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Spatiotemporal programs and genetics of orientation

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Summary. A number of migratory bird species have endogenous annual rhythms that regulate the entire annual cycle including the migratory portion. Moreover, captive migrants display inherited migratory activity; this could theoretically also be used by free-living migrants as a time-program for migration. Finally, this heritable migratory activity is oriented in a seasonally appropriate direction even in naive birds. These characteristics should enable inexperienced migrants isolated from contact with experienced conspecifics to utilize a heritable vector-navigation program to migrate from the breeding grounds to the winter quarters. That is, migrants should reach goal areas they have never experienced by migrating in programmed directions, for as long a period as the genetically fixed time-program for migratory activity induces them to do so. The time-course of migration as established by trapping stations, theoretical influences of environmental variables on migratory programs, and also compensatory behavior and migratory backup measures, are discussed. The present evidence supports the view that a large number of migrants are essentially brought to their wintering areas by vector-navigation systems.

Key words. Bird migration; orientation; navigation; circannual rhythms; genetic programs; inheritance.

Introduction

A worldwide effort (primarily during the past 80 years) of marking ('ringing') individual migratory birds and carrying out population censuses clearly demonstrated that most migrants do not move to winter quarters which vary at random, but are capable of precisely oriented movements between well-defined species- and population-specific breeding grounds and wintering areas[41, 56]. The most difficult task in such a system of movements is the first outward journey from a known area (the breeding grounds) to a totally unknown region (the prospective wintering area). In all later seasons both areas are known. In some highly social groups of birds (e.g., storks, cranes, geese) the problem can be solved by tradition; the offspring are led by experienced adults[50]. It is not possible, however, for there to be any social transmission of migratory information in birds such as brood-parasitic cuckoos, in which migrating fledglings never become acquainted with their parents or other adults before their first migratory journey. This is an extreme example, but the same holds true for the vast majority of migrants that either fly individually, or in varying flocks of inexperienced conspecifics[50]. Since these birds are also able precisely to reach specific winter quarters[41, 56] it is logical to propose that they are equipped with endogenous orientation programs. And because these lonely wanderers, even when commuting over thousands of kilometers, regularly perform their long-distance movements according to rather fixed schedules[34] they must have spatiotemporal programs. In the following sections our present knowledge of such programs is summarized.

Endogenous time-programs

The involvement of endogenous programs in the control of migration has been proposed for a long time. As far back as 1702 von Pernau[44] assumed that a 'hidden urge' in the individual bird was responsible for triggering the initiation of the migratory journey. Later on, it was proposed that endogenous time-programs might control the entire migratory journey (at least during the first migratory season from the breeding grounds to the winter quarters)[51]. About 20 years ago, such programs were actually demonstrated in European warblers[15, 26], and they have currently been established in about 20 bird species of about 10 families[31]. An example is given in figure 1.

In order to demonstrate the existence and performance of endogenous rhythms, organisms have to be kept under constant experimental conditions. Thus, periodicity should not occur within a period length in which the supposed endogenous rhythm would be most likely to

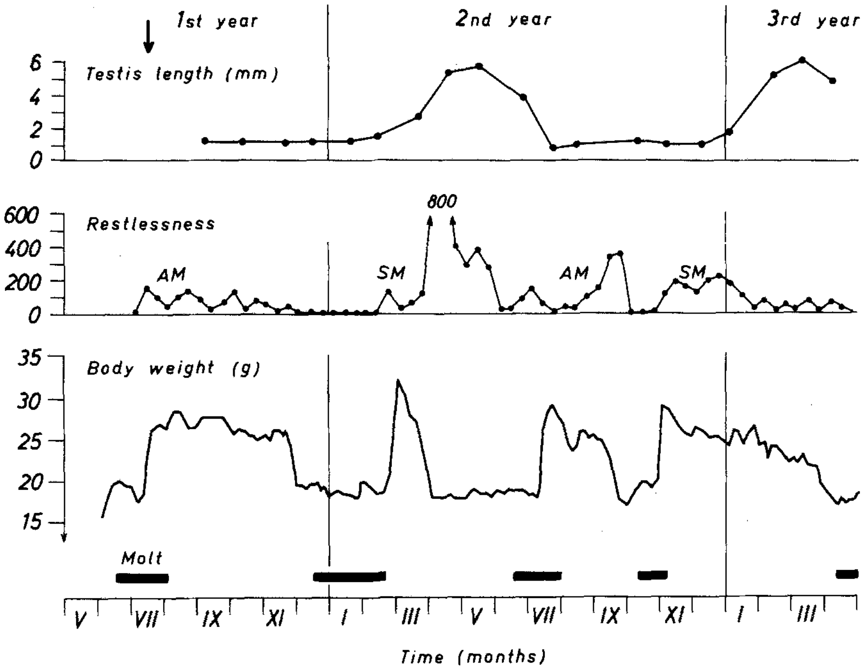


Figure 1. Circannual rhythms of four annual events in an individual hand-raised German garden warbler (*Sylvia borin*) kept in constant conditions (daily light-dark ratio 10:14 h; for further conditions see text). AM and SM: autumnal and spring migratory periods (from Berthold et al.[15]).

operate. In our case, because we were testing for endogenous annual rhythms, any seasonality had to be absent. On the other hand, the conditions have to be permissive enough to maintain the optimal health of experimental individuals, as well as allowing for expression of the programmed rhythms which are of interest[2]. In the example given in figure 1, a young garden warbler (*Sylvia borin*) was taken from the nest five days after hatching (when it was still completely inexperienced with respect to environmental seasonality). It was hand-raised and transferred to a constant daily regime of 10 h light (450 lx), and 14 h dark (0.01 lx); 20 ± 1.5 °C ambient temperature; 60% relative humidity, and a daily food supply constant with respect to quantity and nutrient content. The experimental bird (and many others) were kept in these conditions for ten years; figure 1 covers the first 24 months.

The figure shows that, despite the fact that it was unable to experience any environmental seasonality, the bird nevertheless behaved rhythmically throughout the course of the experiment. The bird first went through a postjuvenile molt (the first black bar); then, while still molting, it started spontaneously to increase its body weight owing to fat deposition (caused by hyperphagia) and began (from July onwards) to display nocturnal migratory restlessness (or Zugunruhe, the expression of migratory activity of migrants in captivity[4]). Towards the winter, restlessness ceased, body weight was reduced to the values of the premigratory season, and a complete winter molt occurred. In late winter body fattening and migratory restlessness started again at the beginning of the period of the homeward migration, and in spring and summer, gonadal development and recrudescence, respectively, occurred. In summary, the bird showed complete annual rhythmicity, and the sequence of the different annual processes and their timing were in full accordance with those of free-living conspecifics. In later seasons, however, processes in the captive birds occurred somewhat earlier than in the wild (fig. 1), and the period length of the rhythm adjusted itself to about 10 months. Such deviations are the norm and are the reason why these rhythms are called 'circa'-rhythms, in this case 'circannual' rhythms. The clear deviation from the calendar year also demonstrates that these rhythms are really endogenously controlled (self-sustained) and not caused by some uncontrolled environmental annual cycles. In a few warblers that were kept for 10 years under constant experimental conditions (i.e., about five times the average life expectancy of free-living conspecifics) we found that these endogenous circannual rhythms are free-running (as are circadian rhythms) and are of life-long efficacy[8]. In the wild, such deviations in endogenous rhythms do not occur because the circa-rhythms are permanently, or temporarily, synchronized with the appropriate external rhythms by Zeitgebers. For the circannual rhythms, photoperiod appears to be the most important Zeitgeber[31]. Of special relevance to our understanding of orientation in migratory birds is the role of circannual rhythms in the endogenous control of fat deposition (expression of the migratory state) and, above all, of migratory restlessness (expression of the urge to migrate) in relation to the distance to migrate. A number of detailed studies of migratory restlessness or Zugunruhe have yielded the following results: 1) there is, as a rule, fairly good accordance between onset, duration, and termination of restlessness in caged birds with the course of actual migration in wild conspecifics[4]; 2) in a few species that have very peculiar migratory journeys due to extreme ecological situations, it was found that the temporal pattern of restlessness mimics fairly well the time course of migration[11]; and 3) comparative studies in groups of warblers of the genera *Phylloscopus* and *Sylvia* (using species and populations with different migratory performances) have shown that long-distance migrants produce large amounts of Zugunruhe, middle-distance migrants medium amounts, and short-distance migrants small amounts of this activity[12,29]. In a study using 13 different *Sylvia* species and populations, a positive significant correlation was found between distance of migration and amount of migratory restlessness ($r = 0.76$, $p < 0.01$)[11]. 4) In nocturnal migrants, migratory restlessness occurs as nocturnal activity, while in diurnal migrants it occurs as additional diurnal activity (and this diurnal migratory activity is based on circadian rhythms[9,25,40]).

From these experimental results it has been concluded that migratory restlessness is closely related to the distance of migration and, as was predicted by von Lucanus in 1929[39] and Stresemann in 1934[51], that the migratory urge might well act as a time-program critical to covering an appropriate distance between the breeding grounds and the winter quarters. Recent quantitative observations of restlessness support that view. When the Zugunruhe of garden warblers was recorded by video-sets under IR illumination we found: 1) almost all migratory restlessness is wing whirring (wing beating in a sitting position) and 2) the total amount of wing whirring displayed by a central European experimental group during the whole first autumn migratory period, multiplied by the known species-specific flight speed during migration, would have brought the experimental group into the center of the species-specific winter quarters in central Africa. Thus, migratory restlessness in sylviid warblers can be interpreted – although with a number of restrictions – as 'traveling by wing whirring in a sitting position'[18].

Orientation programs

In the previous section it was shown that at least some migratory birds appear to be equipped with endogenous time-programs for migration. If, however, inexperienced first-year migrants are to be able to reach their winter quarters on a programmed basis, they will also require information for directional orientation. There is, in fact, increasing evidence for the existence of such programs. In a number of earlier studies (e.g., by Kramer[37], Hoffmann[35] and Sauer[46]) it was observed that warblers, shrikes, starlings and buntings, when being tested in various orientation cages (cages in which birds can demonstrate preferred migratory directions), regularly tried to leave the cages in the direction in which free-living conspecifics normally migrate towards their winter quarters. This behavior was also characteristic of birds which had never migrated and had not had contact with experienced birds.

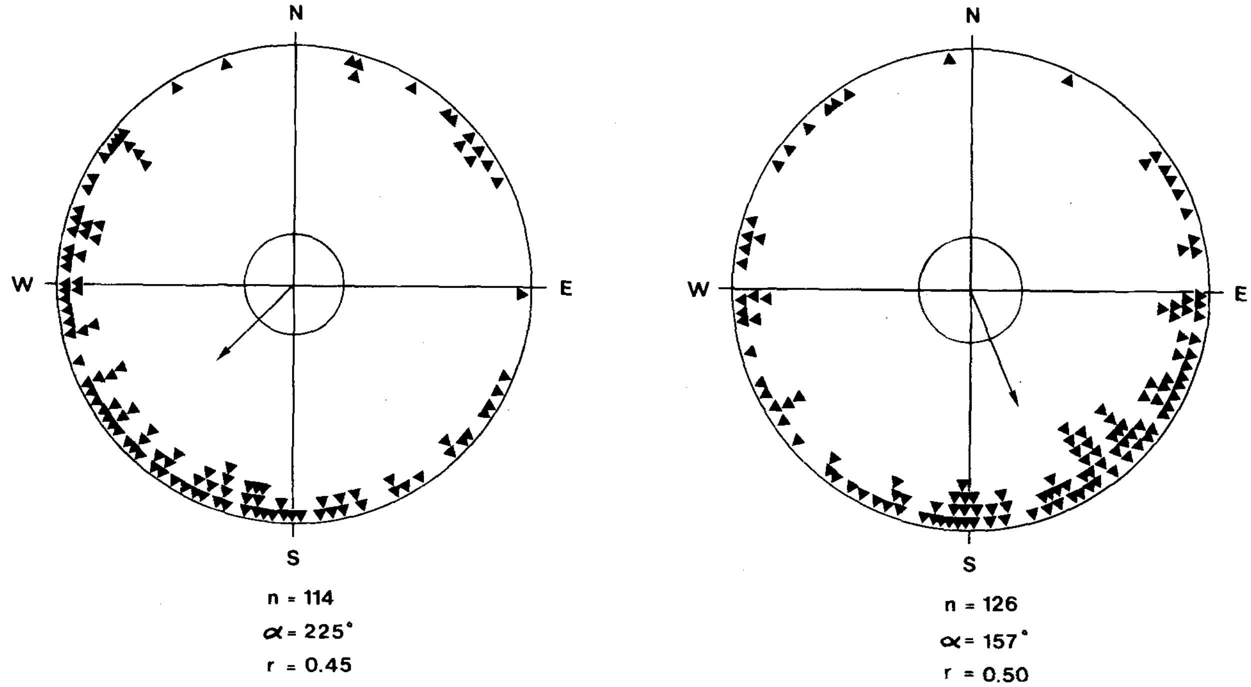


Figure 2. Directional preferences of hand-raised blackcaps (*Sylvia atricapilla*) in autumn in orientation cages (EMLEN funnels). Left: birds from western Germany, right: from eastern Austria. α: direction, r: length of sample mean vector; the inner circles mark the 99 % significance level of the RAYLEIGH test (from Helbig and Wiltschko[33]).

An example from recent studies[33, 42] is given in figure 2. Blackcaps (*Sylvia atricapilla*) are, like many other migratory species, characterized by a 'migratory divide'. Blackcaps from the western parts of central Europe migrate from their breeding grounds in a southwesterly direction (towards western Mediterranean and West African winter quarters), whereas populations breeding in the eastern part of the European breeding range migrate east towards East African wintering areas). Although different populations are not completely separated by this divide, the mean migratory directions of the two groups in the west and east of Europe are separated in a highly significant manner by an angle of about 50 degrees[36]. When blackcaps from both sides of the migratory divide were hand-raised and tested in orientation cages, they showed directionality appropriate to the migratory directions taken by their respective parent populations. Corresponding results were also obtained in a retention experiment by Schüz[49] in which young white storks (*Ciconia ciconia*) were released when the adult individuals had already left the breeding areas. In spite of the lack of experience, experimental birds managed to migrate in the appropriate direction towards the winter quarters[48] (see also Wallraff[54]). Similar results were also found with displacement experiments using white storks from an eastern population transplanted to the western side of the central European migratory divide (separating western birds migrating to Africa via the Iberian Peninsula and eastern birds passing Asia Minor or Greece). These individuals retained their easterly tendency[49]. Young European starlings (*Sturnus vulgaris*) trapped in the Netherlands during their autumn migration from the Baltic region to west European wintering areas and transferred to (and released in) Switzerland, continued their autumn migration to Spain, an area that normally is not reached. Thus, they continued their migratory journey in the programmed direction and to some extent also for the expected distance in spite of the transfer[43].

Empirical support for the existence of endogenous, spatial orientation-programs comes also from a detailed analysis of directional preferences in garden warblers. Garden warblers are broad front migrants that reach their African winter quarters from Eurasian breeding grounds using a variety of migratory directions (depending on the location of the breeding population). Central European populations, however, are uniform in that the initial migratory journey is inevitably in a southwesterly direction to the Iberian Peninsula. Since garden warblers winter exclusively in Africa (and would not be able to cross the Atlantic Ocean and have never been observed in South America) they have to shift their migratory direction somewhere in the vicinity of the Iberian Peninsula more towards the south to reach their African winter quarters (ranging from Gambia and S. Nigeria to southeastern Africa[56]). The necessary shift in migratory direction should take place approximately in the middle of the migratory journey. Figure 3 shows the results of an experiment conducted by Gwinner and Wiltschko[32], in which hand-raised, southern German garden warblers were tested for directional preferences throughout the whole of their first autumn migration season. It is evident from this experiment that caged individuals preferred a more-or-less southwesterly direction during the time when free-living garden warblers migrate in a southwesterly direction. The experimental birds then changed to a southern, or southeastern direction at about the time when wild garden warblers perform a similar directional shift in the western Mediterranean area.

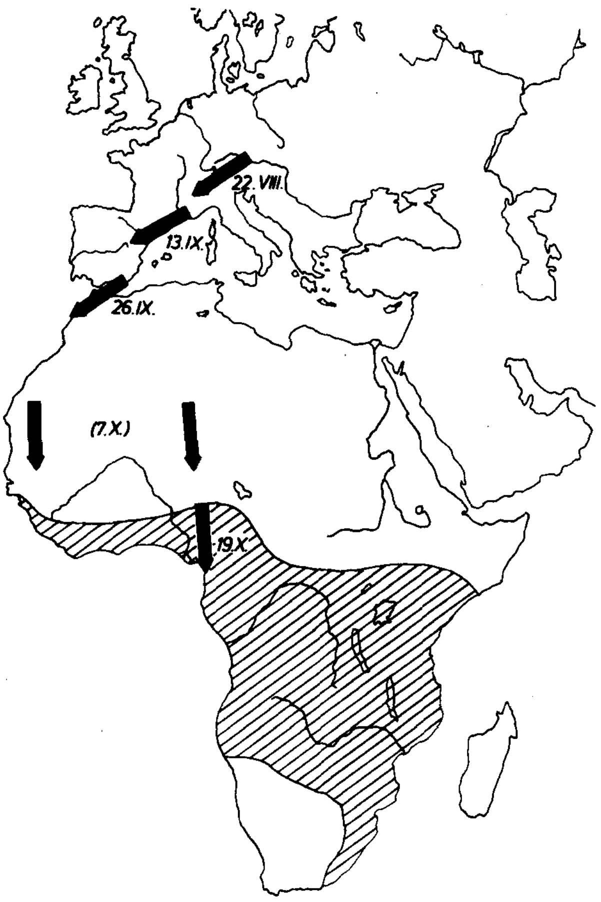


Figure 3. Directional preferences (arrows) shown by hand-raised German garden warblers (*Sylvia borin*), kept in southern Germany, during those periods in which free-living conspecifics pass through certain field stations (average passage dates indicated). Hatched area: winter quarters. The preferred mean directions of the experimental birds (repeatedly tested in orientation cages in southern Germany) are depicted on the map at the places where free-living conspecifics are usually found on passage migration at the corresponding time in the season. In addition, median dates for the passage are given (from Gwinner and Wiltschko[32]).

The most parsimonious interpretation of these results would be to suggest that garden warblers are equipped with specific, programmed, migratory instructions that include a mandatory shift in direction (Zugknick) during the migratory journey. It is likely that the shift of the migratory direction is linked to the circannual rhythms controlling the annual periodicity of the birds (as shown in the previous section). Experimental evidence supports this hypothesis; when the annual periodicity of a migratory species is accelerated (by photoperiodic manipulations) so that subsequent migratory events occur earlier, the shift in directional preferences also occurs earlier in the season[23]. On the basis of these results, garden warblers seem to be equipped not only with a primary, programmed, migratory direction but also with an internal turn-table for shift in direction based on the circannual system.

Inheritance of time-programs and orientation behavior

The existence of endogenous circannual rhythms in migratory birds, which are now considered to be entirely self-sustained and also self-started[31]; the development of migratory restlessness in inexperienced caged migrants, which appears to be the expression of endogenous time-programs for migration; and the demonstration of the presence of programmed migratory directions in young birds, all suggest the existence of heritable behavioral traits. Thus, these traits should be genetically transmitted from parents to their offspring. In the blackcap, inheritance of migratory behavior has indeed been demonstrated through a number of experiments.

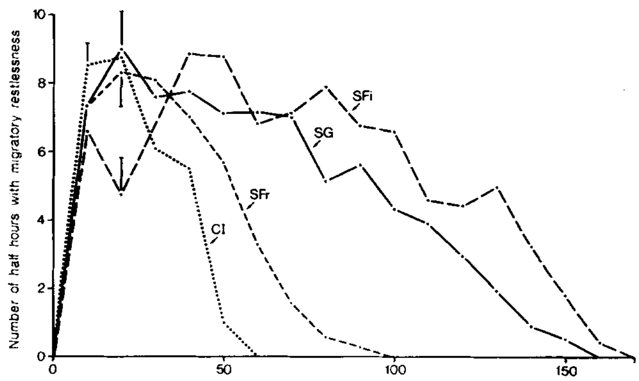
The blackcap is a widely distributed species (it breeds near to the polar circle in Eurasia and nearly up to the equator in Africa) and shows an amazing amount of differentiation in migratory habits in various populations[19]. Basically, the northern-most breeding populations are exclusively long-distance migrants, the middle-temperate zone populations are middle-distance migrants, the Mediterranean and subtropical breeders are partially migratory short-distance migrants, and finally, at least one population is entirely nonmigratory (on the Cape Verde Islands). Patterns of migration are further diversified by the central European migratory divide (discussed earlier).

When experimental birds from these four different populations were hand-raised and tested for migratory restlessness, they showed amounts of restlessness appropriate to their population-specific migratory behavior (thus reflecting the same pattern exhibited by different species – see above). More specifically, the highest amounts of migratory activity were found in the most migratory population from Finland, and progressively less activity occurred in the German, French, and African populations (fig. 4).

When the required conditions for breeding had finally been determined we were able to breed blackcaps from wild populations in aviaries[10]. The large-scale breeding program that ensued made research into the genetics of avian migratory behavior possible. An initial cross-breeding experiment was conducted to test for possible inheritance of the amount of migratory restlessness. For practical reasons, we chose blackcaps from the Canary Islands and from Germany as parental stocks. The results were very clear (fig. 4); the hybrids showed intermediacy with respect to the amount, the temporal pattern and even the variance of the migratory patterns of the parental population. Hence, important population-specific features of migratory restlessness are heritable to a considerable extent, at least in the blackcap.

These results were confirmed and extended when birds from the nonmigratory population on the Cape Verde Islands and from the migratory German population were used in another cross-breeding experiment. 37% of a total of 35 F_1-hybrids exhibited migratory restlessness (indicating that the fundamental urge to migrate can be genetically transmitted), and these hybrids also produced relatively intermediate amounts of restlessness[21].

The next, primary efforts in our genetic studies of migratory behavior were devoted to the inheritance of spatial orientation. In an initial cross-breeding experiment with nonmigratory blackcaps (from the Cape Verde Islands) and migrants (from Germany) we addressed the question of whether directional preferences can be transmitted genetically. From the 35 hybrids obtained from the experiment described above, seven were tested for directional tendencies in orientation cages. These birds showed a clear, significant preference for a southwestern



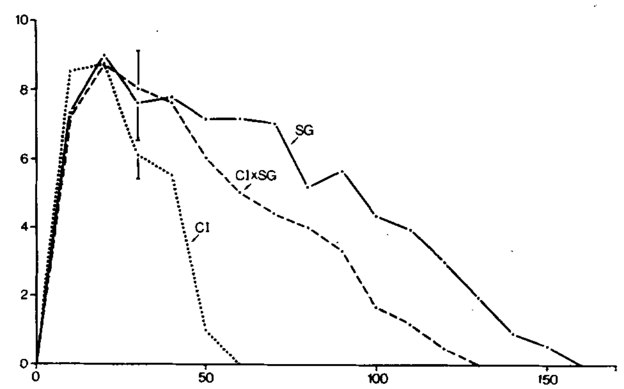


Figure 4. Time course of migratory activity (restlessness, Zugunruhe) in groups of hand-raised blackcaps (*Sylvia atricapilla*) from four populations (left) and of hybrids and their parental stocks (right). SFi, southern Finland; SG, southern Germany; SFr, southern France; CI, Canary Islands, Africa. Vertical lines: standard error, examples (from Berthold and Querner[17]).

direction in autumn (range 15° – 195°) and a northeastern direction in spring (51° – 231°[21]), both of which are in good agreement with the migratory directions used by wild birds of the German parental population. Thus, orientation behavior can be directly inherited, even by offspring of nonmigratory individuals, and, like migratory restlessness, is a heritable, population-specific characteristic.

Present and future studies should shed light on details of how migratory behavior is inherited (i.e., the mechanisms, the heritability values, the extent of genetic determination, and the degree of which genetic-environmental interactions determine the phenotypic expression of various migratory traits). With respect to migratory restlessness, which is clearly a quantitative behavioral trait, both the intermediacy of the hybrids, as well as theoretical considerations[24], support the concept that a polygenous system is involved in its control. It is, however, much more difficult to propose a mechanism for the inheritance of the orientation behavior. To test whether intermediate-, or dominant-inheritance is involved, a crossbreeding experiment was conducted with blackcaps from the eastern and the western side of the central European migratory divide (Helbig, in prep.). The directional preferences of a total of 69 hybrids tested during the first autumn migratory period were compared with those of their parents, which had previously been tested in the same manner (as described above, see fig. 2). These data are still being analyzed, but the results thus far indicate intermediate inheritance.

The vector-navigation hypothesis

As outlined in the introduction, there are in theory four main possibilities with respect to how inexperienced birds might find their specific winter quarters: 1) by tradition, a relatively rare situation in which young birds are led by experienced adults; 2) through inherited knowledge of environmental cues specific to the wintering area that, when recognized, inhibit further migration; 3) by an inherited program that produces temporal schedules and migratory directionality, and 4) by some combination of the above possibilities.

Many years ago, the assumption that endogenous factors are involved in the control of bird migration led to a proposal that outlined how lone, inexperienced migrants might find their winter quarters. Stresemann (1934)[51] wrote: 'The migratory bird moves ahead until its migratory urge fades away; and the migratory urge is active for as many days as, on average, are necessary to cover the distance between its birthplace and the winter quarters'. Over the course of experimental elucidation of endogenous components related to migration, a comprehensive navigation hypothesis has been formulated. It was named the 'vector-navigation hypothesis' by Schmidt-Koenig in 1973[47] on the basis of the evidence that migratory behavior represents a vector composed of an endogenous time-program coupled with a corresponding directional program.

With the experimental evidence summarized in previous sections in mind, one can update the hypothesis as follows. In a young, migratory bird, inexperienced in migration, and without the benefit of experienced conspecifics, endogenous circannual rhythms will control juvenile development (in which detailed genetic programs for temporal course and intensity of the juvenile molt and other processes are involved[12]). When the juvenile molt is progressing appropriately, the endogenous rhythms will trigger the onset of the first processes directly related to migration – normally, migratory disposition and hyperphagia[4]. Hyperphagia, based on the consumption of additional food[5], will lead to fat deposition. When a typical species- or population-specific degree of disposition or amount of fat deposition is reached, the onset of migratory activity is triggered by the program, and the migrant will take off for the first time, and it will do so at the appropriate time of day, e.g., after sunset in case of a nocturnal migrant. Once started, it will follow the endogenous time- and direction-programs. Normally, given obvious constraints, it will proceed in a large number of rather short intervals of active migration interrupted by many stopover periods used for resting and for replenishing fat depots.

At the beginning of the migratory season, phases of active migration will normally be very short (possibly less than one hour, since the average forward movement, e.g. in central European songbirds, is only of the magnitude of 50 km/day). Later in the migratory season, primarily when ecological barriers such as deserts, mountains or seas have to be traversed, migratory activity will intensify greatly. For example, in nocturnal migrants, nocturnal migratory activity will take place for the entire night. Such migratory phases may be controlled by a sliding set-point mechanism provided by the endogenous time-program for migration. An interesting example for this was found in the marsh warbler (*Acrocephalus palustris*). This peculiar migrant leaves its European breeding-grounds as early as mid-July (regardless of the fact that the majority of the breeding population does not arrive before May), and migrates as far as the southern tip of Africa. However, it does not arrive there before late December/January, even though it passes northeastern Africa in mid August and central Africa in October. Thus marsh warblers have a biphasic migration pattern, rapid during the first part and slower in the second. Hand-raised individuals show a pattern of migratory restlessness in which high amounts of activity occur during the first period of autumnal migration and lower activity occurs in the subsequent period[16]. Hence, the pattern of restlessness mimics the course of migration to a considerable extent, or in terms of the vector-navigation hypothesis, a sliding set-point mechanism of program-mediated activity may lead the birds to their wintering grounds, either exclusively or in combination with additional control mechanisms.

Finally, the vector-navigation hypothesis proposes that when endogenously programmed migratory activity ceases, the bird will normally have reached the specific winter quarters. In order to achieve the programmed migratory direction, or directions, used during the course of migration, the migrant has to use compass mechanisms, for which, as in the case of the stellar compass, some experience during juvenile development is necessary (see the paper of Wiltschko and Wiltschko in this issue). If such prerequisites of experience are met, the migrant has, according to the hypothesis, 'automatically' reached its specific wintering area having migrated along its inherited, spatiotemporal vector.

Discussion

We have found that endogenous circannual rhythms in migratory birds control not only the overall annual rhythms but specific migratory events as well. The discovery that migratory activity and directional orientation are both genetically controlled and programmed for coverage of the appropriate distance between the breeding grounds and the winter quarters strongly supports the vector-navigation hypothesis. That is, inexperienced migrants on their first migratory journey are guided by inherited programs so that they can 'automatically' reach their specific winter quarters. Two alternative hypotheses have been discussed in recent years: 1) that the distance to migrate is not measured by endogenous time-programs (via migratory activity) but by endogenous energy-programs (via fat-depots) and 2) that environmental cues in the winter quarters were responsible for the termination of migration[7, 30, 53].

Evidence is weak or even lacking for both alternatives. In captive migrants it can be shown experimentally, for example using interposed periods of starvation, that fat deposition (and thus the body weight cycle) is strictly a product of endogenous control. A sliding set-point mechanism controls the details (e.g. the rate) of initial increase in body weight, the maximum level of fat deposition and finally its maintenance and also the timing and rate of decline following each migratory season[6]. In many captive long-distance migrants, however, the period of fat deposition exceeds the production of migratory activity (restlessness), and also exceeds the known migratory period of wild conspecifics. It is also apparent from studies on wild birds that individuals can reach their goal area with large fat depots remaining[41]. On the basis of these observations, the regulation of migratory distance using fat depots and energy consumption is rather unlikely. There are further problems with this hypothesis as well. In captive migrants fat deposition in a given migratory season can be entirely prevented (by restricted energy availability), but the time program of migratory activity continues normally[7]. Continued migration by extremely lean birds is also well known in the wild. Further, close to their final destinations, migrants often show extremely high variability in fat depots owing to the different, individual energetic demands of their previous journeys[41]. In these cases it is obviously difficult to see how energy consumption, fat stores, or body weight might control a programmed time-course of migration.

Sauer[46] has proposed that migrants have a programmed knowledge of the star patterns of the sky in their specific wintering area and that they terminate their first migratory journey when the observed pattern of stars and the programmed one agree. When European warblers were transported to their wintering areas and were allowed to experience the local sky conditions they did, however, not stop their migratory activity but exhibited it as long as controls in the breeding area did[27]. Thus the stellar-navigation hypothesis is unlikely; it has no other support, and evidence recently obtained on how birds use star patterns for orientation (see Wiltschko and Wiltschko in this issue) also do not favor the idea.

If the vector-navigation hypothesis is valid, a number of intriguing questions arise: 1) to what extent is endogenously controlled 'automatic' migration regularly modified by normally acting environmental factors? 2) Can migrants be led exclusively by their programmed vectors to their winter quarters, and if so, how consistently? 3) Are there specific interactions between migration programs and environmental interferences which produce overt migratory behavior; above all, adaptive compensations and safety measures in case of specific disturbances?

It is clear from numerous observations that unusually extreme environmental conditions (for example, very severe cold spells in autumn) can strongly influence the course of migration of many migrants. They can even hold up the journey, as did an extended, cold, rainy period in 1974 in central Europe (swallows' disaster). But such extreme conditions are relatively rare exceptions. Much more interesting is the question of how normally occurring environmental variables might possibly influence and modify the course of programmed migration. Unfortunately, up to now we have not followed the course of migration of individual birds in nature over long distances. Based on indirect observations of migrants, however, the following picture emerges. In deserts, like the Sahara, the vast majority of migrants apparently pass through in a few continuous steps. Nocturnal migrants land during the day, seek shade in hiding-places in the open desert, take off the next evening, and continue this process for the next few days until the ecological barrier is overcome. Only relatively small numbers of migrants reach oases, and here the majority of staging birds behave in the same manner as those in the open desert, with only about 20% staying longer than one day to replenish depleted fat reserves[3, 22, 38]. Possibly the desert is also traversed via long, non-stop flights, in which case the percentage of strictly passage migrants is even higher.

Similar patterns of resting behavior occur in migrants in normal staging areas in central Europe as well. A long-term trapping program, the 'Mettnau-Reit-Illmitz program' for the study of migration[14], has revealed that approximately 60% of passerines stay for only a single night in a given resting area. The 40% that stay longer are, to a large extent, young individuals that still show considerable juvenile molt and are just in the initial phase of their migration. Thus, the majority of the migrants appear to be in a continuous, 'daily stream' phase of their migratory journey. The average daily movement towards the winter quarters during the first autumn migration (according to ringing recoveries of passerines), is only of the order of 50 km[36]. And since we know from various types of field studies that it takes several months for migrants to arrive safely in central Africa from central Europe, in the average daily migration intervals must be very short in time as well as in distance; around a few hours of active flight. These values may be even lower in the initial phase of the migratory journey, but are surely much higher during the peak migratory period, above all when traversing ecological barriers.

Thus, during considerable periods of the initial migratory journey, the average daily migration intervals are short, and thus migrants should, as a rule, not meet serious difficulties. In addition, climate and food availability should be favorable during the initial stages of migration. Even when birds are forced to stop during migration, for example during a thunderstorm, they should be able to complete a programmed migratory interval, and the overall migration program will not be seriously impaired. As a rule, the situation in which environmental conditions are so nasty or permanently unfavorable that programmed migration intervals will be suppressed or strongly affected should only happen rarely. Thus, if the endogenous migration programs have short migration intervals over a very extended migratory season, migrants should, as a rule, not be much impeded in following them.

In this context, a calculation, carried out by Gwinner[28], is most interesting. First, distances migrated by European warblers in given periods (as revealed by ringing recoveries of banded individuals) were compared to amounts of migratory activity (restlessness) displayed by captive conspecifics during the same periods. Next, a calculation was made of the traveling distance in which the total amount of restlessness of the experimental birds would have resulted. The calculation demonstrated that the programmed migratory activity would just have transported the birds from their breeding grounds to the central areas of their specific winter quarters.

With respect to the other questions raised above, our present knowledge indicates that migrants frequently search for altitudes with favorable (normally not too strong) tail-winds, and that they tolerate drift in favorable wind conditions[1], but show various types of drift compensation[45]. Presently, it is impossible to judge to what extent an 'ideal' course of migration is obtained by these mechanisms, but accidental variation may be considerably damped. Wintering areas of long distance migrants occupy, as a rule, a large, latitudinal area, often over several hundred kilometers. Hence, even when a migration program might be modified to some extent during the course of migration (by environmental variables like wind, etc.) it should still reliably bring migrants into the overall specific goal area. Should a program fail, however, or should migrants become exhausted somewhere during their course of migration, several backup measures are known to operate. If unusual fat depletion occurs, migrants can stay in one place for relatively long periods to replenish their fat depots if food is available[22]. Stopover areas with insufficient resources for maintaining migrants will produce facultative migratory activity. This behavior should lead migrants to more favorable regions, i.e., by continued migration in the previously preferred migratory direction. Such facultative migratory behavior may even occur after termination of the migratory period and before the winter molt period begins[52].

On the basis of mechanisms now known to us, therefore, a considerable number of migrants, migrating for the first time, could be essentially 'brought' by their vector-navigation system to their hitherto unknown winter quarters. Migratory backup systems are known to operate when necessary. In this context a recent computer simulation by Williams and Williams[55] is relevant. Shorebirds migrating from Alaska to the South Sea would still reach their preferred goal area in the Hawaiian archipelago on the basis of vector-navigation even if the worst known meteorological conditions in the take-off area are postulated.

Finally, it should be emphasized that a vector-navigation system does not necessarily imply a rigid, unalterable, migratory program. Provided there is sufficient interindividual, genetic variation such a program may well be able to adapt rapidly to changing environmental conditions. Such a rapid change is apparently in progress in the blackcap in that part of the central European population that has developed a novel migratory direction to the north, to new wintering areas on the British Isles, in just the past 25 years[13, 20].

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