

S19-4 Adaptation and adaptability of migratory behavior

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Abstract Environmental conditions under which extant migration patterns have evolved are diverse and have been changing repeatedly. As a consequence, avian migration is expected to be highly adaptable. Adaptation of migratory behavior in response to changing environments may be accomplished by different mechanisms and at different levels. Adaptive phenotypic plasticity facilitates immediate, fine-tuned response to environmental change at the individual level. At the population level, genetic change in response to natural selection is the mechanism underlying adaptive evolution. Traditionally, these mechanisms have been regarded as mutually exclusive. Current views of evolution, however, consider the plastic response to the environment as a major target of selection. Recent studies have shown that adaptation of migratory behavior may involve both individual adjustment and changes in the genetic composition of populations. Moderate to high levels of genetic variation in migratory traits will facilitate rapid evolutionary change. Extant genetic correlations will accelerate adaptive evolution along an axis of increasing or decreasing migratoriness. However, antagonistic genetic correlations between migratory behavior and other life-history traits may slow down adaptive evolution. Phenotypic plasticity in response to changes in day-length are an important factor in the adaptation of migration to new environments. The response to selection for shorter migration distance, for instance, will be reinforced by phenotypic responses to the photoperiod in the novel wintering area. Photoperiodic responses, however, may become maladaptive if environmental conditions change very rapidly, and birds become desynchronized with food availability.

Key words Genetic correlation, Genetic variation, Phenotypic plasticity, Selection

1 Introduction

Bird migration has evolved as a consequence of seasonal availability of food (Dingle, 1996; Rappole, this symposium). Differences in migration patterns among populations reflect differences in the environments encountered by these populations. Thus it is generally assumed that current migration patterns are adaptations to extant environmental conditions, such as food availability. But environments have forever been changing, and, therefore, migratory behavior has had to readjust repeatedly to new conditions. As a consequence, migratory birds are expected to have evolved specific mechanisms to cope with environmental fluctuations at different spatial and temporal scales (cf. Meyers and Bull, 2002).

Basically, there are two levels at which adaptations can take place: in individuals and in populations. Adaptations in populations, i.e. adaptations in the strict sense, are genetic changes sifted by natural selection. Adaptations at the level of the individual are plastic responses to the environment that do not involve genetic changes. Environmentally-induced changes at the level of the individual, however, are often adaptive and have a genetic basis. If, in a population, there is genetic variation in individual response, this adaptive phenotypic plasticity will become subjected to adaptive evolution, i.e. genetic changes at the population level. Thus phenotypic plasticity may evolve, just as

any other trait, and may be one of the prime targets in adaptive evolution (cf. Pigliucci, 2001). The mechanisms by which adaptive changes in migratory traits are achieved, and their consequences for the evolution of migratory behavior, are the subject of this contribution.

2 Adaptive evolutionary change

Adaptive evolution is the result of natural selection. Natural selection is a process that will work if there is phenotypic variation in a population, if this variation is correlated with fitness differences, and if it is heritable (Endler, 1986). Natural selection in the wild has been demonstrated repeatedly (Kingsolver et al., 2001), but there are a number of factors that may prevent evolutionary change or its detection, such as inherent plasticity, fluctuating selection, genetic correlation (cf., Merilä et al., 2001). Numerous approaches can potentially be used to detect natural selection (Reznick and Travis, 1996). It may, however, be difficult to test for all prerequisites and to obtain reliable models of micro-evolutionary change. In principle, this requires long-term, comprehensive population studies that investigate the ecology and evolution of a population (e.g., Grant and Grant, 2002). Although long-term population studies in birds have probably yielded the best cases for natural selection in the wild, migratory behavior — the incidence, timing, distance and direction of migration — has rarely been the

focus of investigation, partly because it is difficult and labor-intensive to reliably measure migratory traits in individual birds in the wild (cf., Brown and Brown, 2000).

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 both the laboratory and the wild (Pulido and Berthold, 2003). Genetic variation is one prerequisite for rapid evolutionary change. In the blackcap (*Sylvia atricapilla*), for example, the onset of autumn migratory activity was delayed by almost two weeks after two generations of directional artificial selection (Pulido et al., 2001a). Three to six generations of directional selection on migratoriness transformed a partially migratory blackcap population into becoming wholly sedentary or completely migratory (Berthold et al., 1990). These high selection responses are in accord with responses predicted from the amount of genetic variation found in these populations (Pulido et al., 1996; Pulido et al., 2001a).

There are to date only two studies that identify potential genetic constraints on adaptive evolution of migratory behavior. In a field study on Spanish pied flycatchers (*Ficedula 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 migratory activity, which is equivalent to migration distance in the wild (Partecke, 2002). It is unclear why no significant heritabilities of migratory traits were found by these studies. One possible explanation is that the traits under scrutiny were difficult to measure and that measurement error may have inflated phenotypic variation (cf. Pulido and Berthold, 2003). Alternatively, low heritabilities could result from increased sensitivity to environmental variation, and could be adaptive. This has been discussed for the termination of migration in the blackcap and other species (Pulido, 2000). Other possible explanations, such as the erosion of genetic variation by natural selection or bottlenecks, need to be explored.

As migratory traits are part of a syndrome, i.e. a suite of coadapted 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 behavior in the blackcap (Pulido et al., 1996; Pulido and Berthold, 1998; Pulido, 2000), but corresponding phenotypic correlations among migratory traits in other species suggest that these results may apply generally (Pulido and Berthold, 2003). In view of moderate to high genetic correlations among migratory traits in the blackcap, we expect that the response to selection for any migratory trait will be influenced strongly by selection on other traits. Extant genetic correlations may facilitate rapid adaptation to changes in latitude (e.g., as a result of range expansion) or to climatic changes involving shifts in global temperature. 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).

3 Natural selection in the wild

At present, there are only two studies that have investigated adaptive micro-evolution of avian migratory behavior in detail (also Fiedler and Pulido, this symposium). These studies, which are exceptional in elucidating the bases of adaptive change (fitness differences and genetic change), are reviewed here.

3.1 Selection for later spring arrival in the cliff swallow (*Petrochelidon pyrrhonota*)

In a large cliff swallow population in central North America, an exceptionally long cold period caused a high mortality in the spring of 1996. In following years, cliff swallows arrived at their colonies significantly later, as the birds that had survived this cold spell were among the latest that had arrived that year (Brown and Brown, 2000). Thus, there is strong evidence for directional viability selection for later arrival time caused by a cold spell in spring. Brown and Brown (2000) hypothesized that such mortality in years with longer periods of cold weather in spring could mitigate the effects of selection on “normal” years. Birds arriving early in spring usually have the highest breeding success and produce offspring with the highest rate of survival. However, because of these rare yet regularly recurring years with high spring mortality, the arrival date in the cliff swallow population did not change over time. This example shows how fluctuating selection causes evolutionary stasis, without incurring balancing selection.

3.2 Evolution of a novel overwintering area in the blackcap (*Sylvia atricapilla*)

In the early 1960s, a blackcap ringed in Austria and recovered in Ireland puzzled ornithologists, because blackcaps were not known to winter on the British Isles. The traditional wintering areas for central European blackcaps are in the western Mediterranean region and in East Africa. Over subsequent decades, the numbers of blackcaps wintering in Britain, Ireland or northern France increased considerably (cf., Berthold and Terrill, 1988). Several proximate explanations for the increase in blackcaps wintering in these areas were proposed: (1) central European blackcaps could have genetically changed their migration route, (2) birds breeding in Scandinavia — which regularly migrate through Britain — could have started to winter closer to their breeding grounds, and (3) British breeding birds could have become resident. To test these alternatives, Berthold and his colleagues caught blackcaps wintering in Britain, took them to Radolfzell (Germany) and measured their preferred migratory direction in a controlled environment (Berthold et al., 1992).

Their direction of NNW differed significantly from that in south German birds. Subsequently, the English test birds were bred in aviaries; and their offspring too showed

the same mean migratory direction as their parents. Thus, blackcaps breeding in Britain are descendants of birds breeding in central Europe with “genes” for migrating in a new direction. This micro-evolutionary change in wintering area was probably driven by improved survival of blackcaps on the British Isles in winter and higher reproductive success as a consequence of earlier breeding (Berthold and Terrill, 1988).

Evolutionary change in this population not only involved migration direction but also migratory distance and timing. Migration distance for “British winter visitors” is shorter by about one third than for birds migrating to traditional wintering areas around the southwestern Mediterranean. Furthermore, birds wintering in Britain arrive significantly earlier back on the breeding grounds. Although the presence of large amounts of additive genetic variation in migration timing and distance (Berthold and Pulido, 1994; Pulido et al., 2001a) would have allowed this rapid change, phenotypic plasticity responding to photoperiodic conditions in the novel wintering area could alone have advanced spring arrival by more than two weeks (Terrill and Berthold, 1990), shortening migration distance in the process. Thus, it is likely that phenotypic plasticity reinforced selection for this novel wintering area and accelerated the evolutionary changes involved (see below).

4 Adaptive phenotypic plasticity

“Phenotypic plasticity is the property of a given genotype to produce different phenotypes in response to distinct environmental conditions” (Pigliucci, 2001). In principle, phenotypic plasticity may accelerate or slow down adaptive responses. Populations with high levels of adaptive phenotypic plasticity may show fast, immediate responses to environmental change. Such changes, however, will mainly reflect plastic modification of individual phenotypes and not involve genetic change. Yet, evolutionary change is to be expected once directional selection shifts the optimal phenotype beyond the range of environmentally-inducible phenotypes. Although plasticity may enable organisms to survive and reproduce under a wide range of environmental conditions, it is not universal because of the limits and costs to it (cf., DeWitt et al., 1998). Whether adaptive plasticity rather than genetic differentiation is to be expected as the response to changing environmental conditions depends on the spatial and temporal scales at which the changes take place, as well as the frequency and predictability of the changes (cf. Pigliucci, 2001; Meyers and Bull, 2002).

The most important, and probably the best studied, environmental variable influencing migratory behavior is the photoperiod. In seasonal environments, day-length is used by most birds to synchronize the timing of annual life-cycle events with food availability (Gwinner, 1996). In the northern hemisphere, for example, birds experiencing long day-lengths in winter accelerate prenuptial molt, spring migration and breeding. Exposure to short days in summer

and autumn accelerates autumn processes: postnuptial and post-juvinal molt and autumn migration. It has been shown that the strength and direction of these responses have a genetic basis and that there is within- and among- population genetic variation to this response (cf., Widmer, 1999; Pulido, 2000; Pulido et al., 2001b; Helm, 2002; Partecke, 2002).

Inter-population differences in the timing of molt and migration may be largely a consequence of differences in population reaction norms (Helm and Gwinner, 1999; Widmer, 1999; Helm, 2002; Partecke, 2002). Generally, we expect these responses to be adaptive and to reflect inter-population variation in environmental conditions, as in the predictability of food availability (Widmer and Pulido, in prep.). If, however, conditions change rapidly and in directions not previously “experienced” in the evolutionary history of the population, reaction norms may become maladaptive (Schlaepfer et al., 2002), leading to desynchronization of life-cycle events with optimal food availability (Visser et al., 1998), and to an attenuation of selection responses (Coppack et al., 2001). Phenotypic plasticity may also facilitate adaptive evolution if the selection response and environmentally induced change is in the same direction (cogradient variation). The evolutionary response to selection for shorter migration distance, for instance, may be reinforced by the plastic response to the photoperiodic conditions in the new wintering area (Coppack et al., 2003).

In the process of adaptation to current climatic change, a number of rapid changes in avian life-cycle stages, and in migratory behavior in particular (Fiedler 2003), have been observed. Most of the changes in avian breeding have been attributed to phenotypic plasticity (Przybylo et al., 2000; Both and Visser, 2001; Sheldon et al., 2003). Avian migratory behavior may also respond plastically to climatic change. In two recent studies investigating the timing of spring migration, it was found that variation between years in arrival or passage in a number of species was attributable to variation in climatic conditions in the previous winter (Forchhammer et al., 2002; Hüppop and Hüppop, 2003). Although this correlation between phenotypic and environmental variation is indicative of phenotypic flexibility, phenotypic plasticity can only be identified in latitudinal studies (Przybylo et al., 2000). Moreover, if related individuals in a population can be studied, changes in breeding values can be used to estimate the relative contribution of phenotypic and genetic change to adaptive phenotypic change (Sheldon, 2003; Réale et al., 2003).

5 Conclusions

Adaptation to changing environmental conditions may be very complex, as changes can occur at different levels and time scales. Recent breeding experiments and quantitative genetic studies in the wild suggest that different components of migratory behavior may change rapidly in response to directional selection. Moreover, genetic correlations among migratory traits may accelerate the response to selection imposed by global warming. However, unfavourable

vorable genetic correlations between migratory traits and other life-history traits, such as molt, may constrain adaptive evolution. Thus, for predicting adaptive evolution in migration, we need to take into account not only the suite of traits constituting the migratory syndrome, but also those traits to which they are genetically and functionally linked. Moreover, the interaction between selection response and phenotypic plasticity, and the fact that individual birds may modify their migratory behavior by learning from previous experiences, may be important factors determining the direction and rate of evolutionary change. The question how genetic and non-genetic variation interact to facilitate adaptation, and if and why different populations have evolved different adaptive strategies, will be central to future research on the micro-evolution of migratory behavior.

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