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GENETIC BASIS, MODE OF INHERITANCE AND EVOLUTIONARY CHANGES OF MIGRATORY DIRECTIONS IN PALEARCTIC WARBLERS (AVES: SYLVIIDAE)

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Summary

The genetic basis, mode of inheritance and recent evolutionary changes of migratory directions in birds are discussed on the basis of published and new experimental evidence. Displacement experiments with wild-caught migrants and orientation tests with hand-reared passerines illustrate that inexperienced young birds possess genetic information about the direction and approximate distance of migration, but not about the geographic location of the winter quarters. Hand-raised blackcaps *Sylvia atricapilla* from east and west of the Central European migratory divide, when tested under identical conditions, exibited population-specific migratory directions in orientation cages. Cross-breeding of birds from these two populations demonstrated an intermediate mode of inheritance of this behavioural character. New data on the orientation of an F_2 generation suggest that the directional information is encoded by only a few major genes. Migratory adaptations may have evolved recently, in some cases rapidly, as is illustrated by the establishment of a new migration route of central European blackcaps to winter quarters in the British Isles. This new route is shown (in a captive breeding experiment) to be based on a novel, genetically programmed westnorthwesterly migratory direction. It must have spread from almost zero to 7–11 % frequency in parts of central Europe within only three decades. The novel direction is also inherited phenotypically intermediately; its rapid evolution may be mediated by assortative mating based on differential arrival times at the breeding grounds. The evolutionary flexibility of migratory adaptations is discussed in relation to changes in the environment, both natural and accelerated by man.

Key words: bird, migration, orientation, innate directions, inheritance, evolution.

Introduction

One of the fundamental questions of bird migration research is how young birds that initiate migration for the first time know where to fly. The question is especially relevant to species in which young birds migrate independently of experienced adults, i.e. the majority of nocturnally migrating passerines. From a conceptual point of view, we need to distinguish between a bird's 'knowledge' of a migratory direction and the compass mechanisms employed to locate that intended flight direction in space. Compass mechanisms have been studied in detail and, although it is not entirely clear how magnetic and celestial mechanisms interact during ontogeny, it is well established that under most environmental circumstances birds can determine compass directions reliably. This review will be concerned only with the genetic basis of directional information, the mode of inheritance of this character and the ways in which it might change during evolution.

What evidence is there for genetic information of migratory directions?

Two types of experiments have clearly demonstrated that birds possess innate information about their migratory direction.

Displacement experiments

In a classic field experiment, several thousand European starlings *Sturnus vulgaris* were displaced from autumn stop-over sites in Holland perpendicular to the expected migration route (Perdeck, 1958). The results have been comprehensively illustrated by Emlen (1975). Juvenile starlings, ringed and released singly after an 800 km aeroplane flight, continued to migrate from the release site in approximately the same direction as they had flown prior to displacement, i.e. westsouthwest. Adults, however, compensated for the displacement by migrating northwest towards the winter quarters in northern France and southern England, where they had spent at least one previous winter.

An earlier displacement experiment with white storks *Ciconia ciconia* (Schüz, 1951; reviewed by Helbig, 1993) had yielded similar results: nestlings of a southeast-migrating population (eastern Europe) were transferred to the breeding grounds of a southwest-migrating population (western Germany) and reared in captivity. Released after all the local storks had departed, these birds started to migrate towards the southeast, i.e. in the appropriate direction for their population of origin, but clearly on a different heading from that of the local breeding population.

Directional tendencies of hand-raised passerines in orientation cages

From the 1960s onwards, several studies of migratory orientation were conducted with passerine migrants hand-raised from a very early age (e.g. Emlen, 1969; Gwinner and Wiltschko, 1978). When tested in round orientation cages during the migration season, these birds on average hopped or fluttered in a direction that corresponded quite well to the migration direction known from recoveries of ringed birds of the respective species and population (Helbig, 1991*a*).

The conclusion that such spontaneous directional choices do indeed reflect genetically based migratory orientation was most clearly demonstrated by a comparison of two blackcap populations with very different autumn migratory directions (Helbig *et al.* 1989): nestlings from both populations were hand-reared and their orientation was later tested at the same site and under identical conditions. The directional choices of the test birds during the first half of the season differed by about 90° between the two groups, corresponding to the difference between the actual flight paths (known from ringing) of free-living individuals of these populations. Furthermore, birds from the eastern population showed a directional shift about midway through the migration season, whereas birds from the western population did not (Fig. 1). Both the sign (clockwise) and the amount of the shift (approximately 45°) were in agreement with findings derived from recoveries of ringed blackcaps: birds from the eastern population were found to fly around the eastern edge of the Mediterranean Sea and they must alter flight direction southwards to reach their winter quarters in eastern Africa. The western population, in contrast, is known to follow a fairly straight course to winter quarters in the western Mediterranean region.

From both types of experiments, one must conclude that young birds, even in social species such as storks and starlings which normally migrate in flocks, do possess genetic information about the direction in which to migrate. They inherit from their parents not only a general starting direction but also a fairly detailed time-direction programme allowing for programmed changes of direction to circumvent potential barriers. To terminate migration after approximately the right distance, young birds also need a measure of distance to be flown: this may be partly encoded as the duration of endogenously produced migratory activity per season, a quantity that has been measured extensively in cage experiments and correlates roughly with the migration distances observed in the field (Gwinner, 1968; Berthold, 1973).

Taking together all the available evidence on innate

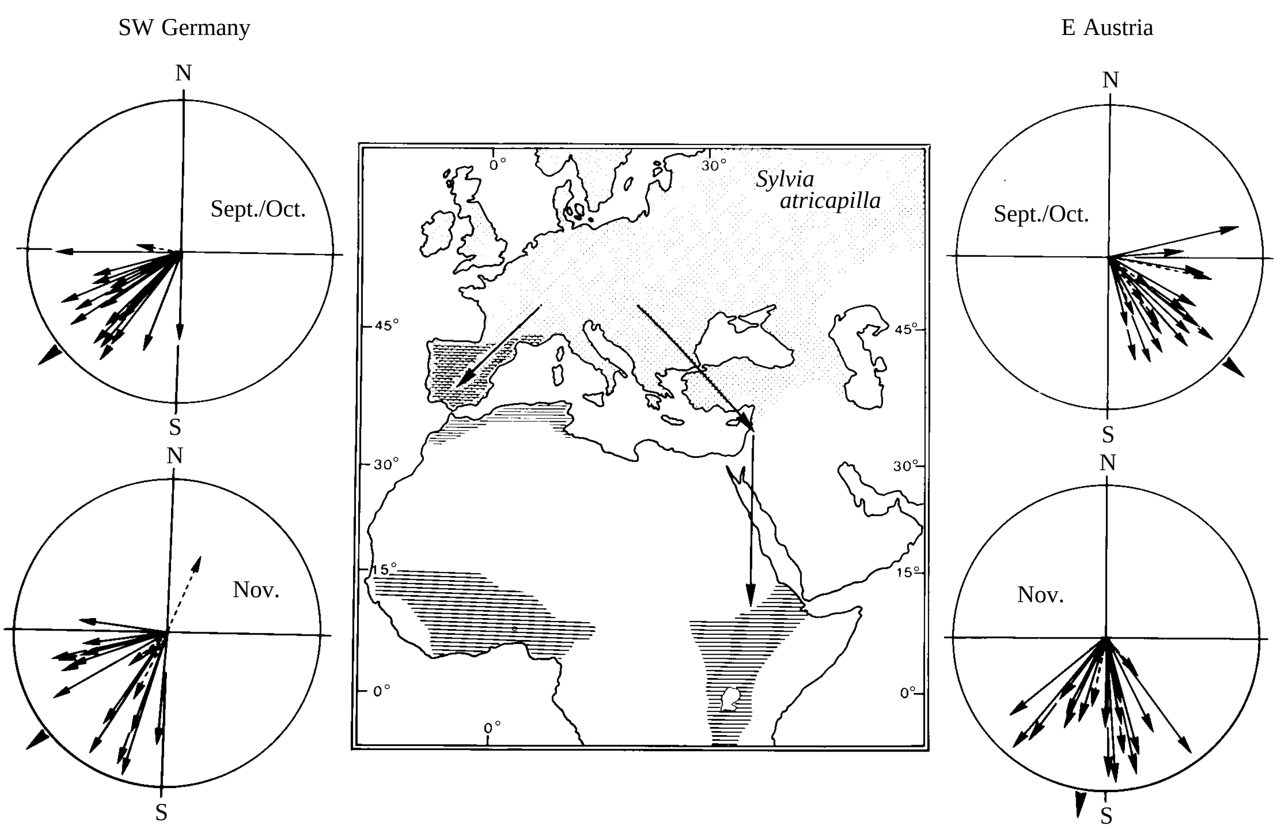

Fig. 1. Map of blackcap breeding (stippled) and wintering (hatched) areas with major migration routes shown by arrows (based on ringing recoveries). Circular diagrams show individual mean vectors of orientation of hand-raised birds from west (left) and east (right) of the central European migratory divide. Each vector is based on 8–15 active tests using a modified Emlen funnel technique (dashed arrows show non-significant vectors; Rayleigh test). The length of vectors is proportional to the directional concentration. Note that west African winter quarters are not used by central European populations (from Helbig, 1994).

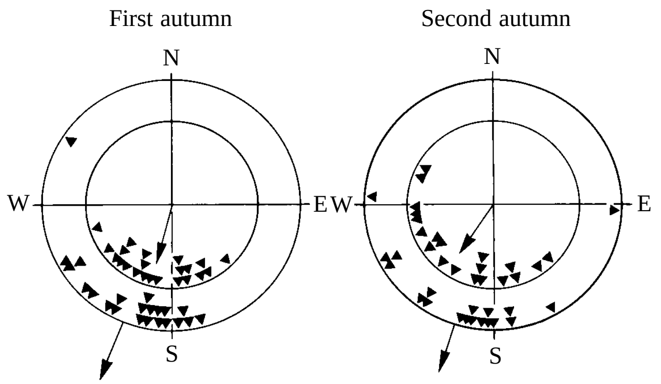

Fig. 2. Individual mean directions (based on 2–9 orientation tests each) of captive-bred blackcaps during the first and second autumn of their lives. Inner circle, October; outer circle, November. Arrows show group mean vectors. Data from both autumns are statistically indistinguishable (from Helbig, 1992*a*).

components of migration, it is appropriate to term this type of behaviour *vector orientation*: direction and distance are encoded genetically, but there is no evidence that young birds possess genetic information about the geographic location of their winter quarters. Only after having spent some time in an appropriate wintering area are young birds able to navigate towards this specific goal area from an unknown location. The cues on which such 'site imprinting' is based and the processes by which it is established are so far poorly understood.

If imprinting on a wintering site is prevented by keeping hand-raised blackcaps in captivity throughout their first and second calendar year, seasonally appropriate migratory orientation can still be demonstrated during the second autumn (Fig. 2; Helbig, 1992*a*). Thus, even in birds unable to gain any migratory experience, the endogenous directional information is not lost.

Inheritance of migratory directions

A divergence between populations migrating towards different directions is a fairly common phenomenon in many bird species breeding in the Palearctic and other parts of the world. Detailed analyses of ringing recoveries (e.g. Zink, 1973–1985) have revealed such 'migratory divides' to be fairly sharp, not only in white stork and blackcap, but also in white wagtail *Motacilla alba*, bluethroat *Luscinia svecica*, willow warbler *Phylloscopus trochilus* and many others. Selection pressures leading to such behavioural differentiation are determined by the costs of migration (in terms of distance and the need to cross topographical and ecological barriers) and the geographical distribution of appropriate wintering habitats (Lundberg and Alerstam, 1986). To European long-distance migrants, the Alps, the Mediterranean Sea and the Sahara Desert constitute significant topographical and ecological barriers, making it advantageous to deviate either towards the east or towards the west from the great circle route to the intended winter quarters.

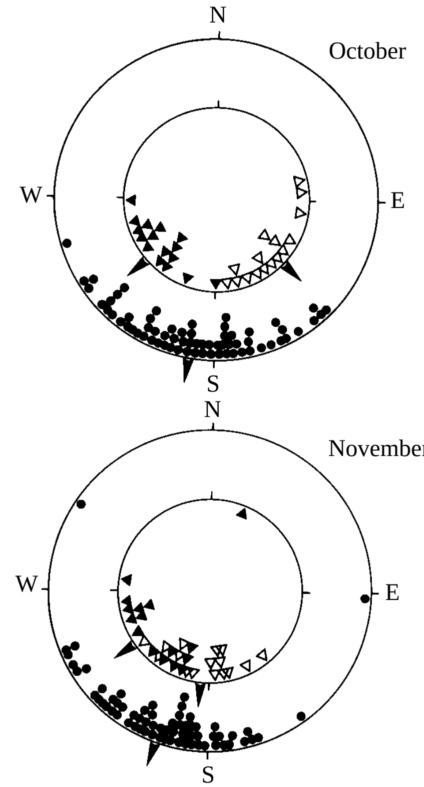

Fig. 3. Inheritance of blackcap migratory directions in a cross-breeding experiment. Symbols show individual mean directions based on 6–10 tests each. Triangles indicate parental populations from southwest Germany (filled) and eastern Austria (open); dots show F_1 offspring of mixed pairs bred in aviaries. Arrowheads indicate group mean directions. Note the seasonal shift of direction of southeast-migrating parents and the intermediate orientation of F_1 offspring (from Helbig, 1991*b*).

The blackcap is an appropriate model organism with which to study the inheritance of such differentiated migratory directions. Two groups of hand-raised blackcaps from east and west of the European migratory divide, whose orientation had already been tested in autumn (see Fig. 1), were cross-bred in outdoor aviaries during their second and third year of life (Helbig, 1991*b*). From 35 mixed pairs of southwest and southeast migrants, 68 F_1 offspring were raised, whose orientation was again tested during the autumn and compared with that of the two parental groups (Fig. 3). The F_1 generation oriented towards directions intermediate between those of the parental groups with no difference in the degree of scatter. Mean directions were significantly different among all three groups in October, and between F_1 birds and the southwest-migrating parents in November, when the eastern parents had shifted their orientation to southsouthwest.

These results not only demonstrated directly the genetic basis of migratory directions through modification by cross-breeding, but also revealed a phenotypically intermediate mode of inheritance of this behavioural character. Some idea about the approximate number of genes involved in determining migratory directions can be gained from studying the

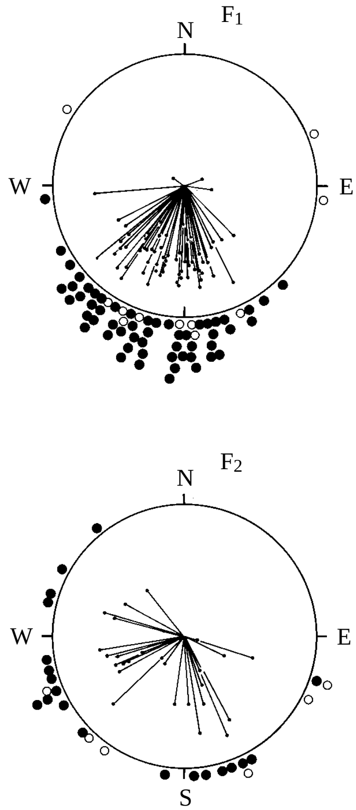

Fig. 4. Comparison of autumn migratory orientation of F_1 and F_2 generations of blackcaps cross-bred from southwest- and southeast-migrating populations (cf. Fig. 3). F_1 birds are the same as in Fig. 3, but mean vectors were here calculated for the entire season. Dots outside circles show directions of individual mean vectors (filled dots, $P<0.05$; open dots, $P>0.05$; Rayleigh test). The difference in scatter between the generations is significant ($P<0.001$ for deviations from group mean; Mann–Whitney *U*-test).

expression of this trait in the F_2 generation. In collaboration with P. Berthold and his coworkers at the Vogelwarte Radolfzell, we managed to breed in captivity 26 F_2 offspring from seven pairs of F_1 blackcaps. Subsequent orientation tests revealed a significant increase in scatter among the F_2 individuals compared with the F_1 individuals, all of which had been reared and tested under identical conditions (Fig. 4; A. J. Helbig and P. Berthold, unpublished data). Surprisingly, the range of directions displayed by the F_2 group surpassed that of both parental groups from which the F_1 group had been bred. This finding strongly indicates that only very few major genes are involved in determining innate migratory directions in this species. In fact, the results are hard to distinguish from what would be expected if only a single locus were responsible for the expression of this trait.

As with all inherited behaviour patterns, there is always an interaction between the genetically determined migratory direction and environmental factors influencing the bird's actual migration course. The extent to which an individual will follow its genetic programme will depend on the degree of its exposure and individual susceptibility to environmental factors such as social influences (of flock members), topography, wind drift, etc. Experimental studies with hand-raised, caged migrants simplify the situation by subjecting all experimental birds to an approximately uniform and rather limited set of environmental influences, thus providing more conclusive information on the underlying genetic programme.

Behaviour of birds in the contact zone between southeast and southwest migrants

Blackcaps are distributed continuously across the central European migratory divide so that mixed matings between southeast- and southwest-migrating birds must be expected to occur. Offspring of such pairs would probably try to cross the Alps and Mediterranean Sea and might end up in very arid parts of northern Africa. Both the increased costs of such a migration and the lowered chances of surviving the winter compared with traditional winter quarters should act as a constant selection pressure against such a behaviour. Some evidence for the behaviour of birds breeding in the suspected contact zone between the two migratory populations north of the Alps is available from ringing recoveries and tests with hand-raised birds (Helbig, 1991*c*). If pure phenotypes mix frequently, a broad spectrum of flight directions between southeast and southwest would be expected. However, few recoveries point directly southwards, and hand-raised birds from the Linz area in Austria oriented predominantly westwards, suggesting that on a regional scale subpopulations have evolved migratory directions that allow them to avoid the mountain crossing. It thus appears that mixing of pure phenotypes, as simulated in the cross-breeding experiment described above, is relatively rare. This is confirmed by the observation that blackcaps, compared with their relative breeding abundance (the species is among the commonest forest and woodland breeding birds in Europe), are decidedly underrepresented among migrants crossing high alpine passes (Jenni and Naef-Daenzer, 1986). So far it is unclear at what geographic scale migratory adaptations are differentiated among blackcap and other bird populations. Gene flow should counteract such adaptation, but assortative mating based on different arrival times on the breeding grounds is a distinct possibility that would restrict gene flow between populations using different winter quarters (such as East Africa *versus* the western Mediterranean area). Unfortunately, no markers for birds of different winter origin are yet available that would allow us to test this hypothesis.

Evolutionary changes of migratory directions: a case study

A new migration route of central European blackcaps to winter quarters in Britain and Ireland (as opposed to the western Mediterranean area) was discovered during the 1960s and 1970s from ringing recoveries (Zink, 1962; Schlenker, 1981). Prior to 1960, blackcaps were rare in winter in Britain, but in the late 1980s thousands of individuals wintered regularly, as was revealed by the nationwide surveys for the atlas of birds wintering in Britain (Lack, 1986). So far, there have been no ringing recoveries indicating a British or Scandinavian breeding origin of these wintering birds. However, many blackcaps ringed during the breeding season in Belgium, southern Germany and the western half of Austria have been recovered in a west to northwest direction, some of them in Britain and Ireland (Berthold and Schlenker, 1991); others even flew north to Scandinavia (Franssen and Stolt, 1993). For the latter, there is good evidence that they represent reverse migration (as suggested by Busse, 1987): blackcaps from east of the migratory divide (southeast migrants) mostly flew northwest, those from west of the divide (southwest migrants) mostly flew northeast, i.e. the opposite of their normal autumn migration direction (Franssen and Stolt, 1993). This explanation does not apply, however, to west and northwest migrants recovered in the British Isles, because almost all of them originated from areas in central Europe where predominantly southwest migrants breed.

It therefore appeared that a fraction of the originally southwest-migrating population had shifted its migration course towards the west and northwest and that the majority of British-wintering blackcaps originated from central Europe. To find out whether this new migration route had a genetic basis (rather than being due to increased wind drift or other environmental factors), it was necessary to breed offspring from blackcaps that had wintered in Britain. The autumn orientation of such birds by itself would be inconclusive, because it might reflect the birds' ability to navigate towards winter quarters with which they had previous experience. We therefore caught a sample of 40 wintering blackcaps in southwest England, transferred them to Germany and bred them in captivity to test the migratory direction that their offspring had inherited (Berthold *et al.* 1992). The autumn orientation of 41 offspring thus produced was tested together with that of their parents and a control group from southwest Germany (expected to orient southwest). Both the parental birds that had wintered in southwest England and their captive-bred offspring did indeed orient towards the westnorthwest, i.e. in a significantly different direction from the southwest-orienting German control group (Fig. 5). Tracing the origin of British-wintering blackcaps by reversal of the autumn orientation they had inherited to their offspring indicates a breeding origin somewhere between Belgium and central Germany. These are areas where indeed the percentage of west to northwest migrants among blackcaps has increased from almost zero before 1960 to 7–11 % in local populations (Helbig, 1992*b*).

These data support the idea that part of the central European blackcap population has evolved a new migration route within only a few decades. This microevolutionary process is probably a geographically restricted frequency shift (of westnorthwest migrants) within the range of pre-existing genetic variation for migratory directions. The selection pressures that may favour wintering of continental blackcaps in Britain rather than in the western Mediterranean region may include the following. (1) Factors acting in the new wintering area such as progressively milder winters in recent decades, reduced competition compared with Mediterranean habitats and improved food supply during cold spells at bird tables provided by man, an important resource exploited by wintering blackcaps (Hardy, 1978), and at berry bushes planted in coastal areas and gardens. (2) Factors related to the geographic location of the new winter quarters: the migration distance is shorter by up to 1500 km and, owing to the earlier increase in daylength, British-wintering birds would be expected to return earlier to the breeding grounds (Berthold and Terrill, 1988). There is some experimental evidence supporting the latter proposition (Terrill and Berthold, 1990), and this has important implications for the understanding of such rapid microevolution: an earlier return to the breeding grounds of British *versus* Mediterranean wintering blackcaps should enable them to pair preferentially among each other (assortative mating based on differential arrival times), to occupy the best territories and to produce most offspring.

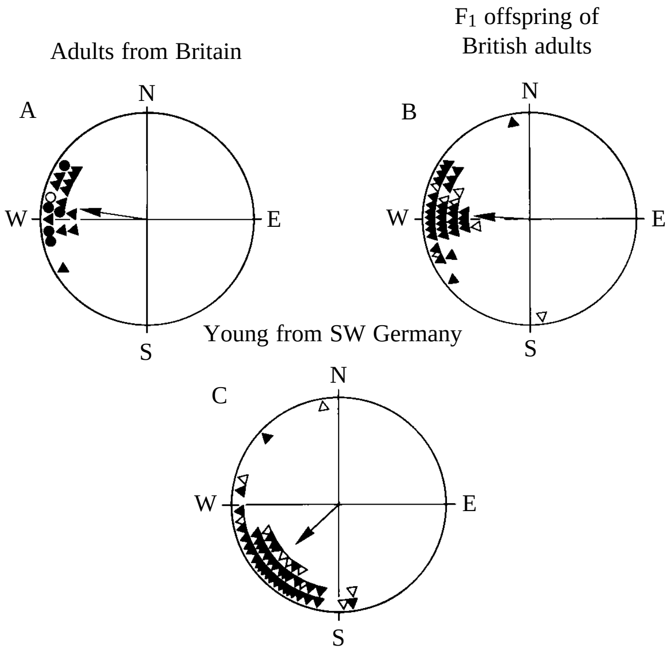

Fig. 5. Orientation of blackcaps caught in winter in Britain (A), their captive-bred F_1 offspring (B) and a control group from southwest Germany (C). In A, triangles show vectors for birds that are parents of F_1 offspring. Each symbol shows the direction of the mean vector of one individual during 15–20 tests. Filled symbols, mean vector significant at $P<0.05$ (Rayleigh test); open symbols, non-significant. Arrows show group mean vectors (from Berthold *et al.* 1992).

Apart from the rapid rate of evolution of this new migration route, it is surprising that British-breeding blackcaps apparently have not yet become partially resident. This is probably because abandoning migration altogether is a much more complex evolutionary process than just changing migratory direction and may require more time. Eventually, however, British blackcaps may evolve into a partially migratory or resident population, and a balance of competition between wintering migrants from the continent and residents may establish itself.

Inheritance of the novel migratory direction of central European blackcaps

How can the rapid rate of evolution of the new migratory direction in some central European blackcaps be explained? Do we need to invoke a different genetic mechanism, perhaps involving a dominant allele that overrides the effect of other genes regulating migratory direction? It has also been suggested that the increase in the number of west to northwest migrants could be due to non-genetic factors. Myers (1992) argued that 'xenobiotic oestrogens' transmitted through the egg might lead to aberrant development of migratory orientation, which – although normally deleterious – in the case of westward migration to Britain happened to be viable. The novel migration behaviour would thus not reflect rapid microevolution, but rather the result of (in general harmful) environmental contamination. To exclude any such maternal transmission effect, sex-linked inheritance must be tested for.

To address these questions, we performed another cross-breeding experiment involving blackcaps from both fractions of the population, i.e. those migrating towards the southwest (the majority of the southern German population) and those migrating westnorthwest (those wintering in southern England), and tested the orientation of the offspring. Again the orientation of the F_1 group was intermediate between, and significantly different from, the migratory directions of the two populations from which their parents originated (Helbig *et al.* 1994), thus confirming the result of the previous cross-breeding experiment between southwest- and southeast-migrating individuals (see above). F_1 individuals were then divided into two groups depending on whether their mother was of German or British origin. The mean orientation of the two groups did not differ (mean directions 254° *versus* 252°; $P \gg 0.05$, Hotelling two-sample test). The inheritance of orientation was therefore independent of whether an individual's parents were a German female and a British-wintering male or *vice versa*.

The evidence shows that the west/northwest migration taking central European blackcaps to new winter quarters on the British Isles can be explained without invoking any novel genetic mechanism of inheritance. Neither can the rapid increase in the frequency of this behaviour be explained by the non-genetic influence of environmental contaminants transmitted maternally. Although some behavioural effects of contaminants have been demonstrated (Colborn and Clement, 1992), our results clearly reject this possibility as an explanation for the westward migration of central European blackcaps.

Conclusions

The findings reviewed here show that, in an evolutionary sense, migratory directions of birds are highly dynamic and, in principle, able to adapt to environmental changes in a relatively short period. However, whether a species is able to adapt and how quickly it does will depend on the population size, the amount of available genetic variation, the severity of selection pressures and, most of all, on the rapidity with which such pressures change. Having demonstrated a rapid evolutionary response and the underlying genetic basis in one species, one cannot assume that all other species will adapt as quickly or even adapt at all to the drastic, partly man-induced, environmental changes we are currently witnessing. We therefore need to investigate what population genetic mechanisms allow for such rapid evolution and what prerequisites must be fulfilled for a bird population to adapt successfully to changing conditions.

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