Microevolutionary Response to Climatic Change

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I. SUMMARY

Organisms may respond to changing environments by evading the new conditions or by adapting to them. Recently, a large body of evidence has been collected indicating that phenotypic adaptation to climate change is widespread. Adaptation may be achieved by phenotypic adjustment or by changes in the genetic composition of populations. Both processes can assure the survival of populations in changing environments, but at different time scales and at different costs. Recent studies indicate that the mechanisms leading to

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ADVANCES IN ECOLOGICAL RESEARCH, VOL. 35
0065-2504/04 $35.00 DOI 10.1016/S0065-2504(04)35008-7

adaptive phenotypic changes in birds may be complex, involving both plastic response and genetic change. Changes in the timing of breeding, for instance, seem to be predominantly caused by phenotypic adjustment to environmental conditions. Shifts in the genetic composition of populations have been demonstrated to be involved in recent changes in morphology and migratory behaviour. The presence of considerable amounts of additive genetic variation within and among avian populations, and examples of rapid evolutionary response to rare climatic events suggest that birds have a high potential for adaptive evolutionary change. However, it is presently unclear whether this is a general pattern, and which factors actually limit the adaptability of avian populations. Antagonistic genetic correlations and maladaptive phenotypic responses (evolutionary traps) are probably the most important constrains to microevolutionary change. Furthermore, the loss of genetic variation due to population declines, and gene flow in the presence of among-population variation in the response to climate change may limit the rate of adaptive evolution. Future research should try to identify the targets of selection and gauge the importance of constraints to microevolutionary change.

II. INTRODUCTION

Currently, climate is changing at an unprecedented rate. Present-day climatic change is characterised by a rapid global increase in temperature, whereby temperatures are not increasing evenly throughout the year and not at the same rate and extent geographically. In the northern hemisphere, temperature increase is higher in winter and early spring than in summer or autumn, and considerably larger at high altitudes and latitudes than at low altitudes and in the south (Houghton *et al*., 2001). But locally these trends may not be apparent or may even be reversed (e.g., Kozlov and Berlina, 2002). The global rise in temperature has caused phenological changes (Menzel and Fabian, 1999; Menzel, 2000; Sparks and Menzel, 2002), shifts in climate zones (Fraedrich *et al*., 2001), and changes in the frequency of extreme weather events like droughts, periods of extreme heat, storms and floods (Easterling *et al*., 2000a,b; Meehl *et al*., 2000).

These environmental changes impose major challenges to animal and plant populations, and may potentially lead to their extinction. Organisms may respond to this climatic change in different ways (Holt, 1990). One possible response is to evade the unfavourable environment. This may result in shifts or expansions of ranges, which has been documented for various plant and animal species (Parmesan, 1996; Parmesan *et al*., 1999), including birds (e.g., Burton, 1995; Thomas and Lennon, 1999; Valiela and Bowen, 2003). Highly mobile organisms, like birds, are expected to more readily respond to environmental change by this means than sessile species and species with low potential of dispersal. However, the availability of appropriate food at the newly colonised site may limit this process (Root, 1993; Huntley, 1994; Price and Glick, 2001). Irrespective of whether organisms colonise a new area, or if they stay within their traditional ranges, populations have to respond to environmental change by adapting to the new environmental conditions (Geber and Dawson, 1993). Traditionally, adaptation is considered to be the result of genetic change in response to selection (see, for instance, Futuyma, 1998), i.e., microevolution. This process of adaptive evolution is relatively slow (but see Hendry and Kinnison, 1999; Rice and Emery, 2003), and may prevent extinction only if selection is not too strong and the lag between the population mean and the optimal phenotype does not become too large (Lynch and Lande, 1993; Lande and Shannon, 1996). Alternatively, or in addition, adaptation to new environmental conditions can be achieved by phenotypic changes of the individual, i.e., phenotypic plasticity (Meyers and Bull, 2002). Individual adjustment may be reversible or irreversible and may or may not be genetically fixed (Piersma and Drent, 2003), in which case it may respond to selection (Pigliucci, 2001; Scheiner, 2002). The evolution of phenotypic plasticity, or its evolutionary change, may be constrained by the costs of plasticity (DeWitt *et al*., 1998; Pigliucci, 2001) and the restrictive selection conditions needed (Scheiner and Lyman, 1991; Scheiner, 1993, 2002). Moreover, moderate levels of plasticity will facilitate evolutionary change (Price *et al*., 2003).

Whether a population will respond to climatic change by phenotypic plasticity or by genetic change seems, at first sight, equally adequate. However, there are some fundamental differences in the consequences of these modes of adaptation. Adaptive responses by phenotypic plasticity are limited by the range of environments in which phenotypic responses are adaptive. Beyond this range phenotypic adjustment may be insufficient or maladaptive (see Coppack and Pulido, 2004, this volume). In a continuously changing environment, adaptation by phenotypic plasticity may, thus, sooner or later lag behind environmental changes, which will confer fitness consequences for the population. Microevolutionary change in response to natural selection can, in principle, enable populations to adapt to ever changing environments. The long-term response to selection is only limited by the amount of additive genetic variation present in the population (Bradshaw, 1991; Bradshaw and McNeilly, 1991). Even this limitation may not be a serious problem as new genetic variation can arise by mutation and transformation of epistatic and dominance variance into additive genetic variation (see Roff, 1997), as indicated by the persisting response in long-term artificial selection experiments (see, for instance, Yoo, 1980 and review by Hill and Caballero, 1992). However, the rate of adaptive evolution critically depends on generation time, and may be very slow in long-lived organisms with overlapping generations (A.J. van Noordwijk, pers. comm.). Therefore, organisms with long generation times and a low potential for population growth may not be able to adapt to rapidly changing environments (see Reznick and Ghalambor, 2001).

Climatic changes, and associated alterations in habitats and biotic interactions have probably been the most important causes for natural selection in the wild, and for this reason one of the driving forces in evolution (Pearson, 1978; Endler, 1986). In a recent review on the biological consequences of global warming, Hughes (2000) predicted changes by four different mechanisms: direct physiological effects, effects on the distribution of animals, phenological changes and adaptive evolution. While he gave a number of examples for all categories of changes, he did not even treat evolutionary changes separately, and gave only one example (Rodríguez-Trelles and Rodríguez, 1998). Although from an evolutionary perspective this categorisation is not intelligible, as physiological and phenological effects may well be a consequence of evolutionary change, it is clear that convincing instances for evolutionary change in response to extant climatic shifts are very rare, and at that time were virtually lacking. Since that review, two studies have been published that have demonstrated that natural populations do respond to climatic warming by evolutionary change (Bradshaw and Holzapfel, 2001; Réale *et al*., 2003). In addition, a number of studies have investigated the causes underlying phenotypic changes in natural populations and the mechanisms responsible for the lack of evolutionary response (e.g., Etterson and Shaw, 2001; Kruuk *et al*., 2001; Merilä *et al*., 2001a,b; Sheldon *et al*., 2003). This work and a number of other studies that are currently under way constitute the fundaments for understanding adaptation to climate change. Although we are only at the beginning of this research, the growing number of studies recently published on this subject justifies writing a review on the evolutionary response to global warming based on empirical results. Because birds are the group of organisms for which we have the best long-term data sets on the composition and behaviour of wild populations, they are central to our understanding of the mechanisms of evolutionary change. In contrast to previous reviews on the evolutionary response to climate change (Holt, 1990; Bradshaw and McNeilly, 1991; Geber and Dawson, 1993; Hoffmann and Blows, 1993; Travis and Futuyma, 1993; Rodríguez-Trelles *et al*., 1998) that have emphasised the potential and limits of adaptive response, the aim of this chapter is to review recent empirical work that has investigated microevolutionary response to climate change and to discuss potentials and shortcomings of different approaches. We shall, in particular, focus on the evolutionary response of avian migratory behaviour.

III. MICROEVOLUTIONARY CHANGE—MECHANISMS AND APPROACHES

Current climatic changes have had, and are persistently having, a profound impact on animal and plant populations (McCarty, 2001; Walther *et al*., 2002; Parmesan and Yohe, 2003; Root *et al*., 2003). The most prominent changes in birds have been changes in the timing of breeding (e.g., Brown *et al*., 1999; Crick *et al*., 1997; Dunn, 2004, this volume) and migration (e.g., Tryjanowski *et al*., 2002; Butler, 2003; Hüppop and Hüppop, 2003; Jenni and Kéry, 2003; Lehikoinen *et al*., 2004, this volume; Fiedler *et al*., 2004, this volume), in clutch size and the number of clutches (e.g., Winkel and Hudde, 1996, 1997; Møller, 2002), in migration distance and the propensity to migrate (reviewed by Berthold, 1998a; Fiedler, 2003), and in body size (e.g., Ludwichowski, 1997; Jakober and Stauber, 2000; Yom-Tov, 2001). These changes in bird populations have been interpreted as being adaptive responses to climate change. However, most of these studies have measured phenotypic change alone without separating genetic and environmental components contributing to that change (Hendry and Kinnison, 1999). Similarly, palaeontologists have assumed that phenotypic changes represent evolutionary change, as they cannot separate the causes of differentiation (Travis and Futuyma, 1993; Barnosky *et al*., 2003).

But to what extent is this assertion correct, or is phenotypic change primarily a consequence of phenotypic plasticity? A recent meta-analysis of rates of change at the genotypic and phenotypic level revealed that the degree of diversification was lower in phenotypic than in genetic studies. One explanation for this finding is that "phenotypic plasticity may make an important contribution to the earliest stages of population divergence or evolution" (Kinnison and Hendry, 2001). Diversification by genetic change may be initially slower than by phenotypic plasticity, but then proceed at a more constant rate over a longer time interval, therefore, on the long run, the net rate of change is expected to be higher (Trussel and Etter, 2001; Pulido, 2004). Furthermore, phenotypic plasticity has been shown to be ubiquitous and to play an important role in the evolutionary response to environmental change (Pigliucci, 2001; Price *et al*., 2003; West-Eberhard, 2003; Coppack and Pulido, 2004, this volume).

Evolutionary change is by definition the "change over time of the proportion of individual organisms differing genetically in one or more traits" (Futuyma, 1998). Thus, to demonstrate that phenotypic changes are a result of evolutionary change, we have to demonstrate that phenotypic differences have a genetic basis. A number of different methods have been proposed and applied for ascertaining genetic differentiation in space and time (see Reznick and Travis, 1996; Reznick and Ghalambor, 2001; Boake *et al*., 2002; Conner, 2003). Among the most commonly used methods are common-garden experiments, reciprocal transplants, reciprocal crossings, artificial selection experiments, longitudinal studies allowing to assess individual phenotypic change, and the estimation of family resemblances from which different quantitative genetic parameters can be derived (e.g., heritability, additive genetic variance, individual estimated breeding values). Moreover, evolutionary change may be demonstrated by showing that actual phenotypic change is in accord with changes expected from selection intensities, genetic variation and among-trait covariation within populations (Grant and Grant, 1995, 2002; Roff and Fairbairn, 1999). None of these methods is without problems, as common-environment effects, including maternal effects, and genotype-by-environment interactions may confound results and suggest genetic differentiation where there is none (Møller and Merilä, 2004, this volume).

Two of these methods have become particularly useful in the study of evolutionary change in response to climate change: common-garden experiments over time and the calculation of estimated breeding values.

Common-garden experiments are based on the idea that if individuals that have been sampled in different areas or at different times express phenotypic differences when held under identical, controlled environmental conditions, these differences are likely to have a genetic basis. The accuracy of this method very much depends on whether it is possible to keep the environment constant and to exactly replicate the conditions of measurement over a long period of time. A group of individuals, which is known not to have changed genetically over time, may serve as a control, and help to minimise this error. Another potentially important shortcoming of this method is its sensitivity to maternal effects. If the phenotype of an individual is not only determined by its genotype and by the environmental conditions it has experienced but also by the phenotype of its mother (including environmental effects), we talk of maternal effects to the phenotype. These effects can be long-lasting and may not be eroded even when individuals are transferred to a common environment very early in life (see reviews in Mousseau and Fox, 1998). This problem may be circumvented if common-garden experiments are combined with breeding experiments where phenotypic differences in the common environment are assessed in the generation of individuals produced by mothers held in the controlled environment, i.e., in the F_1 generation. Strong and persistent maternal effects, however, may not be totally removed after one "round of breeding". The breeding of an F_2 generation in a common environment will in most cases be sufficient to minimise these effects. Because of the difficulties associated with this method it is particularly well suited for monitoring organisms for which controls can easily be preserved (e.g., clonal organism), and for studying traits which are known to be influenced only by few environmental variables—preferably only one—that can be experimentally controlled.

A common garden approach over time was used by Bradshaw and Holzapfel (2001) to demonstrate microevolutionary response of photoperiodism in pitcher plant mosquitoes *Wyeomyia smithii*. They collected mosquitoes from 31 locations covering more than 20 degrees of latitude in 4 years from 1972 through 1996, and measured in two different approaches critical daylengths of pupation and of the initiation and maintenance of diapause under controlled conditions. The comparisons of the changes between 1972 and 1996 and between 1988 and 1993 yielded similar results. In both periods the critical photoperiod had changed towards shorter daylengths, whereby changes in the northern populations were more pronounced than in southern populations. These results were in accord with temperature changes in North America that have been strongest at highest latitudes. The observed change in the critical photoperiod between 1972 and 1999 was equivalent to a delay of diapause by 9 days. Although the data had been collected for other reasons than for studying evolutionary change, and controls were not kept, this study is a convincing example for the use of a controlled environment to elucidate genetic variation in time and space. We have used a similar approach to study evolutionary change in migratory behaviour in a bird population (see below).

An alternative approach for studying the causes of phenotypic change over time is the estimation of breeding values of individuals. The breeding value is a statistical measure of the "individual genotype" in a particular population, and is defined as "the sum of the average effects of the genes an individual carries for a trait" (Falconer and Mackay, 1996). Breeding values have previously been estimated by animal and plant breeders for identifying those individuals with the prospect of yielding the highest selection gain. With the development of new statistical techniques (Henderson, 1986; Knott *et al.*, 1995) and the increase of computer power it is now possible to estimate breeding values for large, unbalanced data sets, like those obtained in long-term studies on natural populations in the field (Kruuk, 2004). One of the advantages of these new statistical approaches is that different genetic (e.g., maternal, paternal) and environmental effects (condition, age, food availability, temperature, etc.) can be estimated separately, and their importance can be evaluated. The accuracy of breeding value estimates critically depends on the accuracy of the quantitative genetic estimates (i.e., genetic variances and covariances). It is, therefore, potentially dependent on family size, pedigree size and complexity, and the number and diversity of environments considered. However, to our knowledge, biases and limitation of this approach for detecting and quantifying microevolutionary change in the wild have hitherto not been studied, and have remained largely unconsidered in the interpretation of results.

The study of the correlation between breeding values and fitness has been shown to predict selection intensities and responses more accurately than the classical approach based on the correlation between phenotypic values and fitness because selection gradients based on breeding values are not biased by environmental covariation (Rausher, 1992; Kruuk *et al*., 2003). For this reason, this method has provided new insight into the process of natural selection in wild populations by detecting cryptic evolutionary change (Merilä *et al*., 2001a), and the cause for the lack of evolutionary change in the presence of additive genetic variation and selection (Kruuk *et al*., 2002). It has recently become the most important tool in the study of evolutionary response to climate change. This method has been applied, for instance, to investigate changes in antler size in red deer *Cervus elaphus* (Kruuk *et al*., 2002), parturition date in red squirrels *Tamiasciurus hudsonicus* (Réale *et al*., 2003), tarsus length (Kruuk *et al*., 2001), body weight at fledging (Merilä *et al*., 2001a,b), clutch size and timing of breeding in the collared flycatcher *Ficedula albicollis* (Sheldon *et al*., 2003), and timing of spring arrival in barn swallows *Hirundo rustica* (A.P. Møller, unpubl.; see below).

Merilä *et al*. (2001b) investigated the change in condition in the collared flycatcher population of Gotland (Sweden) from 1980 through 1999. They found a phenotypic decrease in condition over time despite selection favouring individuals in better condition and the presence of significant amounts of additive genetic variation for this trait (Figure 1a). However, mean estimated breeding values for condition increased over time as expected from the direction and strength of selection (Figure 1b). This discrepancy between changes in condition at the phenotypic and at the genotypic level can be explained by changes in the environment that may induce changes in opposite direction to evolutionary change (countergradient variation). In the case of the Gotland flycatcher population, the deterioration of environmental condition was probably due to a reduction of the availability of caterpillars—the primary food of nestlings—as a consequence of an increasing asynchrony between the caterpillars and bud burst of their host trees, i.e., oaks (Visser and Holleman, 2001).

It is currently unknown how widespread this phenomenon is. There are a number of studies that have reported countergradient variation (Conover and Schultz, 1995), but because this kind of work needs long-term data sets on individually marked related individuals, there are only few studies that have been able to investigate this phenomenon. Irrespective of whether this phenomenon is common or not, this study cautions against drawing conclusions about evolutionary change based on phenotypic change alone. In the presence of countergradient variation, phenotypic change in one direction may be paralleled by strong evolutionary changes in that direction, no evolutionary change, or genetic changes in the opposite direction. Without knowing how environmental variation influences the expression of a trait and whether there have been changes in the relevant environmental variables, no inferences on evolutionary response may be drawn from phenotypic changes.

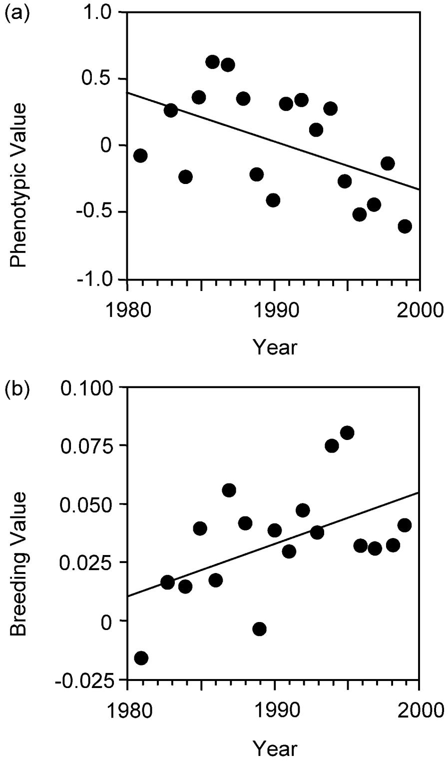

Figure 1 Observed annual changes in body condition in a collared flycatcher population from Gotland (Sweden). (a) Changes in mean phenotypic value of condition index. (b) Changes in mean estimated breeding values of condition index (from Merilä *et al.*, 2001c, with permission from *Nature*).

IV. THE PROSPECTIVE IMPORTANCE OF DIFFERENT EVOLUTIONARY PROCESSES TO ADAPTIVE EVOLUTIONARY CHANGE

A. The Response of Bird Populations to Natural Selection

There is probably no other group of organisms in which the impact of natural selection on trait distribution in natural populations has been studied in more detail than in birds. One reason for this is that the offspring of birds can be easily marked individually and trait distributions and fitness, as measured, for instance, as lifetime reproductive success, can be followed over several generations. Selection studies in natural bird populations have shown that extreme weather events are probably the most important and strongest selective agents in nature (Price and Boag, 1987).

One of the first, and probably the best analysed, studies of natural selection in the wild was the study by Bumpus (1899) who investigated the effects of a snow storm on morphological trait distribution in house sparrows *Passer domesticus*, overwintering in Rhode Island. He measured 10 morphological traits in the sample of birds that had died and in birds that had survived the storm. He found that birds of intermediate size were those that had survived best. Later analyses revealed among-sex differences in selection, e.g., directional selection for large males (e.g., Johnston *et al.*, 1972; Lande and Arnold, 1983). This approach of measuring trait distributions before and after a selection event has been the prevailing method used to detect and reconstruct selection. If, in addition, genetic variances and covariances for the traits under scrutiny are known, selection intensities can be estimated (Lande and Arnold, 1983; Arnold, 1988, 1994; for a review of selection intensities in the wild, see Kingsolver *et al.*, 2001). However, one major problem with this method is that the traits under selection may not be measured. Moreover, the samples taken before and after the selection event may not be representative, and immigration after the selection event may bias trait values in the presumed "survivors" (Price and Yeh, 1999; Price *et al.*, 2000; Møller and Merilä, 2004, this volume). Another problem is that selection may act on environmental deviations, or that differential survival may be a consequence of environmental covariation between trait expression and fitness (see above; Merilä *et al.*, 2001c; Kruuk *et al.*, 2003).

Using this approach a number of selection events caused by extreme climatic events have been studied in wild bird populations (see references in Price and Boag, 1987), of which the best known are the studies by Peter and Rosemary Grant on the medium ground finch *Geospizia fortis* and the cactus finch *G. scandens* on the Galapagos island Daphne Major (Grant and Grant, 1989, 1993, 2002). In a nutshell, the results of these studies can be summarised as follows: (1) Evolutionary response to extreme climatic events can be considerable and (2) high evolutionary rates are both due to high selection intensities and high heritabilities. Moreover, studies following more than one selection episode indicate that selection often fluctuates in direction and intensity and, therefore, over longer periods of time, rates of evolutionary change are much lower than predicted from one selection episode (e.g., Grant and Grant, 2002; see also meta-analysis by Kinnison and Hendry, 2001).

Although many studies suggest that selection imposed by climatic change may lead to very rapid evolutionary changes, it is doubtful whether these results can be generalised. First, most studies have investigated morphological traits which are known to have high heritabilities (e.g., Mousseau and Roff, 1987;

Roff, 1997). Second, selection has been predominantly studied after extreme climatic events (cold spells, droughts, flooding, etc.). The response to such strong selection, however, may differ substantially from continuous directional selection. While extreme events often involve high mortality of birds and predominantly affect viability selection, persistent selection is often weaker and may involve fitness differences in both viability and fecundity (e.g., Sheldon *et al*., 2003). Moreover, under less extreme environmental changes, adjustment at the individual level (e.g., by phenotypic plasticity) is likely to be more important (Meyers and Bull, 2002).

B. The Effects of Gene Flow

As a consequence of habitat changes, range expansions and shifts, we expect patterns of gene flow to change. Populations previously separated by distance, by ecological or geographic barriers may come into contact and interbreed (see Rhymer and Simberloff, 1996). The strength of the effects of such a mixing of populations will depend on the degree of introgression (i.e., mating system), among-population differentiation, effective population size and mutation rates (Edmands and Timmerman, 2003). One possible consequence of population mixing could be a reduction in fitness as a consequence of the disruption of local co-adapted gene complexes and the occurrence of detrimental gene interactions, i.e., outbreeding depression (Frankham *et al*., 2002). Moreover, gene flow may constrain local adaptation (Slatkin, 1987; Storfer, 1999; Lenormand, 2002). However, gene flow may also increase fitness by increase genetic variation and disrupting unfavourable genetic correlations (Grant and Grant, 1994). This could facilitate rapid evolution. It is currently not known whether these effects of gene flow will be important in the adaptation to climate change, or as a consequence of changes in breeding ranges.

Yet, gene flow may become an important component for the adaptation to climate change by another mechanism. The expected directional expansion of ranges of populations dwelling at lower latitudes to higher latitudes, and from lower altitudes to higher altitudes, will most probably cause asymmetrical gene flow from populations adapted to warmer climatic conditions to populations adapted to colder environments. We predict that this inflow of pre-adapted genotypes will facilitate evolutionary adaptation to novel environmental conditions. Although we currently have no evidence for such adaptive unidirectional gene flow it may not be uncommon, but often overlooked, as evolutionary changes in response to local environmental change will have the same effect. Furthermore, gene flow could be reduced as a consequence of a reduction of migratoriness in northern populations (see below; Møller and Merilä, 2004, this volume), as dispersal and geographic differentiation are associated with migratoriness in birds (see Paradis *et al*., 1998; Belliure *et al*., 2000). This process could accelerate local adaptation by reducing introgression of genes from migratory to other populations.

Global climate change is also likely to increase the frequency of interspecific hybridisation. As a consequence of differential effects on population sizes in different species, abundances of some species will dramatically increase while other species will decline to the brink of extinction (Berthold, 1990; McCarty, 2001; McLaughlin *et al*., 2002; Lemoine and Böhning-Gaese, 2003). Under the situation that one of two potentially hybridising species is rare and the other common, the frequency of hybridisation is expected to increase (Wirtz, 1999; Randler, 2002). Hybridisation can have dramatic effects, particularly on the rarer species, extending its evolutionary and ecological potential. This has been extensively studied in Galapagos finches. Here, climatic change has been shown to increase the rate of hybridisation by changing the abundance of intermediate seed sizes, which can best be exploited by hybrids (Grant and Grant, 1992, 1994, 1996). In other species there is also evidence for introgressive hybridisation as a consequence of changes in population sizes, for instance, in European redstarts (*Phoenicurus phoenicurus* and *P. ochruros*; Berthold *et al*., 1996; Grosch, 2003), and warblers (*Hippolais icterina* and *H. polyglotta*; Faivre *et al*., 1999). These instances need, however, to be verified by molecular methods, and may not hold under closer scrutiny (S. Bensch, pers. comm.).

C. The Effects of Inbreeding

If populations suffer rapid and strong declines and when, thereafter, population sizes remain small for a longer period, or when new populations are founded by a few individuals, inbreeding coefficients are likely to increase. Elevated levels of inbreeding may have negative, fitness-reducing effects ultimately leading to the extinction of populations (Frankham, 1995a; Keller and Waller, 2002). In birds, inbreeding is associated with reduced hatching success, reduced survival and lower recruitment into the next generation (e.g., Kempenaers *et al*., 1996; Daniels and Walters, 2000; Keller *et al*., 2002; Spottiswoode and Møller, 2004). Even moderate population bottlenecks (<600 individuals) can have significant fitness consequences for many bird populations (Briskie and Mackintosh, 2004). However, population declines will not inevitably cause an increase of the level of inbreeding if the more inbred individuals do not survive population crashes. This has been shown in the song sparrow *Melospiza melodia* population on Mandarte Island (Keller *et al*., 1994). If population crashes increase as a consequence of increasing frequency of extreme climatic events, recessive deleterious alleles causing inbreeding depression could be purged from the population and reduce inbreeding effects (e.g., Templeton and Read, 1984; Barrett and Charlesworth, 1991). But purging may be efficient only under particular environmental conditions, and may not work under changing or stressful environmental conditions (e.g., Bijlsma *et al*., 2000; Kirstensen *et al*., 2003). Thus, inbreeding effects due to population bottlenecks may persist for long periods of time, as was shown in birds introduced to New Zealand (Briskie and Mackintosh, 2004), probably because they are caused by a reduction of "overdominance effects" rather than by the expression of recessive deleterious alleles.

Another effect of inbreeding has been recently found in an endangered North American breeding bird: the red-cockaded woodpecker *Picoides borealis* (Schiegg *et al*., 2002). During the last decades, laying date has significantly advanced in two populations of this species. This was most probably due to individual adjustment of the timing of breeding to changes in temperatures and the timing of food availability. Breeding experience, the age of the mother and the level of inbreeding affected the adjustment of laying date. A trend for earlier laying was found among non-inbred birds, but not among inbred individuals, suggesting that the effect of climate on laying date depends on the level of inbreeding. It is unclear why inbred female red-cockaded woodpeckers do not adjust to climate change. One possible explanation would be that inbreeding reduces plasticity, because inbred individuals are in inferior condition and cannot allocate energy into plasticity. Low immunocompetence, which has been found to be associated with inbreeding in birds (Reid *et al*., 2003), may affect the timing of breeding, as recently shown in tree swallows *Tachycineta bicolor* (Hasselquist *et al*., 2001). Unfortunately, experiments testing for the association between levels of inbreeding and phenotypic plasticity are lacking.

V. CHANGES IN THE LEVEL OF GENETIC VARIATION

It is not clear how climate change will affect the level of genetic variation in natural populations. To what extent changes are to be expected depends on a number of factors, primarily on the form, strength and constancy of selection, on the size of the population and population trends, and on the degree of isolation, i.e., gene flow (Lacy, 1987; Booy *et al*., 2000). Furthermore, sex ratio and mating system are major determinants of effective populations size (e.g., Frankham, 1995b; Nunney, 1995). Although we currently have some evidence that sex ratio in birds can be adaptively modified (but see Ewen *et al*., 2004, this volume), we do not know if and in which direction changes could take place. Potential factors influencing the sex ratio are the quality of territories (i.e., resource availability), and the quality of males (Sheldon, 1998). Mating system is also highly dependent on resource availability. The higher the availability of resources, the higher is the level of promiscuity in the population (Forstmeier *et al*., 2001; Leisler *et al*., 2002). A reduction of food availability or quality may thus result in lower effective population size not only because of the reduction of the carrying capacity of an area but also because of changes in mating systems. Habitat deterioration in combination with habitat loss, and the increase of fragmentation, will increase the effects of inbreeding and genetic drift by reducing population size and decreasing gene flow (e.g., Gibbs, 2001). Moreover, persistent natural selection as imposed by ongoing climate changes is accompanied by a reduction of population fitness, because adaptive evolution will lag behind rapid environmental changes, and the optimal phenotype cannot evolve in time (Lynch and Lande, 1993; Gomulkiewicz and Holt, 1995; Nunney, 2003). The increase of the frequency of rare climatic events will exert strong viability selection that may drastically reduce population sizes (to the point of extinction). As a consequence, the likelihood for the loss of genetic variation by genetic drift and inbreeding will increase. The potential for adaptive response to climate change may be further reduced by anthropogenic changes of quality, size and distribution of suitable habitats. Many bird populations have already suffered declines as a consequence of habitat deterioration and destruction (Bauer and Berthold, 1997). Population declines and habitat fragmentation are consequences of this process that will reduce the genetic variability within populations and thereby their evolvability and fitness (Booy *et al*., 2000; Gaggiotti, 2003; Reed and Frankham, 2003). Generally, we predict that populations in disturbed and fragmented habitats are less likely to survive environmental changes as both their potential for adapting to new conditions *in situ* and the potential for evading these conditions by dispersal to areas with more favourable environmental conditions, i.e., range shifts, are restricted (Simberloff, 1995; Travis, 2003). Moreover, competition with invasive species may further accelerate population declines, especially in endemic species and ecological specialists (Benning *et al*., 2002; McLaughlin *et al*., 2002). It is controversial whether peripheral and isolated population will be able to endure new climatic conditions because they are adapted to resist extreme climatic conditions and environmental perturbation (Safriel *et al*., 1994; Reed *et al*., 2003), or if, alternatively, they will be the first to go extinct because of increased levels of stress and reduced levels of genetic variation (e.g., Parsons, 1990; Hoffmann and Parsons, 1997; Hoffmann *et al*., 2003). Probably one crucial determinant of the evolutionary potential of peripheral populations is the time they had for evolving genetic adaptations to transition areas and sub-optimal habitats, and whether they could maintain a sufficiently large effective population size over evolutionary time (Lesica and Allendorf, 1995).

VI. ADAPTIVE CHANGES IN LAYING DATE IN RESPONSE TO CLIMATE CHANGE

Probably, the best studied and supported effect of climate change on birds is the trend for earlier egg laying (Winkel and Hudde, 1996, 1997; Crick *et al*., 1997; Brown *et al*., 1999; Crick and Sparks, 1999; Dunn and Winkler, 1999; Koike and Higuchi, 2002; Sergio, 2003; Visser *et al*., 2003). This trait is known to have a significant heritability in many populations (see Boag and van Noordwijk, 1987), and to respond to selection (Flux and Flux, 1982). But laying date seems also to be a trait which is adjusted individually to local conditions, both by phenotypic plasticity and by individual learning (e.g., van Noordwijk and Müller, 1994; Juillard *et al*., 1997; Grieco *et al*., 2002).

All studies that have investigated the causes of changes in laying date have found that currently observed trends for earlier laying are best explained by individual adjustment to increasing temperatures (Przybylo *et al*., 2000; Both and Visser, 2001; Schiegg *et al*., 2002; Sergio, 2003; Sheldon *et al*., 2003). Convincing evidence for this conclusion has been provided by longitudinal population studies (Przybylo *et al*., 2000; Both and Visser, 2001). They show that the response of individual birds to among-year variation in temperature is not different from the populational response in laying date. As a consequence, no change in the genetic composition of the population needs to be inferred to explain the trend for earlier laying. The most detailed study to date on the evolution and causes of phenotypic change in response to climatic variation is the study by Sheldon *et al*. (2003) that investigated phenotypic and genetic changes in the timing of breeding and clutch size from 1988 to 1999 in the collared flycatcher population from Gotland (Sweden). Despite using large sample sizes and powerful statistical techniques, no evidence for evolutionary change towards earlier laying was found in this study. The previous finding that among-year correlation between NAO and laying date is caused by phenotypic plasticity (Przybylo *et al*., 2000) was confirmed.

These results on adaptive changes in the timing of breeding in birds are very consistent among studies and seem to indicate that there are general principles in the mode of adaptation of temperate-zone birds to climate change. We currently do not know whether this high phenotypic flexibility in the timing of breeding is also found in birds breeding in habitats with less among-year variation of weather conditions (e.g., in the tropics). Moreover, there seem to be limits to the adjustment of the timing of breeding to climatic conditions, as has recently been shown in a migratory bird species (Both and Visser, 2001). Constraints on the adjustment of laying date may be determined by the flexibility of the phase relationship between timing of spring migration, breeding and post-juvenile and post-nuptial moult (Coppack and Pulido, 2004, this volume; Pulido and Coppack, 2004).

VII. MICROEVOLUTIONARY RESPONSE OF MIGRATORY BEHAVIOUR

A. The Adaptability of Migratory Behaviour: The Role of Genetic Variances and Covariances

In the last two decades, a number of studies have demonstrated the presence of moderate to high amounts of additive genetic variation in migratory traits in the laboratory and in the wild. Mean heritabilities for migratory traits obtained under laboratory conditions are in accordance with estimates obtained in the wild ($h^2 = 0.40$ and 0.45, respectively), and also there is currently no indication that phenotypic variation is lower under controlled laboratory conditions (see review by Pulido and Berthold, 2003). Therefore, experimental studies may help us to predict evolutionary responses of migratory behaviour to natural selection in the wild.

Most studies on the control and the evolution of migration have been conducted in the blackcap (*Sylvia atricapilla*), the model species for nocturnal passerine migrants. In a series of common-garden, crossbreeding and selection experiments it has been shown that this species has an extraordinarily high adaptability, and a high potential for evolutionary change (Berthold, 1998b; Pulido, 2000). In an artificial selection experiment, for instance, the onset of autumn migratory activity was delayed by almost 2 weeks after two generations of directional artificial selection (see Figure 2; Pulido *et al*., 2001a). Three to six generations of directional selection on migratoriness transformed a partially migratory blackcap population into a sedentary or completely migratory population (Berthold *et al*., 1990). These strong selection responses were in accord with responses predicted from the amount of genetic variation found in these populations (Figure 3; Pulido *et al*., 1996, 2001a). Recent selection experiments have further demonstrated that other adaptive changes that are expected as a response to climatic warming, like the decrease in migration distance and the evolution of sedentariness in migrants can very rapidly be achieved in a few generations (F. Pulido and P. Berthold, unpubl.; see Pulido and Berthold, 2003).

As migratory traits are part of a syndrome, i.e., a suite of co-adapted traits, we expect genetic correlations to be major determinants of evolutionary trajectories and of the rate of adaptive evolution (Dingle, 1996). Presently, genetic correlations have only been estimated for migratory behaviour in the blackcap (Pulido *et al*., 1996; Pulido and Berthold, 1998; Pulido, 2000), but similar phenotypic correlations among migratory traits in other species suggest that these results may be of general validity (Pulido and Berthold, 2003). In the blackcap, moderate to high genetic correlations among migratory traits, i.e., incidence, intensity and timing of migratory activity, suggest that selection on

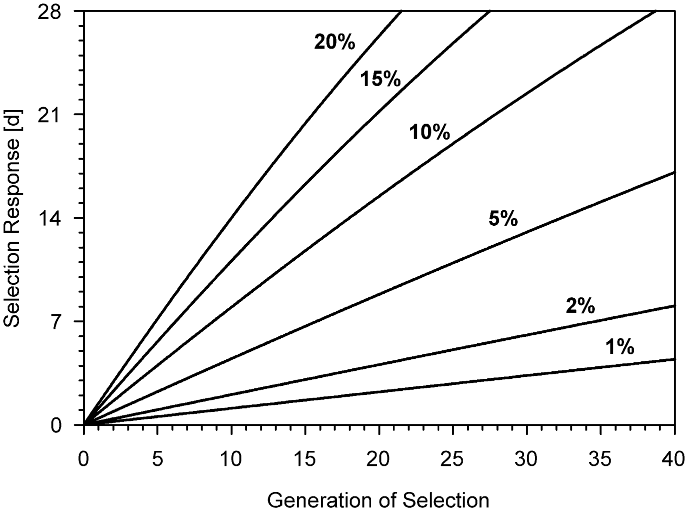

Figure 2 Expected response to directional selection for later onset of migratory activity in southern German blackcaps. Selection responses were estimated from mean phenotypic and genetic variation of this trait in this population (see Pulido *et al.*, 2001a,b). Lines give selection responses under different selection intensities. Percentages above lines give selection intensity as the proportion of individuals that were not allowed to reproduce (from Pulido and Berthold, 2003).

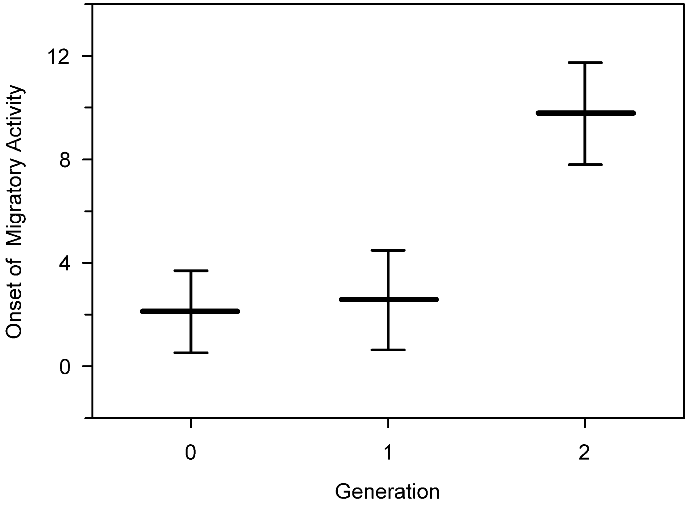

Figure 3 Observed response of the residual onset of migratory activity to two generations of artificial selection for later onset of migratory activity in southern German blackcaps (from Pulido *et al.*, 2001a). Bars give standard errors.

one migratory trait will strongly influence many other traits. Extant genetic correlations among migratory traits may facilitate rapid adaptation to changes in breeding and wintering latitude or altitude, and to phenological changes. The correspondence between the direction of selection vectors and genetic correlations is most probably the result of recurrent and persistent environmental changes in the evolutionary history of migratory bird populations (Pulido and Berthold, 1998). But not all correlations are in the expected direction of selection vectors. Recent studies on the relationship between hatching date, timing of migration and timing of moult suggest that genetic correlations may prevent or delay independent adaptive evolution of timing of breeding, juvenile moult and migration (Coppack *et al.*, 2001; Pulido and Coppack, 2004; Coppack and Pulido, 2004, this volume). We currently do not know whether this will impose serious constraints on the adaptability of birds to global warming. Although genetic correlations have been shown to strongly determine evolutionary trajectories during a relatively long period of time (see Björklund, 1996; Schluter, 1996, 2000), recent experimental studies suggest that rapid response to multivariate selection may be possible despite antagonistic genetic correlations (Beldade *et al.*, 2002). Intraspecific variation in variance–covariance matrices (i.e., **G**-matrices) in birds (e.g., Badyaev and Hill, 2000; Roff *et al.*, 2004) may be an indication that genetic correlations may be adaptively modified in a short time (see discussion on the evolution of reaction norms in Coppack and Pulido, 2004, this volume).

B. Constraints on Adaptive Evolution of Migration

At present, there are only two studies that identified potential constraints on adaptive evolution of migratory behaviour due to the lack of additive genetic variation on migratory traits. In a field study on Spanish pied flycatchers *F. hypoleuca*, no evidence for genetic variation in the timing of spring arrival was found (Potti, 1998). In a common-garden experiment on European blackbirds *Turdus merula*, a corresponding result was obtained for the amount of migratory activity, which is equivalent to migration distance in the wild (Partecke, 2002). We do not know why in these particular studies no significant heritabilities of migratory traits were found. One possible explanation is that the traits under scrutiny were difficult to measure and that measurement error may have inflated phenotypic variation (Pulido and Berthold, 2003). Alternatively, low heritabilities could result from increased sensitivity to environmental variation or strong genotype–environment interaction (e.g., Stirling *et al.*, 2002), and this may be adaptive. This has been discussed for the termination of migration in the blackcap and other species (Pulido, 2000). Other explanations, like the erosion of genetic variation by natural selection or bottlenecks, need to be further explored.

Migratory birds, and long-distance migrants in particular, may have problems to adapt because of their complex life cycles and their vulnerability to changes in different areas (Coppack and Both, 2002). In fact, there are a number of examples of migratory species that have undergone population crashes as a consequence of rare climatic events on the wintering area, e.g., droughts (e.g., Cavé, 1983; Jones, 1987; Peach *et al.*, 1991; Szép, 1995), and in the breeding area, e.g., due to cold spells in spring or autumn (e.g., Brown and Brown, 1998, 1999, 2000). Milder conditions on the breeding grounds in winter might aggravate the situation for migratory birds, as survival of resident bird species and short distance migrants is likely to increase under these conditions (Forsman and Mönkkönen, 2003; Lemoine and Böhning-Gaese, 2003). This will lead to increased competition within and among species. As a consequence of the competition of long-distance migrants with an increasing number of birds that do not migrate, or that winter close to the breeding grounds, long-distance migrants are expected and have been shown to decrease in numbers (Berthold, 1991; Berthold *et al.*, 1998; Lemoine and Böhning-Gaese, 2003). Moreover, long-distance migrants may take longer to adapt to changing conditions on the breeding grounds than short-distance migrants because they are less phenotypically flexible and/or may not be exposed to the "climatic information", like the NAO, that is correlated with conditions on the breeding grounds (Butler, 2003; Hüppop and Hüppop, 2003). Moreover, differential changes in phenology *en route* may constrain adaptation to the advancement of spring on the breeding grounds, i.e., birds may be unable to arrive earlier on the breeding grounds because conditions at stopover sites do not allow earlier migration (Strodde, 2003).

C. The Study of Adaptive Change in Migratory Birds

A number of recent changes in migratory behaviour have been attributed to climate change. Increasing number of residents, decreasing migration distances, later departure from and earlier return to the breeding grounds, and the change of migratory direction as a consequence of the establishment of new wintering areas have been the trends reported for numerous bird species (reviewed by Berthold, 1998a, 2001; Fiedler, 2003). These changes in migratory behaviour in response to global warming are characterised by a general trend for reduced migratoriness which may be a consequence of increasing survival probabilities at or near the breeding grounds outside the reproductive seasons (Berthold,1998a; Pulido and Berthold, 1998; Coppack and Both, 2002).

There have basically been three approaches used to detect and study these trends: population monitoring (trapping, banding, song recording), population studies with individually marked birds and experimental studies including common-garden and selective breeding experiments (see Fiedler and Pulido, 2004). Monitoring studies have provided the largest body of evidence for phenotypic changes in migratory behaviour, but only few have been able to investigate the causes of these changes (Fiedler, 2003; Møller and Merilä, 2004, this volume). Long-term population studies are the only means by which fitness differences among different migration strategies can be assessed. Moreover, population studies have helped to assess the amount of additive genetic variation and covariation present in the wild (e.g., Potti, 1998; Møller, 2001; reviewed by Pulido and Berthold, 2003). However, in contrast to avian morphology and breeding biology (see above), migratory behaviour has rarely been the focus of investigation in long-term population studies. The main reasons are that most model species in long-term population studies are non-migratory (e.g., tits), and that reliable measurements of migratory traits are difficult to obtain. Moreover, such studies require high recovery probabilities both on the breeding, and—for studies on migration distance and direction—on the wintering grounds, which are not given in small bird species (Fiedler and Pulido, 2004).

D. Phenotypic Changes in Migratory Behaviour and Their Potential Causes

Apart from changes in laying date, shifts in the timing of migration, spring arrival in particular, are probably the most frequently reported and best investigated responses of avian migratory behaviour to recent climatic change (e.g., Gatter, 1992; Mason, 1995; Sparks, 1999; Forchhammer *et al.*, 2002; Tryjanowski *et al.*, 2002; Butler, 2003; Cotton, 2003; Hüppop and Hüppop, 2003; Jenni and Kéry, 2003; Lehikoinen *et al.*, 2004, this volume). Although these monitoring studies have revealed patterns of change, hitherto, only one study has discussed the potential mechanism underlying these changes. In their analyses of long-term trapping data from the island of Heligoland, Hüppop and Hüppop (2003) found a trend for earlier spring migration in 23 of 24 species. Among-year-variation in spring passage was best explained by the NAO in the preceding winter in long-distance migrants, and local temperatures during migration in short-distance migrants. This finding prompted them to conclude that variation in the timing of spring arrival is a consequence of phenotypic flexibility rather than microevolutionary change. Moreover, they hypothesised that this flexible response is an adaptation to large among-year variation in winter and spring temperatures. Correlations of the timing of spring arrival with the NAO (Forchhammer *et al.*, 2002; Sokolov and Kosarev, 2003), with temperatures on migration (Huin and Sparks, 1998, 2000; Sokolov *et al.*, 1998), on the breeding sites (Sparks and Braslavská, 2002; Tryjanowski *et al.*, 2002), and with temperatures and precipitation in Africa (Cotton, 2003; Sokolov and Kosarev, 2003) have been reported for a number of species, including long-distance migrants. Butler (2003), Forchhammer *et al.* (2002) and

Tryjanowski *et al.* (2002) found that the immediate influence of climate on the timing of spring migration in long-distance migrants is smaller than in short-distance migrants. Migration in this group of birds has been previously considered to be predominately determined by endogenous spatio-temporal programmes that are insensitive to environmental perturbation (Berthold, 1996).

But to what extent does the correlation between migration phenology and temperatures (or climatic indices) provide evidence for assuming that changes have solely occurred as a consequence of adaptive phenotypic plasticity? We think that such a conclusion is only justified if alternative models that include climate variables at the presumed time of selection, e.g., spring temperatures in the preceding year or temperatures on the wintering site, are tested for best fit and can be excluded (e.g., Forchhammer *et al.*, 2002). It is, for instance, conceivable that due to the correlation between climatic conditions on the breeding grounds in spring and in the non-breeding area in winter, climate-induced selection in winter causes an apparent correlation between spring temperatures in the breeding areas (and on migration) and spring arrival (Møller and Merilä, 2004, this volume). For conclusively demonstrating that populational variation in migration phenology, or in any other trait, is a consequence of phenotypic plasticity alone, longitudinal data, i.e., data from individually marked birds measured in more than one year, are required (see Przybylo *et al.*, 2000; Møller, 2002; Sheldon *et al.*, 2003; Saino *et al.*, 2004). By comparing individual response with the population response to changes in temperature it can be assessed whether phenotypic change in the population can be explained by the mean reaction norm in the population. However, it is likely that phenotypic adaptation to climatic change often involves both phenotypic response at the individual level and genetic changes at the population level (Pulido *et al.*, 2001b; Pulido, 2004; see Réale *et al.*, 2003 for an example in a mammal).

A different approach for studying the genetics of migration is monitoring the number of overwintering birds. Fluctuations in the numbers of birds observed in winter in different areas can provide circumstantial evidence for the genetic basis of migratory behaviour and residency. In an analysis of ringing recoveries of stonechats *Saxicola torquata* wintering in Belgium, Dhondt (1983) showed that fluctuations in the number of wintering birds was correlated with winter temperatures in the previous year indicating that "differential survival of overwintering and migratory individuals takes place and that individuals differ in their tendency to migrate". Although Dhondt could not test whether the consistency of individual behaviour was due to inheritance, cultural transmission, imprinting, or to other mechanisms, he concluded that in view of the rapidity of changes in the proportion of migrants a genetic basis of migratory behaviour was "plausible". Assortative mating according to migratory habits—which was found to be strong in this population — could explain the strong response to selection caused by severe winters. Further evidence for assortative mating according to migratory status has been recently provided in the blackcap using stable isotope signatures (S. Bearhop *et al.*, unpubl.). Strong selection in combination with assortative mating may indeed lead to fast rapid evolutionary change, although evidence from ringing studies can at best be circumstantial. However, this potential for fast evolutionary change should be considered when drawing inferences on the causes of phenotypic change only from the rate of phenotypic change. Without any other evidence, long-term phenotypic change cannot be attributed to changes through phenotypic plasticity, as has been done in some recent studies.

Another population study providing evidence for evolutionary changes in migratory behaviour was conducted by Adriaensen *et al.* (1993) on the great crested grebe *Podiceps cristatus*. Their analysis of ring recoveries revealed that the proportion of Dutch grebes wintering in the breeding area had increased from 22% for the period before 1970 to over 80% in the years after 1980. This increase of residents in the Netherlands was paralleled by an overall increase of the number of great crested grebes breeding in northwestern Europe, and a significant decrease in the number of birds wintering in Switzerland. Circumstantial evidence based on the time lag between numbers of overwintering birds in different areas and on migration distances of Dutch grebes hatched at different times of the year supported the hypothesis that this change in the proportion of resident bird was a consequence of evolutionary change. Other studies have tried to explain changes in migratory behaviour in terms of adaptive evolution of inherited traits (e.g., Able and Belthoff, 1998; Hill *et al.*, 1998). These studies, however, could not rigorously test the hypothesis of genetic change.

E. Microevolutionary Change in Migratory Behaviour

Currently, there are three studies that have investigated evolutionary change of migratory behaviour in response to climate change (see also Berthold *et al.*, 1992 for microevolutionary change caused by other selective agents).

Brown and Brown (2000) demonstrated that in a cliff swallow (*Petrochelidon pyrrhonota*) population in central North America a long period of cold weather in spring had caused strong viability selection on the timing of spring arrival. They found that first-capture dates (an indicator of spring arrival) in the years before selection had been significantly later in survivors than in non-survivors, and that in the generation hatched after selection the frequency of birds arriving early in the season had significantly decreased. Brown and Brown (2000) hypothesised that this mortality in years with longer periods of cold weather in spring could mitigate the effects of selection in “normal” years in which birds arriving early in spring have the highest breeding success and produce the offspring with the highest survival. Because of these rare but regularly recurring years with high spring mortality, however, arrival date in this cliff swallow population does not change in the long run. Although, it could not be tested whether this population actually possesses significant amounts of additive genetic variation for this trait, all evidence provided (e.g., significant repeatability) favours this assertion.

This study currently provides the strongest case for microevolutionary change of migratory behaviour in response to an extreme climatic event (Pulido, 2004). Furthermore, this study shows how oscillating selection may slow-down or prevent long-term evolutionary changes (see also Grant and Grant, 2002). In view of the expected increase of climate extremes like droughts and floods (e.g., Easterling *et al*., 2000a), and a possible reduction of frosts in spring (Scheifinger *et al*., 2003), this finding may be particularly important for interpreting and predicting long-term microevolutionary changes in phenology.

In another long-term study on a Danish barn swallow population, Møller (2004; Møller and Merilä, 2004, this volume) found a significant trend for earlier spring arrival in the period from 1971 to 2002. This trend was predominantly due to a marked advancement of spring arrival since 1985, and was paralleled by a decrease of estimated breeding values for arrival dates over time, suggesting that phenotypic change was, at least, partly caused by genetic changes in the population. Møller hypothesised that mean arrival data is early when environmental conditions in Northern Africa during migration are unfavourable, because birds migrating late, which presumably are in bad condition, do not arrive on the breeding grounds. In years when conditions at northern African stopover sites are favourable, more birds may survive migration (Møller and Szép, 2002). Thus, a larger number of birds with late arrival should be found in the population.

Although this study could potentially be the first in demonstrating evolutionary change in migratory behaviour in response to climatic change, it is not without problems. The reliability of estimated breeding values depends very much on the influential environmental variables being considered, and the depth and the complexity of the pedigree used. If only little pedigree information is available, estimated breeding values will not differ from phenotypic values (E. Postma, pers. comm.). Because in Møller's analysis only arrival dates of fathers and sons were used, the changes in estimated breeding values may not reflect genetic but rather phenotypic change. Moreover, in northern Italian barn swallows, among-year variation in arrival date was caused by individual phenotypic adjustment of adult birds to environmental conditions in the wintering area (Saino *et al*., 2004), as is the case for some of the variation in arrival date in Denmark (A.P. Møller, unpubl.). If different populations of the same species have similar mechanisms of adaptation, it is likely that the trend for earlier spring arrival in Danish barn swallows may partly represent adaptation by phenotypic plasticity rather than microevolutionary change.

In contrast to these field studies, we used a common garden experiment to study changes in autumn migration in the blackcap (F. Pulido and P. Berthold, in prep.). From 1988 through 2001, each year (but one) we collected nestlings randomly from a southern German population and transferred them to the laboratory. There, we hand-raised them and kept them under standardised conditions. In autumn, we registered migratory activity of each individual using an identical protocol throughout the study period (see Pulido *et al*., 2001a; Pulido and Coppack, 2004). Some of these birds were used for breeding experiments, which made it possible to exclude maternal effects and served as a control. By using this experimental protocol, we could show that in the course of 13 years, the amount of migratory activity has dramatically decreased by about one standard deviation. This change in the amount of migratory activity has been primarily caused by a strong reduction of the intensity of migration, i.e., the activity per night, and to a lesser extent as a consequence of a delay of the onset of autumn migration. Changes in the termination of migration were not significant, as was expected from the low heritability of this trait. Variation in migration distance assessed by ringing data is very large and the number of recoveries too low to be able to show this trend in the reduction of migration distance. However, in the last decade, an increasing number of anecdotal observations of blackcaps wintering in central and northern Europe has been reported (e.g., Andres and Bersuder, 1992; Fransson and Stolt, 1994), which may reflect a reduction of migratoriness in these areas. We think that the genetic changes in migratory behaviour found in southern German blackcaps are very likely to result from adaptive response to selection imposed by recent climate change and not from massive gene flow, as neither ringing recoveries nor biometrical data obtained from trapping programmes show a tendency for an influx of individuals from other populations. Moreover, the changes observed are in accord with the changes predicted under a global-warming scenario (see above, and Pulido and Berthold, 1998). Unfortunately, we currently have no field data on survival and reproduction that would allow us to test whether the observed changes are actually in accord with predictions from selection intensities and heritabilities.

Using different approaches, the three studies described suggest that migratory behaviour may readily respond to selection imposed by climatic change. They support previous findings reporting high potential for adaptive change of migratory behaviour in birds (reviewed by Berthold, 1998b; Pulido and Berthold, 2003; Pulido, 2004). The study by Møller (2004, unpubl.) is an example of how ecological, demographic and pedigree data could be used to study the causes of phenotypic change in the timing of spring arrival. The experimental studies in the blackcap highlight the role of genetic variation and covariation for reconstructing selection events. Studies combining both approaches, using long and complex pedigrees (as available for many hole-nesting birds), and extending the set of characters under scrutiny to other life-cycle stages (see Coppack and Pulido, 2004, this volume) are urgently needed to understand the adaptation and evolution of life cycles. This will probably only be possible by incorporating new methods (e.g., stable isotopes, genetic markers, satellite tracking; cf. Fiedler and Pulido, 2004) into the research agenda, and by combining the efforts of several research groups to study one or a few model system(s).

VIII. CONCLUSIONS AND OUTLOOK

Birds may very rapidly respond to changing environmental conditions imposed by global climatic change. Although fossil records in other taxa suggest that the most likely response to climatic change is range shift rather than adaptive evolution (e.g., Cronin and Schneider, 1990; Parmesan *et al*., 2000), the validity of this inference for the current evolutionary response is questionable (Travis and Futuyma, 1993). Adaptability to temperature changes is likely to have evolved by correlational selection, as a result of environmental fluctuation during the evolutionary history of many bird populations (Burton, 1995). High levels of genetic variation, favourable genetic correlations, cogradient variation and adaptive plasticity may allow rapid responses to current environmental changes (Pulido, 2000, 2004; Pulido and Berthold, 2003; Coppack *et al*., 2003). Moreover, unidirectional gene flow from populations or species better adapted to warmer environmental conditions may further accelerate adaptive evolution. If climate change persists and is accompanied by an increase of climatic variability—as currently predicted (Houghton *et al*., 2001)—the rate of evolutionary change may be much lower than found in studies on single selection events, because of oscillating selection and the erosion of genetic variation. In addition, environmental variation may not be buffered by phenotypic plasticity, or may become maladaptive (Schlaepfer *et al*., 2002; Coppack and Pulido, 2004, this volume), which may further accelerate the erosion of genetic variation. Unfavourable genetic correlations are likely to constrain the rate of adaptive evolution (Etterson and Shaw, 2001), but adaptive changes in the variance–covariance matrix could evolve if the direction of selection remains constant over a longer period of time (Endler, 1995). Alternatively, genetic covariances may not change, probably because they are caused by pleiotropic gene effects. Then, unfavourable genetic covariation could determine evolutionary trajectories over a long period of time (Schluter, 1996, 2000).

A complete understanding of adaptive evolution will only be achieved if ecological and genetic studies are integrated, and the influences of the environment, different fitness components, phenotypic plasticity, genetic covariation and gene flow can be evaluated at the same time. Recent studies have followed such an integrative approach, and have revealed that adaptive evolution is determined by a variety of factors and their complex interactions (see, for instance, Sheldon *et al*., 2003). Data from other long-term population studies should be used to reconstruct adaptive changes in the same way, and to unravel among-population differences in evolutionary response (e.g., using the data on blue and great tits analysed by Visser *et al.*, 2003). Such an approach will help us to reveal general patterns of adaptation, and to study changes in the adaptability of particular traits and populations in response to changes in the environment.

ACKNOWLEDGEMENTS

We thank Timothy Coppack, Anders Møller, and two anonymous reviewers for critically reading the manuscript.

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