

# Heritability of the timing of autumn migration in a natural bird population

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In recent decades, global temperature has increased at an unprecedented rate. This has been causing rapid environmental shifts that have altered the selective regimes determining the annual organization of birds. In order to assess the potential for adaptive evolution in the timing of autumn migration, we estimated heritabilities of the onset of migratory activity in a southern German blackcap (*Sylvia atricapilla*) population. Heritabilities ( $h^2 = 0.34\text{--}0.45$ ) and coefficients of additive genetic variation ( $CV_A = 4.7\text{--}5.7$ ) were significant and consistent when estimated by different methods, irrespective of whether they were derived from birds hatched in the wild or bred in captivity. In an artificial selection experiment, we selected for later onset of migratory activity, simulating expected natural selection on this trait. We obtained a significant delay in the mean onset of migratory activity by more than one week after two generations of selection. Realized heritability ( $h^2 = 0.55$ ) was in agreement with expected heritability in the cohort that the selection line was derived from. Our results suggest that evolutionary changes in the timing of autumn migration may take place over a very short time period and will most probably be unconstrained by the lack of additive genetic variation.

**Keywords:** selection response; genetic variation; adaptive evolution; zugunruhe; climate change

## 1. INTRODUCTION

Evidence is accumulating that, during the last century, global temperature increased at an unprecedented rate due to human activities (Crowley 2000; Intergovernmental Panel on Climate Change 2001). One of the regions most affected by this temperature rise is the Holarctic where major changes in the length of the vegetation period and in phenology have been documented (Bradley *et al.* 1999; Menzel & Fabian 1999). These environmental changes have had a major impact on birds, affecting their distribution, behaviour and annual cycle (Berthold 1998a; Crick & Sparks 1999; Thomas & Lennon 1999; Hughes 2000). Migratory bird populations are expected to respond to global warming by increasing the time spent on their breeding grounds (which is achieved by arriving earlier and delaying departure), by shortening their migration distance, by evolving residency and by shifting or expanding their ranges (Berthold 1991, 1996, 1998a). All of these predicted changes, including shifts in the timing of autumn (Gatter 1992; Bezzel & Jetz 1995; Bergmann 1998) and spring migration (Mason 1995; Sparks 1999) have been found in natural bird populations (reviewed in Berthold 1998a).

However, it is not known whether these changes in migratory behaviour that have been attributed to global warming are due to phenotypic plasticity or whether they are a consequence of adaptive evolution, i.e. changes in the genetic composition of populations. Whether a population will respond to new selection regimes and at what rate adaptive evolution may proceed depends on the amount of additive genetic variance present and the sign and amount of genetic covariance with other traits (Roff 1997). The most important genetic constraint on adaptation to changing conditions is probably the lack of genetic variation (Bradshaw 1991). Therefore, we need to know

the pattern of genetic covariation in migratory traits in order to interpret current changes in avian migration and predict responses and limits to selection (see Berthold & Pulido 1994; Pulido 2000).

The timing of autumn migration is an important fitness-correlated trait as it is the main determinant of how long a migratory bird will stay on its breeding grounds and, therefore, of the time it has available for breeding and moulting (cf. Berthold 1996; Hall & Fransson 2000). It further determines the environmental conditions a bird will encounter when it prepares for migration, during migration and on the wintering grounds (see McNamara *et al.* 1998). Finally, the timing of the onset of migration determines how far a juvenile bird will migrate and, as a consequence, where it will overwinter (Pulido & Berthold 1998; Pulido 2000).

It has been shown previously in hybridization and common-garden experiments that differences in the timing of autumn migration between the common redstart (*Phoenicurus phoenicurus*) and the black redstart (*Phoenicurus ochruros*) (Berthold 1998b) and differences between two garden warbler populations (*Sylvia borin*) (Widmer 1999) have a genetic basis. In a comparative analysis of 18 species, Berthold (1990) found that the onset of migratory activity in caged birds held under controlled conditions was strongly correlated with the onset of migratory activity in the wild, suggesting that the timing of departure from the breeding grounds is controlled by a genetic programme. This programme appears to be part of an endogenous circannual rhythm, which also controls the timing of breeding, moult and fat deposition (Gwinner 1986; Berthold 1996).

Heritabilities for the timing of migration in birds have hitherto only been estimated for three species: Bewick's swan (*Cygnus columbianus bewickii*) (Rees 1989), the pied flycatcher (*Ficedula hypoleuca*) (Potti 1998) and the barn swallow (*Hirundo rustica*) (Møller 2001). Low heritabilities reported for the timing of arrival on and departure from

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the wintering grounds (Rees 1989) and for the date of arrival on the breeding grounds (Potti 1998) have suggested that the evolution of the timing of migration may be genetically constrained. However, two studies on swallows have recently shown the presence of genetic variation in the timing of spring arrival (Møller 2001) and evolutionary change in response to natural selection (Brown & Brown 2000).

Significant additive genetic variation has previously been found in the blackcap for other migratory traits, such as the amount of migratory activity (Berthold & Pulido 1994) and the frequency of migrants (Berthold *et al.* 1990; Pulido *et al.* 1996). Moreover, central European blackcaps have recently evolved a new migration strategy involving changes in migration distance and direction (Berthold *et al.* 1992).

Here we report on estimates of expected and realized heritabilities for the timing of autumn migration in a migratory bird population. We show for the first time, to the authors' knowledge, that there is significant additive genetic variation in the timing of the onset of migratory activity and that considerable evolutionary changes in the timing of autumn migration may take place in a few generations, potentially enabling migratory birds to track rapid environmental changes.

## 2. MATERIAL AND METHODS

From 1988 to 1999, we collected a total of 534 blackcaps from 148 nests hatched in the environs of Radolfzell (at 47°46' N, 9°58' E) and transferred them to our institute at ages of five to seven days. We selected 80 individuals from this sample for breeding in outdoor aviaries. This group of birds comprised 33 individuals that were mated assortatively for their amount of migratory activity (see Berthold & Pulido 1994), 10 birds selected for their late onset of activity (see below) and 37 individuals selected for their low amounts of migratory activity. They produced a total of 203 individuals ( $F_1$  generation). Another 93 blackcaps were bred from 24 breeding pairs selected from birds of the  $F_1$  and subsequent generations. All birds were hand-reared and kept under identical controlled conditions. Artificial light to dark cycles simulated the natural photoperiodic cycle of this population (see Berthold *et al.* (1970) for details of the rearing and maintenance conditions).

Migratory activity was quantitatively recorded in registration cages during each bird's first autumn migratory period. Zugunruhe or migratory restlessness is the extra activity performed by captive birds during the migratory season (Berthold 1996). It has been shown that the pattern of timing and amount of migratory restlessness, particularly in hand-reared birds during their first autumnal migratory season, is a reliable measure of migratory activity in the wild (Berthold 1973, 1996; Gwinner 1986; Berthold & Querner 1988; Berthold *et al.* 2000) and of the timing of autumn migration in particular (Berthold 1990). As autumn migratory activity in the blackcap appears not to be correlated with condition-dependent traits such as body weight or wing length (P. Berthold, unpublished data), we did not consider condition dependence, as found for the timing of spring arrival in the barn swallow (Møller 2001), in our analyses.

The onset of migratory activity was defined as the first night on which a bird was active during at least five 30-min intervals. This criterion yielded biased results in a few individuals with low activity levels or with interrupted activity (constituting less

than 2% of the total sample). The onset of activity in these birds was better defined by the beginning of a continuous period with night activity above the basal level.

One major methodological problem when estimating heritabilities of the onset of migration is that the date at which birds initiate migratory activity is strongly correlated with their hatching date (Berthold 1996; Pulido 2000). This hatching-date effect was taken into account by fitting a linear regression model with hatching date as the independent variable and date at onset of migratory activity as the dependent variable. The residuals of this regression model (in the following referred to as 'residual onset of migratory activity') were used for estimating quantitative genetic parameters (Pulido 2000). One complication of this approach is the presence of a considerable hatching date  $\times$  year interaction (Pulido 2000; F. Pulido and P. Berthold, unpublished data). However, as we were interested in decomposing variance components in the onset of migratory activity at the population level and we have evidence that between-year effects are partly due to sampling error (results not shown), we generally used the residuals obtained from the regression on the complete data set (onset of migratory activity =  $174 + 0.559 \times$  hatching date) ( $r^2 = 0.515$ ,  $F_{1,828} = 879$  and  $p < 0.0001$ ).

We estimated repeatabilities ( $r$ ) of the residual onset of migratory activity among clutches within and between years using all offspring produced by breeding pairs that bred more than once in captivity. Repeatabilities were based on clutch means and calculated from variance components derived from one-way ANOVA, as described in detail by Lessells & Boag (1987).

We estimated narrow-sense heritabilities ( $h^2$ ) by computing the intraclass correlation between full-sibs derived from one-way ANOVA (Falconer & Mackay 1996). As there was heterogeneity in the mean onset of migratory activity between birds hatched in different years (i.e. cohorts) and because we wanted to identify potential environmental effects on family resemblances, we estimated intraclass correlations and  $h^2$  separately for each cohort of birds collected in the wild and bred in captivity. The mean heritability for the population was obtained by computing the arithmetic mean of within-cohort heritabilities weighted by the number of individuals within each cohort.

A second set of heritability estimates was obtained from the weighted regression of mid-offspring on mid-parental onset of migration and from single-parent–mid-offspring regression. Regressions were weighted by the number of offspring produced by each breeding pair. Heritabilities from regressions on single parents (mother or father) were corrected for assortative mating (see Falconer & Mackay 1996). For estimating heritabilities from parent–offspring resemblances we exclusively used the data of the  $F_1$  generation, as the data from subsequent generations were not independent of these.

Coefficients of additive genetic variation ( $CV_A$ ) and of residual variation ( $CV_R$ ) were computed using mid-parent–mid-offspring covariances and covariances among full-sibs as described by Houle (1992). Standard errors of all estimates were calculated using a bootstrapping approach (Efron & Tibshirani 1993). An empirical bootstrap distribution was generated by resampling the original number of families 100 000 times with replacement. Means and errors of variance components were derived from this distribution. Bootstrap estimates were calculated using H2BOOT (Phillips 1998).

We conducted an artificial selection experiment for directly assessing the response of the timing of the onset of migratory activity to selection using the birds collected in the wild in 1994

Table 1. Heritability estimates and coefficients of additive genetic and residual variation derived from the resemblances among full-sibs hatched in the wild (above line) and in aviaries (below line) in different cohorts

('Cohort' gives the actual hatching year for birds hatched in the wild and denotes the hatching years of the progenitors (parents or grandparents) that hatched in the wild for birds bred in captivity. Abbreviations:  $n$ , number of individuals;  $k$ , number of families;  $h^2$ , narrow-sense heritability;  $CV_A$ , coefficient of additive genetic variation;  $CV_R$ , coefficient of residual variance.  $p_1$  gives the error probability for hypothesis  $H_0$  that  $h^2 \leq 0$  and  $p_2$  gives the error probability for hypothesis  $H_0$  that  $h^2 \geq 1$ .)

cohort	$n$	$k$	$h^2$	s.e.	$p_1$	$p_2$	$CV_A$	$CV_R$
1988	50	12	0.996	0.296	0.004	0.533	8.57	0.00
1989	36	9	0.386	0.276	0.089	0.001	2.01	7.65
1990	30	7	0.297	0.400	0.244	0.030	5.07	7.22
1991	20	5	0.024	0.279	0.462	< 0.001	0.00	7.85
1992	47	13	0.518	0.268	0.026	0.036	5.25	5.31
1994	45	12	0.650	0.315	0.020	0.136	7.69	5.54
1995	59	16	0.266	0.300	0.184	0.010	4.06	7.96
1996	54	15	1.085	0.268	< 0.001	0.666	6.30	5.42
1997	47	12	0.299	0.291	0.184	< 0.001	0.00	8.79
1998	49	14	-0.175	0.319	0.732	< 0.001	1.59	9.50
1999	93	29	0.285	0.336	0.208	0.018	5.33	8.38
1988/1988	32	6	0.608	0.306	0.036	0.073	4.09	7.57
1988/1989	26	5	0.569	0.489	0.119	0.167	8.69	10.00
1990/1991	29	7	0.373	0.349	0.093	0.051	5.11	6.75
1994/1994	39	8	0.491	0.367	0.079	0.109	6.09	7.05
1995/1995	93	16	0.242	0.159	0.049	< 0.001	5.23	9.35
1995/1997	18	4	0.271	0.417	0.241	0.024	8.01	11.58
1997/1997	11	4	0.853	0.380	0.061	0.487	10.11	1.90
1997/1998	26	5	0.289	0.356	0.184	0.054	4.38	6.54

( $n=45$ ), a cohort with very high family resemblances in this trait (see table 1). We selected ten birds with the latest residual onsets of migratory activity for breeding and, out of the 26 offspring produced by this group of birds, we selected four breeding pairs with late onset of activity for producing a second generation ( $n=14$ ). The selection response obtained in this selection experiment allowed us to estimate realized heritabilities by dividing the cumulative selection response by the cumulative selection intensity (cf. Falconer & Mackay 1996).

### 3. RESULTS

On average juvenile southern German blackcaps started autumn migratory activity on 17 September ( $\pm 14.7$  days) at an age of  $105.5 \pm 12.2$  days. The earliest onset of migratory activity was recorded on 15 August and the latest on 1 November.

The overall between-clutch repeatability ( $r=0.396$ , s.e. = 0.143,  $F_{24,37}=2.62$  and  $p=0.004$ ) was significantly different from zero, as was the between-clutch repeatability within years ( $r=0.370$ , s.e. = 0.157,  $F_{22,27}=2.28$  and  $p=0.022$ ). The repeatability among clutches hatched in different years was of similar magnitude ( $r=0.305$ , s.e. = 0.335,  $F_{6,8}=1.94$  and  $p=0.190$ ), although it did not reach significance, probably due to the small number of families sampled. The similarity of the within-year and between-year repeatabilities clearly indicate that variation in environmental conditions between years cannot account for variation in the timing of autumn migration or in family resemblances among cohorts.

Heritability estimates for the onset of migratory activity derived from the resemblances among full-sibs collected in the wild varied considerably between years

and were significant in 4 out of 11 years (table 1). The mean within-cohort heritability was  $0.431 \pm 0.377$ . The combination of the results for the 11 cohorts (table 1) provided strong statistical evidence for rejecting the hypothesis of  $h^2 \leq 0$  (Fisher's combination test,  $\chi^2_{22}=59.7$  and  $p < 0.0001$ ).

Despite smaller sample sizes, the heterogeneity in heritability estimates derived from the resemblance among full-sibs bred in aviaries was smaller than in birds hatched in the wild (see table 1). The mean heritability derived from birds bred in captivity ( $h^2=0.415 \pm 0.210$ ) was in good agreement with estimates derived from birds collected in the wild and significantly different from zero (Fisher's combination test,  $\chi^2_{16}=37.7$  and  $p=0.002$ ). Heritabilities derived from the intraclass correlation between full-sibs hatched in captivity were correlated with heritabilities in their respective parental cohorts (Spearman's rank correlation,  $r_S=0.667$ ,  $n=8$  and  $p=0.071$ ) but not with heritabilities derived from birds collected in the wild that had hatched in the same year ( $r_S=0.024$ ,  $n=8$  and  $p=0.955$ ).

The heritability estimated from the weighted regression of mid-offspring on mid-parent residual onset of activity was significantly different from zero ( $h^2=0.345 \pm 0.155$  and  $p=0.013$ ) (figure 1). There was neither a significant influence of offspring hatching year (ANCOVA,  $F_{7,187}=1.22$  and  $p=0.293$ ) or of paternal ( $F_{6,186}=1.22$  and  $p=0.298$ ) or maternal ( $F_{4,175}=1.51$  and  $p=0.201$ ) birth year on the regression coefficient. Single-parent-mid-offspring regressions yielded similar heritability estimates, but only the regression of mid-offspring on father was significantly different from zero (father-mid-offspring regression,  $h^2=0.470 \pm 0.236$  and  $p=0.038$ , and

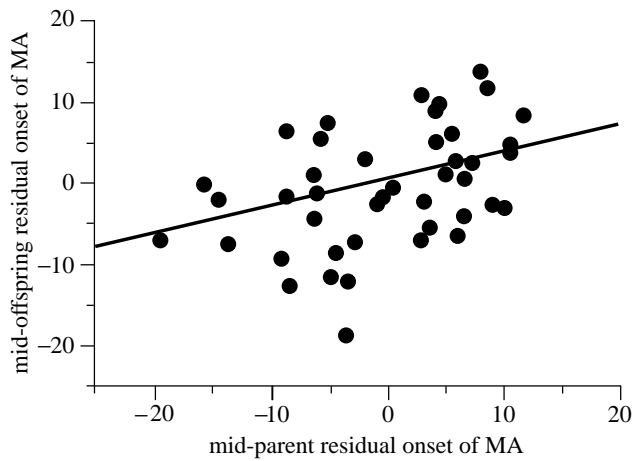


Figure 1. Weighted mid-parent–mid-offspring regression of the residual onset of migratory activity (MA).

mother–mid-offspring regression,  $h^2 = 0.355 \pm 0.365$  and  $p = 0.202$ ). The difference between the mid-offspring on mother and mid-offspring on father regressions was not significant (ANCOVA,  $F_{1,400} = 1.50$  and  $p = 0.221$ ).

The coefficients of additive genetic variation ( $CV_A$ ) and residual variation ( $CV_R$ ) derived from full-sib resemblances did not vary significantly between birds collected in the wild (median  $CV_A = 5.09$ , median  $CV_R = 7.51$  and  $n = 11$ ) and birds bred in captivity (median  $CV_A = 5.66$ , median  $CV_R = 7.31$  and  $n = 8$ ) (Mann–Whitney  $U$ -test,  $CV_A$ ,  $U = 32$  and  $p = 0.322$ , and  $CV_R$ ,  $U = 43$  and  $p = 0.934$ ) (see table 1). These coefficients of variation were in agreement with the coefficients obtained by mid-parent–mid-offspring regression ( $CV_A = 4.70$  and  $CV_R = 6.44$ ). There was no trend of an increase or decrease in the heritabilities ( $b = -0.028 \pm 0.032$ ,  $F_{1,9} = 0.788$  and  $p = 0.398$ ) or coefficients of additive genetic variation ( $b = -0.152 \pm 0.25$ ,  $F_{1,9} = 0.361$  and  $p = 0.563$ ) and residual variation ( $b = 0.151 \pm 0.140$ ,  $F_{1,8} = 1.15$  and  $p = 0.315$ ) with time.

We obtained a shift in the population mean of 7.65 days in two generations of artificial selection for later onset of migratory activity (figure 2). The selection gain in the first generation was only minimal and non-significant (Dunnnett's T3 pairwise comparison test, mean difference = 0.45, s.e. = 2.46 and  $p > 0.5$ ). The mean residual onset of migration in generation 2 was significantly different from the means in both preceding generations (Dunnnett's T3 pairwise comparison test, generation 0, mean difference = 7.65, s.e. = 3.05 and  $p = 0.015$ , and generation 1, mean difference = 7.20, s.e. = 3.30 and  $p = 0.040$ ). The realized heritability estimated by dividing the cumulative selection response (0.72) by the cumulative selection intensity (1.30) was 0.55.

#### 4. DISCUSSION

To the authors' knowledge, this is the first report of a heritability estimate of the timing of autumn migration in a migratory species. We obtained consistent heritability estimates using different methods and sets of birds hatched in the wild or in captivity. Based on the extensive data on migratory activity in a blackcap population, we

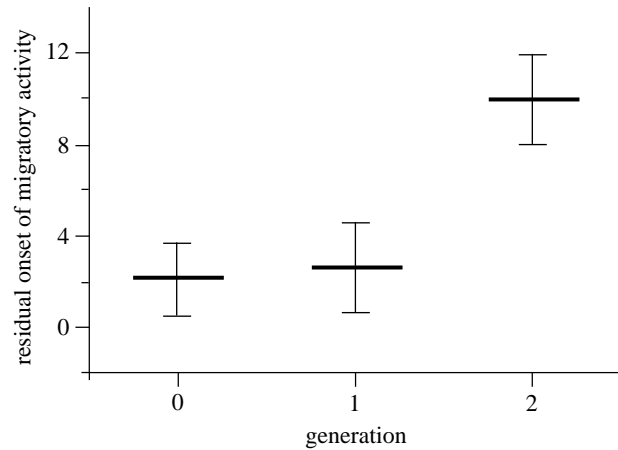


Figure 2. Two generations of selection for later onset of migratory activity. Means and standard errors of the residual onset of migratory activity in the parental and the two selected generations are given.

demonstrate the evolvability of the timing of migration by the presence of significant additive genetic variation as derived from the resemblances among relatives and in an experiment showing that the timing of migration can be rapidly changed by directional selection for delayed migration. Even though we conducted this selection experiment for only two generations and the sample size was limited, we obtained a shift in the mean departure date by more than one week. This selection response was in close correspondence to the response expected from the heritability estimates derived from family resemblances in the cohort the selection line was derived from.

The fact that the resemblances among full-sibs bred in captivity were correlated with the resemblances in their progenitors' cohort and not with resemblances among birds hatched in the same year in the wild suggests that hatching and being reared under artificial conditions does not change family resemblances. This conclusion was further supported by the finding that within-year repeatabilities were no larger than between-year repeatabilities. We are thus confident that common-environment effects did not bias our heritability estimates. Our analyses further demonstrate that the between-year variation in family resemblances was not caused by fluctuations in the 'laboratory environment' but was due to between-year variation in the genetic composition of the population. We currently do not know whether the between-cohort genetic variation in the samples reflects changes in the composition of the population or whether it reflected sampling error. Lack of directional changes in family resemblances and limited sampling in some years suggested that the between-year variance in heritabilities may have been partly due to sampling variance.

The heritabilities of the timing of onset of migratory activity in the southern German blackcap population are in accord with the heritability of arrival date in the barn swallow ( $h^2 = 0.54$ ) (Møller 2001) and with heritabilities of the termination of juvenile moult in the stonechat *Saxicola torquata* (mean of four estimates  $h^2 = 0.42$ ) (see table 5 in Helm & Gwinner (1999)) and the garden warbler (mean for two populations  $h^2 = 0.55$ ) (Widmer

1999). Heritability estimates for these traits are not available for the blackcap but we expect the heritability of the termination of juvenile moult to be in the same range as the heritabilities of the onset of autumn migratory activity as there is a strong correlation between the timing of the end of moult and the onset of migration (F. Pulido and T. Coppack, unpublished data).

Using the estimates for the heritability, mean and variance of age at onset of migratory activity, we can predict the rate of evolutionary change in this trait by the formula  $\Delta\bar{z} = CV_p \times \bar{z} \times h^2 \times \bar{\beta}$ , where  $\bar{z}$  is the mean age at onset of migratory activity,  $CV_p$  is the coefficient of phenotypic variation and  $\bar{\beta}$  is the standardized selection gradient (cf. Falconer & Mackay 1996; Roff 1997). An analysis of the relationship between the trait mean and coefficient of variation in different blackcap cohorts revealed that the coefficient of variation decreased slightly with the mean ( $b = -0.170$ ,  $F_{1,17} = 2.43$  and  $p = 0.137$ ), which we take into account when estimating selection responses. Using this quantitative genetic model and assuming that heritabilities remain constant during the selection episode, we predict very rapid changes in the timing of migratory activity even under weak to moderate selection intensities.

For example, assuming a heritability of 0.3 and a coefficient of phenotypic variation of 11.5%, a delay in the mean onset of migratory activity by one week would be achieved in six generations if 20% of the population with the earliest departure dates were to fail to reproduce. If only 5 or 2% of individuals with the earliest onset of migration were not to breed each generation, a delay in the mean onset of migration by one week would be achieved after 18 and 40 generations, respectively. Considering the strong genetic correlations of the timing of the onset of migratory activity with other migratory traits (Pulido 2000) and that a global increase in temperature will cause fitness differences in suites of traits, we do, in fact, predict stronger selection responses than those calculated above. A multivariate response to correlational selection of migratory traits due to global warming would be reinforced by the pattern of genetic correlations (Pulido & Berthold 1998). Assuming equal selection intensities on all migratory traits, the selection response of the onset of migration could increase by ca. 70%.

Even though we found significant additive genetic variation in the timing of migratory activity, we cannot currently predict whether adaptation will be hampered by antagonistic genetic correlations with other traits under selection or by unfavourable changes in the genetic variance-covariance matrix (cf. Holloway *et al.* 1990; Holt 1990). Our data suggest that changes in additive genetic variances have probably not occurred, as there was no trend for directional changes in heritabilities or the coefficients of additive genetic and residual variance during the study period (1988–1999). However, there were significant climatic changes in the breeding area of this population during this period (Bergmann 1998), which have probably caused evolutionary changes in migratory traits (Pulido 2000; F. Pulido and P. Berthold, unpublished data).

Another uncertainty in the predictive power of our selection model is whether heritabilities obtained in the

laboratory are valid under environmental conditions in the wild. If the expression of migratory activity is modified by conditions in the laboratory (see Lambrechts *et al.* 1999) it will be impossible to make predictions about selection response in the wild using laboratory data. However, in view of the fact that the endogenous spatio-temporal programme controlling the onset of migratory activity is insensitive to most environmental variables except the photoperiod (Berthold 1996) and that there is a tight correlation between migratory behaviour in the laboratory and in the wild (Berthold 1973, 1990), we are confident that the genetic parameters obtained in this study reflect the variance components in the natural southern German blackcap population. Moreover, it has been shown in a number of studies that laboratory estimates of heritability are strongly correlated with heritability estimates in field populations (reviewed in Weigensberg & Roff 1996; Roff 1997). The observation that field heritability estimates are often lower than laboratory estimates for behavioural traits may be an artefact due to the low measurement repeatability of these traits (Hoffmann 2000).

Although the presence of additive genetic variation and favourable genetic correlations in migratory traits may prompt us to take an optimistic view regarding the response of migratory birds to climatic change, we should caution about not seeing the limits of their adaptability. Migratory birds are particularly vulnerable to global climatic changes as their annual cycle, which involves breeding, moult and two migration events, is more complex than that of resident birds. Moreover, the timing of these routines requires a fine-tuned adjustment to the timing of environmental conditions. Synchronization with environmental seasonality is achieved by the interplay of an endogenous circannual rhythm and environmental cues used as indicators for annual processes (Wingfield & Jacobs 1999). Changes in the phase relationship of environmental factors due to global environmental changes (cf. Visser & Holleman 2001) may have profound consequences for the annual organization of birds. By disrupting their synchronization with food availability, migratory birds may suffer serious fitness declines (e.g. Myers & Lester 1992; Inouye *et al.* 2000). Moreover, due to rigid phase relationships between annual life-history stages that are probably accompanied by high genetic correlations, the evolution of the timing of individual events to new optima may be constrained (e.g. Visser *et al.* 1998; Coppack *et al.* 2001). Thus, we need to know more about heritable variation in and covariation between life-history stages before we can definitely settle the question of whether migratory birds will be able to adapt to global warming.

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