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On the evolution of characters associated with migration

Bernd Leisler & Hans Winkler

ABSTRACT

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Migration is a powerful factor that shapes the flight apparatus and other morphological features of birds. Previous analyses have shown that morphological characters are excellent predictors of migratory distances. Here we show with examples from five different oscine lineages that a change to migratory features can occur in a very short evolutionary time and that the opposite change to residential ones may be equally pronounced. Factors that may account for these rapid reversals include the advantage of maneuverable flight and the trade-off between forelimb and hind-limb development. Sexes of residential birds interact for longer periods. These interactions are predicted to foster sexual dimorphism in traits that would be otherwise constrained by the stringent demands of migration.

Introduction

Environmental change is certainly an important driving force behind any evolutionary change in the features of organisms. Migratory behavior may be one of the responses to changes in seasonality, spatio-temporal distribution of resources, changes in habitat, predation, and competition (Alerstam & al. 2003). The evolution of migratory adaptations is complicated by different constraints (ecological, physiological, morphological) that may limit adaptive changes in different traits. Morphological changes are often considered to be slow compared to behavioral and physiological changes, and could therefore cause substantial evolutionary inertia for adaptive change. Previous work has shown that morphology, behavior and ecology have coevolved in the context of migration, producing various convergent adaptations for long-distance flight: The flight apparatus has exhibited the most pronounced changes, with a co-evolving suite of external structures, especially the wing

tip and tail, being the most affected by these changes (Leisler & Winkler 2003, Fiedler 2005). However, trade-offs between locomotory styles and energetic demands associated with a migratory life-style produce morphological changes in other domains, such as habitat use, as well (Winkler & Leisler 1992, Leisler & Winkler 2003, Winkler & al. 2004).

Several recent molecular phylogenetic studies have shown that not only have migrants evolved from (tropical) residents, but these studies also documented that non-migratory populations may originate from migratory ones (Zink 2002, Helbig 2003, Joseph 2005). This implies that evolutionary change may occur in either direction from characters that are more suited for a residential life to those needed for migration, and vice versa. Details of morphological evolutionary changes, especially those from migrants to residents, have not been studied yet, although changes in the wing tip have been investigated already by Stegmann (1962). In particular, an open question is whether morphological changes from adaptations to migration, back to adaptations of residents are as pronounced. If they are, one has to assume that there are selective forces that operate in that direction, and that these forces have to be identified.

In the current investigation we present evolutionary analyses of morphological traits and migratory behavior in different avian lineages (basically at the taxonomic level of genera) from different passerine superfamilies. Specifically, we analyze trade-offs between the development of hind and forelimbs, changes in the flight apparatus, and the constraints migration imposes on the evolution of sexual dimorphism. We focused on convergent adaptations for migration in lineages with different predispositions.

Material and Methods

Our comparative data came from the following species-rich lineages of passerine birds with resolved molecular phylogenies (partly used in previous analyses, Leisler & Winkler 2003, Winkler & Leisler 2005): Mimidae (Gulledge 1975), Acrocephalidae, *Sylvia*, *Anthus*, Parulidae (data measured for W. J. Bock, Columbia University, by Jaydeep Bhatt), and *Piranga*.

Other data sets pertain to published information on muscle masses of 385 bird species from different families (Hartman 1961) and skeletal measurements of falcons (Falconidae, Kemp & Crow 1993).

We generally compare at the species' level (using species means, for sample sizes see Leisler & Winkler 2003), but in *Anthus* we also included subspecies with marked differences in migratory behavior.

To describe shape differences in external morphology between species we used measurements of study skins as defined in Leisler & Winkler (2003) and corrected for size.

Phylogenetic trees were constructed using sequences deposited in Genbank. Trees were constructed according to the maximum likelihood principle using the PhyML software (Guindon & Gascuel 2003). The model of nucleotide substitution was set to GTR, with parameters optimized by the program (four categories for the discrete gamma-model). For *Sylvia*, the sequences comprised the complete mitochondrial *cyt-b* gene, and the tree was rooted with *Garrulax canorus* and *Bradypterus cinnamomeus* as an outgroup. We constructed the acrocephalid tree with 1041 bp of the mitochondrial *cyt-b* gene and rooted it with *Locustella lanceolata*, *Garrulax canorus*, and *Sylvia borin* in the outgroup. Calculations for the *Piranga* tree were based on 1044 bp of the *cyt-b* gene with *Thraupis bonariensis* and *Tangara varia* as outgroup taxa. The tree given by Voelker (1999) served as basis for our *Anthus* phylogeny. To accommodate the two subspecies of *A. hodgsoni*, which differ greatly in migratory behavior, we arbitrarily split the branch leading to this species in the original tree in the middle.

We analyzed the evolution of traits with the method of Schluter & al. (1997), and code adapted from their program ancml.c. Based on maximum likelihood estimates of character states at all nodes, rates of change were computed by dividing differences of character states along a branch with branch length. The original rates were then normalized by the mean rate at all branches to facilitate comparisons across lineages. Absolute values greater than 1 thus indicate above average rates. To avoid cluttering of the figures, only those relative rates discussed in the text were indicated in the trees of figures 4–7.

Results and Discussion

Trade-offs between hind and forelimb

A general allocation problem of muscle mass of forelimb and hind-limb seems to exist in birds (Leisler & Winkler 1991). This together with other constraints leaves forbidden morphological space (Fig. 1); Hindlimbs vary more than forelimbs with migration (Fig. 2). Long-distance migrants tend to have less leg muscle mass than either short distance migrants or residents ($p = 0.01$, Anova).

In the morphological space depicted in Fig. 1 migrants occupy a restricted

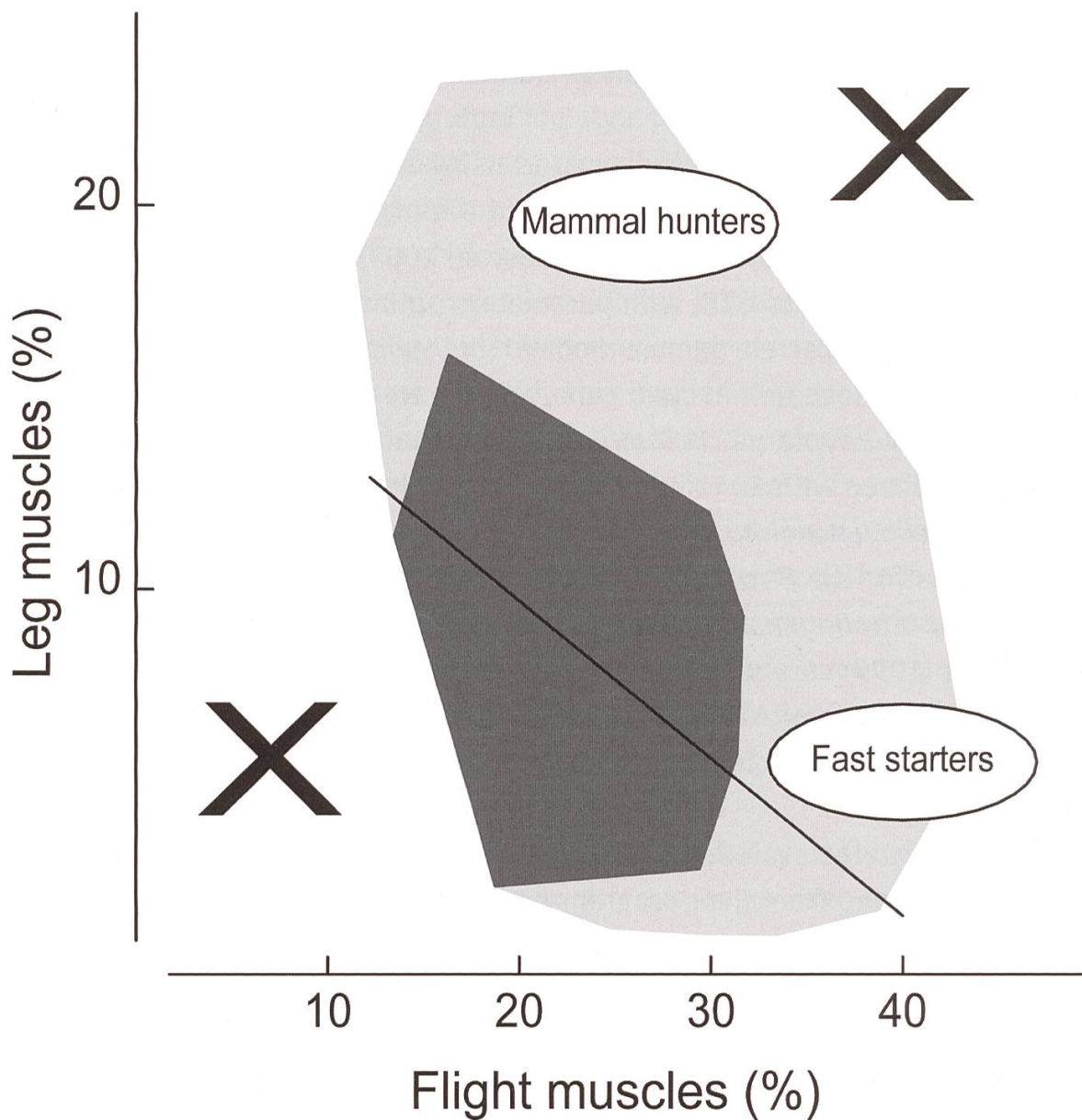


Fig. 1. Negative relationship ($r = -0.47529$, $p < 0.00001$) between forelimb and hind-limb muscles given as percentage of total muscle mass of 385 bird species (light grey). Migrants (dark grey) occupy a restricted subspace. X illustrates "forbidden morphological space", i.e. combinations of heavy legs with heavy forelimbs or light wings with light legs have not evolved. Data from Hartman (1961).

subspace. Birds with especially heavy hind-limbs, such as mammal hunting raptors and birds that obtain fruits by reaching down (Winkler & Preleuthner 1999, Moermond & Denslow 1983), and birds with massive breast muscles, those that forage on the ground and can take off rapidly ("fast starters" such as columbids, phasianids), are not found among long-distance migrants. Generally, birds that combine heavy legs with heavy forelimbs, or light wings with light legs have not evolved.

Sit-and-wait foragers, aerial foragers, and twig-hoppers have light hind-limbs and can easily evolve into long distance migrants. Athletic, independent use of the legs (like in tits), ground scratching, and vertical climbing, on the

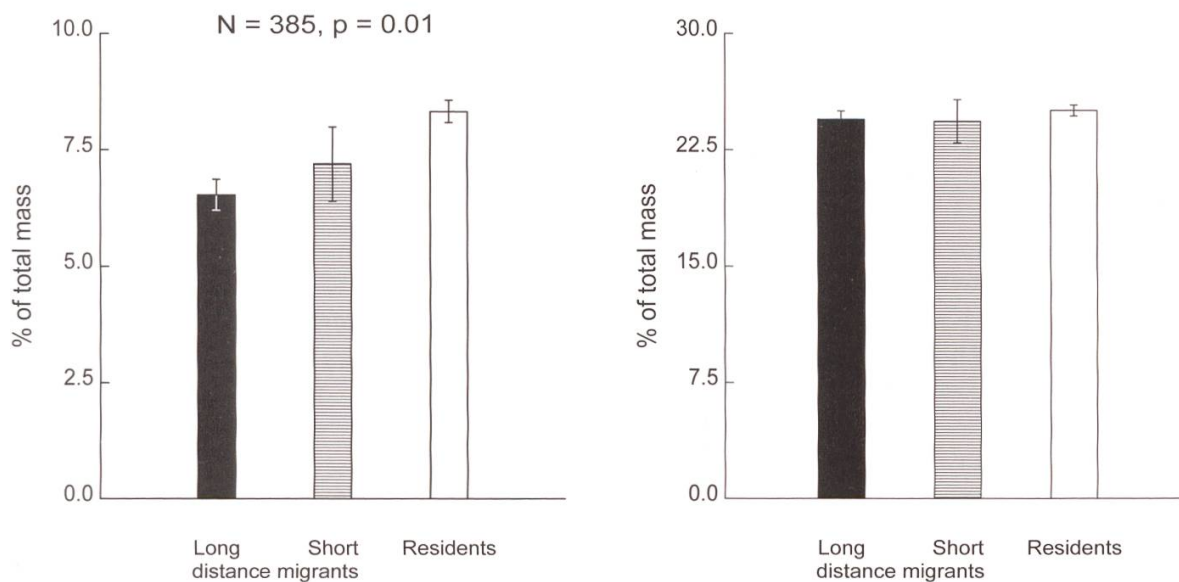


Fig. 2. Relative muscle mass of hindlimb (left) and forelimb (right) in residents, short distance and long-distance migrants. Whiskers indicate standard errors of the mean; only hindlimbs differ significantly (Anova). Data from Hartman (1961).

other hand require strong musculature which is hard to reconcile with migration. This trade-off between legs and wings relates to the same allocation principle discussed above (Fig. 1), and is not necessarily related to migration alone as the example of mimids demonstrates (Fig. 3). The skeletal data comprise two distal leg measurements, and two distal wing bones. All these measurements were corrected for size with humerus length. The highly significant ($p < 0.001$) Canonical Correlation between these two data sets was 0.819. A phylogenetic analysis showed that a change in the distal wing parallels an opposite change in the proximal leg element (Winkler & Leisler 2005).

The changing fate of wings and tails

Ultimately, flight performance depends on the size and shape of the aerofoils involved: the wing and tail. Since aerodynamics does not leave many alternatives, convergence is especially pronounced here. Based on this assumption, we computed a migration score by forming two groups, long-distance migrants (birds that migrate distances over 2500 km), residents, and short-distance migrants, with 234 species from various oscine groups (*Sylvia*, *Acrocephalidae*, *Anthus* and *Piranga* and parulids). After computing a discriminant analysis with a set of external characters belonging to all functional complexes (bill, flight apparatus, hindlimb), we found that only four traits contributed to the characterization of long-distance migrants in all these groups: wing length, primary projection, tail length, and tail graduation. Therefore,

| Variable | F-value | p | Bonferroni-corrected p | | | | |
|-----------------|---------|---------|------------------------|------|-------|-------|--------|
| | | | < 0.05 | 0.01 | 0.005 | 0.001 | 0.0001 |
| Wing-length | 24.8638 | 0.00000 | * | * | * | * | * |
| Tail length | 9.0226 | 0.00317 | * | | | | |
| Prim projection | 52.7094 | 0.00000 | * | * | * | * | * |
| Tail graduation | 14.4585 | 0.00021 | * | * | * | * | |

Tab. 1. Univariate F-Tests (dgfs 1,138) of those characters that consistently characterized long distant migrants, and from which our "migration scores" were computed (see text).

we ran the analysis again with only these four characters (Tab. 1). The resulting "migration scores" of a species (positions on the discriminate axis) were used to study the evolutionary change of migration adaptations in each of the included lineages separately. Wing length and primary projection contribute positively to this score, while tail length and tail graduation enter negatively. Thus migrants are characterized by long and pointed wings and short and square tails.

In New World *Piranga* tanagers migrants have evolved from tropical residents (Fig. 4, Burns 1998). However, resident forms (*bidentata*, *flava*) are nested within the migrant group. Therefore, this small set of species offers a good example of the evolutionary changes we are interested in. We analyzed the evolution of those scores with the method outlined above. There is a significant change to migratory features at the base of the group comprising *olivacea*, *flava*, *rubra*, *bidentata*, and *ludoviciana*. The trend reverses in the short branches that lead to *bidentata*, and populations of *flava* residential in northern South America.

In the Acrocephalidae (conventional genera *Acrocephalus* and *Hippolais*) the number of migratory species exceeds tropical residents (Fig. 5). The latter are mainly found in a clade consisting of *A. gracilirostris*, *brevipennis*, *rufescens*, *newtoni*, and *sechellensis*. Its sister group (*arundinaceus-stentoreus*) contains residents, short-distance and long distance migrants. Thus, the reconstructed score changes towards migratory features at the basal branch, with a strong further change in the branch associated with the Great Reed Warbler (*A. arundinaceus*). Both "*Hippolais*" clades showed a steady, but slow, trend towards a migratory morphology. Of the small streaked *Acrocephalus* species *schoenobaenus*, *bistrigiceps* and *paludicola* tend to have high migratory scores. This trend is reversed in the branches to the short-distance migrant *melanopogon*. However, much stronger reversals occur in other clades. High contrasting rates of change occur in the migrant-resident pair *australis-taiti*, and even between *icterina-polyglotta* (Fig. 5). In the latter

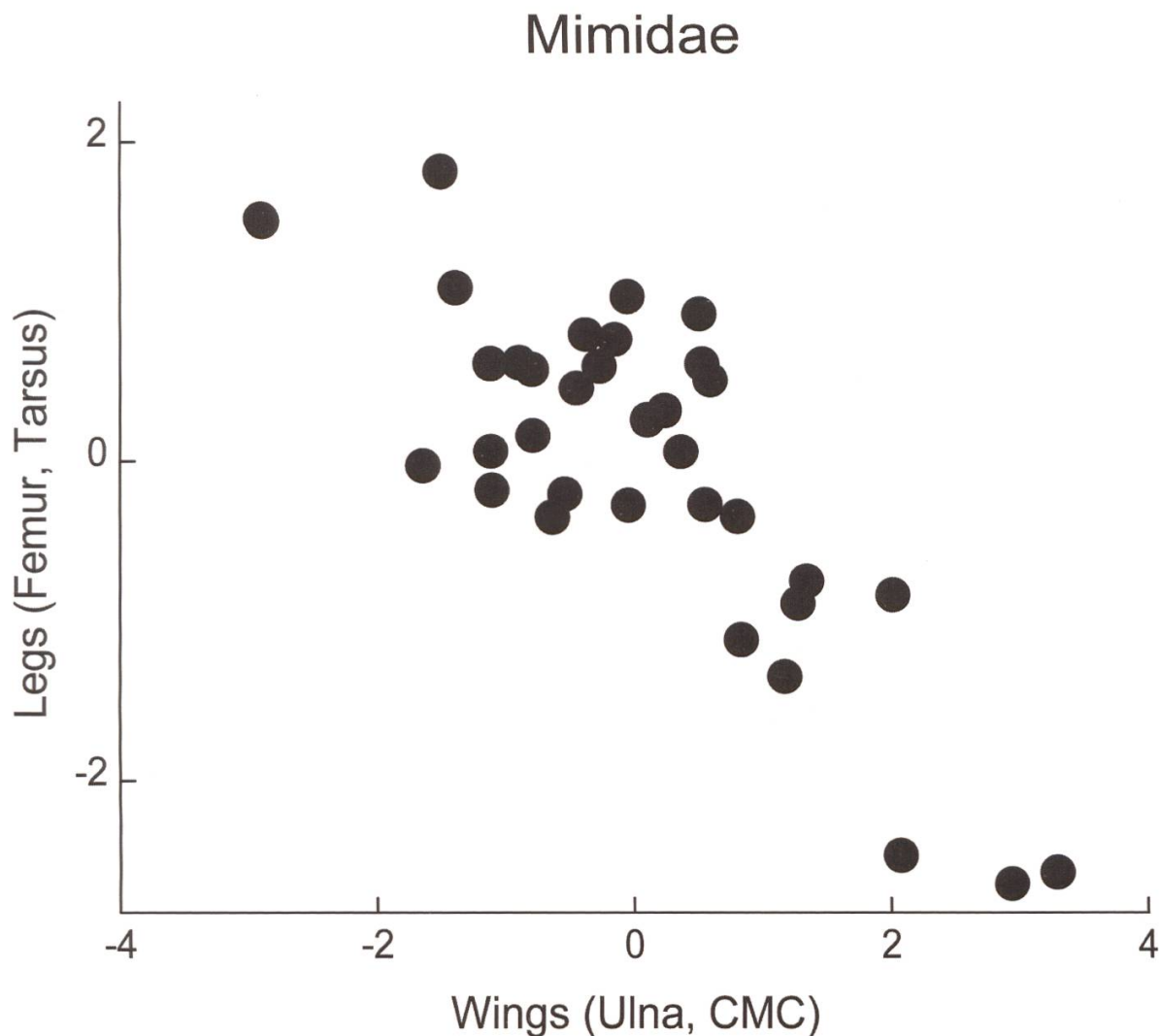


Fig. 3. Canonical correlation between leg elements (femur, tarsus) and distal wing elements (ulna, CMC carpometacarp) in 35 spp of mockingbirds. Data from Gullledge 1975.

pair, *icterina* migrates about eight, and *polyglotta* about four thousand kilometres, yet scores are lower in this species. The transitions in the *scirpaceus* superspecies (including *baeticatus* and *avicenniae*) constitute the most extreme cases, however. The basically non-migratory (some short distance movements do occur) *baeticatus* and *avicenniae* developed a "residential" flight apparatus in a very short evolutionary time (see branch lengths in Fig. 5).

The pipits of the genus *Anthus* frequently inhabit open habitats and one would expect that species in this group already possess wings and tails that allow for efficient long-distance flight (Leisler & Winkler 2003, Winkler & Leisler 2005). Consequently, changes are expected to be less dramatic than in other groups. This has proved to be true, although migrants still differ from residents significantly (Voelker 2001, Leisler & Winkler 2003, Winkler & Leisler 2005). Furthermore, Outlaw & Voelker (2006) argue that the main driving force for the evolution of migration in this group was seasonality. Another complicating factor is the occurrence of song flights (Hedenström &

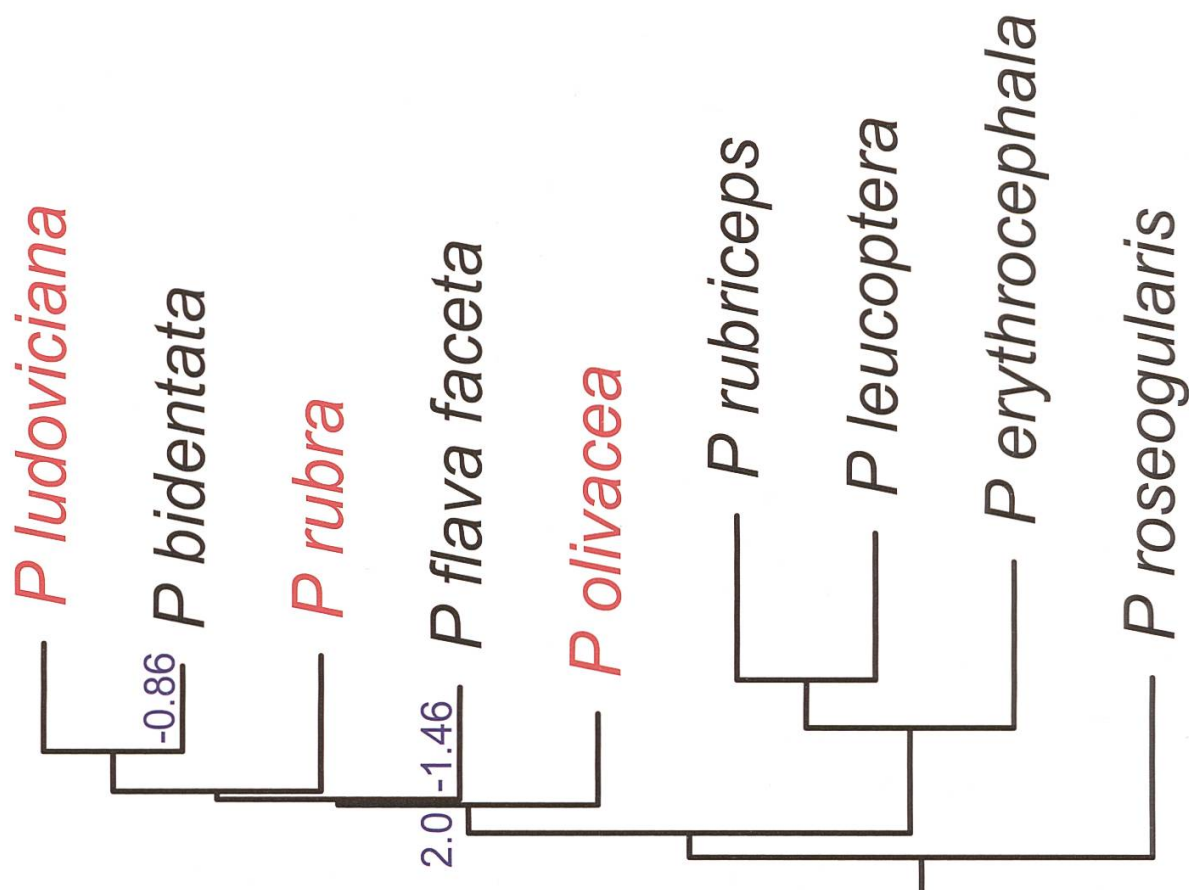


Fig. 4. Phylogenetic tree of *Piranga*. Rates (relative to the mean rate) on some branches discussed in the text indicate change towards a migratory (positive signs) or resident (negative signs) morphology summarized with discriminant scores (see text). Species names in red indicate long distance migrants.

Møller 1992, Voelker 2001). With respect to changes from migratory features to more sedentary ones, one could hypothesize that in this group corresponding selective forces are less stringent than in other groups that exploit, for instance, denser vegetation. The data do not support this idea, however (Fig. 6). High rates of change away from a migratory flight apparatus still do occur in the pairs *spinoletta spinoletta* (migrant)-*spinoletta coutellii* (from Turkmenistan, resident/partial migrant), *hodgsoni yunnanensis* (migrant)-*hodgsoni hodgsoni* (short-distance migrant), and *campestris* (migrant)-*berthelotii* (resident).

The species of the genus *Sylvia* comprise mostly sub-tropical to temperate species that inhabit dense vegetation, with several long-distance migrants, embedded in the large, mostly tropical, radiation of babblers (Cibois 2003, Jönsson & Fjeldså 2006). In this genus we can observe a complex mosaic of changes from residents to migrants and vice versa (Fig. 7). Long distance migration evolved five times in this group (Helbig 2003). High evolutionary rates towards migratory features are found in the branches leading to *cantil-*

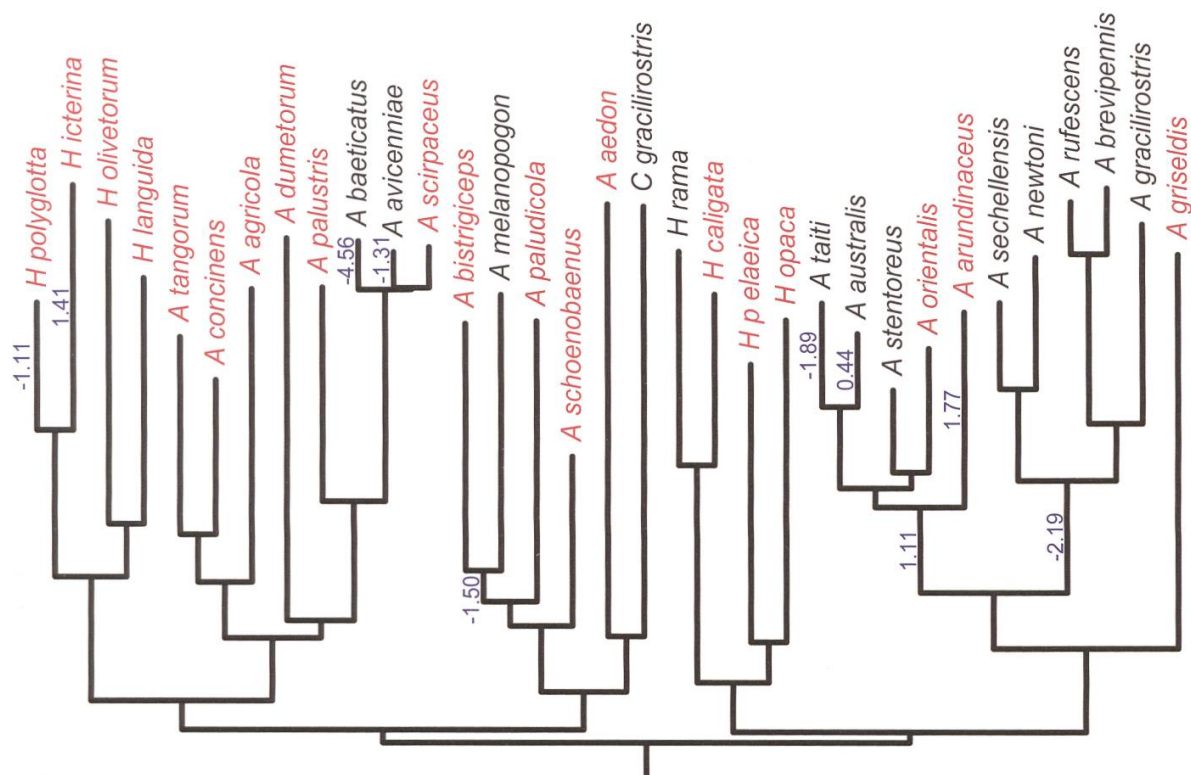


Fig. 5. Phylogenetic tree of acrocephalid warblers. Rates (relative to the mean rate) on some branches discussed in the text indicate change towards a migratory (positive signs) or resident (negative signs) morphology summarized with discriminant scores (see text). Species names in red indicate long distance migrants.

lans and *nisoria*. Much higher rates occur in those cases in which migrants and residents are closely related. The Mediterranean *sarda* and *undata*, largely sedentary, contrast strongly with *conspicillata*. Sedentary *leucomelaena* contrasts with the trans-Saharan migrant *hortensis*. At the base of the radiation of Mediterranean warblers (*undata-rueppelli*) a change away from a migratory flight apparatus occurred, contrasting with migratory *communis*. The ancestor of this group may well have been a migrant.

Sexual dimorphism

Because migration exerts strong selective demands on wings and tails, sexual dimorphism in these characters is expected to be low, when both sexes migrate (Winkler & Leisler 2005). Migration has consequences for the interactions between the sexes. Opposite sex individuals may meet for only a brief period in the breeding season, and even then the sexes may forage separately. Pair-bonds and joint foraging forays all year round, on the other hand, lead to frequent and intense interactions and competition. Sexual dimorphism

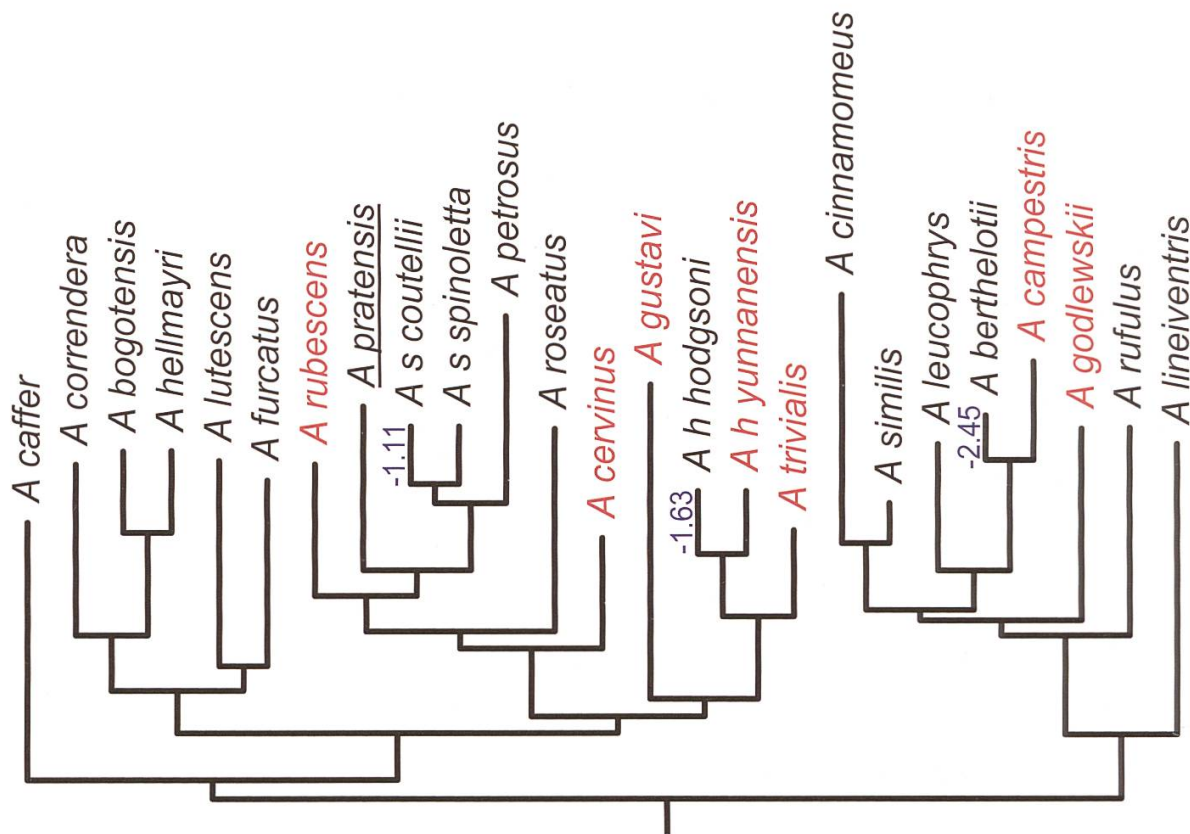


Fig. 6. Phylogenetic tree of *Anthus*. Rates (relative to the mean rate) on some branches discussed in the text indicate change towards a migratory (positive) or resident (negative signs) morphology summarized with discriminant scores (see text). Species names in red indicate long distance migrants. Underlined is species *pratensis* which migrates approx. 2500 km.

especially in the feeding apparatus may therefore be common among residents and less so among migrants. Willson & al. (1975) present data on the bill morphology of North American birds that we reanalyzed for the purpose of this paper focusing on songbirds only (Fig. 8). The results show that sexually dimorphic species are more likely found in residents compared to long-distance migrants, with short-distance migrants falling between these extremes (but closer to residents). Even in the falcons, which like other raptors are generally known to be size dimorphic, bill and head dimensions vary between the sexes of migrants significantly less than in residents (Fig. 9).

Discussion

The results confirm that migration is a powerful factor shaping the flight apparatus of birds, although other factors, such as habitat use (Rayner 1988) or flight displays (Voelker 2001) intuitively may seem to be more important. Previous analyses showed that morphological characters are excellent predictors of migratory distances (Winkler & Leisler 1992, Leisler & Winkler 2003).

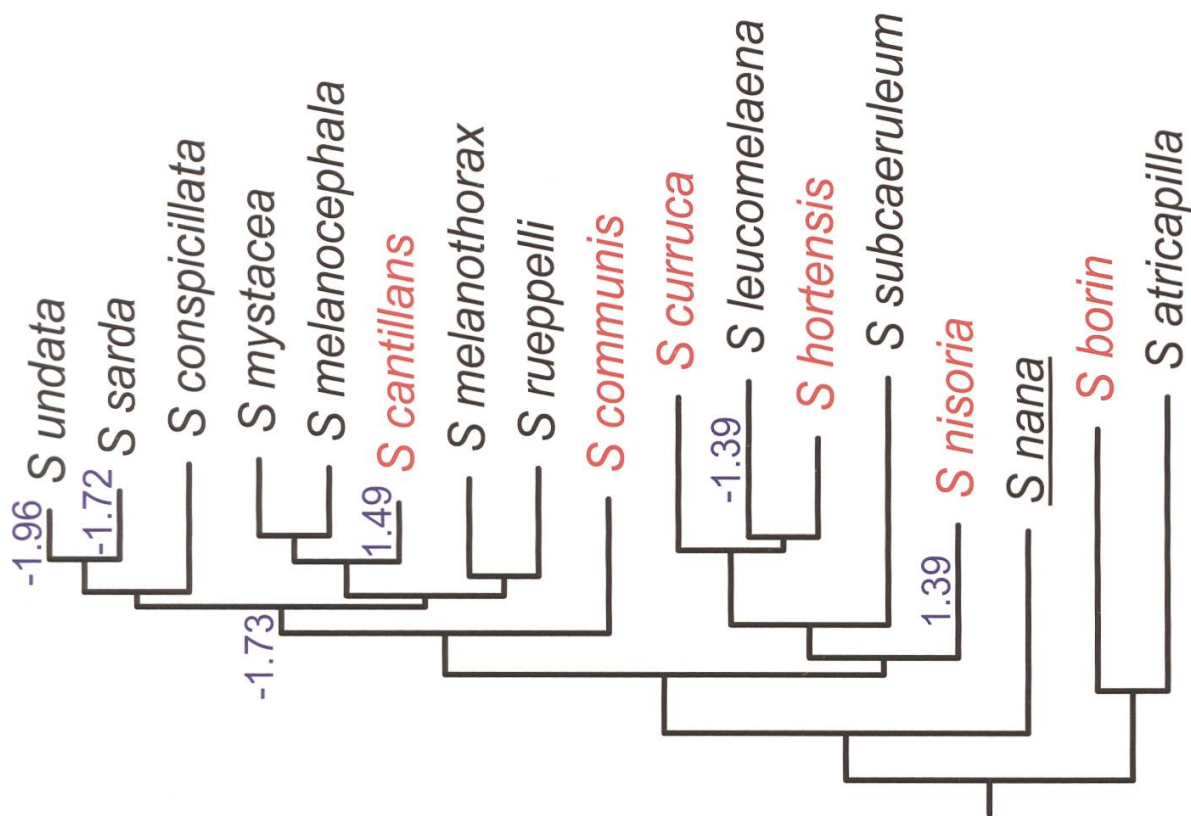


Fig. 7. Phylogenetic tree of *Sylvia*. Rates (relative to the mean rate) on some branches discussed in the text indicate change towards a migratory (positive) or resident (negative signs) morphology summarized with discriminant scores (see text). Species names in red indicate long distance migrants. Underlined is species *nana* which migrates approx. 2500 km.

Here we show that a change to migratory features can occur in a very short evolutionary time. This strengthens the notion that migration and flight performance associated with it are strong evolutionary factors. Our analyses also showed that the opposite change from a migratory to a residential life-style is equally pronounced (*Piranga*, *Anthus*). This raises the question of what the forces are that strongly select for a non-migratory morphology. Researchers have noted that young birds do not develop a full migratory wing with a high aspect ratio and pointed tips (Alatalo & al. 1984, Fiedler 2005). They explain these findings as a trade-off between the ability to escape from predators and efficient long-distance flight. Only experienced birds are supposed to fully exploit the higher efficiency of pointed high aspect ratio wings. Predation and habitat use may indeed be forceful factors that form the flight apparatus as soon as the demands of migration cease. Hall & al. (2004) argue that stabilizing selection on wing characteristics acts in Reed Warblers (*Acrocephalus scirpaceus*), explaining it with the opposing demands of long-distance migration and maneuverability. Studies like this one, or those by Nowakowski (2000) or Nowakowski & Wojciechowski (2002) in which the influence of different environmental conditions on the survival of birds with different morphologies

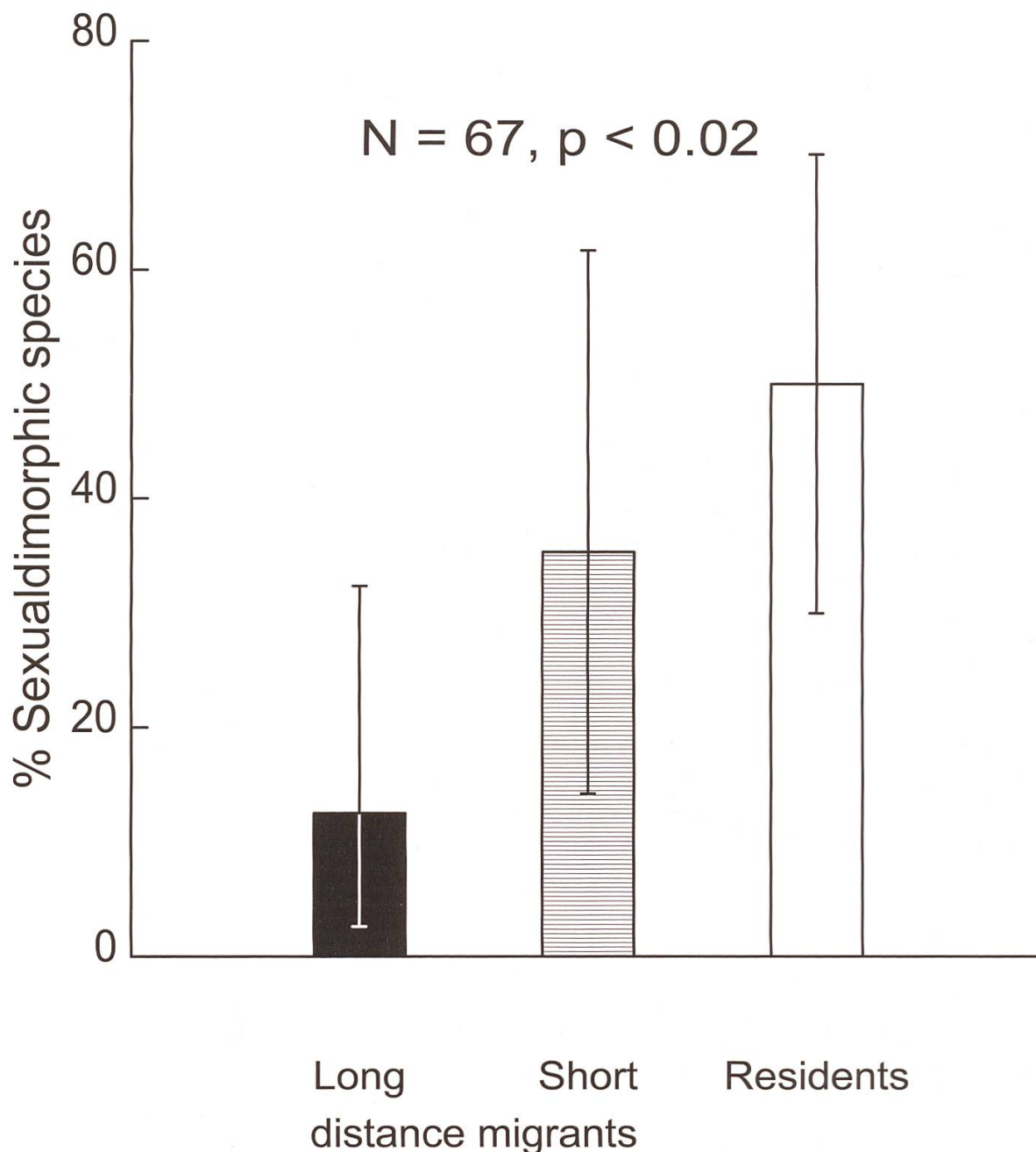


Fig. 8. Percentage of sexualdimorphic species (in beak dimensions) in residents, short-distance and long-distance migrants (67 species, data from Willson & al., 1975). Shown are 95% confidence limits; tested with an exact test of the 2 x 3 contingency table.

are measured could help to identify relevant selective forces on morphological shape (not specifically studied by Hall & al. and Nowakowski). Maneuverability versus efficient flight is not the only trade-off that acts on wing morphology. The ability to escape predators also depends on fast take-off, which is not necessarily coupled with maneuverability. The negative relationship between a migratory phenotype and hind-limb development is another factor that may account for the fast loss of character states related to long-distance migration.

The fast changes reported here are possible only if there are no substantial genetic constraints. One such constraint may originate from genetic correl-

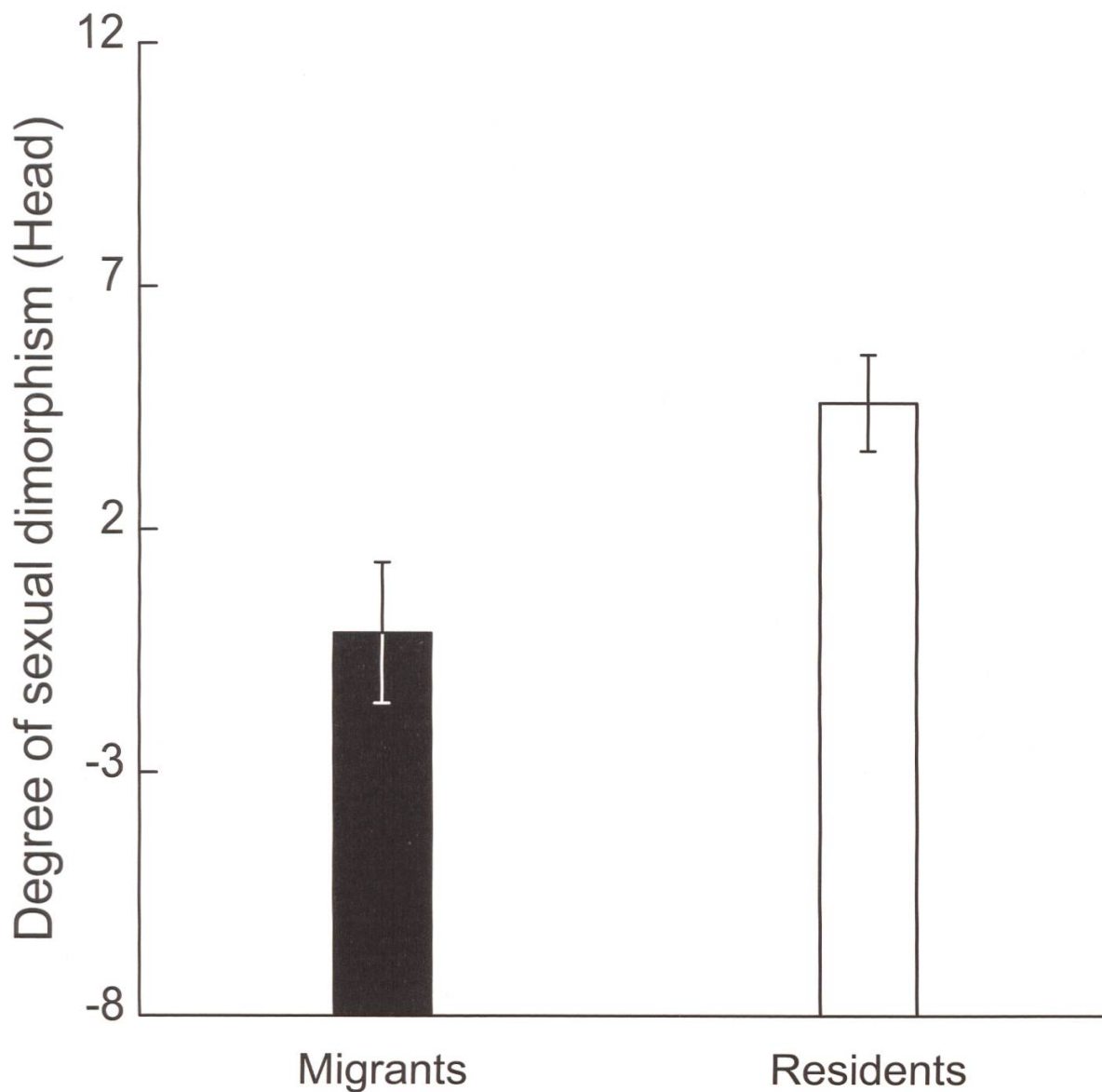


Fig. 9. Degree of sexual dimorphism in (head and beak dimensions) in 26 resident and migrant *Falconidae* species (data from Kemp & Crow 1993). Shown are the differences between male and female scores of a discriminant analysis of sexual differences in nine characters on the head. Whiskers indicate standard errors of the means.

ations among characters (Steppan & al. 2002). These kinds of constraints do not seem to play a major role in the evolution of characters associated with migration. Winkler & Leisler (2005) and Leisler & Winkler (2006) have shown that these changes occur orthogonally to the so called line of least resistance (Björklund 1996, Schluter 1996, Steppan & al. 2002) as easily as along it.

The method of Schluter & al. (1997) reconstructs ancestral character states by assuming constant and independent (among branches) rates of evolution and weighing with relative branch lengths. Thus, among other things, the inferred character state of an ancestor must always lie within the range observed in its descendants. Our results concerning the relative rates of acquisition and loss of character states related to long-distance migration are not severely affected by these limitations, because we talk mainly about

changes close to the tips. However, more faithful reconstructions of ancestral character states will eventually be possible by including the morphology of outgroups and more sophisticated methods of inference (e.g. Ronquist 2004).

Kissner & al. (2003) discussed the effects that early arrival of males on the breeding grounds may have on sexual size dimorphism. They argue that survival of these males in adverse weather conditions would be more likely with larger body size. They found a larger dimorphism in New World species with larger differences in arrival time, as predicted, after the effects of the negative correlation between migration distance and sexual dimorphism had been removed. Rubolini & al. (2005) found no supporting evidence with data from European migrants. Another example of the complex interactions in relation to sexual dimorphism, migration, and sexual selection was presented by Sandercock (2001). He found that migration had little influence on size dimorphism. The aerial display of males had an influence because it favors smaller, more agile males. Long-distance migration, however, was clearly associated with aerial displays. In his study of *Anthus* display flights, migration, and morphology, Voelker (2001) found that migration correlated with a particular display, namely parachuting. That may mean that others, such as circling, are constrained by migration. The dimorphism in long-distance migration relevant features of flight apparatus (aspect ratio) in songbirds was found to be least in migrants by Hedenström & Møller (1992). Stutchbury & al. (2005) suggested that in species with female winter territoriality, females are larger. This would be compatible with the decreased dimorphism in migrants in case this social system is more common among migrants.

Most of the studies cited above considered size only. The examples presented in our results, however, refer to differences in shape. While it is not hard to imagine that migration exerts similar pressures on the flight apparatus of both sexes, the observed greater uniformity in other traits still needs to be explained. We suggest that inter-sexual competition is reduced in migrants. Birds that do not migrate may often form pairs even outside the breeding season and forage together, a situation that may lead to inter-sexual niche differentiation (e.g. woodpeckers, Selander 1966, Leisler & Winkler 1985, Matthysen & al. 1991). In summary, sexual size dimorphism has many, partly opposing, selective forces of which migration is certainly a powerful one.

We left aside many other aspects of traits associated with migration and their evolution. Some of these may not be under selective pressures directly associated with migration. We therefore suspect that evolutionary changes may not be as conspicuous as in the morphological characters treated here. For example, with respect to singing behavior migration correlates positively

with the repertoire of song types in comparisons within genera, whereas the number of different syllables sung does so in inter-generic comparisons only (Read & Weary 1992). Mountjoy & Leger (2001) discovered a strong positive correlation between repertoire size and migration distances within the New World genus *Vireo* (see also Barlow & Bortolotti 1988). Good explanations for these findings are still missing. The fact that social bonds in migrants cannot be maintained as long as in residents may play an important role because sexual selection is stronger when mate acquisition is confined to a shorter breeding season (Irwin 2000). This is obvious in the social systems of *Acrocephalus* warblers: only resident species or partial migrants are likely to develop systems that involve helpers (Leisler & al. 2002). Migrants also differ from residents in cognitive abilities, such as exploration, and other personality traits (Mettke-Hofmann & Greenberg 2005, Mettke-Hofmann & al. 2005). One of the problems here is, among other things, to translate correlations into causalities. A good example for this is the discussion on the reasons for the smaller brain size in migrants. Whereas Winkler & al. (2004) suggest that this is an adaptation to the energetic or other demands of migration, Sol & al. (2005) believe that smaller brain size forces birds to migrate.

Research has produced many exciting findings about the ways birds can adapt to the demands of migration. They do so from different sets of adaptations and preadaptations (Piersma & al. 2005). Only recently researchers have begun to ask the relevant evolutionary questions about the magnitude of the changes involved. The general opinion seems to be that these changes are easily achieved, like those in *Zugunruhe* produced in the laboratory (Berthold 1999). The results of this paper seem to corroborate this view for certain morphological characters. Still, more such comparative studies, with more lineages and more characters, are needed to separate convergent from innovative solutions to the ubiquitous challenges of bird migration.

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