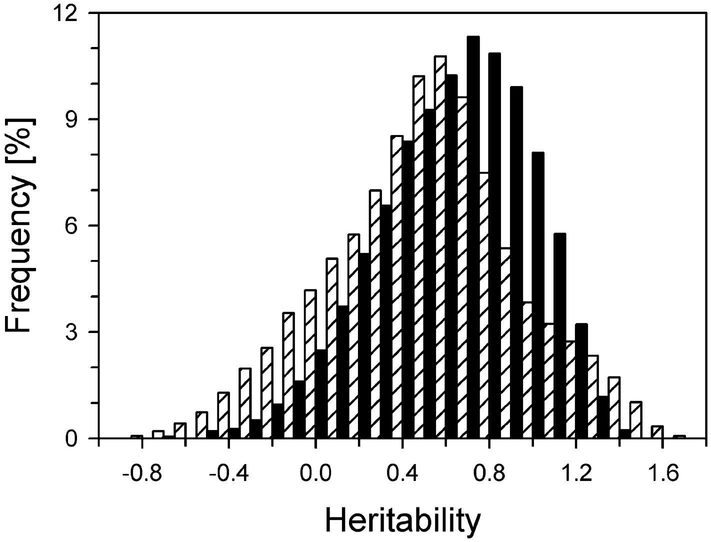

FIGURE 2. Pooled bootstrap distribution of heritability estimates of the residual timing of autumn migration in two garden warbler populations (*solid bars*), and combined bootstrap distribution of heritabilities in 12 blackcap cohorts from southern Germany (*hatched bars*). The total number of bootstrap samples used to generate the distribution of heritabilities was 65,000 for the blackcap and 20,000 for the garden warbler.

sample sizes as phenotypic variance increases with increasing sample sizes in the blackcap ($b = 0.75$, $t_{10} = 2.47$, $P < .05$), and mean within-cohort samples were smaller in the garden warbler than in the blackcap. However, if only cohorts with comparable sample sizes were considered ($N \leq 50$), mean phenotypic variance in the blackcap changed only little ($V_P = 106.6$), and was still significantly higher than in the garden warbler ($F_{1,531} = 5.72$, $P < .05$).

High phenotypic variance in the blackcap was due to high residual variance in this species (TABLE 1). Residual variance in southern German blackcaps was on average 3.6 times higher than in the garden warbler ($t_{10} = 2.86$; $P < .05$). As a consequence, mean heritability of the onset of autumn migratory activity in the blackcap was on average about 30% lower than in the garden warbler (FIG. 2). This difference is marginally significant if mean heritability in the garden warbler was tested against the among-cohort distribution of heritabilities in the blackcap ($t_{10} = 2.26$; $P < .05$). But if the blackcap mean or the pooled bootstrap distribution of heritabilities (see FIG. 2) was tested against the bootstrap distribution in the garden warbler, this result was not confirmed ($P > .2$). Moreover, we found no statistical evidence for interspecific differences in the amount of additive genetic variance, irrespective of the statistical method used (bootstrap test and *t*-test: $P > .5$).

DISCUSSION

Currently, climate is rapidly changing, and to cope with these changes organisms have to adapt.[1,60–62] It has repeatedly been reported that long-distance migrants may change migratory traits, particularly the timing of migration, at a slower rate than migratory birds wintering close to the breeding grounds.[6–10] In this study we investigate whether differences in the amount of genetic variation present in populations differing in migratory behavior could be the cause for differences in the rate of adaptive change. We predicted that bird populations subjected to strong stabilizing selection should maintain lower levels of genetic variation in migratory traits than populations in which selection on migration is weaker. Contrary to this prediction we found no evidence for a reduction of genetic variation in the timing of autumn migration in the species migrating long distances (the garden warbler) relative to its sister species migrating shorter distances (the blackcap). In both garden warbler populations, we demonstrated high, statistically significant heritabilities and genetic variance components for the onset of migratory activity. The amount of additive genetic variance expressed was practically identical in both species. Most remarkably, however, phenotypic variance in the garden warbler was lower than in the blackcap (on average by about 30%). This was primarily due to low amounts of residual variances found in both garden warbler populations.

In the intraspecific comparison, we expected the garden warbler population living in the mountain habitat to experience stronger stabilizing selection on the timing of autumn migration. This expectation was borne out of the fact that the breeding season of this population is almost four weeks shorter compared to the lowland population.[48,49] We predicted finding reduced levels of additive genetic variation in the mountains. As expected, heritability estimates and coefficients of additive genetic variation were both higher in the lowland population. The difference to the mountain population, however, was moderate and had a large variance; as a consequence, it was not statistically significant. Corresponding results were obtained for the timing of spring migration and the amount of migratory activity.[17,49] In this latter trait, genetic variation was larger in the mountains, though the difference was not statistically significant. This inconsistent pattern of among-population genetic variation in migratory traits could be a consequence of different traits being subjected to different selection intensities. However, large sampling variances suggest that inconsistent results are probably due to low, negligible differences in combination with small sample sizes and to considerable among-year fluctuations in the amount of additive genetic variation in these populations (see Pulido *et al.*[22] for results in the blackcap). If among-population differences in genetic variation exist, they are probably small. The intraspecific comparison suggests that differences in the intensity of stabilizing selection among populations did not lead to significant differences in genetic variation. Although this conclusion could be challenged by the fact that genetic drift and migration can potentially mask selection effects on genetic variation, we believe that our result cannot be explained by these processes. Because effective population size and rate of immigration are most probably larger in the Upper Rhine Valley than in the Urseren Valley population (M. Widmer, unpublished), we predict that these processes alone would cause a reduction of genetic variation in the mountain population. This would increase the expected effect of stabilizing selection on genetic variances rather than canceling it out. Since we find only moderate differences in genetic variation for the timing of autumn migration, we can exclude that stabilizing selection strongly reduces the amount of genetic variation maintained in the mountain population. Moreover, stronger isolation and lower effective population size could be the cause for the somewhat lower amounts of genetic variation found in the mountain population.

Environmental Canalization

There are several potential causes for low residual variation in the timing of migration found in garden warblers as compared to the blackcap. Because residual variance is composed of environmental and nonadditive (mostly dominance) variance,[54] both of these variance components could, in principle, be reduced in long-distance migrants. However, there are a number of arguments supporting the idea that it is the environmental variance component that is reduced in garden warblers:

(1) Theoretical considerations and empirical findings suggest that in traits closely correlated with fitness, nonadditive genetic variance components, and above all dominance variance, should increase.[29,59,63,64] As a consequence, we expect high residual variances in traits closely correlated with fitness and low residual variances in "nonfitness" traits. This is opposite to our finding of reduced residual variance in the garden warbler, that is, the species in which this trait is supposedly subjected to stronger stabilizing selection.

(2) Environmental and genetic canalization increase under stabilizing selection.[31–33,65] "Environmental canalization is the reduction in the phenotypic variation caused by an environmental perturbation."[66] Thus, we would expect a reduced response to environmental variation in the species under stronger selection.

(3) The finding of low phenotypic variance and environmental canalization in the timing of autumn migration in the garden warbler is in accord with field observations, and experimental results suggesting that long-distance migrants generally display less variation in migratory traits, particularly in the timing of spring migration, than short-distance migrants.[4,26]

In British and eastern European blackcaps, ranges and standard deviations of the distribution of among-year means of spring arrival date are about two times larger than in garden warblers.[8,67,68] Moreover, Berthold *et al.*[69] studied *zugunruhe* under controlled laboratory conditions and found higher coefficients of among-individual variation of the amount of migratory activity in the blackcap than in the garden warbler. They concluded that "this result could be interpreted by assuming that migratory activity is less rigid endogenously programmed in the blackcap than in the garden warbler," and that environmental factors have a stronger impact on migratory activity in the blackcap. Similar results were obtained in a comparative study of migratory activity in the chiffchaff (*Phylloscopus collybita*), a short-distance migrant, and the willow warbler (*Phylloscopus trochilus*), a long-distance migrant. Coefficients of variation for duration, amount, and maximum intensity of migratory activity were smaller in the short-distance migrant.[70] In a comparative study of blackcap and garden warbler migration based on ringing recoveries, Klein *et al.*[71] found stronger among-year and geographic variations (correlated with isotherms) of the timing of autumn migration in blackcaps than in garden warblers. They concluded that "there are numerous differences between the migration of *S. borin* and *S. atricapilla* that fit into the picture of a lower environment-dependent migration in *S. borin* as compared to *S. atricapilla.*" Moreover, two other studies found that distributions of autumn passage dates of long-distance migrants are characterized by small variances and high skewness. These findings were interpreted as indicators for the predominantly endogenous control of the timing of autumn migration in this group of birds.[72,73]

In line with the hypothesis of environmental canalization of migratory traits in long-distance migrants, we found a reduction of phenotypic variance in the garden warbler for the timing of molt and the onset of vernal migration, but not for the termination, duration and amount of autumn migratory activity (F. Pulido and M. Widmer, unpublished). These latter traits are not expected to be subjected to stronger selection in the garden warbler than in the blackcap, as the large winter range of the garden warbler permits considerable variation of migration distances in this species.[71] The preliminary analysis of other migratory traits in the garden warbler and the blackcap thus seems to corroborate the conclusion derived from this study that strong stabilizing selection reduces phenotypic variation by increasing environmental canalization. As migratory traits, particularly those traits related to the timing of migration, are likely to be under strong selection in long-distance migrants, we expect to find reduced levels of phenotypic variation in this group of birds as a consequence of environmental canalization. We further predict that the degree of canalization in long-distance migrants will decrease if populations are subjected to strong directional selection, as currently caused by rapid environmental changes.

Consequences for Adaptive Evolution

Environmental canalization is equivalent to the lack of plasticity in response to environmental variation.[74] Phenotypic plasticity could in principle accelerate or slow down adaptive responses. Simulations using genetic algorithms, however, have shown that under a large spectrum of conditions phenotypic plasticity will slow down evolutionary change.[75] Although populations with high levels of phenotypic plasticity may show fast adaptive responses to environmental changes, these changes will be individual adjustments and will not involve genetic changes in the population. If directional selection persists and the optimal phenotype shifts beyond the range of environmentally inducible phenotypes, then evolutionary change is to be expected. Populations with a high degree of environmental canalization will show more immediate responses to selection. However, their degree of genetic adaptation will be lower, and the time needed to reach an adaptive peak will be considerably larger. For the adaptation of migratory traits in long-distance migrants, this means that compared to short-distance migrants we should expect lower rates of phenotypic change as immediate response to environmental change. Rapid immediate changes in short-distance migrants, however, would not involve changes in the genetic composition of the population, but would result from phenotypic plasticity. In the long term, populations of long-distance migrants could theoretically evolve at a faster rate than short-distance migrants, if they are large and survive the initial phase of selection.

CONCLUSIONS

There is currently no evidence that the amount of additive genetic variance present in populations of long-distance migrants is smaller than in short-distance migrants. Our results suggest, however, that differences in the speed of adaptive phenotypic change between long-distance and short-distance migrants could potentially be caused by differences in phenotypic plasticity. Unfortunately, strong evidence for this hypothesis is currently lacking. Although there are a number of studies suggesting low plasticity of migration timing in long-distance migrants and lack of response to climatic variation,[76] other studies indicate that long-distance migrants can adjust migration speed to weather conditions and plant phenology.[77] To date all evidence is at best circumstantial, as it is based on correlations and means of groups of migrating birds. To understand if and how short- and long-distance migrants differ in their mode to adapt to changing environmental condition, we urgently need longitudinal studies and quantitative genetic studies of migratory behavior in the wild.

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