Is There a "Migratory Syndrome" Common to All Migrant Birds?

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ABSTRACT: Bird migration has been assumed, mostly implicitly, to represent a distinct class of animal behavior, with deep and strong homologies in the various phenotypic expressions of migratory behavior between different taxa. Here the evidence for the existence of what could be called a "migratory syndrome," a tightly integrated, old group of adaptive traits that enables birds to commit themselves to highly organized seasonal migrations, is assessed. A list of problems faced by migratory birds is listed first and the traits that migratory birds have evolved to deal with these problems are discussed. The usefulness of comparative approaches to investigate which traits are unique to migrants is then discussed. A provisional conclusion that, perhaps apart from a capacity for night-time compass orientation, there is little evidence for deeply rooted co-adapted trait complexes that could make up such a migratory syndrome, is suggested. Detailed analyses of the genetic and physiological architecture of potential adaptations to migration, combined with a comparative approach to further identify the phylogenetic levels at which different adaptive traits for migration have evolved, are recommended.

KEYWORDS: behavioral syndrome; bird migration; life history; phenotype; comparative method; trade off; coadapted trait complex; evolution of migration; exaptation

INTRODUCTION

Many people worldwide, including the community of professional biologists, continue to be impressed, inspired, and challenged by the seasonal movements of

migratory birds around the globe. Perhaps as a result, the phenomenon of bird migration has attracted much focused scientific attention in the past few decades, and this has generated several dozens of volumes dealing exclusively with bird migration.[1–6] All these efforts seem to have subsumed, or inspired, the idea that bird migration is a truly biologically distinct and unique phenomenon, that birds (and perhaps a few other groups of animals) possess an integrated group of special traits that enable these migrations. This is the migratory syndrome of birds. Here we summarize and develop the discussions at the ESF workshop "Are There Specific Adaptations for Long Distance Migration in Birds? The Search for Adaptive Syndromes" at the Max-Planck Institute for Ornithology in Andechs/Seewiesen, Germany, from January 6–8, 2005. In several different ways we actually develop the theme "evolution of bird migration" beyond the discussions provided by Zink and Rappole.[7,8]

Sih *et al.*[9] recently defined a *behavioral* syndrome as "a suite of correlated behaviors reflecting between-individual consistency in behavior across multiple (two or more) situations. A population or species can exhibit a behavioral syndrome. Within the syndrome, individuals have a behavioral type (e.g. more aggressive versus less aggressive behavioral types)." When referring to the *migratory* syndrome, we tend to mean something deeper and older than a set of traits that is distinct at the individual or population level (but see below). An important aspect of (life history) syndromes in general is that they are highly integrated at the morphological, sensory, physiological, and behavioral levels.[10] Although we restricted our search to birds, a clade of derived dinosaurs, Dingle[11] took it a step further by searching for a migratory syndrome in all animal groups. He defined five basic migration characteristics: (1) persistent movement between distant sites; (2) directional movement; (3) inert behavior to arresting stimuli; (4) zugdisposition (i.e., distinct behavior for departure and arrival); and (5) energy allocation (i.e., migratory fueling). These characteristics all hold for migrating birds.

To structure our discussion, we first briefly discuss what it takes to be a long-distance migrant in general, starting off with some clear exaptations to seasonal migration (i.e., traits that evolved as responses to diverse selection pressures not related to migration, but later turned out to be useful preadaptations for a migratory lifestyle);[12] we then compile a listing of the set of biological traits required for a migratory lifestyle. We would expect all these traits to be integrated in a single migratory syndrome at some phylogenetic level, if there is such a thing. We therefore proceed by putting some of these expected traits in a phylogenetic context (how old and phylogenetically deep are these traits), and round up by discussing whether the idea of an old and integrated migratory syndrome can be upheld.

EXAPTATIONS AND ADAPTATIONS TO LONG-DISTANCE MIGRATION

To start our search for a migratory syndrome, we first seek to define traits that, in isolation or combined, characterize birds with a migratory lifestyle. It seems particularly relevant to search for traits that are more elaborate in migrants compared with (most) residents, and which may therefore represent true adaptations to migration.

To be able to move efficiently over long distances, a land animal needs wings to reduce the cost of locomotion—that is, to fly.[13] It also needs modest body size to be able to become airborne in the first place, as well as pointed wings (and other morphological features) to make flight energy efficient.[14–16] To reduce the mass carried aloft, a flying animal would do well with a particularly light skeleton (e.g., two-layered skull bones or generalized reduction of bone structures), and migrants would also need efficient respiratory systems, such as the lungs of birds that recirculate air to ensure rapid and complete oxygen extraction.[17] Birds possess all these traits (flight capacity including light bones, modest size, aerodynamic morphology, and an efficiently extracting respiratory system), but as these traits are general to almost all birds, they should be regarded as preadaptations, or exaptations. Although such exaptive traits—or more specifically, trait values—may increase fitness of migrants compared with alternative trait values, they need to be distinguished from true adaptations, which are derived characters built by selection *for their current roles*.[12,18,19]

More to the point, perhaps, would be a listing of the traits directly associated with the specific issues of long-distance migration. During the ESF workshop we came to the following listing of migration-related problems and their phenotypic solutions. Our list is neither novel nor very original. It has been put forward in various disguises in the older literature.[20] However, so far no attempt has been made to distinguish between preadaptations and true adaptations to migration.

Long-distance migrant birds typically need to deal with the following issues and have come up with the following solutions.

(1) *Precise timing of seasonal physiological events*: taken care of by the development of sophisticated endogenous circannual clocks that function as evolutionary ecological memory systems.[21–26] Circannual clocks help to predictably time a very diverse range of aspects of a bird's life cycle, including molt,[2,24] migratory fattening,[21,23,27] migratory direction and distance,[25,28–30] gonadal growth,[21,24] and changes in the bird's internal organ physiology.[31–34]

(2) *Finding the way over large distances*: solved by evolution of sophisticated long-distance orientation systems, including long-distance compass orientation based on global cues such as the stars, the sun, and Earth's magnetic field[35–40] combined with endogenous information about migratory direction,[25,30,41,42] to which learned components are added with experience (e.g., detection of North based on celestial rotation[43] and identification of cues needed to relocate a bird's first breeding and wintering site[44]). Nighttime compass orientation in particular may require special physiological and molecular adaptations.[45,46] In some species, evolution of social behaviors facilitating successful orientation have evolved; some birds use a so-called guiding strategy, during which young birds follow parents or other adult conspecifics during first migratory journeys.[44,47]

(3) *Endurance performance (extended fasting and intense exercise)*: this is achieved by (a) quick adjustments of metabolism—for instance, extremely fast and efficient fat metabolism and storage;[48–52] (b) seasonally predictive fueling and molt;[26,53] (c) organ flexibility (e.g., reduction of digestive tract size and subsequent rebuilding of digestive system within a few days);[54–56] (d) endurance musculature;[57–60] and (e) specialized hemoglobin with par-

ticularly high oxygen affinity (left-displaced oxygen extraction curves) enabling high-altitude flight exercise.[61–63]

(4) *Contrasting environments (different food, competitors, predators, and parasites)* necessitate (a) flexible digestive systems (e.g., gizzard changes in shorebirds;[54] (b) nutritional flexibility;[51,52] (c) broad-spectrum immune defense systems;[64] (d) physiological flexibility;[65] and (e) specific cognitive abilities.[66]

(5) *Predation and potential for overheating during flight:* taken care of in some groups of birds by night-time migration,[67,68] which demanded the evolution of orientation mechanisms specialized for nighttime travel [see (2)].

(6) *Tracking or predicting food resources*: possible with the capacities listed under (2), but also needs orchestrated seasonal changes in physiology and metabolism (1, 3), as well as concomitant life-history adjustments, resulting from the combination of the reproductive benefits of exploiting seasonal habitats and the mortality costs associated with migration.[69]

(7) *Seasonal time pressures*, which can be solved by (a) multitasking (overlapping of physiological changes, e.g., testicular development during northward migration,[70] special abilities to speed up physiological processes); (b) accurate circannual clocks [see (1)]; (c) special adaptations allowing migrants to cope with sleep deprivation;[71] (d) selection for speeding up physiological capabilities; and (e) optimization of flight speed and efficiency (e.g., aerodynamic shape, long and pointed wings, ontogenetic variation in shape of the flight apparatus[72–75]); and (f) optimization of stopover and flight.[76,77]

(8) *Continuous variation and some degree of unpredictability of resource distribution*. Unpredictability in the environment has led to relatively large genetic variability in migratory traits within migrant populations. This genetic variation combined with the fact that phenotypic expression of migratory behavior seems to be determined by a genetic threshold, at which birds abruptly change from being migratory to being sedentary (the so-called Zugschwelle) means that changed selection pressures can result in bird populations switching between sedentary and migratory lifestyles within a few generations.[8,25,78,79]

EMPIRICAL FINDINGS

A review of the occurrence of the just-mentioned traits in various birds suggests that many specific traits are correlated with migration distance, but that no single trait seems to be unique to migrants. The single exception to this rule could be nighttime compass orientation and the consequential physiological and molecular adaptations, which may be unique to night migrants.[45,46] The reason seems to be that although long-distance migration results in several problems and constraints, most of these are of a more general nature such as endurance capabilities and coping with food-type variability, which are also facing several resident species living in special or extreme environments. Thus, while no single trait seems to be unique to long-

distance seasonal migrant birds, migrants do seem to be found at one extreme end of several more or less continuous trait distributions.

PHYLOGENETIC PERSPECTIVES: MAPPING MIGRATORY TRAITS ON PHENOGRAMS

Arguably, the best way to decide whether the previously listed migration-related traits or trait complexes represent aspects of one or more highly integrated and old migratory syndromes is mapping of the traits onto phylogenetic trees.[7,8,18] By studying migration in a phylogenetically explicit context, several studies have shown that migratory habits of birds are evolutionarily labile (FIG. 1). The whole range from
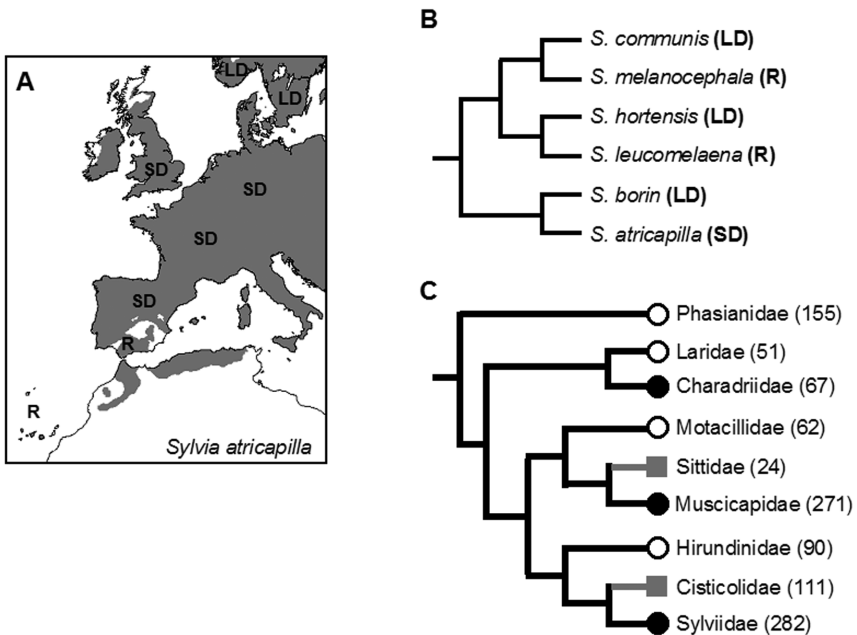

FIGURE 1. The complexity of the evolution of the "migratory syndrome" can be understood by analyzing its components in a phylogenetically explicit context. Variation in migratory behavior may be extensive within a single species, as shown in (**A**) by blackcaps *Sylvia atricapilla*, which include long-distance migrant (LD), short-distance migrant (SD), and resident populations (R) across their range (*shaded*). The same pattern is observed among closely related species, as shown in (**B**), by six *Sylvia* warblers (family Sylviidae[94]). However, evolutionary constraints are revealed at higher phylogenetic levels, as shown in (**C**), by nine bird families (the number of species in each family is shown in brackets). The tree (based on Refs. 95 and 96) shows six families that are primarily migratory (*circles*), contrasting with two families with conserved absence of migration (*gray branches* and *squares*). Within migratory families, the occurrence of nocturnal migration (*filled dots*), as opposed to diurnal migration (*open circles*), has been mapped as well. Although nocturnal migration seems to have repeatedly been gained and lost during the evolutionary history of birds, flying time is mostly constant within families.

long-distance migration to complete residency can be found within a single family or genus,[80] and such variation, together with the consequent changes in important components of the migratory syndrome like morphology, seasonal fattening, life history, and others, can evolve within a single species in just a few thousand years.[25,81] This circumstance makes us wonder whether or not the migratory syndrome is evolutionarily constrained.

However, looking at the occurrence of migration between bird taxa gives us little information on evolutionary constraints on each presumably adaptive trait. Migration is likely to be as old as the birds themselves (or even older), yet different bird taxa have evolved completely different solutions for moving long distances. For example, some species rely on endogenous programs to decide when and where to move, whereas others mostly follow social influences[47,82] or environmental cues.[83] Similar differences can be found for most of the traits common to all migratory birds (listed earlier), such as having orientation abilities (nocturnal and diurnal migrants use quite different clues) or putting on fat seasonally (warblers, waders, and geese may have quite different physiological mechanisms of fat deposition and use).[84]

Diverse solutions to the same problems posed by migration have probably evolved as independent responses to dissimilar selection pressures—not necessarily related to migration—in different bird taxa. As a consequence, if we are to identify evolutionary constraints on migratory syndromes, we first need to dissect such syndromes into traits and then determine whether such traits are homologous among the birds that share them or if they have evolved as independent adaptations in each group. For example, the occurrence of nocturnal migration is quite scattered along the phylogeny of birds, with nocturnal migrants being paraphyletic with respect to diurnal migrants (FIG. 1C). The presence of suspected physiological and molecular mechanisms for night orientation in nocturnally migrating garden warblers (*Sylvia borin*), but not in sedentary zebra finches (*Taeniopygia guttata*) or chickens (*Gallus gallus*) (which are included in mostly resident or otherwise diurnally migrating families[45,46]) suggests that diurnal migrants lack the machinery for nocturnal orientation (rather than keeping it unexpressed). Future studies should determine whether nocturnal migration evolved early and was repeatedly lost by different families or whether extant nocturnal migrants have independently evolved different physiological mechanisms of nighttime orientation (FIG. 1C).

The preceding example also illustrates the need to analyze the evolution of different potentially adaptive traits at different phylogenetic levels. The fact that all migratory families in FIGURE 1C include species with different behaviors (from resident to long-distance migrant) shows that some adaptations to migration can evolve very rapidly. Such traits can most elegantly be studied in species with diverse migratory behaviors, such as the blackcap (*Sylvia atricapilla*),[25] or in partial migrants and facultative migrants [e.g., redpoll (*Carduelis flammea*)[85]]. Considering the high susceptibility of migratory behavior to microevolution, different populations of the same species, or different species of the same genus, are likely to have the physiological and the molecular machinery needed to shift from migrant to nonmigrant in a relatively short time, as a response to ecological conditions.[79] However, such an evolutionary flexibility is not common to all species: although the adaptability of migratory patterns of some species seems little constrained,[27] other species retain apparently suboptimal migration patterns due to historical constraints.[86] Also very importantly, evolutionary flexibility is not common to all adaptations to migration.

Coming back to our example, all migratory families in FIGURE 1C are quite invariable with respect to time of migration (nocturnal or diurnal). This pattern indicates that some more fundamental physiological differences, such as the molecular or physiological machinery needed for nighttime orientation and/or magnetodetection, may be evolutionarily more constrained,[87] so their significance as true adaptations to migration can be evaluated only by comparing distantly related groups (families or higher taxa).

DISCUSSION

As we have seen, birds need many different adaptive traits to do a good job as a seasonal, long-distance migrant, even though any single species may possess only some of them. The phylogenetic perspective confirmed that there is no evidence for a single highly integrated and deep-rooted migratory syndrome. In fact, in various clades of birds, long-distance migrating species make up the tips of the trees, indicating that a migratory lifestyle, along with the necessary morphological, physiological, and behavioral adaptations, evolve and reevolve relatively quickly. At a deeper level, the ancestors to most birds (and certainly many of the dinosaurs[25]) have been migrants. Such an ancestry most likely provided them with the sensory acuity, clock-and-compass systems, and the basic performance machinery to become specialized long-distance migrants when the ecological need arose. However, with the evidence available today, we cannot discard the possibility that important traits associated with migration are true adaptations evolved during the radiation of birds, as innovative solutions to the same problems faced by their migratory ancestors (e.g., finding the way, putting on fat seasonally). To resolve this important issue, we need to disentangle the genetics, morphology, physiology, and ontogeny of the relevant traits. And such studies need to be combined with comparative analyses of the different trait features—from character architecture to current function—both within birds and between birds and other animals with variable migratory habits.

When considering adaptations to a migratory lifestyle, it is important to realize that migration requires a complex, highly integrated set of traits and that solutions to one problem may limit the possible solutions to another. For example, imprecision of the navigation system could limit the highest possible site fidelity and homing abilities of young birds.[44,88,89] In a similar way, remembrance of natal latitude[44] may limit otherwise adaptive breeding range change between years in individual birds.

Understanding the evolution of migratory adaptations is complicated by the different constraints (ecological, physiological, historical, and/or interactive) limiting adaptive changes in different traits. This also makes it difficult to predict how well migratory birds will be able to adapt to environmental change, either natural or induced by humans, which is an important conservation concern nowadays. Great advances in this direction have been achieved using some model species, such as the blackcap,[79] but an important implication of our review is that extending the conclusions obtained for one species to another may be problematic, particularly if the two species are distantly related.

One of the most critical challenges facing researchers in this field will be to understand the environmental triggers, cues, and regulators controlling seasonal and

predictive changes in morphology, metabolism, and neuronal signaling, and how these changes are controlled on the molecular and physiological level in birds with different migratory strategies. Such approaches may enable us to identify truly integrated sets of traits (migratory syndromes) specific to one or more bird taxa with well-known evolutionary histories. Furthermore, understanding the architecture, integration, and evolution of particular traits or sets of migratory traits is not only important from a purely scientific perspective but will also help us to anticipate possible adaptive responses of migratory birds faced with natural or manmade environmental changes.[90–93]

CONCLUSION

Different evolutionary constraints on the various adaptations to migration make us discard the idea of the existence of an old and integrated migratory syndrome common to all migratory birds. Some traits may have been inherited from preavian common ancestors, whereas others have independently evolved at different times during the radiation of birds. We believe that different bird taxa, at various phylogenetic levels, share different sets of adaptations and preadaptations, which are expressed or suppressed depending on particular ecological circumstances. This hypothesis explains why birds like the blackcap can shift from resident to long-distance migrant in a few generations, changing endogenous programs, morphology, or life history adaptively. But it also explains why single species, or even whole families, rarely abandon an endogenous program in favor of socially influenced migrations or shift from nocturnal to diurnal migration.

ACKNOWLEDGMENTS

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