GENETIC VARIATION AND PHENOTYPIC PLASTICITY MAY EXPLAIN ADAPTIVE CHANGES IN THE TIMING OF AUTUMN MIGRATION

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ABSTRACT

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Here, we review recent experiments on the genetic and environmental control of the timing of autumn migration in the Blackcap (*Sylvia atricapilla*) with the aim of predicting the potential for adaptive evolution in response to climatic changes. The environmental variable most strongly influencing the onset of migratory activity is the photoperiod. Birds born late in the season develop migratory activity at an earlier age than birds born early. This response of the age at onset of migratory activity to differences in hatching date can be described as an adaptive norm of reaction, which enables all birds to initiate migration before conditions deteriorate on the breeding grounds. Significant among-family variation in this reaction norm suggests that there is a potential for responding to natural selection. In a split-brood experiment, in which we exposed nestlings to daylength simulating photoperiodic conditions six weeks before their actual hatching date, we found that although experimental birds initiated migratory activity at a significantly earlier age, it was interrupted as daylength increased, thus initiating migratory activity at the same age as control birds. Consequently, if we take into account the trend for earlier breeding, the delay in the timing of autumn migration currently observed in a number of bird species cannot be due to plasticity of the phenotype. As an immediate adaptive response to improved conditions on the breeding grounds, we expect a differential delay of the onset of migration and a flattening of the population reaction norm due to relaxation of selection for fast development in late-hatched birds.

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INTRODUCTION

To migratory birds, the onset of autumn migration is an important trait, strongly correlated to fitness. It not only determines how long a bird stays on the breeding grounds, and which conditions it encounters when it prepares for migration (*i.e.* for moulting and building up fat reserves), but also determines, as we have recently shown, how far a bird migrates (Pulido 1998, Pulido and Berthold 1998). We therefore expect that each species has an optimal departure date under particular environmental conditions. Indeed, in many bird species there is only little among-year variation in autumn departure date (see, for instance, Berthold 1993). However, as environmental conditions change, the optimal departure date also changes. We are currently witnessing an increase in global temperature, and are therefore interested in predicting to what extent and in which way birds can alter the timing of autumn migration in response to these changing conditions on the breeding grounds (*cf.* Berthold 1991, 1996).

The photoperiodic cycle has been identified as the most important environmental factor influencing the timing of migration in birds (Gwinner 1986, 1996; Berthold 1996), thus synchronising their annual activities with seasonal processes. The influence of the photoperiod on bird migration has predominantly been studied with the aims of identifying the conditions under which photorefractoriness is broken in autumn (*e.g.* Gwinner 1987, 1989), and the conditions under which the photoperiod functions as a „zeitgeber" of circannual rhythms (Gwinner 1986). Moreover, it has been investigated to what extent interspecific and interpopulational differences in the development of migratory disposition, and in the timing and course of migratory activity, are due to different genetic programs, differences in the photoperiodic conditions experienced, or genetic differences in the response to photoperiodic conditions (see, for instance, Gwinner *et al.* 1971, 1972; Berthold *et al.* 1972; Berthold 1977; Widmer 1999). In these studies, differences in endogenous programs were identified as the major cause for differences in juvenile development and migratory behaviour.

Recently, there have been a number of studies showing that among-population differences in the timing of breeding (Lambrechts *et al*. 1996, 1997, 1999; Visser and Lambrechts 1999), moulting (Helm and Gwinner 1999), autumn (Pulido 1998, Widmer 1999, Pulido and Berthold in prep.) and spring migration (Widmer 1999) are to a large extent due to differences in the response to environmental cues, *i.e.* the photoperiod. In these studies, the relationship between daylength variation and the timing of seasonal events has been studied using a reaction-norm approach (see, for instance, van Noordwijk 1989, Via *et al.* 1995, Schlichting and Pigliucci 1998). The reaction norm is „the set of phenotypes produced by a single genotype across a range of environmental conditions" (Stearns 1992). By using this quantitative genetic approach, we may be able to elucidate the evolutionary processes leading to adaptive changes in the timing of migration. In addition, the assessment of the amount of additive genetic variation in reaction norms may enable us to predict the rates of evolutionary change in this trait.

Here, we summarise recent experimental results on the control and the adaptability of the onset of autumn migratory activity in a southern German Blackcap population using a reaction-norm approach.

MATERIAL AND METHODS

All experiments reviewed in this paper were conducted at Vogelwarte Radolfzell. The results presented are based on data on migratory restlessness of almost 700 first-year Blackcaps from a southern German population collected in the past 12 years. All birds were either bred in aviaries or collected in the wild. They were hand-raised, and kept under standardised, controlled conditions. Migratory activity was measured in registration cages with movable perches throughout the migratory season (for methods and a description of the population, see, for instance, Berthold and Pulido 1994).

RESULTS

Within-environment genetic variation

Genetic variation is the prerequisite for adaptive evolution, and a measure of the amount of genetic variation available to selection in a population is the heritability. The most straightforward way of estimating heritability is to plot mid-offspring trait values on mid-parental values. The slope of the regression line fitted to these data points gives an unbiased estimate of the heritability (Falconer and Mackay 1996). If we remove the effect of hatching date, the heritability of the residual onset of migratory restlessness obtained by this method was 0.36. Heritabilities estimated using the resemblances among full sibs were on average a little higher ($h^2 = 0.42$). We should thus expect that in this Blackcap population about 40% of the phenotypic variance is caused by genes with additive effects (Pulido 1998, Pulido and Berthold in prep.).

In an artificial selection experiment, we tested the prediction of rapid evolutionary change in this trait. We selectively bred birds with the latest onset of activities for two generations (Pulido and Berthold in prep.). Surprisingly, the response to this truncation selection was much higher than we anticipated. The mean onset of migration of the population was delayed by about two weeks in only two generations, yielding a realised heritability of about 0.8. This unexpected result was probably due to correlated responses to selection on other migratory traits we did not control for in our experiment, as a consequence of reinforcing genetic correlations (see Pulido and Berthold 1998).

All these experiments suggest that there is a relatively high amount of additive genetic variation present in this population, and that we should expect rapid responses of within-environment trait means to selection.

Phenotypic plasticity

It is well established that the photoperiod is the environmental variable having the strongest influence on the timing of migration in most birds (Gwinner 1986, 1996; Berthold 1996). Variation in photoperiodic conditions within a population is a consequence of variation in the timing of breeding. Birds hatching late in the season experience shorter daylengths during their development than birds hatching earlier in the season.

There is a strong positive correlation between hatching date and date of onset of migratory activity: the later a bird hatches, the later it starts migration (Pulido 1998, Pulido and Berthold in prep.). However, even though we expect selection on the date of onset of migration, it is not the trait selected for. For understanding the selection process leading to changes in the date of onset of migratory activity, we have to gain insight into the mechanisms causing the photoperiodic response. Differences in the onset of migration in birds hatched at different times are caused by differences in developmental time, *i.e.* the time a bird needs to moult and acquire migratory disposition. Birds hatched late in the season do start migration later, but not as late as we would expect if all birds needed the same time to develop (see Gwinner 1986, 1996; Berthold 1988, 1996).

If we plot the age at onset of migratory activity against hatching date of each individual southern German Blackcap, we find a strong linear relationship between these two variables (Fig. 1). The later a bird hatches the faster it develops, and the younger it is when it leaves the breeding grounds. This function can be described as a population reaction norm, *i.e.* the set of phenotypes that on average is produced within a population exposed to different environmental conditions (van Noordwijk 1989). For studying individual reaction norms, we looked at the performance of the offspring of one breeding pair hatched at different times of the season. Even though full sibs are not genetically identical (unless they were monozygotic twins), they are the most genetically homogeneous group available in birds. Figure 2 shows the re-

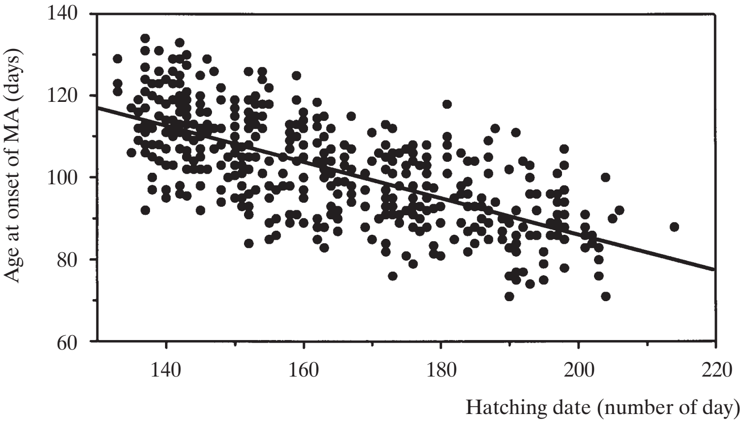

Fig. 1. The effect of hatching date on age at onset of migratory activity (*MA*, in days after hatching). The regression line gives the mean population reaction norm (cf. van Noordwijk 1989). The linear regression coefficient (b = -0.440) is highly significantly different from zero (from Pulido 1998; Pulido and Berthold, in prep.).

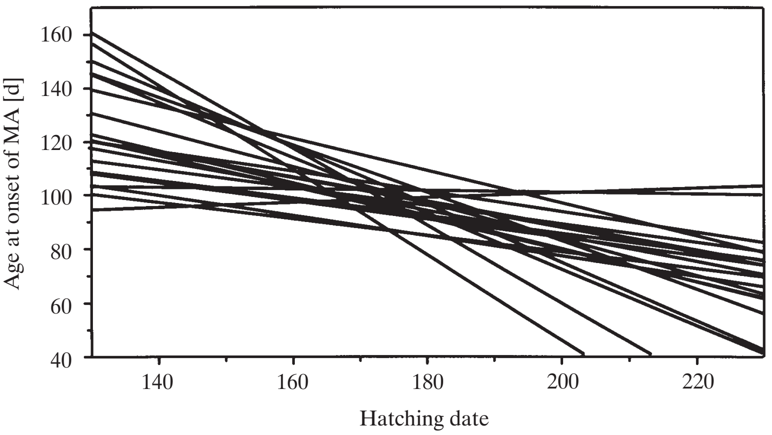

Fig. 2. Among-family variation in reaction norms of the age at onset of migratory activity (*MA*) in response to differences in hatching date. Each line gives the linear regression fitted to the data on the onset of migratory activity of one of 20 full-sib groups (*F1* generation) with variation in hatching dates. The among-family variation of regression coefficients (i.e. the family-by-hatching-date interaction term) is significantly different from zero (from Pulido 1998; Pulido and Berthold, in prep.).

action norms of 20 full-sib groups. On average the relationship is similar to the one found for the total population. The slopes of most family reaction norms are close to the mean slope of the population. However, there is also some heterogeneity: in some families, there is practically no response to the photoperiod; in other families, the compensatory effect is much stronger. This heterogeneity in slopes (which mathematically is identical to the genotype-by-environment interaction) is important, as it is a prerequisite for reaction norms to respond to natural selection.

For adapting to a global increase in temperature, it is not sufficient to delay the departure from the breeding grounds, but also the response of the onset of migration to differences in hatching date has to change. There is now growing evidence from field studies that not only autumn migration is delayed but also that breeding is considerably advanced (see, for instance, Crick and Sparks 1999). Because conditions in early spring have improved on the breeding grounds, birds return earlier in spring and start breeding earlier. On the other hand, conditions in autumn have also improved and allow birds to stay longer on the breeding grounds. However, as there is a strong positive correlation between timing of breeding and timing of migration, an advancement of laying date should cause an advancement of autumn migration. So, how could both laying date and onset of migration adapt to these new environmental conditions? One solution to this problem would be the modification of the population reaction norm. This may be possible as there is some evidence for additive genetic variation in the slope of reaction norms (see above). However, first estimates of the heritability of the slope of the reaction norm in this population (h^2 lies between 0.04 and 0.14 and is not significantly different from zero – Pulido and Berthold unpubl.) suggest that the amount of additive genetic variation in phenotypic plasticity is too low to adapt to a rapidly changing environment. Moreover, it is not enough to have a different slope of a linear reaction norm, but its shape has to change – it has to become curvilinear. We have good evidence that in the range of current hatching dates the reaction norm is linear (see Fig. 1; Pulido 1998). However, what would happen if a bird hatched much earlier, at a time when daylength is relatively short, and still increasing? This is a scenario to be expected if the trend for earlier breeding in the Blackcap continues. It is possible that the mean reaction norm in this population is already adapted to very early hatching. If the reaction norm was curvilinear outside the range of studied hatching dates, then a delayed onset of migration could be induced by the photoperiodic conditions experienced during development in very early-hatched birds.

We conducted a photoperiodic experiment with Blackcaps from southern Germany to investigate whether a delayed onset of migration could be induced by the photoperiodic conditions experienced by birds hatching very early in the season (Coppack 1998, Coppack *et al.* in prep.). Nestlings were reared under a time-shifted light-dark regime simulating conditions six weeks before their actual hatching date. Experimental birds started migratory restlessness at a significantly earlier age compared to siblings held under photoperiods similar to natural conditions. However, this early migratory activity was interrupted as daylength subsequently increased (Fig. 3). This experiment shows that the photoperiodic response alone cannot ex-

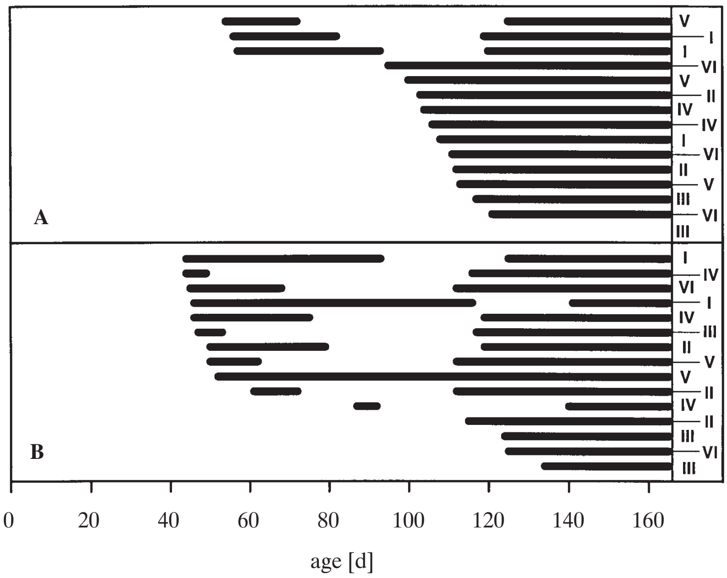

Fig. 3. Results from a split-brood experiment testing the shape and variation of reaction norms in very early-hatched birds. Patterns of migratory restlessness of 30 individual juvenile Blackcaps derived from 6 families (I-VI) hatched around May 15. In *A*, migratory activities in birds from the control group – held in natural photoperiodic conditions – are given. In *B*, migratory activities for the experimental group – held in photoperiodic conditions simulating a hatching date 6 weeks earlier, i.e. around April 6 – are given. Birds within each treatment are sorted by the age at onset of migratory activity (from Coppack 1998; Coppack *et al.,* in prep.).

plain current changes in the timing of migration. Moreover, some individuals from single families did not respond to the photoperiodic shift, indicating that there is variation of reaction norms within this population. This may suggest that adaptive responses to very early hatching may already be present in this population, and that we can expect reaction norms to adapt to the expected environmental changes.

DISCUSSION

The studies reviewed here clearly demonstrate the presence of additive genetic variation in the onset of migratory activity in autumn, thus the potential for evolutionary change. However, adaptive changes in the onset of migratory activity cannot be understood if the tight correlation between the age at onset of migratory activity and hatching date is disregarded. The timing of the onset of migration is controlled by the speed of development of juvenile birds. Thus, it is this trait that may be modified by natural selection for earlier or later autumn migration. The later a bird hatches the faster it develops, and the earlier it starts migration. This response of developmental time to differences in hatching date can be regarded as a reaction norm, where the photoperiod (*i.e.* daylength or changes in daylength) is the environmental variable modifying the expression of developmental rate. The reaction-norm approach has previously been successfully applied to studying the adaptation and evolution of laying dates (*e.g.* Nager and van Noordwijk 1995; Lambrechts *et al.* 1997, 1998, 1999; Visser and Lambrechts 1999) and the timing of moult (Helm and Gwinner 1999). Here, we show that this approach can successfully be used to predict adaptive evolution in the timing of autumn migration.

The study of family reaction norms revealed some additive genetic variation in the slope of the reaction norm. This variation, however, seems to be too small to facilitate rapid adaptive changes. Similarly, experimental results in *Drosophila* (Hillesheim and Stearns 1991, Scheiner and Lymann 1991) and *Daphnia* (Scheiner and Yampolsky 1998) suggest that although selection may result in significant changes of reaction norms, direct selection responses are small compared to correlated responses to selection on within-environment trait means (see Via 1993, Scheiner 1993, Scheiner and Yampolsky 1998). In our proposed model for adaptive changes in the timing of autumn migration in response to global warming, the change in the reaction norm is primarily achieved by relaxed selection for fast development in birds born late in the season (Fig. 4). As rapid development is costly (for an evaluation of the costs of rapid moult in birds, see Murphy 1996, Hedenström 1999, Hedenström and Sunada 1999), we expect strong selection for a longer developmental time in late-hatched birds as a first, immediate evolutionary response to improved conditions on the breeding grounds. Because of this selection process, a flattening of the reaction norm should follow as a correlated response (see Fig. 4). However, as selection proceeds, both late-hatched birds and birds hatched early in the season will be affected. As laying dates are becoming progressively earlier, birds will hatch

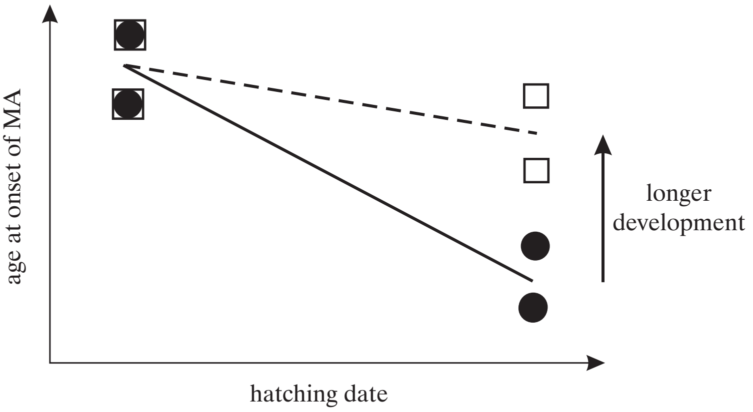

Fig. 4. Model predicting changes in the age at onset of migratory activity in response to global warming. Filled circles represent the current population mean for the age at onset of migratory activity (*MA*) for two different hatching dates. The solid line gives the present reaction norm. Open squares and broken lines represent expected population means for two hatching dates, and the respective reaction norm after selection. The arrow indicates the predicted direction of selection.

earlier and should, therefore, be initiating migration earlier. Thus, if selection persists for a long enough period, we not only expect changes in within-hatching-date means and in the slope of the reaction norm, but also in its shape.

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