

REVIEW

The study of bird migrations – some future perspectives

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Capsule Routes and destinations have been unveiled but modern techniques offer the chance to explore much more.

Summary Ringing of birds unveiled many mysteries of avian migrations, notably routes and destinations. However, there is still much to be explored by the use of ringing and other marks. Satellite tracking, geolocation and global positioning systems, and even electronic tags may enable much more detailed insights into the migration patterns of individual birds and populations. But also a more elaborated colour-marking approach is recommended. Moreover, particular chemical and molecular markers appear to be very useful in the study of bird migration by delineating the origin of birds and connectivity between breeding and non-breeding grounds. Co-ordinated, collaborative, standardized and large-scale migration networks provide another elaborate tool to study differential migration and patterns of migratory timing and fuelling. Although our understanding of bird migration has gained much from captive studies about the internal mechanisms in the control of bird migration, we still lack knowledge about external factors, such as food availability, weather, competitors, parasites or diseases. Such data are also required to refine theoretical models of migration strategies. Future migration research must aim at much more comparative research and a more integrative approach at various spatial and temporal scales, and link various subdisciplines. It must also consider that migration is only one part of the life of a migrating species. Thus, linking migration and breeding is another future challenge, both for basic science and for effective protection of migratory birds.

By the introduction of bird ringing about 100 years ago, many of the former mysteries of bird movements were unveiled (Bairlein 2001). Hundreds of thousands of recoveries of ringed birds clarified the annual movements of many bird species and contributed substantially to a better understanding of the spatial and temporal course of migrations. Various 'Atlases' compiled recoveries on a transnational (Schüz & Weigold 1931, McClure 1974, Zink 1973, 1975, 1981, 1985, Zink & Bairlein 1995) or national scale (Yamashina Institute for Ornithology 1996, Fransson & Petterson 2001, Wernham *et al.* 2002), and hundreds of other papers analysed recoveries of single species or species groups in great detail. Consequently, the general migration routes of many species are well known – in particular for the northern hemisphere.

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Moreover, numerous observational data exist that describe the spatial and temporal distribution of migratory bird species in considerable detail (Glutz von Blotzheim & Bauer 1966–98, Moreau 1972, Cramp *et al.* 1977–94, Keast & Morton 1980, Curry-Lindahl 1981, Brown *et al.* 1982–2000, Hagan & Johnston 1992, Poole *et al.* 1992–2002, Rappole *et al.* 1995). In addition, exciting behavioural and physiological work give insights into the general principles of bird migration (Alerstam 1990, Gwinner 1990, Berthold 1996, Berthold 2001, Berthold *et al.* 2003). Consequently, one may argue that not much is left for future research in the field of bird migrations. However, the contrary is true. There is still much to be explored with respect to migration routes and the distribution of migrants, migration systems, winter ecology of migrants, the integration of migration in the annual cycle of a migratory species, and life-history aspects of

migrations. This paper briefly sketches a few of these future perspectives. For the sake of conciseness and space, I have chosen examples relevant to Europe and mostly landbirds. Many other examples could have been used, so this is not a complete review of the subject.

Identifying migration routes

Ordinary ringing normally provides start- and end-points of movements, and routes can only be identified and evaluated by the analyses of many such recoveries. However, new tools of tracking migrants have become available during the last decade. Satellite telemetry has proved fascinating in delineating migration routes of birds (Berthold *et al.* 1997, Fuller *et al.* 1995, 1998). It enables a much more detailed spatial and temporal resolution of avian migrations (Fig. 1; Berthold *et al.* 2002) and helps to identify migration routes, stopover sites and winter grounds – especially in species for which comparatively few recoveries are available or could be obtained, such as larger or rare species. The technique is so far applied only to comparatively large species (e.g. storks, cranes, geese, raptors) owing to the mass of the transmitters, but miniaturization of transmitters and improved receiver sensitivity may enable application to even smaller species.

Geolocation (GLS) and global positioning system (GPS) are two other new tools which can be used to track migrating birds on a worldwide scale (von Hünenbein *et al.* 2000, Weimerskirch & Wilson 2000, Gauthier-Clerc & Le Maho 2001, Wilson 2001). Geolocation is based on real-time measurement of the ambient light intensity to determine the geographic coordinates, while GPS receives data from satellites for calculating the position of the bird. Both require an archival tag on the birds to collect the data and thus necessitate recapture of the birds and the recovery of the logger. However, recent developments to link GLS and GPS to satellite transmitters may allow the stored data to be downloaded without recapture.

In contrast to ringing, tracking systems enable continuous and worldwide information on the migrant birds' locations. Data can even be obtained from very remote areas that are normally not accessible to man. Tracking studies can also help to identify important bird areas for migrants (e.g. Golden Eagle *Aquila chrysaetos*, Fuller *et al.* 1995; Spectacled Eider *Somateria fischeri*, Petersen *et al.* 1999).

Electronic tags are used to re-identify tagged individuals on particular sites such as nests or perches, where

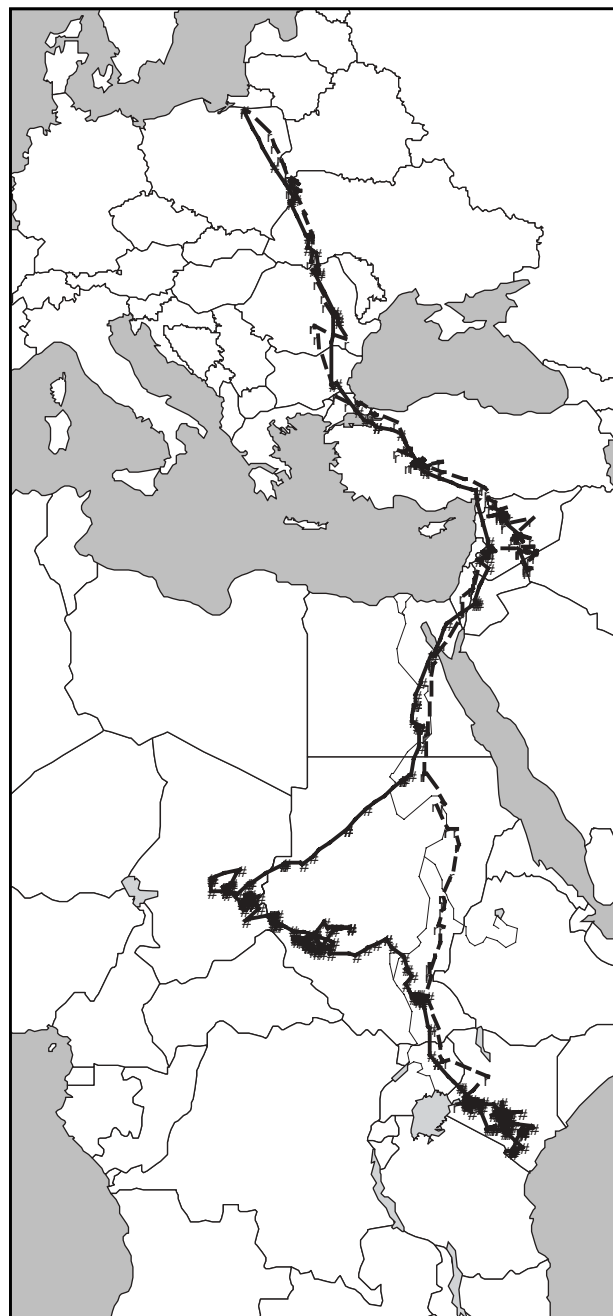


Figure 1. Migration patterns of an individual satellite-tracked White Stork. Reproduced from Berthold *et al.* (2002) *J. Ornithol.* **143**: 490, with permission of the German Ornithologists' Society.

the birds regularly return or pass. Their use is currently limited by the short reading distance of the antennae. However, technical progress may increase the reading distances and one may speculate that electronic tags may even become available for reading birds in flight (Gauthier-Clerc & Le Maho 2001).

Besides new electronic tools, recently established

chemical and molecular markers appear to be very useful in bird migration research (Webster *et al.* 2002). The earth's surface varies in its chemical composition. Through diet, birds carry a signature of that chemical composition in their tissues. Stable isotopes are found to function as natural markers and provide new insight into the location histories of highly mobile animals by delineating the origin of birds feeding in areas where diets differ in isotope composition (Alisauskas & Hobson 1993, Hobson & Wassenaar 1997, Alisauskas *et al.* 1998, Bensch *et al.* 1999, Hobson 1999, Chamberlain *et al.* 2000, Rubenstein *et al.* 2002, Hobson 2003, Lott *et al.* 2003). Similarly, trace-element composition of plumage can be used to identify origins of birds (Parrish *et al.* 1983).

Molecular techniques analysing polymorphisms of genetic markers, such as DNA sequences, can also be applied to determine different populations and to track them at stopover sites and wintering grounds (Webster *et al.* 2002).

Finally, there is another potential tool for the identification of migratory routes, not yet fully explored – the large-scale use of co-ordinated colour banding. By using marks which can be read at distance, the number of 'recoveries' can be much increased simply by stimulating the many bird observers to resight marked birds and report to a centralized database. There are already several colour ringing schemes established (Flamant 1994, Clark 1996, Marchant 1996; see also <http://www.cr-birding.be>), but there is still a huge unused potential, namely in larger species where even coded colour-rings such as the new ELSA (European laser-signed advanced; Fig. 2) ring (Fiedler *et al.* 2002) can be applied (e.g. swans *Cygnus*, geese *Anatidae*, herons *Ardeidae*, storks *Ciconiidae*, raptors, several waders *Charadriiformes*). In the past, the use of colour rings was mainly limited by our capabilities and capacities for collaborating on an international scale – minimizing duplication of codes by people working in different places and passing observations of colour-banded birds back to the ones who marked. Another



Figure 2. The new ELSA (European laser-signed advanced) ring (Fiedler *et al.* 2002).

limitation was the capacity to handle a large number of resightings. The latter is being solved by computerization and electronic submission of data. The first problem could be solved by appropriate funds to bodies like EURING, IWRB and the Wader Study Group.

While recoveries of ringed birds revealed a lot about migration routes, and origins and destinations of migrating birds of the northern hemisphere, still very little is known of bird movements in the southern hemisphere and within the tropics (Dowsett & Davies 1988, Fullagar *et al.* 1988, Lane & Parish 1991, Chesser 1994, Bairlein 1998a). More ringing projects in these regions are to be established. Ringing in the tropics is also very efficient in determining population-specific wintering grounds of northern migrants, as shown by Wood (1982) in the Yellow Wagtail *Motacilla flava*.

Analyses of differential migration

Despite considerable knowledge of the general to-and-fro migrations of many bird species, little is known concerning questions of differential migration (Ketterson & Nolan 1983), i.e. differences in the migration of age classes, of sexes, and of populations as well as seasonal variation in routes and behaviour. Owing to the hundreds of thousands of recoveries, there is a great potential for more refined analyses of already existing recoveries of ringed data applying recently developed statistical techniques (Nichols & Kaiser 1999).

In some irruptive migrants, such as Brambling *Fringilla montifringilla* (Fig. 3), Redpoll *Carduelis flammea* or crossbills (*Loxia* spp.), inter-year variation of migration routes and destinations deserves interest. Identifying differential migration has considerable consequences for understanding migration strategies (Alerstam & Hedenström 1998), migratory connectivity (Webster *et al.* 2002), and conservation needs (Van der Have 1991, Salathe 1991).

While to-and-fro migrating species may use approximately the same routes in both autumn and spring, others follow a 'loop-migration', i.e. using a different route in each season (Bairlein 2001, Wernham *et al.* 2002).

Population-specific migration routes are most evident in species with a 'migratory divide' separating adjacent populations with different migratory directions, such as White Stork *Ciconia ciconia* or Blackcap *Sylvia atricapilla*, where the western European breeding birds follow a southwesterly route while the eastern birds migrate southeast. However, there also other types of separation of migration routes of adjacent populations. In Lapwings *Vanellus vanellus* different breeding popu-



Figure 3. Recoveries of Bramblings ringed in winter in Great Britain and recovered in a successive winter. Reproduced from Wernham *et al.* (2002) *The Migration Atlas*: p. 642, with permission of the British Trust for Ornithology.

lations have quite distinct population-specific migration routes heading to different wintering grounds (Imboden 1974). In Chaffinches *Fringilla coelebs* different populations follow more or less parallel migration routes in autumn, following almost the same principal direction but not merging (Zink & Bairlein 1995, Bairlein 2001).

First-year birds may migrate along different routes or may have different winter grounds from adults (Bairlein 2001, Wernham *et al.* 2002). Comparatively little is known about sex-related migration patterns, routes and destinations. However, there is a fair amount of evidence that sexes can differ in the spatial and temporal course of their migration and wintering grounds. In Chaffinches ringed at the Courish Spit (Kaliningrad region), males winter further north in central Europe than females (Zink & Bairlein 1995), while in Siskin *Carduelis spinus* males winter further south than females (Payevsky 1994).

While many species migrate to the same wintering places each year, and individual birds may return even to the same site as the winter before (Curry-Lindahl

1981, Rappole 1995, Salewski *et al.* 2000a, 2000b), other species are more flexible and may winter in different regions in different years (Zink & Bairlein 1995, Bairlein 2001, Wernham *et al.* 2002). The causes of variation in winter quarters from year to year may be related to the availability of food (Jenni 1987) or to the weather conditions during the start of migration (Richardson 1991).

We still have insufficient knowledge about the occurrence and the extent of partial migration. Partial migration involves only a part of the population. It may be obligate, with some individuals leaving the breeding area every year on a genetic basis, or facultative, when migration occurs only in some years owing to annual variation in environmental conditions such as weather or food (Berthold 2001). The occurrence and the extent of partial migration may vary between species and with geographical location. However, apart from numerous descriptive studies and compilations of evidence on partial migration (Zink 1973, 1975, 1981, 1985, Zink & Bairlein 1995, Fransson & Petterson 2001, Wernham *et al.* 2002), very few studies evaluated the extent and consequences of partial migration in detail. The study of partial migration becomes particularly interesting in the light of recent global climate changes which are likely to affect bird life considerably (Berthold 1998, Bairlein & Winkel 2001, Walther *et al.* 2002). Namely, partial migrants may become mainly resident as a consequence of global warming and improved winter survival, and owing to their micro-evolutionary potentials (Berthold 2001).

Moult migration

A largely neglected subject is moult migration. Although it is known in some species – such as ducks, geese, raptors – even more species may regularly undertake prebasic moult migrations. Such movements may vary within a given species owing to population-specific environmental conditions, and they may vary between sexes and age groups (Jehl 1990, Storer & Jehl 1985, Rohwer & Manning 1990, Rohwer 1999, Butler *et al.* 2002). Thus, it is worthwhile exploring in more detail the relationship between the species' ecological requirements and the ecological conditions and the occurrence and extent of pre-moult movements.

Migration networks

Differential migration and partial migration, especially in small landbirds, could be efficiently explored by co-

ordinated, collaborative and standardized projects following a broader geographical and even flyway perspective (Jenni *et al.* 1994, Buckley *et al.* 1998, Tautin *et al.* 1999). The EURING *Acrocephalus* project (Jenni *et al.* 1994), the European Science Foundation Network on European–African Songbird Migration (Bairlein 1993, 1998b), the Southeast European Migration project (Busse 2000) and the recent EURING Swallow Project (van Noordwijk & Oatley 1998, Spina 1998) are examples showing the great value of continent-wide approaches. Such planned and targeted ringing is more likely to meet the conservation needs of migratory birds (Salathe 1991) than mere local studies. The potential for co-ordinated large-scale bird ringing research is immense thanks to the large numbers of amateur ringers. The great value of such network approaches lies in the use of more evaluated parameters to study the migration of birds rather than relying on recoveries as the sole source of information. The study of variables such as wing-length and wing-shape are of particular interest as these features are closely linked to flight performance (Pennycuik 1989). Their analysis across geographical regions can reveal the spatial and temporal courses of migration in more detail (Fig. 4) than can recoveries in species that can be caught in good numbers but which produce comparatively few recoveries, such as many songbirds (Pilastro *et al.* 1998, Bairlein 1998b). These measurements also make it possible to calculate how birds may migrate and how fuel is used – by applying recently developed approaches to the mechanics of the bird and the physical and physiological performance of migration (Pennycuik 1998, Rayner & Maybury 2003).

Implicit in current theories of migration strategies are two distinctive forms of variation encountered by migrants. This is the trade-off between locally experienced performance at a site and the expected performance at future sites (Weber 1999, Weber *et al.* 1999). Thus, understanding the migration strategy of a species requires both detailed local single-site studies as well as large-scale ones. This will help us learn more about variation between sites and large-scale geographical variation. So far, most studies have been conducted as single-site approaches. Many of these studies provide excellent insights into site-specific details of migratory passage and performance. However, they all investigate their own subset of species using their area, and use their own procedures and routines in trapping and taking bird measurements, thus making comparisons across a wider geographical scale difficult. Large-scale approaches are still rare, although under-

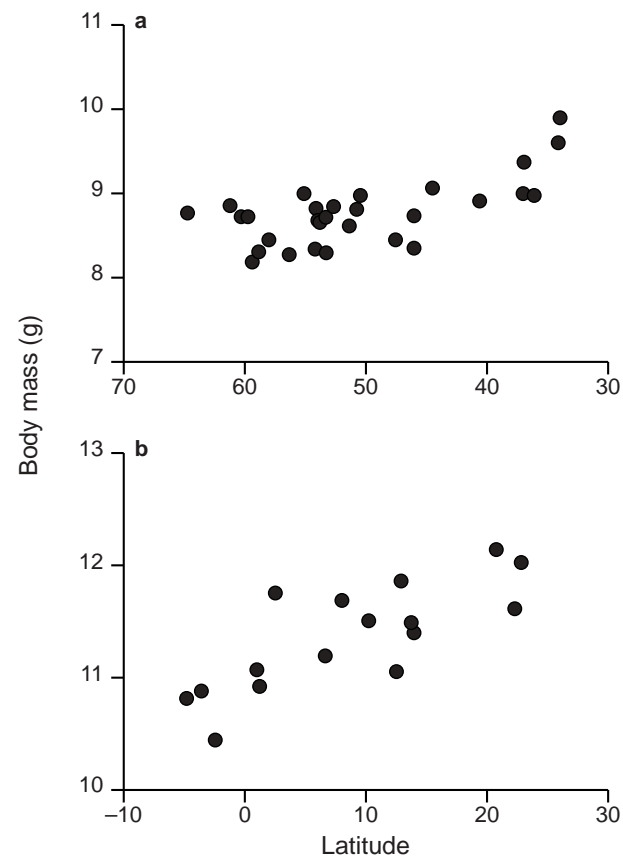


Figure 4. Latitudinal (a) and longitudinal (b) patterns of body mass of two migratory species during autumn migration (data from the European Science Foundation Scientific Network on Palaearctic–African songbird migration).

standing of natural patterns needs a broader view of spatial and temporal scale (Simons *et al.* 2000). Well-designed large-scale and co-ordinated networks of study sites can achieve this task. They can be used to identify timing and speed of migration, and to evaluate the fuelling strategies of migrating birds (Lindström *et al.* 1996, Bairlein 1998b, Grattarola *et al.* 1999, Schaub & Jenni 2000a, 2000b, 2001a, 2001b).

External factors ruling migration – the study of optimality

While we have gained a lot of information about internal mechanisms in the control of avian migration, i.e. timing of migration, the spatial control of migration, the directional cues used for orientation and the energetic background for successful migration (for reviews see Berthold 2001, Bairlein 2002) and although we know much about patterns of migration (Fransson & Pettersson 2001, Wernham *et al.* 2002), to

understand migration and reveal the different migration strategies we need to learn more about external factors ruling migration and shaping an innate template into realized migration (Fig. 5). Among these factors, some have already been studied, in particular the role of food and physiological adaptations for migration (Biebach 1998, Jenni & Jenni-Eiermann 1998, Piersma 1998, Bairlein 2002, 2003, Jenni & Schaub 2003). Others, however, have been largely ignored, such as intra- and inter-specific competitors or parasites and diseases. In order to achieve better insight into the role of these factors, we have to apply a much more integrated approach combining field observations, field experiments and captive studies.

Evolution by natural selection is a process of optimization. In recent years, considerable theory has been built up to predict various aspects of bird migration using optimality models (Alerstam & Lindström 1990, Alerstam & Hedenström 1998). The theory of bird flight yields quite specific predictions about gliding and soaring performance of different species, and about the speed in flapping flight and how this speed is expected to vary in relation to environmental cues – such as flight altitude, wind, or fuel burden. Several ‘ecological’ criteria can be added to the models to explain the temporal and spatial course of migration and the adaptations that enable birds to accomplish their migratory journey successfully. The optimal policy for a migrating bird to reach its destination within the appropriate time varies with the demands that act on the bird. Time, energy, and safety from predators are of main current concern. Using dynamic programming models, the adaptive aspects of flight behaviour, fuel deposition and responses to environmental cues can be evaluated, and patterns of stopover, fuel load at departure, responses to different fuel-deposition rates and habitat selection in migrating

birds can be predicted.

However, empirical evidence is still scarce and only few studies have tried to test the derived hypotheses in field studies.

Migration of birds is flying and stopover, with about 90% of entire migration time spent at stopovers (Hedenström & Alerstam 1997). Consequently, models dealing with optimality in bird migration refer mainly to stopover conditions. Crucial for testing models of optimal migration is the relationship between fuel-deposition rate and departure fuel load in individual birds during stopover. Consequently, these studies rely on birds that are repeatedly retrapped after their first catch. Thus, many more studies should focus on this issue and ringers should intensify their efforts to retrap and reweigh birds during their stopovers. Moreover, some species may even be good candidates for using remote techniques that avoid recatching. Individual colour-ringing and the use of remote electronic balances were applied successfully by Carpenter *et al.* (1983) on migrant Rufous Hummingbirds *Selasphorus rufus*, by Lindström & Alerstam (1992) on Bluethroats *Luscinia svecica*, by Fransson (1998) on Whitethroats *Sylvia communis* and Wheatears *Oenanthe oenanthe* (Dierschke & Delingat 2001, Dierschke *et al.* 2003). Species using open areas for stopover, such as Wheatears, are particularly interesting as they are comparatively easy to access and to observe, which allow quantification of stopover behaviour (Delingat & Dierschke 2000, Dierschke & Delingat 2001, Dierschke 2003). In addition to colour-ringing, transponders could be used to mark the stopover migrants and to identify them automatically on remote balances placed beneath regularly used perches, thus being less dependent on visibility and observer capacities. Using these new technical developments will significantly improve our under-

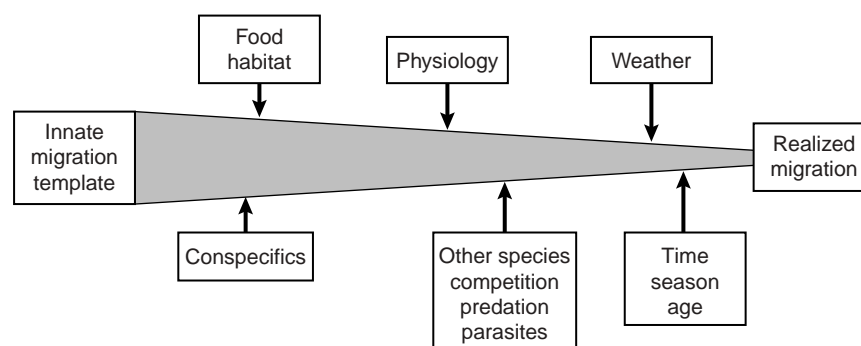


Figure 5. A complex set of factors is involved in shaping an innate migration template into realized migration. The order of the factors does not imply a hierarchy of relevance.

standing of stopover behaviour and ecology, and of migration strategies.

Quantifying migration

Migration can be spectacular, but quantifying migration is still mostly an unsolved task. It can be achieved by using various modern radar facilities, ranging from airport surveillance radars to tracking radars (for a summary see Bruderer 1997). Recently, the use of comparatively cheap modified marine radar systems was powerful in quantifying migration in space and time (Harmata *et al.* 1999, Biebach *et al.* 2000, Klaassen & Biebach 2000). Major achievements using radars include the altitude of migration, the diurnal and nocturnal patterns and courses of migration, and the influence of meteorological conditions on bird migration. The analysis of migration heights becomes important in the light of the recent debate about the possible impact of offshore windfarms on migrating birds (Hüppop *et al.* 2002).

Migrants in winter

Migrants are facing at least two worlds. Wintering in other areas and habitats, and meeting different bird communities to those during breeding is an integral part of their life-cycles. Consequently, a number of studies investigated the ecology and behaviour of migrants at their wintering grounds (Keast & Morton 1980, Hagan & Johnston 1992, Jones *et al.* 1996, Salewski *et al.* 2002a, 2003) but much is still to be learned about wintering ecology, in particular for Afrotropical migrants which are little studied. Moreover, surprisingly few studies quantified winter ecology, although it is already well-known that survival and even subsequent breeding success may depend on the ecological conditions during wintering (Cave 1983, Møller 1989, Kanyamibwa *et al.* 1990, Peach *et al.* 1991, Szep 1995, Bairlein & Henneberg 2000; Fig. 6), irrespective of the fact that the extent to which migrants are limited by circumstances on their winter grounds is much debated (Alerstam & Högstedt 1982, Svensson 1985, Rappole & McDonald 1995, Sherry & Holmes 1998, Latta & Baltz 1997). Winter subsistence and survival largely depend on habitat quality and food resources, but the impact of ecological factors other than food is less studied and largely unsolved (Sherry & Holmes 1998). The role of intra- and inter-specific competition of migrants on their winter grounds is still much debated (Greenberg 1986, Leisler 1992, Rappole

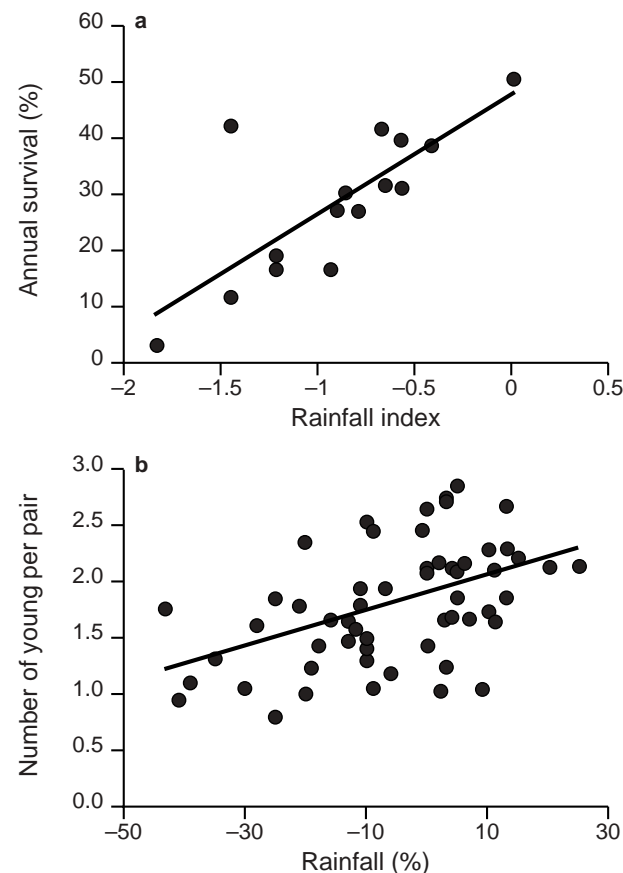


Figure 6. Annual survival in Sedge Warbler *Acrocephalus schoenobaenus* (a) and breeding success in White Stork *Ciconia ciconia* (b), both Palaearctic migrants, in relation to rainfall in the Sahelian winter quarters. Rainfall is expressed in (a) as an index and in (b) as percentage deviation from the long-term (1900–85) average. (a) Redrawn from Peach *et al.* (1991) with permission of the British Ornithologists' Union; (b) redrawn from Bairlein & Henneberg (2000) with permission.

1995, Sherry & Holmes 1998, Salewski *et al.* 2002b).

Closely related to habitat use and competition of migrants on their winter grounds is the question of how these migrants affect the local bird communities and how these communities support the influx of migrants which can often double the number of native birds in a given habitat. Consequently, many more detailed analyses are required before we will be able to understand the ecology of migrants on their winter grounds, to relate winter conditions to survival and breeding, and to draw consequences for conservation. In addition, we should notice that most studies on the wintering ecology of landbird migrants are conducted in the tropical winter ranges. That many arctic and higher latitude species spend their non-breeding lifetime in the temperate zone, however, is mostly

neglected. Recent studies by Dierschke (2001, 2002) revealed that Shorelarks *Eremophila alpestris*, Snow Buntings *Plectrophenax nivalis*, and Twites *Carduelis flavirostris* depend largely on very particular habitat and food resources during wintering in the salt marshes of the North Sea coast, and that their populations may be limited by the ecological conditions in winter. As several tropical migrants, they show high but species-specific winter site fidelity, which is, in both cases not as well understood as winter territoriality. The same also holds for many short-distance and partial migrants that move to specific habitats at, for example, lower altitudes – such as the Skylark *Alauda arvensis* in Britain (Gillings & Fuller 2001).

Connecting migration and breeding

Migration is an integral part of the annual life-cycle and the life-history of a migrant species. However, surprisingly few studies connect migration and breeding. In arctic geese and waders, breeding success depends on the conditions upon arrival from migration and the body condition of the parents – which is mainly gained before departure on spring migration (Ebbinge 1989, Klaassen *et al.* 2001). American Redstarts *Setophaga ruticilla* have a higher reproductive success when they arrive with more body fat (Smith & Moore 2003). Thus, reproductive performance in long-distance passerine migrants is likely to be closely connected to migration performance and the individual migrant's energetic condition encountered during prebreeding migration can have important fitness consequences. This relationship becomes particularly challenging with respect to possible global warming where either spring arrival or onset of breeding may advance (Crick *et al.* 1997, Huin & Sparks 1998, 2000, Sæther *et al.* 2000, Sillett *et al.* 2000, Bairlein & Winkel 2001, Walther *et al.* 2002, Hüppop & Hüppop 2003) and where the two events may mismatch (Both & Visser 2001, Strode 2003). On the other hand, parental investment may have consequences for the condition of the offspring and their subsequent migratory performance, as well as having costs for the parents and their subsequent migration. So far, I do not know a single study on this subject.

Conclusions

Research on bird migration by both professional scientists and the many citizen scientists has revealed considerable insights into the patterns of migration and

the behaviour of migrants during recent decades. However, bird migrations are far from being understood. We need a much closer and detailed look at the ecological circumstances of migration, not only for the sake of science but also for conservation. Migrant bird species, in particular, have been subject to population declines in recent decades (Terborgh 1989, Marchant *et al.* 1990, Bauer & Berthold 1997).

New techniques have become available that allow detailed tracking of migrants to identify key areas for stopover and wintering and to reveal connectivity between breeding and non-breeding areas. These methods will not replace ordinary bird ringing by both professional scientists and the many skilled volunteer ringers. However, future ringing for bird migration research must emphasize the need for more project-related approaches and objectives. Future research must consider that migrants are connected to different parts of the world and must focus on quantifying the geographical distributions, habitat requirements and behavioural ecology of migrants, as well as their survival rates, and it requires much more comparative research and a more integrative approach at various spatial and temporal scales.

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