BIRD MIGRATION: THE PRESENT VIEW OF EVOLUTION, CONTROL, AND FURTHER DEVELOPMENT AS GLOBAL WARMING PROGRESSES

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Abstract
Studies during recent decades have shown that bird migration in general is to a great extent under direct genetic control. There is evidence indicating the existence of an innate migratory drive as well as genetic control of (i) the onset, duration and end of the migration period, (ii) the amount of migratory activity, a genetically prescribed parameter that determines the distance over which the bird flies, (iii) the migration directions and (iv) physiological parameters, in particular fat deposition during the migratory period, but also those determining which individuals will migrate and which will not in forms that are obligatorily partial migrants. A two-way selection experiment has shown that within only a few generations partial migrants can be converted by selection into pure migrants or nonmigrants. Selection for a new migration direction, leading to new winter quarters, can occur equally rapidly in free-living birds. At least in the species most closely studied so far (the blackcap, Sylvia atricapilla), the attributes "migrant" or "nonmigrant" are inherited in conjunction with the characteristic amount of migratory activity (as a time program), and the former are evidently controlled by a threshold mechanism. A new bird migration theory postulates that even in forms that at present are exclusively migratory, selection for lower levels of migratory activity can cause a threshold to be crossed, below which nonmigrants appear. Accordingly, conversion of a population from migratory to nonmigratory can occur by selection with a transition through partial migration. This intermediate stage is prevalent among the recent bird species; it appeared early in the evolution of organisms and in the case of birds was probably acquired from ancestral, pre-avian forms. Model calculations indicate that with strictly directed selection, migratory birds can be converted to sedentary in about 40 years and conversely. This explains the changes in migratory behaviour currently observable in so many bird species in the course of global warming; in particular, migratoriness is decreasing in various respects at higher latitudes. The new theory also enables us to predict the ways in which avifaunas are likely to be restructured if warming continues; these scenarios are briefly outlined.

Key words
Birds, Migration, Evolution, Genetics, Global warming

1 Introduction
Our institute, the “Vogelwarte Radolfzell”, was established 100 years ago, in 1901. It was then called “Vogelwarte Rossitten” and was situated in East Prussia, far to the northeast of its present site. The first “ornithological biological observation station” in the world, it was brought to life as a result of proposals made at the First International Ornithological Congress, held in 1884 in Vienna. From the outset it was directed primarily towards the study of bird migration, and throughout its history it became progressively more focused on that area of research. It was only for a short period that the work relied on pure field observations. Beginning as early as 1903, data were obtained from a broadly based ringing system, an approach that had recently been developed in pioneer studies by the Danish teacher C. C. M. Mortensen. By the time that the end of World War 2 brought activities at the original institute to a halt, about a million birds had been ringed. Since the institute was re-established at Radolfzell in 1946, the number has risen by about 4.5 million. The insights obtained from recoveries of

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Brief introduction to the author
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ringed birds have been presented in many original and review articles, in particular in two publications entitled *Atlanten des Vogelzugs* (see, e.g., Zink and Bairlein 1995). As early as the 1920s the founder of our institute—Prof. Dr. Johannes Thienemann began front-line research in the area of orientation. At first this involved retention and displacement experiments, using the swallows (*Hirundo rustica*) and then mainly white storks (*Ciconia ciconia*); the work was then continually extended by his collaborators. Research on the physiology and control of bird migration, initiated during the 1920s in Canada by Rowan (1925), was taken up in Rossitten during the 1930s and then adopted as a major project in Radolfzell after the war. To summarize: workers at our institute have been investigating all the basic aspects of bird migration almost uninterruptedly for a century.

Because Thienemann’s successors over the years have progressively built on and added to a vast resource of experience, mostly accumulated in our own institute, we have been able to develop a number of new approaches. Most prominent in recent years are the introduction of satellite tracking of migratory birds in Europe in 1990 (Berthold et al., 2000) and the incorporation of experimental genetics and experimental evolution research into the study of bird migration during the 1970s. The last two research areas, in particular, have produced novel insights, hypotheses and theories, which will now be considered in detail.

### 2 Circannual rhythms and their implications

For species that migrate late in the year, for instance not until the first snow falls, it has long been postulated that they are induced to depart by exogenous signals generated directly by environmental factors, such as cold temperatures or lack of food (e.g., Farner, 1955). In the case of species that migrate very early—such as the marsh warbler (*Acrocephalus palustris*) which leaves higher latitudes during summer, beginning in mid-July—the possibility that their departure is caused by endogenous factors was raised centuries ago, by von Pernau (1702). As he put it, they are “pulled away at the right time by a hidden force.” Ideas about endogenous initiation and control of migration multiplied from the 1950s on (Aschoff 1955), and after evidence to this effect had been obtained for mammals, in particular, beginning in the 1960s researchers in our institute produced the first demonstrations of endogenous annual rhythms (circannual rhythms, i.e., biological clocks or internal calendars related to the calendar year; e.g., Gwinner, 1967, 1986; Berthold et al., 1971; Berthold, 1988).

These circannual rhythms are cyclic changes in physiological body functions that are controlled by the central nervous system, though it is not yet known exactly how they are produced. They have now been demonstrated in about 20 species of migratory birds, belonging to various systematic groups and distributed over five continents. In these birds they govern the periodicity of migratory activity, rhythms in body weight (especially fat deposition), food preferences, the basic features of orientation behaviour, and probably many fundamental physiological and endocrinological periodicities. As an example, Fig. 1 shows four circannual body rhythms of a garden warbler (*Sylvia borin*). Circannual rhythms of birds persist under constant experimental conditions, and in this situation it becomes evident that their periods are normally less than 12 months, usually of the order of about 8-10 months. Under natural conditions, this deviation of circannual rhythms from the calendar year is counteracted by external synchronizers—especially photoperiodicity—which adjust the rhythms to the calendar year, matching them to the appropriate biological seasons.

It was an intriguing question whether endogenous circannual rhythms can trigger migratory processes even when uninfluenced by environmental factors, which often appear to affect migratory events especially in late-migrating species. There is indeed convincing evidence that they can in some cases: for instance, the initiation of the first departure from the breeding grounds by young individuals, migrating for
Fig. 1 Endogenous annual periodicity (circannual rhythms) of (from top to bottom) testes length, migratory restlessness (Zugunruhe, as measured by nocturnal locomotor activity, "hopping"), body mass and moult of a male garden warbler (Sylvia borin).

The hand-raised bird hatched at the end of May and was transferred to constant conditions (a light-dark regime of 10:14 hrs) in June (arrow) and kept there for 10 years; results are depicted from the first three study years.

RM: return migration  OM: outward migration period
(modified from Berthold, 2001)

The discovery of circannual rhythms and the demonstration that they can directly initiate migratory events made it seem highly probable that bird migration could to a considerable extent be under direct genetic control. Similar hypotheses had previously been put forward by Rowan (1931), Nice (1933), Lack (1943/44) and others. So as to proceed along this line of thought, it was necessary to open a new area of research: experimental bird-migration genetics. This was not an easy task. But after a long search we finally struck gold with one species: the blackcap (Sylvia atricapilla). This species is widely distributed, ranging from the Cape Verde islands over other Atlantic islands such as the Azores and Madeira and through almost the whole European continent as far as western Siberia; it includes sedentary, migratory and partially migrant populations, and its migration routes have various directions and distances. Furthermore, it is common everywhere, can readily be kept in cages and aviaries, and now—after more than 5 years of pilot experiments—can be bred quite well in our institute. During the last 25 years or so we have hand-reared over 3,000 individuals from various populations, and a good 1,600 have been bred in our aviaries in the course of crossing and selection experiments. We have also achieved similar breeding results, though involving fewer individuals, with the common redstart (Phoenicurus phoenicurus) and black redstart (P. ochruros) (Berthold, 2001). These two species cross-breed regularly in the field and can also be crossed in aviaries, producing fertile hybrids and thus enabling genetic studies beyond the species boundary. Because these warblers and redstarts in nature migrate by night, their migratory activity (or its absence, in the case of non-migrating individuals) can easily be measured quantitatively as nocturnal migratory restlessness (Zugunruhe) in automatic registration cages (Fig. 2).

3 Results of genetic and experimental evolutionary studies

Since 1980 blackcaps and redstarts have been tested for genetic mechanisms directly underlying the following characteristics and events associated with migration: (i) the presence of a “migratory drive” (instinct in the sense of Konrad Lorenz), i.e. the spontaneous, inherited appearance of migratory

The comparative study in 19 species of European leaf and reed warblers, small thrushes and some others showed a very high correlation coefficient of 0.967 between onset dates of migratory activity (restlessness, see below) in hand-raised caged birds and the actual migration of conspecifics belonging to the same populations in the wild. This finding implies that the endogenous mechanisms triggering migratory activity in captive individuals also initiate actual migration, and that environmental factors in these cases are of minor, if any, importance for the initiation of departure. The same is likely to apply to birds flying to the breeding grounds from winter quarters near the equator, because in equatorial regions there are very few regular seasonal changes that could act as migration-elicitting factors (Berthold, 1996).
activity in hybrids produced by experimental cross-breding of migratory and sedentary birds; (ii) the species- and population-specific onset, duration and end of the first outward migration (Fig. 3); (iii) the amount of migratory activity produced in the first outward migration period—which, according to the vector navigation hypothesis (see below), in the case of young birds migrating for the first time, with no prior experience, represents a time program that determines the migration distance and hence the location of the winter quarters; (iv) directional preferences for migration, including both the maintenance of a particular direction and changes of direction (which often occur as sharp turns, flying in curves etc.) in the course of migration; (v) increases in body weight during the migration period, such that the bird can become as much as twice as heavy, primarily owing to fat deposition but also by protein accumulation etc.; (vi) the determination of migrants and nonmigrants in partially migrant populations; (vii) the phenotypic and genotypic variability and the heritability of individual characters, in particular the amount of migratory activity and of partially migrant behaviour; (viii) the timing of migration in accordance with other processes having annual periodicity, namely juvenile development, moulting and breeding. For all of these characteristics and events it has been possible to demonstrate direct genetic control. Furthermore, considerable phenotypic and additive genetic variability has been found, which together with intermediate heritability values (around 0.4) suggest a high potential for rapid selective and microevolutionary processes. Two examples follow.

Common redstarts are long-distance migrants, travelling about 5000 km from central Europe to overwinter in central Africa, south of the Sahara; to cover this distance takes from mid-August to mid-December. Black redstarts start from the same area but migrate over the much shorter distance of about 1000 km to winter quarters in the Mediterranean region, from October/November to December. Correspondingly, hand-reared individuals of the two species kept in registration cages exhibit migratory restlessness that differs in duration and appears when the birds have reached different ages. When avairy birds of the two species are cross-bred and the hand-reared hybrids are tested in the same way, the time of onset and the duration of their migratory activity are intermediate. This result shows that these parameters are under direct genetic control, which is evidently neither monogenic nor dominant, but polygenic; that is, these are evidently quantitative genetic characters (Fig. 3).

The second example relates to partial migration. This is a form of the regular yearly migratory period in which only part of the population leaves the breeding grounds, while the other birds stay there for
the winter. Regarding control of obligatory partial migration (i.e., occurring regularly every year), two completely disparate hypotheses have been proposed. According to the “behavioural-constitutional hypothesis,” weaker individuals are displaced during post-breeding skirmishes over food etc., and are eventually forced to migrate, whereas the stronger winners of these disputes can remain resident. The “genetic hypothesis” states that the decision as to whether an individual will later be a migrant or a nonmigrant is already made in the egg by the combination of parental genes. We have carried out the first experimental tests of these hypotheses, with birds from a partially migrant blackcap population in southern France that is composed of 75% migrants and 25% nonmigrants. A two-way selection experiment (Fig. 4) yielded a strong selection response even in the F1 generation. Continued selection gave very striking results: it was possible to obtain a fully migratory population after just 3 generations and an (almost) resident one after only 5-6 generations. Thus partial migration in the blackcap has an extremely high evolutionary potential towards full migratoriness or sedentariness.

Such rapid changes on a genetic basis also occur in nature. The central European blackcaps had always migrated exclusively southward, to winter quarters in the Mediterranean region and in Africa, until about 40 years ago; then some birds began to migrate in a new, northwestern direction and to overwinter on the British Isles. We tested the directional preferences of birds taken from these new winter quarters and then raised their progeny in aviaries and tested them in the same way. Although this novel migratory behaviour has just arisen in recent decades, the new migration direction is already genetically fixed: it is inherited by the descendants, and accordingly has very recently been brought about by rapid selection. Evidently a considerable number of selection pressures have contributed to its quick development, such as a shorter migration distance, ideal winter quarters in a mild climate with only slight intraspecific competition, an ample food supply and relatively short days in winter, which cause a timely return to the breeding grounds and hence optimal choice of habitat, early gonadal development and breeding and probably also assortative pairing with partners from the same overwintering area (Berthold, 2001).

4 □ A novel comprehensive theory of avian migration

In addition to the results of the two-way selection experiment with blackcaps described above—that the distinction between migrants and nonmigrants is genetically determined, and that partial migration can rapidly evolve into pure migratory or sedentary behaviour by selection—we also gained two other important insights. When migratory birds mate with one another (or sedentary
ones do), initially some of the offspring are sedentary (or migrants), but their proportions gradually decline as selection proceeds. It follows that the inheritance process involves neither a single nor a dominant gene, but rather that migrating and not migrating are under polygenic control and are quantitative genetic traits. Second, we learned that during selection for more migrants, the level of migratory activity (which, as a time program, determines the distance travelled) also rises significantly, whereas during selection for sedentary birds it decreases until eventually it disappears altogether and all the birds are nonmigrants. That is, migrating or not migrating on one hand and the amount of migratory activity (the migration-distance program) on the other are controlled by one and the same genetic mechanism. It is probably a threshold mechanism: those individuals in a population that have migratory activity levels above a particular threshold behave phenotypically as migrants, whereas others with below-threshold activity are phenotypically nonmigrants, and the result for the population as a whole is partial migration. The finding that both the alternative migrant/nonmigrant and the amount of migratory activity are controlled by a single common mechanism (and hence are inherited as a so-called migratory syndrome) has the following implications. Even in a bird population that at present is exclusively migratory, with all its members producing high levels of migratory activity (all above a critical threshold), directed selection towards progressively lower activity levels would be expected to bring the population to the critical threshold below which nonmigrants will appear “automatically”, in the absence of any other influences such as mutations. That is, partial migration should be brought about purely by selection for lower levels of migratory activity. But then, as shown above, exclusively sedentary behaviour can be selected from partial migration. These novel findings essentially compel us to formulate a new bird migration theory, namely: migration and nonmigration are not mutually exclusive forms of behaviour but can change into one another. The transition takes the form of partial migration, which arises by selection with no need for any further mechanism such as mutations. Hence partial migration acts as a kind of turntable between migrating and not migrating. In our institute we are currently carrying out two large-scale experiments in which, according to the theory, we should be able to breed sedentary birds from migrants and conversely; the results obtained so far are very promising.

It is not difficult to demonstrate that partial migration is the most common life form in birds. For instance, identification keys for European birds explicitly list as partial migrants about 35% of the over 400 species considered. According to the specialist literature as many as 70% of the species are partial migrants, the remaining 30% comprising mainly migratory birds although some are to a great extent sedentary. However, even the entirely typical migratory and sedentary bird species repeatedly produce individuals that are clearly physically intact but nevertheless do not migrate, or that migrate over fairly long distances, respectively. This applies even to species that exhibit such pronounced migratory or nonmigratory behaviour as swallows or the house sparrow (Passer domesticus). It is not unlikely, therefore, that all the bird species currently breeding in Europe are genotypically partial migrants—most of them phenotypically so, and the rest at present having been strongly selected for the phenotype migratory or sedentary.

Partial migration is similarly common in higher-latitude regions outside Europe. Furthermore, recent studies have shown that even tropical species often undertake migratory journeys—far more often than had previously been thought (Rappole, 1995; Winker et al., 1997). Because tropical species tend to migrate only for short distances, it is quite possible that partial migration is also common in the tropics; we can expect future investigations to produce abundant evidence in this regard.

Furthermore, partial migration is phylogenetically very old and, accordingly, is also a widespread form of behaviour in other groups of animals; it is even observed in plants, in the form of differently formed seeds, some of which are distributed close to
the plant and others further away. A number of fossil finds suggest that even in the Cretaceous period, about 80 million years ago, the toothed, flightless birds Hesperornis had subpopulations that made migratory journeys by swimming. These findings have produced two further important viewpoints for the new bird migration theory. The disposition towards partially migratory behaviour either arose early in the evolution of birds or—more probably—was inherited from the ancestors of birds, as were orientation mechanisms (compass and other navigation systems) and metabolic processes (ability to store fat as an energy source). In either case partial migration, having proved to be an extremely successful life strategy, would have developed further into an evolutionarily stable form of behaviour that soon became part of the basic equipment of birds. It is therefore likely that genes for migrating and not migrating (genotypic, “potential” partial migration) became part of the basic avian genome (Berthold, 1999).

Bird migration and global warming: recent findings and prospects

During the last 100 years the global climate has warmed up by about 0.6 °C and due to the Intergovernmental Panel on Climate Change (www.ipcc.ch) the last decade was the warmest recorded worldwide since weather recording began. Results are becoming evident; as just a few examples, the onset of spring at higher latitudes has advanced by at least a week, glaciers and parts of the polar ice caps have receded, and the sea level has risen. By the year 2100 a further global warming amounting to 1.4–5.8 °C is predicted (Berthold, 1998; Kerr, 2001).

Even the moderate climate warming that has occurred so far has had a marked effect on the bird world, distinctly altering the birds’ annual rhythmicity and their behaviour. A recent compilation of the relevant data (Berthold, 1998) showed, primarily for the northern hemisphere, the following major changes. (i) Many species have extended their breeding areas to higher latitudes; a particularly striking example is the immigration of Mediterranean and African species into Europe and their continuing expansion, so that within a few decades some have advanced into northern parts of central Europe. (ii) Some species with a northern distribution have withdrawn to even higher latitudes by shrinking the previous area of their breeding range. (iii) There have been marked changes in reproductive biology, especially an earlier onset of breeding in many species, but in some cases lengthening of the breeding period, altered laying pattern, increased clutch size and better breeding success. (iv) A number of resident birds plus some less pronounced migrants show reduced winter mortality, hence larger populations. (v) Changes in population size include not only the increases cited in (iv) but, among long-distance migrants, predominantly declines; these can result partly from greater competition with the more numerous sedentary birds, and also from habitat deterioration and the like, e.g. by the climate-induced expansion of the Sahara and the progressive desertification of marginally arid regions. (vi) Finally, there have been many changes in migratory behaviour, which are of particular interest in the present context. Recent alterations in behaviour of migratory birds are characterized by the following criteria: 1. in many species, increasingly and significantly later departure from the breeding grounds, maximally by up to 14 days, which is evident even to the layman; 2. correspondingly, in many species a substantially earlier return to the breeding grounds, with maximal advances of a month or more; 3. in a number of partial migrants, a distinct increase in the proportion of sedentary individuals, which no longer migrate but instead overwinter in the breeding grounds; 4. similarly, the appearance of a progressive tendency to overwinter in the breeding grounds in species that used to be almost entirely short-distance migrants, and even in long-distance migrants such as the white stork, the swallows (Hirundo rustica) and (Delichon urbica) or yellow wagtails (Motacilla flava); 5. shortening of migration distances and a greater tendency to overwinter closer to the breeding grounds in a number of species; and finally 6. choosing new winter
quarters in a new migration direction and at a shorter distance than previously, as described above for the group of central European blackcaps that now migrate to the British Isles rather than to the Mediterranean region and Africa as formerly.

As matters stand, we can expect the anthropogenic global climate warming to continue. Given that the last climate conference in Bonn, Germany, in July 2001 achieved so little, and in particular that the USA—the main contributor to this warming—has shown itself so reluctant to reduce its emission of atmospheric pollutants to an appropriate degree, the warming is actually likely to accelerate. If it should amount to over 5 °C as predicted above, meteorologists await a climatic “catastrophe” (Kerr, 2001) for which at present no even somewhat realistic prognoses can be formulated, regarding either the meteorological details or the effect on ecosystems. If warming proceeds less rapidly, remaining in the lower range of about 1.5 °C, the following scenario is probable. For higher latitudes we can expect three specific developments. (i) Progressively milder winters, hence a further decrease in the winter mortality of nonmigrant birds and the sedentary members of partially migrant populations, so that these generally become more numerous, especially because the breeding period is simultaneously advanced and extended. (ii) A rapid conversion of partial and short-distance migrants to nonmigrants. Model calculations based on our estimates of variance and heritabilities have shown that with strictly directed selection, long-distance migrants can change to short-distance migrants in about ten generations or 15 years, and a conversion of pure migrants into sedentary birds (or conversely) could occur in only 25 generations or 40 years. Because in nature selection is rarely strictly directed but usually proceeds in forward and backward steps, these values are theoretical minima. Nevertheless, periods of 20 or 100 years, respectively, seem entirely realistic for the two cases considered here. For example, European blackbirds (Turdus merula) in central Europe were once exclusively migratory, and in less than 200 years they evolved sedentary populations (Berthold, 2001).

Regarding decidedly migratory birds (iii), mainly long-distance migrants, the future is more difficult to predict. At present the populations of most of them are declining, and two groups of factors are probably involved here. First, these birds experience loss of their habitats not only in the breeding grounds, like sedentary birds, but also in their winter quarters and along the migration route, so that some of them have suffered harm in several regions. Second, the increased populations of nonmigratory species are likely to cause problems because they exert more competitive pressure in the breeding grounds (O’Connor, 1990). There are indications that the genetic—as well as documented measures of phenotypic—variance is distinctly less in long-distance migrants than in short-distance and partial migrants. It follows that processes of selection and microevolution would take place more slowly in the long-distance migrants, so that by the time these birds had been converted to permanent residents in the breeding grounds, a large proportion of the ecological niches suitable for them would already be occupied. In this situation it is not unlikely that some of the long-distance migrants will be crowded out of avifaunas. This loss of biodiversity might be compensated locally by a northward advance of Mediterranean and African species such as is currently well underway in Europe for, e.g., the great white egret (Egretta alba), cattle egret (Bubulcus ibis), and bee-eater (Merops apiaster).

Another problem faced by long-distance migrants is adjustment to the annual periodicities of their environments. These birds obtain the precise seasonal information they need to time migration, breeding and so on from the interaction of circannual rhythms and annual rhythms of day length; in some cases only the photoperiodic conditions characteristic of particular latitudes can act as synchronizers (Gwinner, 1986). Very recently some European long-distance and trans-Saharan migrants have begun overwintering in the Mediterranean region rather than in Africa south of the Sahara (Berthold, 1998). There they experience much shorter day lengths in winter than they had normally encountered in central or southern
Africa, which raises the question of how they cope with this. Photostimulation experiments with three songbird species have shown that the annual periodicity is favourably accelerated when they spend the winter near the Mediterranean rather than in more southern parts of Africa. The birds display a migratory disposition for their return migration sooner and their gonads grow more rapidly, so that after an earlier return to the breeding grounds they could also breed earlier (Coppack, 2001). Accordingly, long-distance migrants that increasingly overwinter in the Mediterranean region could probably enhance their potential for competition against other species.

For still lower latitudes, other kinds of development are to be expected. Major changes are likely in the so-called desert belts of the earth and the adjacent regions, in which increasing aridity has already brought about a progressive desertification. If this desertification should spread further—in the case of Europe, for instance, encompassing large parts of the Mediterranean region—we can predict two results: the development of new migration patterns in the form of escape from aridity, and the loss of breeding areas for sedentary species and of winter quarters in particular for short- and medium-distance migrants. If the rising sea level in far northern regions should cause flooding of enormous parts of the tundra, at present it is an entirely open question whether the limicoles, geese, ducks etc. that now breed there would have any chance of settling elsewhere, or whether they would simply disappear from our avifauna.

6 Some aspects of conservation measures

So far it is almost impossible to make even moderately reliable prognoses for the medium-term prospects of individual species. Even if sedentary birds at the higher latitudes are currently finding the climate advantageous, it is far from the case that all species in this group are increasing in population size, or increasing uniformly. On the contrary, in Europe a considerable number of them are just now undergoing dramatic population declines in quite diverse regions: for instance, the capercaillie (Tetrao urogallus) in montane coniferous forests, the grey partridge (Perdix perdix) in farmland or the house sparrow in human settlements (Bauer et al., 1997). There are various reasons for this, including the loss of suitable habitats, the reduction of the food supply as agricultural practices change, and factors such as a lack of calcium for forming eggshells, which has been observed for example in great tits (Parus major) that live in places where acid rain makes calcium unavailable (Graveland et al., 1994). As hard as it may be in the case of sedentary birds, it is much more difficult to predict population development and design whatever conservation measures may be necessary for migratory birds—in particular long-distance migrants, for which strongly regulatory factors that have been previously ignored may suddenly become apparent in the most diverse parts of their overall habitat, in part as a result of climate-related environmental changes. For example, the succession of vegetation that follows logging of tropical rainforests turns out to bring advantages for some overwintering species (Hutto, 1989), whereas the cultivation of new kinds of coffee that are planted in an open, sunny situation tends to be disadvantageous for overwintering songbirds (Greenberg et al., 1996). The logical conclusion to be drawn from all these uncertainties is undoubtedly this: that we should depart from the pure conservation of species, especially where it is directed towards single species or small species groups, because at present no one can say how well any particular species will be able to survive rapidly changing environmental conditions. Instead, more effort should be made to protect habitats, with particular concentration on species-rich biocoenoses in conservation regions that are made as large as possible, so that relatively large ecosystems are preserved or can develop anew. Then these habitats, with sufficient internal dynamics, will be able to adapt themselves continuously to rapid environmental change, and their biodiversity need not suffer as a result of such change.
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天的迁徙动因并涉及以下几方面的遗传调控：（1）迁徙过程的起始、持续以及结束；（2）迁徙活动量，即决定鸟类飞行距离的遗传参数；（3）迁徙方向；（4）生理参数，特别是迁徙期间的脂肪贮存，以及对于那些部分个体迁徙的鸟种而言，决定个体迁徙与否的生理参数。双因素选择实验表明，部分迁徙群经由几个世代的选择即可转变成完全的迁徙群或非迁徙群。新迁徙方向以及由此导致的新越冬区的改变，也能在野生鸟类中迅速实现。至少在以往研究得最为透彻的鸟种（黑顶林莺 Sylvia atricapilla）中，“迁徙”或“非迁徙”是先天性的，与特异性迁徙活动量相关（尤如一时间程序），前者（迁徙的）已证实是由一种阈机制所控制。一项新的鸟类迁徙理论假设，即使好些完全迁徙的类群，较低水平的迁徙活动量选择也会导致阈的异位，低于这一阈值就会出现非迁徙个体。因此，通过选择作用，一个迁徙型种群可以通过部分迁徙型转变为非迁徙型。这种中间阶段在现存鸟类中十分普遍。它始见于生物演化早期，就鸟类而言，可能在原始鸟类就已具备。模型运算表明，在施以强定向选择情况下，迁徙鸟类经过约40年可转变为留鸟，反之亦然。这就解释了在全球变暖的形势下，近来所观察到如此众多的鸟种在迁徙行为方面的变化。特别高纬度地带鸟类迁徙性在多方面的衰退。新理论还使我们能够预测，在气候继续变暖的情况下鸟类区系重组的方式。本文对以上内容作了简要概述。

关键词：鸟类 迁徙 演化 遗传 全球变暖

书讯
《四川两栖类原色图鉴》由中国科学院成都生物研究所费梁研究员和叶昌媛研究员编著。本图鉴主要依据作者多年野外和室内的研究积累，并参阅大量文献资料编著而成。全书共分为绪论和各论两部分：绪论包括四川省自然概况、两栖动物研究简况、区系特征、物种生态类型、资源和保护、两栖动物概述、分类学术语和量度、纲、目、科、属、种的主要鉴别特征及各阶元成体、蝌蚪、卵群检索表；各论共记载四川省包括3新种在内的已知两栖动物111种，每个种均有成体外形彩绘图，文字叙述包括形态特征、生物学资料和地理分布。书内共有各类图片651幅，其中彩绘图254幅、彩色照片261幅以及墨线图136幅，绝大多数彩绘图依据模式标本、地模标本或四川的实物标本绘制而成。书后并附有“四川省两栖动物地理分布表”、“国家及四川省野生两栖动物保护名录”、中文索引和拉丁学名索引。本图鉴是第一部全面系统记述四川省两栖类的彩色图鉴，书内多数种的成体有背面、腹面、蝌蚪和卵群图片，从全方位展示了各物种生活史特征，是一部科学性和实用性相结合、图文并茂的学术性专著及工具书。本图鉴可供有关科研单位、高等院校和各级学校、农林牧业和珍稀、濒危、经济动物养殖单位及野生动植物保护管理部门使用，也可供海关、商检、邮政、交通、防疫和卫生等单位有关人员参考，同时还具有观赏和收藏价值。该书定价180.00元。联系方式如下：

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