Naturwissenschaften (2007) 94:268–279
DOI 10.1007/s00114-006-0186-y

REVIEW

The evolution of bird migration—a synthesis

Volker Salewski · Bruno Bruderer

Received: 30 June 2006 / Revised: 29 August 2006 / Accepted: 19 October 2006 / Published online: 10 January 2007

Abstract We approach the problem of the evolution of bird migration by asking whether migration evolves towards new breeding areas or towards survival areas in the non-breeding season. Thus, we avoid the ambiguity of the usually discussed "southern-home-theory" or "northern-home-theory". We argue that migration evolved in birds that spread to seasonal habitats through gradual dispersal to enhance survival during the non-breeding season; this in contrast to the alternative idea suggesting that migration evolved towards new breeding areas to increase reproductive success. Our synthesis is based on the threshold model explaining how migratory traits can change rapidly through microevolutionary processes. Our model brings former theories together and explains how bird migration, with the appropriate direction and time program, evolves through selection after genetically non-directed events such as dispersal and colonization. The model does not need the former untested assumptions such as competition as a reason for migration and for the disappearance of sedentary populations or higher reproductive success in temperate breeding areas. Our theory offers answers to questions such as how birds with a southern origin may gradually reach northern latitudes, why migration routes may follow historical expansion routes and why birds leave an area for the non-breeding season and move back instead of breeding on their wintering grounds. The theory proposes gradual change through selection and not sudden changes such as long distance dispersal or mutations and can be applied to migration at all latitudes and in all directions. The scenario provides a reasonable concept to understand most of the existing migratory phenomena on the basis of the ecology and genetics of migratory behaviour.

Keywords Bird migration · Migration system · Seasonality

Introduction

Bird migration is a phenomenon on which research efforts have been concentrated for many decades, but the processes leading to the evolution of migratory behaviour are still debated. Early theories about the evolution of bird migration were summarized by Cox (1968) and Gauthreaux (1982). With respect to the origin of bird migration, two theories were discussed: (1) the "northern-home-theory", which assumes that due to climate changes, birds had to shift their non-breeding activities away from high latitude breeding grounds [see references in Gauthreaux (1982)] and (2) the "southern-home-theory", which assumes that bird migration evolved in tropical species that started to breed at higher latitudes [see references in Gauthreaux (1982); Levey and Stiles (1992); Rappole and Tipton (1992); Safriel (1995); Rappole and Jones (2002); Böhning-Gaese and Oberrath (2003); Jahn et al. (2004)]. Some authors, however, suggested that the two theories are not mutually exclusive (Duncker 1905; Mönkkönen et al. 1992). Cox (1985) and Jahn et al. (2004) proposed for the Nearctic–Neotropical migration system that migrants are species of the temperate–tropical borderlands, which extended their ranges into the temperate zone to breed and their wintering ranges southwards into the tropics.

Bell (2005) pointed out that the ancestral home of a species and the origin of the evolution of migration need not be geographically identical. The problem becomes obvious in the statement of Berthold (2001, page 5):

V. Salewski (✉) · B. Bruderer
Swiss Ornithological Institute,
6204 Sempach, Switzerland
e-mail: volker.salewski@vogelwarte.ch

"Finally, two contradictory views emerged about the geographical origin of bird migration: the hypothesis of a northern origin, which assumes that bird migration originated in the current northern temperate zone, and the hypothesis of a southern origin, which assumes that migrants stem from the tropics". Two different issues are thereby opposed to each other, although they are not necessarily connected and are not mutually exclusive: The evolution of seasonal movements in a particular geographical region (bird migration originated in the current northern temperate zone) need not be linked to the phylogenetic origin of the birds (migrants stem from the tropics); that is, phylogenetic origin and evolution of certain traits must not be linked geographically. In addition, the clear dichotomy of the discussion ignores the great diversity of avian migration, including temperate–tropical migration in the southern hemisphere and intra-tropical migration. Therefore, the crucial question for the evolution of bird migration is not whether birds start to migrate from a low latitude origin towards higher latitudes or vice versa, but whether bird migration evolved from the original breeding areas towards new breeding areas because of enhanced fitness through enhanced reproduction or from breeding areas towards non-breeding areas because of enhanced fitness through better survival in the non-breeding season.

In this paper, we will derive a synthesis for the evolution of bird migration. None of the ideas will be completely new; most have been previously presented to some extent especially by Berthold (1999) and Bell (2000, 2005). We hope, however, that our contribution will help to mitigate current controversial discussions (e.g. Bell 2005; Rappole 2005) by showing that many discrepancies are due to inappropriate use of terms, ambiguous formulation of questions or unclear definitions. We will first review some former theories about the evolution of bird migration and then present a scenario for the evolution of bird migration which can be applied to all migration systems although it may not explain all directional movements of birds.

Basic definitions

In former papers, crucial terms such as migration, dispersal, origin and evolution were often not clearly defined or not used in the sense of a certain definition or were just used interchangeably. In this paper, we define *evolution* of bird migration in the sense of "maintenance and modification" of migratory behaviour (Zink 2002) and not the first appearance of migration in evolutionary history. The change in allele frequencies through selection instead of the occurrence of new genetic traits through mutations is of prime interest when discussing migration phenomena (Rappole et al. 2003). In other words, it is ecology and not phylogenetic relationships that influences the appearance of migratory behaviour in a species or population (Helbig 2003).

We define *avian migration* as a regular, endogenously controlled, seasonal movement of birds between breeding and non-breeding areas. Therefore, migration always includes two trips: from breeding grounds to non-breeding grounds and back. This definition does not include foraging trips during the breeding season, which might be quite extended (albatrosses, penguins and swifts). If the condition "endogenous control" is included in a strict sense, we can exclude facultative migration such as irruptions, which are triggered primarily by proximate environmental factors and are thus not regular (Schwabl and Silverin 1990). Partial migration occurs when some individuals of a population migrate, whereas others are residents. This definition draws a clear line between migration and *dispersal*, although some authors have included dispersal as a migratory strategy (Gauthreaux 1982) or interpreted migration as a form of dispersal (Winker 2000; Nathan et al. 2003; Rappole 2005). However, migration and dispersal have different ultimate and proximate causes, and the different functions of dispersal and migration expose them to different selective pressures (Winkler 2005). Dispersal was defined as a movement from one location where an individual was born or has bred to another location where it will breed (South et al. 2002; Boyd 2002). Dispersal is a one way movement, not regular in terms of a cyclic change of sites and not controlled endogenously with respect to time and direction and is also characterized as a Brownian (random) movement [e.g. Bullock et al. (2002); Hengeveld and Hemerik (2002); Newton (2003)]. Although active dispersal (in contrast to drift) has no genetically fixed directional component, environmental factors and resource tracking may influence its direction.

The evolution of bird migration—a brief review

A bird migration system need not have evolved in response to one set of environmental factors operating at one time (Joseph et al. 2003). However, two main factors have usually been discussed as being crucial for the evolution of migration: competition and a seasonal environment with variation in resource availability.

Migration was often interpreted as a result of birds escaping *intraspecific competition* during the breeding season, (Taverner 1904; Cox 1968; Alerstam and Enckell 1979; Rappole and Tipton 1992; Safriel 1995) although Taverner (1904) and Cox (1985) suggested that competition is only one of several factors such as climate, resource availability, predation or parasitism which makes species to shift their breeding ranges and become migrants. However, Alerstam and Enckell (1979) saw competition in the highly seasonal African savannas during the breeding season as a prerequisite for the evolution of the Palearctic–African migration system. Rappole and Tipton (1992) developed a scenario to explain how bird migration could have evolved stepwise in resident tropical species through dispersal into favourable breeding areas. These ideas were further elaborated by assuming that migration developed in tropical resident species as a response to pressure on young individuals to locate uncontested feeding and breeding habitat (Rappole 1995; Rappole and Jones 2002). For the evolution of the Palearctic–African migration system, Safriel (1995) assumed that migrant populations originated from southern regions, shifting their range northwards through long-distance dispersal. All the mentioned studies made competition in the tropical breeding ranges responsible for the evolution of migration out of their ancestral home, whereas Lack (1968) discussed intraspecific competition in the northern breeding areas during the non-breeding season as being the driving force for at least some individuals (juveniles and females) to migrate out of the breeding areas.

Seasonality of crucial resources was seen as a second important factor for the evolution of migratory behaviour. Some authors interpreted migration as an adaptation to the lack of critical resources in the non-breeding season in temperate regions, optimizing survival during the non-breeding season (von Lucanus 1929; Mayr and Meise 1930; Bell 2000). Others assumed that migration is an adaptation of tropical birds to use seasonally abundant resources in temperate regions to optimize breeding success (Taverner 1904; Alerstam and Enckell 1979; Stiles 1980; Safriel 1995; Rappole 1995; Rappole and Jones 2002). Berthold (2001) mentioned that both strategies are possible, and Alerstam et al. (2003) saw migration as an adaptation for both, exploiting seasonal peaks of resources and avoiding seasonal resource depression. Taverner (1904) and Rappole (1995), although clearly advocating the “southern-home-theory”, mentioned deterioration of resources in temperate regions as the reason why birds migrate back to the tropics. Levey and Stiles (1992) developed a scenario for the evolution of Neotropical–Nearctic bird migration where temporal and spatial variation of resources, especially for frugivorous and nectarivorous birds, led to altitudinal intra-tropical migration, predisposing these birds to migrate out of the tropics.

In conclusion, most recent studies have seen bird migration as a result of low latitude populations evolving migration to exploit seasonal resources in temperate regions for breeding. An alternative hypothesis was proposed by Bell (2000), who is the only recent author to propose that bird migration evolved primarily in seasonal breeding areas to spend unfavourable periods on wintering grounds enhancing survival during the non-breeding season. He further elaborated his ideas by discussing that migratory populations arise as a consequence of gradual expansion at the edge of the breeding range (Bell 2005), a theory which came close to the scenarios proposed by Taverner (1904) and Mayr and Meise (1930).

Problems and shortcomings

Most of the scenarios mentioned above have several shortcomings:

(1) Some authors (Levey and Stiles 1992; Rappole and Tipton 1992; Rappole 1995; Rappole and Jones 2002) argue for the “southern-home-theory” and southern origin of bird migration on the basis of taxonomic relatedness of high latitude migrants with tropical species. However, this is only an argument for the phylogenetic origin of migrants, but it is questionable whether the present centre of species diversity of a taxon indicates its geographical centre of origin (Zink 2002).

(2) Some of the above mentioned studies stress the role of competition as a first step for the evolution of migration when young birds are forced to find new breeding areas. In support of this, there is evidence that natal dispersal rates and distances are density dependent and caused by effects such as competition, social crowding and individual condition (Sutherland et al. 2002; Matthysen 2005). Furthermore, in unpredictable environments, random dispersal and random settlement are the best strategies to avoid competition (Ferriere et al. 2000). We do not reject the possibility that either intra- or interspecific competition can influence migratory behaviour or resident–migrant relations; also, its role may be negligible (see discussion in Salewski et al. 2006). However, the untested assumption that migration, as defined above, is the normal consequence of competition (Cox 1968; Alerstam and Enckell 1979) is speculative. By definition, migration is a round trip. Therefore, competition in the original breeding areas cannot explain why inferior individuals forced out of the original area to uncontested breeding sites through competition should return to the point of origin in the non-breeding season. Furthermore, in many resident species, intraspecific competition for resources does not induce migration. Competition may even lead to a reduction of migration: Adult males of European blackbirds *Turdus merula* show less migratory activity compared to first-year males and females, presumably due to competition for suitable nesting sites early in the breeding season (Schwabl 1983). In conclusion,

competition may be important in influencing dispersal rates but its role in the evolution of regular return movements is questionable.

(3) Some studies presume that bird migration evolved from the low latitudes to new breeding sites because of a fitness gain through enhanced reproductive success at higher latitudes. This argument was based on the idea that birds breeding at high latitudes lay larger clutches compared to birds breeding at low latitudes on an inter- and intraspecific level (Lack 1947; Hussell 1972; Skutch 1985; Böhning-Gaese et al. 2000; Russell et al. 2004). However, clutch size may not be the primary fecundity trait on which selection is acting (Martin 1995). Northern temperate zone birds have lower life expectancies compared to tropical birds (Yom-Tov et al. 1994; Peach et al. 2001; Martin 2004), and a strong negative relation has been found between clutch size and adult survival within and between regions (Ghalambor and Martin 2001). Therefore, higher annual fecundity at higher latitudes may be a trade-off against lower annual survival. High adult mortality can favour increased reproductive effort such that selection through mortality can drive the evolution of reproductive effort rather than the converse (Martin 2004). It is therefore impossible to assess whether individuals are selected to shift their breeding ranges to high latitudes because of an enhanced reproductive success or whether there is selection to have a larger reproductive output per time unit at high latitudes because of latitude-dependent mortality (Martin 2004).

(4) The main problem with the theory of southern evolution of bird migration, i.e. that migration evolves from originally southern breeding sites towards new northern breeding sites, is that the offspring of the first migrants cannot have an inherited program to migrate to their parents origin (Rappole and Tipton 1992; Bell 2005). If the first northward movement is assumed to be migration already (Fig. 1a,b), the offspring of those birds will inherit this migration program; that is, they will stay at the new breeding site until the next breeding season instead of migrating south to avoid deteriorating conditions (Fig. 1c). Consequently, most of them will die. Even if they survive, they will move further north to breed at the beginning of the next breeding season (Fig. 1d). Sooner or later, this will lead to the extinction of the population as it moves step by step closer to the poles. The drastic change of the migration program between parents and offspring would require a mutation, which seems to be an unlikely explanation given the repeated and fast changes between migratory and sedentary behaviour of some bird populations (Berthold 1999). The explanation of how the offspring of migrants that moved north to breed could find their way south, namely that young birds follow conspecifics on their first trip south, which later becomes regular inherited migration (Rappole 2005), is a Lamarckian argument (Bell 2005) because it assumes that a tradition could become inherited. Additionally, the theory that migrants learn migration routes on their first journey from more experienced birds in general had already been rejected by von Lucanus (1929), who pointed out that birds of different ages migrate at different times in many species and often first year birds migrate before adults (Rappole and Tipton 1992; Berthold 2001; Newton 2003; Carlisle et al. 2005).

A new synthesis

Considering the above mentioned problems with theories about the evolution of bird migration, we will further elaborate the theories of Berthold (1999) and Bell (2000, 2005) to develop a new synthesis, the dispersal–migration-theory, to explain how bird migration evolved based on the following assumptions:

1) All birds have the potential to migrate with respect to their orientation capabilities, physiology and morphology, and although migration may need adaptations for long-distance flights, it does not require dramatic changes (Terrill 1991; Wiltschko and Wiltschko 1999a,b; Helbig 2003; Leisler and Winkler 2003).
2) Migratory traits of birds are universal and ancestral; their expression is explained by the threshold model (Berthold et al. 1990; Pulido et al. 1996; Pulido and Berthold 2003). According to the threshold model, all birds without phenotypic migratory activity have activity levels below a limit of expression or detection. The expression of migratory activity is then subject to selective pressures. Consequently, every bird population is partially migratory, but the proportion of individuals that express migration phenotypically can range from close to 0 (fully resident) to close to 1 (fully migratory) along a continuous distribution of migratory activity levels (Berthold et al. 1990; Pulido et al. 1996; Berthold 1999). Recent findings of migratory restlessness in a tropical resident species (Helm and Gwinner 2006) seem to confirm this assumption. Piersma et al. (2005), however, concluded from phylogenetic analyses that there is no general migration syndrome in birds. Nevertheless, from the results they presented, it is not clear whether the lack of migrants in certain families (e.g. Sittidae, Fig. 1c in Piersma et al. 2005) is

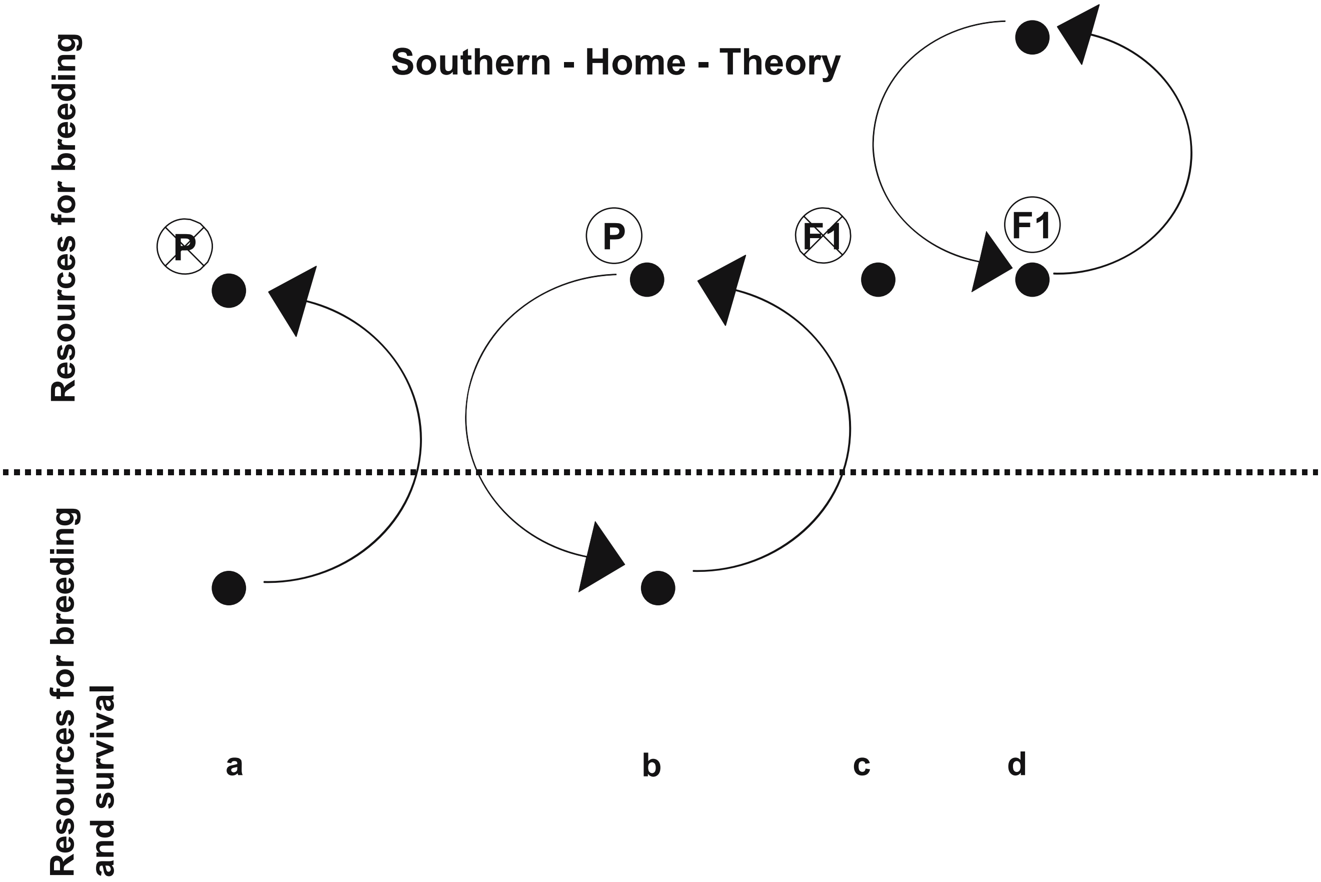

Fig. 1 Results of bird movements according to the southern-home-theory for the evolution of bird migration. *Arrows* show migration, i.e. a regular movement with an inherited time and direction program. *P* means parent generation and *F1* means first offspring. *Simple letters* mean that the individual survives, *crossed letters* mean that the individual dies. The scenario starts with an individual born in an area with sufficient resources during a breeding and a non-breeding season, which moves to its first breeding site in an area with sufficient resources during a breeding season only. When the first movement is migration northwards before the non-breeding season (**a**), this individual will not survive the non-breeding season. When an individual stays at the southern site where it was born, it will survive and can migrate north before the breeding season, breed successfully and migrate south for the non-breeding season (**b**). The offspring will, however, have inherited to stay at the non-breeding site for the non-breeding season and will therefore probably die (**c**). Provided that the offspring manage to survive, they will move further north before the breeding season. Consequently, the whole population will shift its range further northwards with every generation until the population either reaches habitats with insufficient resources and vanish or it stops migration. The southern-home-theory can, therefore, not explain the origin of bird migration

due to a phylogenetically based lack of pre-adaptations for migration, or because migratory activity remains below the threshold for its phenotypic expression in all members of a taxon due to similar conditions acting on selection. An example may be the woodpeckers Picidae among which the typical species in Europe are completely resident, whereas migratory species occur in the Nearctic, and one deviating migratory species, the wryneck *Jynx torquilla* occurs in Europe. In the migratory species, specific ecology favours migration, whereas the other species in the family are particularly well-equipped for sedentariness.

3) According to the threshold model, every bird population has the potential to become phenotypically migratory (or resident), and the proportion of migrants in a population can change rapidly if favoured by selection without new mutations (Lack 1968; Berthold et al. 1990; Pulido et al. 1996; Able and Belthoff 1998; Pulido and Berthold 2003). Migration is then controlled by an inherited endogenous time and direction program, which is subject to selection and rapid adaptation through microevolution (Berthold 1996).
4) Species or population-specific ecology is the main factor for the expression of migratory behaviour implying only minor or no phylogenetic constraints (Helbig 2003; Winkler and Leisler 2005) as proposed by Zink (2002).

Considering these assumptions, we start to develop our scenario from a phenotypically resident population with the proportion of phenotypic migrants being close to zero where juveniles may disperse to find their own breeding sites. These dispersal movements are not constrained by inherited directions. At the fringe of the population's range, some individuals will disperse out of the present range of the population. Many will vanish because they end up in habitats that lack the species-specific requirements for survival and reproduction. Others, however, may find habitats that meet the species' requirements and will settle there and breed successfully. The process will continue and will lead to a range extension into favourable habitats. When favourable habitats are only found in one direction, the species' range expansion will apparently be directed. This is not due to endogenously controlled directed movements but is a consequence either of the ability to track resources or of selection favouring the individuals that reached suitable habitats for survival and reproduction. This is not migration because birds settle in the new range to breed without a priori returning to the ancestral breeding areas; that is, range extension is a consequence of dispersal.

As long as the range of the population extends only into habitats that provide crucial resources throughout the year, there will be no selective pressure on the change of allele frequencies responsible for the expression of migratory traits. When, however, some individuals will reach areas with seasonal variation of crucial resources (Fig. 2a,b), selection may increase the proportion of individuals expressing migratory traits because only they and their offspring will survive (Fig. 2b,c). When the range extension follows a gradient of increasing seasonality of critical resources, the frequency of individuals that express migratory activity above the threshold will increase until above a certain degree of seasonality when almost all individuals express migratory behaviour. In this way, a gradual range extension of a resident population along a gradient of increasingly seasonal resources will give rise, via a partial migratory population, to an almost fully migratory one.

With this scenario, the question remains whether resources for breeding or for non-breeding are crucial for the evolution of migration. As explained above, the reason for dispersal is to gain fitness advantages by moving to suitable reproduction sites. In habitats with constant resources for reproduction and survival, any further movement after successful reproduction should be avoided

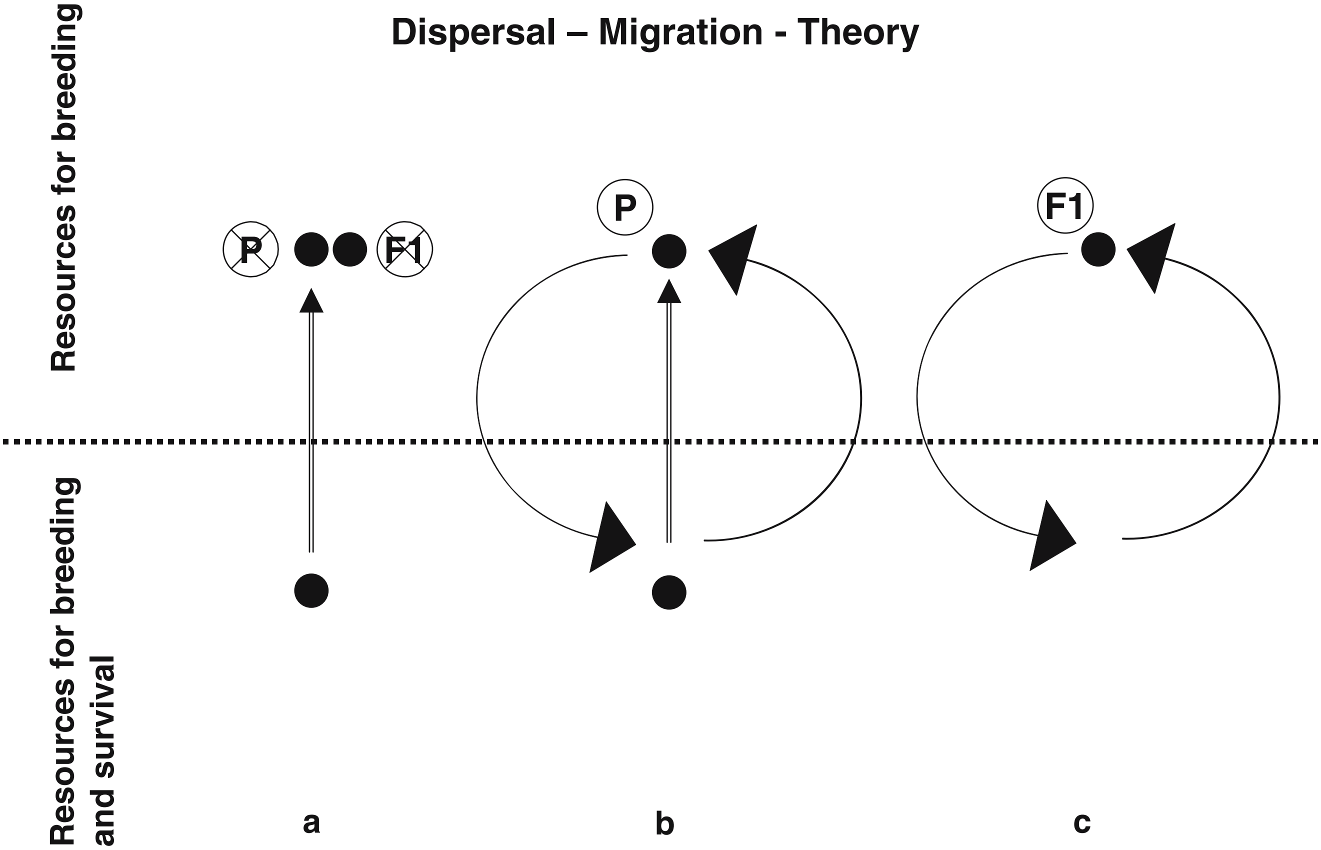

Fig. 2 Results of bird movements according to the dispersal-migration-theory for the evolution of bird migration. *Arrows* show migration, *double arrows* show dispersal, i.e. a non-regular movement without an inherited time and direction program. Letters mean as in Fig. 1. The scenario also starts with an individual born in an area with sufficient resources during a breeding and a non-breeding season, which moves to its first breeding site in an area with sufficient resources during a breeding season only. When according to the dispersal-migration-theory, the first movement is dispersal towards the area with sufficient resources before the breeding season the dispersed individual will breed successfully. If it does not migrate, however, after the breeding season (**a**) it will die together with its offspring. If the dispersed individual will migrate after breeding (**b**) it will survive and return for the next breeding season, as will be its offspring (**c**) which have inherited the parents' migration program. Timing and directional components of migration are then modified by selection

because movements such as dispersal and migration generate costs (Alerstam and Lindström 1990). Selection will therefore favour residency when movements provide no fitness advantage. Hence, if dispersal leads to successful new breeding grounds in new habitats with constant resource availability, the proportion of individuals that express migratory behaviour should remain low. If dispersal leads to new habitats with resources for successful breeding but insufficient resources to survive the non-breeding season, only those individuals showing phenotypic expression of migration will survive together with their offspring. Because of this fitness gain of migratory individuals, the entire population at the new site may become migratory within only a few generations through selection (Pulido and Berthold 2003). The movement (dispersal) towards the new breeding grounds takes place first, and first breeding can take place even when resources for the incoming non-breeding period are critical. Therefore, dispersal may lead to enhanced fitness in the breeding season, whereas a fitness gain through survival based on critical resources in the non-breeding season leads to the evolution of regular migration. Migration therefore evolves as a movement away from breeding grounds to survival areas in the non-breeding season.

The endogenous control of the migration program and migration as a movement from breeding sites to survival areas also explains why migrants do not stay in the survival areas to breed. Migration is a round trip. The realization of the whole program can be either suppressed or realized through selection but not interrupted once it has started until the bird is back on its breeding grounds. Therefore, migrants, once they have left their breeding sites, do not breed in the survival areas even when conditions are apparently good. Again, no untested assumptions like, e.g. competition with tropical residents, is necessary to explain why northern migrants do not breed in their wintering areas (exceptions see below).

Timing and direction of migration are equally the result of selection. Migrants will initially show a large scatter in migratory directions because there is no selective pressure for a particular direction in the ancestral resident population from which they derive. Many directions will lead to areas where survival is impossible. However, because survival habitats will be found in the direction of the ancestral population, this is very likely to be the migration route favoured by selection through enhanced survival of those individuals flying into these directions. This could support the suggestion that migratory populations may follow their historical expansion routes, which was supported for the North American Swainson's thrush *Catharus ustulatus* by a recent molecular study (Ruegg and Smith 2002). When the range of the partially migratory population extends gradually further, there is already a growing proportion of migrants with the inherited migration route back towards the ancestral home. The scatter in orientation can, however, lead to quick adaptations in migratory directions and wintering areas when the suitability of nearby non-breeding areas changes or new suitable non-breeding areas are reached by some individuals. This is shown by the blackcap *Sylvia atricapilla population in Central Europe, a small but increasing proportion of which now winters in southern Britain instead of the Mediterranean, implying a shift in migratory direction of at least 30° and a reduction in migration distance of about 30% within few generations (Berthold 1995; Fiedler 2003).*

Evidence from field data—recent range extensions

There are field observations supporting our scenario about the evolution of bird migration: A spectacular example is the range extension of the serin *Serinus serinus* in Europe during the last 200 years (Mayr 1926; Berthold 2001). Until about 1800, the species was found exclusively in the Mediterranean area but then started to extend its range quickly to the north and northwest, reaching southern Scandinavia by 1990. Along with the range extension into western and northern Europe, populations north of the Alps contain partially or completely migratory individuals, whereas individuals in the populations of southern and western Europe are resident. The range extension involved no long-distance dispersal, as proposed in the model for the evolution of migration by Safriel (1995). Indeed, the model of Pulido et al. (1996) explains why range extension via long distance dispersal of resident populations is unlikely to lead to fully migratory populations. When individuals of a population with a proportion of migrants close to zero disperse over long distances, the new population will be composed of mostly non-migratory individuals. Consequently, when long-distance dispersal leads to regions where there are no resources to survive the non-breeding season, the population will not establish itself. The situation is different if range extension by dispersal is gradual. Then, allele frequencies in the dispersing population can change slowly, and the proportion of migrants and migration distances will be selected according to the local availability of resources during the non-breeding season. Long-distance dispersal out of resident populations with the establishment of founder populations distant from the ancestral range is only likely to happen when long-distance dispersal leads into regions where resources allow year round survival. An example for the latter is the range extension of the collared dove *Streptopelia decaocto* into central Europe. Until about 1900, the range of the species was restricted to western Turkey. By the 1930s, the species had already spread over the whole Balkan Peninsula and had reached Scandinavia and Ireland by the 1980s. Hengeveld (1993) indicated that the range extension included various bridgeheads where populations established themselves beyond the front of the actual distribution. This is only possible when the founder population has enough resources available for both breeding and survival in the non-breeding season and can therefore remain sedentary over the entire range as the collared dove (Glutz v Blotzheim and Bauer 1980).

Insights in the relation between range expansion and change in migratory behaviour was given by the documentation of both traits for two introduced species in North America, the European starling *Sturnus vulgaris* and the house finch *Carpodacus mexicanus* (Kessel 1953; Able and Belthoff 1998). Both species, the starling from Europe and the house finch from southwestern USA, were introduced to the northeastern USA, being artificial long-distance dispersal. Both species extended their ranges quickly. The starling is a partial migrant in Europe. In North America, starlings also established partial migratory populations with the proportions of migrating individuals varying with locality (Kessel 1953). Migration phenology is similar to European populations due to similar seasonal patterns, but the geographic pattern of migration is different. The latter can be explained by differential selective pressures acting on birds after dispersal, favouring those birds which, according to the scatter of migratory directions, happened to find favourable non-breeding areas. It is well known from ring recoveries that migratory directions of juveniles scatter more than those of adults (e.g. Fransson and Stolt 2005), which may be the basis for changes in migratory routes through selection when conditions change. The house finches introduced to the northeastern USA were introduced from an apparently sedentary population but which contained 2–3% migratory individuals (Able and Belthoff 1998). As the introduced population extended its range, the proportion of migrants has increased. Thus, we have an example from a large unintended field experiment under natural conditions supporting the scenario that even a small fraction of migrants in a population can increase rapidly when favoured by selection.

Open questions and alternative scenarios

Although the scenario for the evolution of bird migration proposed in this paper does not have the problems outlined for former models, it cannot explain all directional movements of birds. We made a clear distinction between (natal) dispersal and migration, although the distinction may not be clear-cut in all cases because bird movements are so varied that they do not always fall into discrete categories (Newton 2003). This problem is due to the difficulties to determine in the field whether an individual movement is dispersal or migration (Able and Belthoff 1998), especially in species that are about to extend their range. We have to accept that a clear distinction between different kinds of movements is not always possible because the evolution of migration is a process rather than an event, and in permanently changing environments, evolutionary processes are in progress constantly.

It is obvious that migration cannot only evolve in birds colonizing seasonal habitats but also in resident populations adapting on site to changes in the degree of seasonality or resource availability. In a changing environment, directed selection will favour the expression or suppression of migratory activity, and therefore a mainly resident population can become migratory or vice versa. There is no recent example of a sedentary population becoming migratory, probably because recent climatic changes may have been more favourable to sedentary behaviour (Berthold 2001). Examples of a decrease in migratoriness are found, e.g. in lesser black-backed gull *Larus fuscus*, great crested grebes *Podiceps cristatus* and blackbird in Europe, where migratory populations became sedentary within a few decades (Lack 1968; Adriaensen et al. 1993; Berthold 2001; Fiedler 2003). In the introduced population of house finches in the northwestern USA, some individuals migrate in some years but not in others (Able and Belthoff 1998), as has already been suggested for European starlings in the USA (Kessel 1953). It is well known that many species may increase or decrease their migratory behaviour under certain conditions; for example, a common trait of long-distance migrants among long-lived larger birds (waders, raptors and terns), which do not breed until they are several years old, is to remain on the wintering grounds during their first summer(s) (Hockey et al. 1998). In short-lived passerines, however, migration may be more pronounced in juveniles than in adults; for example, in house finches, young birds may migrate in their first autumn but stay on the breeding grounds in subsequent years (Able and Belthoff 1998), and in European blackbirds, the proportion of migrants in first year males was found to be higher than in older males (Schwabl 1983). This suggests that the possibility of a fitness gain through staying at rewarding breeding sites may override an endogenous migration programme, and the realization of an endogenously controlled migration program is not inflexible to the influences of environmental and population-inherent factors (Berthold 1996). Another example are male waterfowls that accompany females to their breeding areas, which can be at a great distance from the natal or former breeding sites of the males. In this case, long-distance dispersal is mediated through directed migration towards the species winter quarters when the endogenous direction program of males on spring migration is overlaid by an external social factor, the flyway of the female partner.

We argued against the theory that bird migration had evolved simply by moving from one breeding area to another or that migrating birds start breeding in their non-breeding areas because in this cases, drastic changes in the endogenous migration program with respect to timing and direction would be necessary. This seems to be impossible on evolutionary grounds, but the argument appears to be rebutted by the fact that some species of Palearctic long-distance migrants (white stork *Ciconia ciconia*, black stork *C. nigra*, booted eagle *Hieraäetus pennatus*, Eurasian bee-eater *Merops apiaster* and house martin *Delichon urbica*) have at least temporarily founded breeding populations on their wintering grounds in southern Africa. However, these populations did not migrate to new breeding areas outside the species' regular ranges but started breeding on the regular wintering grounds south of the Equator, with the exception of the black stork in which the range of the African breeding population does not or no more overlap with the wintering range of the European birds (Salewski and Underhill, in preparation). Individuals that now breed in the former winter quarters seem to have switched their endogenous migration program with respect to timing and direction of migration. An explanation of how birds can get "confused" about the time program was provided by Gwinner and Helm (2003), who showed in cage experiments that when Palearctic birds (garden warblers *Sylvia borin*) were exposed to southern hemisphere photoperiods, some individuals became "time trapped"; that is, they switched to an annual cycle of southern hemisphere residents. When this happens in nature, these individuals are able to migrate towards the equator in the non-breeding season, as suggested for the southern populations of booted eagle and European bee-eater (Harrison et al. 1997) and shown for southern-bred white storks by ring recoveries and satellite telemetry (McLachlan 1963; Underhill 2001). Birds use, among other compasses, a magnetic inclination compass for orientation (Wiltschko and Wiltschko 1999b). According to this compass, Palearctic migrants are not moving southwards according to their endogenous migration program but equatorwards to their non-breeding grounds. Orientation based on the magnetic inclination compass will therefore lead migrants from new populations in the southern hemisphere towards the equator, i.e. northwards to non-breeding areas without a switch in the directional component of the migratory program.

Implications of the new synthesis

Our scenario for the evolution of bird migration stresses the importance of dispersal into seasonal habitats as the initial step for a selective advantage of migration. However, under stable conditions, selection against dispersal is often strong because most organisms are better adapted to local conditions than to conditions elsewhere, and mortality during dispersal is usually high (Dynesius and Jansson 2000). Therefore, individuals of species and populations with a high dispersal capacity, i.e. with traits that decrease the costs of dispersal and increase colonization abilities, will be prone to evolve migratory habits as a consequence of dispersal into new habitats. Such traits may include the ability to track resources due to morphological adaptations for long flights (Winkler and Leisler 2005). Even when dispersal is gradual, it may lead individuals towards slightly different habitats and resources, and therefore, those individuals that show an increased flexibility in the use of available resources and reduced neophobia should be the more successful dispersers. These characteristics have been found in long-distance migrants (Leisler 1993; Salewski et al. 2002, 2003; Mettke-Hofmann and Gwinner 2004; Mettke-Hofmann and Greenberg 2005). Many of the traits proposed to lead to migration like competition or sufficient breeding resources at higher latitudes (Cox 1985; Rappole 1995) could well explain range extensions but not the evolution of return movements, i.e. migration. However, those traits may be a prerequisite for individuals to settle in habitats where migration may evolve. We also do not, in general, refuse that migrants may have evolved in present-day non-breeding ranges (Rappole 1995; Joseph 2005), but even if a "southern-home-theory" may be valid in a phylogenetic sense for some species (e.g. Joseph et al. 1999; Outlaw et al. 2003), it does not explain the evolution of migration.

Our scenario can also explain the differences between the three Holarctic–Tropical migration systems. Few migrant species in the Palearctic–African migration system have conspecifics breeding in the Afrotropics (16%, own analysis). Some authors assume that competitively superior migrants invading the ancient breeding grounds may drive the conspecific residents to extinction (Alerstam and Enckell 1979; Bell 2000). The idea fails to explain why there are much higher proportions of long-distance migrants with conspecific populations in the tropics in the Nearctic–Neotropical (48%) and Palearctic–Asian (31%) migration systems (Rappole and Jones 2002), although the general factors leading to the evolution of migration may be the same. However, the continuous N–S availability of suitable habitats for most migrants in the Americas and Asia, allowing gradual range extensions of forest birds to higher or lower latitudes, is in contrast to the Palearctic–Afrotropical system, where the 2,000-km-wide Sahara and Arabian desert intervene (Bell 2000; Rappole and Jones 2002). This may explain the lack of resident tropical populations in most migrant species of the Palearctic–African migration system and why relatively few Palearctic migrants have affinities to tropical forest avifaunas, this without involving speculative competition between migratory and resident conspecific populations.

The scenario presented here has implications for how we view bird migration. We propose that the first step towards the phenotypic expression of bird migration is genetically undirected dispersal. Schüz (1952) and Alerstam (1990) suggested that birds migrate because the earth's axis is tilted 23.5°, which is the reason why we have seasons, and birds can thereby make use of the high resource availability at northern latitudes to breed (but see above for doubtful reproduction advantages). When this argument is meant in a directed sense, i.e. that evolution had to lead to migration to northern breeding grounds, it does not conform with our theory. In this case, it is a teleological argument because it implies that evolution is directed towards a certain endpoint (Kutschera and Niklas 2004; Bell 2005). If, however, the argument is meant in the sense that birds, once dispersed to high latitudes, can only survive the non-breeding season if they can migrate away during a resource depression, the argument conforms with the theory presented in this paper. In conclusion, we argue that the evolution of bird migration is a result of selective pressures after chance events, in contrast to the directed approach of former scenarios, which suggest that bird migration evolved to take advantage of abundant resources for higher reproductive success.

Acknowledgement We thank L. Jenni, P. Jones, J. Korb, F. Liechti and F. Pulido for the many inspiring discussions.

References

Able KP, Belthoff JR (1998) Rapid 'evolution' of migratory behaviour in the introduced house finch of eastern North America. Proc R Soc Lond B 265:2063–2071

Adriaensen F, Ulenaers P, Dhondt AA (1993) Ringing recoveries and the increase in numbers of European great crested grebes (*Podiceps cristatus*). Ardea 81:59–70

Alerstam T (1990) Bird migration. Cambridge University Press, Cambridge

Alerstam T, Enckell PH (1979) Unpredictable habitats and evolution of bird migration. Oikos 33:228–232

Alerstam T, Lindström Å (1990) Optimal bird migration: the relative importance of time, energy and safety. In: Gwinner E (ed) Bird Migration. Springer, Berlin Heidelberg New York, pp 331–351

Alerstam T, Hedenström A, Åkesson S (2003) Long-distance migration: evolution and determinants. Oikos 103:247–260

Bell CP (2000) Process in the evolution of bird migration and pattern in avian ecogeography. J Avian Biol 31:258–265

Bell CP (2005) The origin and development of bird migration: comments on Rappole and Jones, and an alternative evolutionary model. Ardea 93:115–123

Berthold P (1995) Microevolution of migratory behaviour illustrated by the Blackcap *Sylvia atricapilla*: 1993 Witherby Lecture. Bird Study 42:89–100

Berthold P (1996) Control of bird migration. Chapman and Hall, London

Berthold P (1999) A comprehensive theory for the evolution, control and adaptability of avian migration. Ostrich 70:1–11

Berthold P (2001) Bird migration. A general survey. Oxford University Press, Oxford

Berthold P, Mohr G, Querner U (1990) Steuerung und potentielle Evolutionsgeschwindigkeit des obligaten Teilzieherverhaltens: Ergebnisse eines Zweiweg-Selektionsexperiments mit der Mönchsgrasmücke (*Sylvia atricapilla*). J Ornithol 131:33–45

Böhning-Gaese K, Oberrath R (2003) Macroecology of habitat choice in long-distance migratory birds. Oecologia 137:296–303

Böhning-Gaese K, Halbe B, Lemoine N, Oberrath R (2000) Factors influencing the clutch size, number of broods and annual fecundity of North American and European land birds. Evol Ecol Res 2:823–839

Boyd IL (2002) The measurement of dispersal by seabirds and seals: implications for understanding their ecology. In: Bullock J, Kenward R, Hails R (eds) Dispersal ecology. Blackwell, Malden, pp 72–88

Bullock J, Kenward R, Hails R (2002) Dispersal ecology. Blackwell, Malden

Carlisle JD, Kaltenecker GS, Swanson DL (2005) Molt strategies and age differences in migration timing among autumn landbird migrants in south-western Idaho. Auk 122:1070–1085

Cox GW (1968) The role of competition in the evolution of migration. Evolution 22:180–192

Cox GW (1985) The evolution of avian migration systems between temperate and tropical regions of the New World. Am Nat 126:451–474

Duncker H (1905) Wanderzug der Vögel. Verlag von Gustav Fischer, Jena

Dynesius M, Jansson R (2000) Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. Proc Natl Acad Sci 97:9115–9120

Ferriere R, Belthoff JR, Oliveri I, Krackow S (2000) Evolving dispersal: where to go next? Trends Ecol Evol 15:5–7

Fiedler W (2003) Recent changes in migratory behaviour of birds: a compilation of field observations and ringing data. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian migration. Springer, Berlin Heidelberg New York, pp 21–37

Fransson T, Stolt B-O (2005) Migration routes of North European reed warblers *Acrocephalus scirpaceus*. Ornis Svec 15:153–160

Gauthreaux SA (1982) The ecology and evolution of avian migration systems. J Avian Biol 6:93–168

Ghalambor CK, Martin TE (2001) Fecundity–survival trade-offs and parental risk-taking in birds. Science 292:494–497

Glutz v Blotzheim U, Bauer KM (1980) Handbuch der Vögel Mitteleuropas. Vol. 8/II. Aula Verlag, Wiesbaden

Gwinner E, Helm B (2003) Circannual and circadian contributions to the timing of avian migration. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian migration. Springer, Berlin Heidelberg New York, pp 81–95

Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V, Brown CJ (1997) The atlas of southern African birds, vol. I: Non-passerines. Bird Life South Africa, Johannesburg

Helbig AJ (2003) Evolution of bird migration: a phylogenetic and biogeographic perspective. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian migration. Springer, Berlin Heidelberg New York, pp 3–20

Helm B, Gwinner E (2006) Migratory restlessness in an equatorial nonmigratory bird. PLOS Biol 4:611–614

Hengeveld R (1993) What to do about the North American invasion by the collared dove? J Field Ornithol 64:477–489

Hengeveld R, Hemerik L (2002) Biogeography and dispersal. In: Bullock J, Kenward R, Hails R (eds) Dispersal ecology. Blackwell, Malden, pp 303–324

Hockey PAR, Turpie JK, Velásquez CR (1998) What selective pressures have driven the evolution of deferred northward migration by juvenile waders? J Avian Biol 29:325–330

Hussell DJT (1972) Factors affecting clutch size in Arctic passerines. Ecol Monogr 42:317–364

Jahn AE, Levey DJ, Smith KG (2004) Reflections across hemispheres: a system-wide approach to new world bird migration. Auk 121:1005–1013

Joseph L (2005) Molecular approaches to the evolution and ecology of migration. In: Greenberg R, Marra PP (eds) Birds of two worlds. Johns Hopkins University Press, Baltimore, pp 18–26

Joseph L, Lessa EP, Christidis L (1999) Phylogeny and biogeography in the evolution of migration: shorebirds of the *Charadrius* complex. J Biogeogr 26:329–342

Joseph L, Wilke T, Alpers D (2003) Independent evolution of migration on the South American landscape in a long-distance temporal-tropical migratory bird, Swainson's flycatcher (*Myiarchus swainsoni*). J Biogeogr 30:925–937

Kessel B (1953) Distribution and migration of the European starling in North America. Condor 55:49–67

Kutschera U, Niklas KJ (2004) The modern theory of biological evolution: an expanded synthesis. Naturwissenschaften 91:255–276

Lack D (1947) The significance of clutch size. Part I. Intraspecific variations. Ibis 89:302–352

Lack D (1968) Bird migration and natural selection. Oikos 19:1–9

Leisler B (1993) Habitat use and coexistence of Palearctic migrants and Afrotropical residents. Proc VIII Pan-Afr Orn Congr 565–570

Leisler B, Winkler H (2003) Morphological Consequences of Migration in Passerines. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian migration. Springer, Berlin Heidelberg New York, pp 175–186

Levey DJ, Stiles FG (1992) Evolutionary precursors of long-distance migration: resource availability and movement patterns in Neotropical landbirds. Am Nat 140:447–476

Martin TE (1995) Avian life history evolution in relation to nest sites, nest predation, and food. Ecol Monogr 65:101–127

Martin TE (2004) Avian life-history evolution has an eminent past: does it have a bright future? Auk 121:289–301

Matthysen E (2005) Density-dependent dispersal in birds and mammals. Ecography 28:403–416

Mayr E (1926) Die Ausbreitung des Girlitz (*Serinus canaria serinus* L.). J Ornithol 74:571–671

Mayr E, Meise W (1930) Theoretisches zur Geschichte des Vogelzuges. Vogelzug 1:149–172

McLachlan GR (1963) European Stork *Ciconia ciconia* ringed as nestling in South Africa recovered in Northern Rhodesia. Ostrich 34:48

Mettke-Hofmann C, Greenberg R (2005) Behavioral and cognitive adaptations to long-distance migration. In: Greenberg R, Marra PP (eds) Birds of two worlds. Johns Hopkins University Press, Baltimore, pp 114–123

Mettke-Hofmann C, Gwinner E (2004) Differential assessment of environmental information in a migratory and a nonmigratory passerine. Anim Behav 68:1079–1086

Mönkkönen M, Helle P, Welsh D (1992) Perspectives on Palearctic and Nearctic bird migration; comparisons and overview of life-history and ecology of migrant passerines. Ibis 134:7–13

Nathan R, Perry G, Cronin JT, Strand AE, Cain ML (2003) Methods for estimating long-distance dispersal. Oikos 103:261–273

Newton I (2003) The speciation and biogeography of birds. Academic Press, Amsterdam

Outlaw DC, Voelker G, Mila B, Girman DJ (2003) Evolution of long-distance migration in and historical biogeography of *Catharus* thrushes: a molecular phylogenetic approach. Auk 120:299–310

Peach WJ, Hanmer DB, Oatley TB (2001) Do southern African songbirds live longer than their European counterparts? Oikos 93:235–249

Piersma T, Pérez-Tris J, Mouritsen H, Bauchinger U, Bairlein F (2005) Is there a "migratory syndrome" common to all migrant birds? Ann N Y Acad Sci 1046:1–12

Pulido F, Berthold P (2003) Quantitative genetic analysis of migratory behaviour. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian migration. Springer, Berlin Heidelberg New York, pp 53–77

Pulido F, Berthold P, van Noordwijk AJ (1996) Frequency of migrants and migratory activity are genetically correlated in a bird population: evolutionary implications. Proc Nat Acad Sci USA 93:14642–14647

Rappole JH (1995) The ecology of migrant birds—a neotropical perspective. Smithsonian Institution, Washington

Rappole JH (2005) Evolution of old and new world migration systems: a response to Bell. Ardea 93:125–131

Rappole JH, Jones P (2002) Evolution of old and new world migration systems. Ardea 90:525–537

Rappole JH, Tipton AR (1992) The evolution of avian migration in the Neotropics. Ornitol Neotrop 3:45–55

Rappole JH, Helm B, Ramos MA (2003) An integrative framework for understanding the origin and evolution of avian migration. J Avian Biol 34:124–128

Ruegg KC, Smith TB (2002) Not as the crow flies: a historical explanation for circuitous migration in Swainson's thrush (*Catharus ustulatus*). Proc R Soc Lond B 269:1375–1381

Russell EM, Yom-Tov Y, Geffen E (2004) Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. Behav Ecol 15:831–838

Safriel UN (1995) The evolution of Palearctic migration—the case for southern ancestry. Isr J Zool 41:417–431

Salewski V, Jones P, Vickery J (2002) Niche partitioning between immigrant Palearctic willow warblers *Phylloscopus trochilus* and resident Afrotropical warblers in three woodland habitats in Zimbabwe. Avian Sci 2:207–216

Salewski V, Bairlein F, Leisler B (2003) Niche partitioning of two Palearctic passerine migrants with Afrotropical residents in their West African winter quarters. Behav Ecol 14:493–502

Salewski V, Bairlein F, Leisler B (2006) Paläarktische Zugvögel in Afrika-Konkurrenz mit tropischen Arten? Vogelwarte 44:1–15

Schüz E (1952) Vom Vogelzug. Grundriß der Vogelzugskunde. Verlag Dr. Paul Schöps, Frankfurt /Main

Schwabl H (1983) Ausprägung und Bedeutung des Teilzugverhaltens einer südwestdeutschen Population der Amsel *Turdus merula*. J Ornithol 124:101–116

Schwabl H, Silverin B (1990) Control of partial migration and autumnal behaviour. In: Gwinner E (ed) Bird migration. Springer, Berlin Heidelberg New York, pp 144–155

Skutch AF (1985) Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. Ornithol Monogr 36:575–594

South AB, Rushton SP, Kenward RE, MacDonald DM (2002) Modelling vertebrate dispersal and demography in real landscapes: how does uncertainty regarding dispersal behaviour influence predictions of spatial population dynamics. In: Bullock J, Kenward R, Hails R (eds) Dispersal ecology. Blackwell, Malden, pp 327–349

Stiles FG (1980) Evolutionary implications of habitat relations between permanent an winter resident landbirds in Costa Rica. In: Keast A, Morton ES (eds) Migrant birds in the neotropics: Ecology, behavior, distribution, and conservation. Smithsonian Institution, Washington, pp 421–435

Sutherland WJ, Gill JA, Norris K (2002) Density-dependent dispersal in animals: concepts, evidence mechanisms and consequences. In: Bulloch JM, Kenward RE, Hails RS (eds) Dispersal ecology. Blackwell, Malden, pp 134–151

Taverner PA (1904) A discussion of the origin of migration. Auk 21:322–333

Terrill SB (1991) Evolutionary aspects of orientation and migration in birds. In: Berthold P (ed) Orientation in Birds. Birkhäuser Verlag, Basel, pp 180–201

Underhill LG (2001) Four of our white storks vanish into the clouds; one keeps going. Promerops 246:12–14

von Lucanus F (1929) Die Rätsel des Vogelzuges. Hermann Beyer und Söhne, Langensalza

Wiltschko R, Wiltschko W (1999a) Das Orientierungssystem der Vögel-IV. Evolution. J Ornithol 140:393–417

Wiltschko R, Wiltschko W (1999b) Das Orientierungssystem der Vögel-I. Kompaßmechanismen. J Ornithol 140:1–40

Winker K (2000) Migration and speciation. Nature 404:36

Winkler DW (2005) How do migration and dispersal interact. In: Greenberg R, Marra PP (eds) Birds of two worlds. Johns Hopkins University Press, Baltimore, pp 401–413

Winkler H, Leisler B (2005) To be a migrant. Ecomorphological burdens and chances. In: Greenberg R, Marra PP (eds) Birds of two worlds. Johns Hopkins University Press, Baltimore, pp 79–86

Yom-Tov Y, McCleery R, Oatley T (1994) The survival rates of some southern African passerines. Ostrich 65:329–332

Zink RM (2002) Towards a framework for understanding the evolution of avian migration. J Avian Biol 33:433–436