Ringing and the study of mechanisms of migration

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The ringing of birds has unveiled many mysteries of avian migration, notably routes and destinations, but has also contributed to the elucidation of migration mechanisms. The understanding of orientation and navigation mechanisms, stopover and fuelling strategies, and of migration strategies has gained much from the analyses of recoveries from ringed birds, and ringing and recapture approaches still make a major contribution to our understanding of migration. Detailed single-site studies could reveal internal and environmental factors governing stopover strategies, especially with sophisticated field experiments, but comparative multi-site approaches would be of considerable value to unravel migration strategies and carry-over effects between non-breeding and breeding periods. This is particularly important in view of the fact that long-distance migratory species are the ones with the most serious population declines.

The ringing of birds has unveiled many mysteries of avian migration, notably routes and destinations, and has also made a considerable contribution to understanding the mechanisms of migration. Many, if not all, migratory birds are equipped with internal, innate mechanisms to control their migration in terms of timing, migratory distances, orientation, and migratory fuelling (for reviews see, for example, Gwinner 1990, Berthold 1996, Wiltschko & Wiltschko 2003). These internal mechanisms set the framework for migration, but external factors shape migration during the real journey. Thus, to understand migration we need to elucidate these external factors as well, and ringing makes a significant contribution because data are required on individual birds. Analyses of recoveries from ringed birds contribute particularly to our understanding of (1) orientation and navigation mechanisms, (2) stopover and fuelling strategies, and (3) migration strategies.

MIGRATORY ORIENTATION AND NAVIGATION

One of the very first fields where ringing contributed greatly to the understanding of mechanisms of migration was migratory orientation and navigation. In the very early 1900s, Loos (1907) translocated colour-marked swallows, Starlings *Sturnus vulgaris* and pigeons to study homing. More-thorough displacement experiments were conducted in the late 1920s (Stimmelmayr 1930), and in particular in the 1930s with White Storks *Ciconia ciconia*,

Sparrowhawks *Accipiter nisus*, ducks, Starlings, Barn Swallows *Hirundo rustica*, and Hooded Crows *Corvus cornix* (Schüz 1931, Drost 1934, Rüppell 1934, 1944). Most of these studies aimed to elucidate the homing capabilities of migratory birds (Wiltschko 1992) but several studies also considered orientation mechanisms during migration. For example, Drost (1938) caught Sparrowhawks on the island of Helgoland during autumn migration and displaced them 700 km southeast to Silesia. Young birds continued their migration southwest, in parallel to the normal migration route of non-displaced birds, whereas the adult birds headed northwest towards the population-specific wintering grounds of Sparrowhawks passing Helgoland. This experiment showed that young birds follow innate, inherited, migratory directional information, whereas the adult birds compensated for the displacement through navigational mechanisms.

These first results were later confirmed by the most extensive displacement experiment ever with migratory birds, which was carried out by Perdeck (1958). During autumn migration, he displaced some 11,000 Starlings from the Netherlands to Switzerland. Recoveries of ringed birds during the first autumn and winter after release showed that the young Starlings continued their migration in parallel to the normal route Starlings take from Holland, thus ending up in southern France and Spain. In contrast, ring recoveries from the released adult Starlings were obtained from northwesterly locations, revealing that these adult birds corrected for the displacement and migrated towards their normal winter range. Later, Wolff (1970) repeated Perdeck's Starling experiments with Teals *Anas crecca* which he also displaced from the Netherlands to Switzerland during autumn migration. Displaced juvenile

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Teals continued to migrate in a southwesterly direction whereas adult Teals migrated northwestwards to their normal winter quarters. In later seasons, adults returned to their normal range, whereas the displaced juveniles continued to winter in their new winter quarters and they bred in more-easterly areas than the non-displaced birds. These data gave convincing evidence that young migrants use inherited directional information, whereas adult birds are able to conduct true navigation towards a known goal. However, as pointed out in detail by Mouritsen (2001), Perdeck's experiment is not as convincing as is often claimed. Starlings normally migrate in flocks. Thus, the displaced young Starlings might have joined migrating flocks of local Swiss Starlings which are known to winter in Spain and they might simply have followed these Swiss Starlings.

Even before Perdeck's experiment, Schüz (1949) was able to show that social relationships could override internal mechanisms determining compass directions. Young White Storks from the southeast-migrating population of East Prussia, released in western Europe in contact with the southwest-migrating western storks, followed these birds rather than their population-specific compass direction (Schüz 1949). In contrast, translocated young birds released without contact with the westerly migrants followed their inherited southeasterly route (Schüz 1950), as did young White Storks displaced from East Prussia to England and Scotland (Schüz 1938). The role of social effects in influencing migratory behaviour had earlier been revealed by Välikangas (1933) and Putzig (1938). These authors aimed to elucidate the genetic basis of the control of migration. They took eggs from the non-migratory English population of Mallards *Anas platyrhynchos* to Finland and East Prussia, respectively, reared the birds at these places and released them in contact with the local migratory Mallards prior to their autumn migration. The birds that hatched from the English eggs departed with the local population and followed them to their normal winter ranges.

Although there are some pitfalls in interpreting the results of the previous displacement experiments (Wiltschko 1992, Mouritsen 2001), they gave important hints on the inherited backgrounds and orientation and navigational mechanisms of migratory birds, and they stimulated many subsequent studies with birds in captivity (for review see, for example, Wiltschko & Wiltschko 2003).

While it might be very unlikely, in view of the logistics involved, that such a displacement experiment as conducted by Perdeck (1958) might be performed again with species that migrate alone and without any influence or guidance from other birds, existing ring recoveries can also be used to elucidate orientation and navigation mechanisms of migration. Ring recoveries from Pied Flycatchers *Ficedula hypoleuca* and European Robins *Erithacus rubecula* strongly support the assumption that first-migrating birds follow an inherited migratory direction and that they use only a clock-and-compass strategy if they migrate alone (Mouritsen 2001).

MIGRATORY STOPOVER AND FUELLING

In most migratory birds, migration consists of flying interspersed with intermediate stopovers, with about 90% of the entire migration time spent at stopover sites (Hedenström & Alerstam 1997). Stopovers are necessary for resting and/or fuelling. Fuelling is the major issue for most species because of the tremendous energetic requirements for flight. Consequently, successful migratory fuelling and fuel accumulation prior to migratory flights play a pivotal role for all migrants that do not feed in flight. This is particularly so for species which cross huge ecological obstacles such as oceans or deserts. Therefore, an understanding of the migratory journeys and of migration strategies relies on understanding migratory fuelling and stopover behaviour. From an evolutionary point of view, recent theories on optimal bird migration predict that migrating birds should minimise either the time spent on migration or their total energy expenditure, with predation risk as a further criterion to be considered (Alerstam & Lindström 1990). However, empirical evidence is still scarce and only a few studies have tried to test the derived hypotheses in field studies (Lindström & Alerstam 1992, Fransson 1998, Dierschke & Delingat 2001, Delingat *et al* 2006). Crucial for testing models of optimal migration is the relationship between fuel deposition rate and departure fuel load in individual birds during stopover, because this relationship tells us about the overall migration strategies. Birds which are 'energy-minimisers', *ie* minimising the overall cost of migration, do not invest in achieving maximum departure fuel load and thus show almost no relationship between fuel deposition rate and departure fuel load during stopover. In contrast, migrating birds which have a strong drive to reach their destinations should minimise their overall time spent on migration and, consequently, these 'time-minimisers' should show a positive relationship between fuel deposition rate and departure fuel load, meaning that they put much effort into gaining maximum departure fuel load for achieving long migratory flights.

These relationships are exemplified for spring migrating Northern Wheatears *Oenanthe oenanthe* staging at the island of Helgoland in the southern North Sea (Fig 1). The relationship between fuel deposition rates and departure fuel loads in spring is significantly positive in male *leucorhoa*, the subspecies migrating to Iceland and Greenland. In
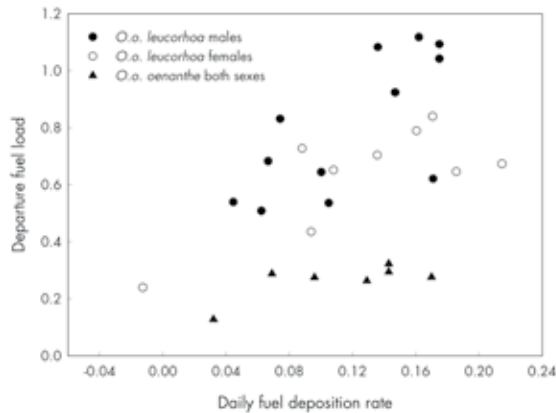
Figure 1. Relationship between departure fuel load (in relation to lean body mass) and total daily fuel deposition rate in Northern Wheatears on Helgoland (from Bairlein 2008).

Figure 2. Body mass of Garden Warblers at first capture (left) and individual body-mass changes of stopover birds in a northern Algerian stopover site during autumn migration (from Bairlein 1987).

Figure 3. A complex set of factors is involved in shaping an innate migration template into realised migration. The order of the factors does not imply a hierarchy of relevance (from Bairlein 2003).

female *leucorhoa* the relationship is weaker, and it is absent in nominate *oenanthe*, which migrate to Scandinavia. Thus, male *leucorhoa* could be considered time-minimisers while *oenanthe* are energy-minimisers. Female *leucorhoa* illustrate a compromise between the two strategies (Dierschke *et al* 2005, Delingat *et al* 2006, Bairlein 2008).

Fundamental questions are when, where and for how long a migrant should stop for rest or fuelling, what is the fuelling success and which factors influence these stopover decisions. Consequently, such studies rely on individually marked birds. Capture–recapture and capture–resighting are the most important approaches where ringing and marking make a major contribution to elucidating staging and migration mechanisms. As a consequence, numerous studies have used these techniques, of which only a few are discussed below as examples. Capture–recapture studies reveal that many trans-Saharan migrants cross the desert in stages, in contrast to previous assumptions that birds have to overfly the desert in one long non-stop flight (Bairlein 1985, Biebach *et al* 1986, Safriel & Lavee 1988, Schmaljohann *et al* 2007). Crucial for successful desert crossing is fuelling at staging sites prior to final take-off. At such fuelling sites trans-Saharan migrants accumulate bodily reserves at an amazing rate. For example, Garden Warblers *Sylvia borin* arrive at a northern Algerian stopover site during autumn migration with, on average, only moderate reserves which would not enable subsequent crossing of the Sahara Desert (Fig 2). During stopover, they fuel at an average rate of 10–15% of initial body mass per day upon arrival, with only very few birds losing mass (Fig 2); this identifies such sites as major fuelling sites.

A complex set of factors is involved in shaping an innate migration template into realised migration (Fig 3), but comparatively few studies have investigated them. Stopover
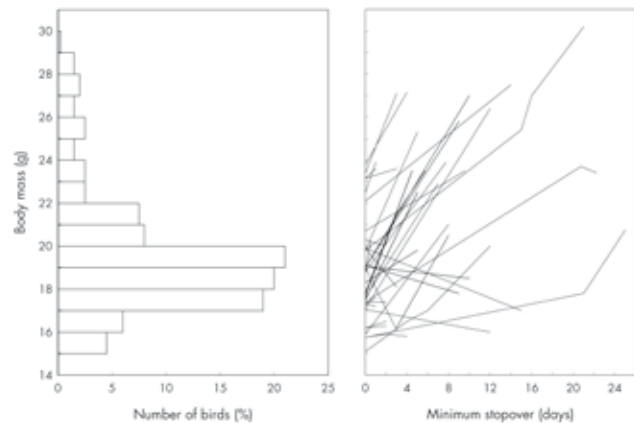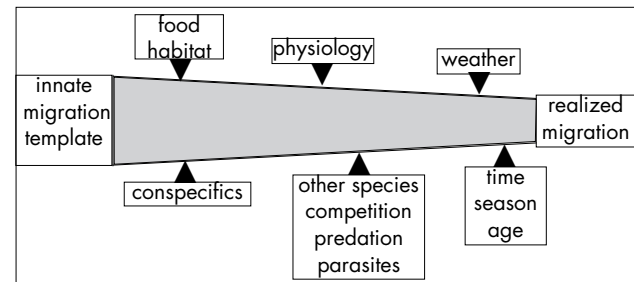
body-mass gain could be influenced by various factors such as the geographical location of the stopover site (Moore *et al* 1990, Rubolini *et al* 2002, Fitzgerald & Taylor 2008), the kind of habitat (Ktitorov *et al* 2008), food abundance and availability (Dierschke *et al* 2003), the amount of fat stores (Bairlein 1985), density (Kelly *et al* 2002), dominance status and competition (Moore & Yong 1991, Dierschke *et al* 2005), predation risk (Lindström 1990, Dierschke 2003, Schmaljohann & Dierschke 2005), weather (Dierschke & Delingat 2001, Schaub & Jenni 2001, Tsvey *et al* 2007), season (Tryjanowski & Yosef 2002), or by endogenous factors, such as age and sex (Ellegren 1991, Jones *et al* 2002, Dierschke *et al* 2005), physiology (Jenni-Eiermann & Jenni 2003) or internal timing mechanisms (Berthold 1996).

Capture–recapture approaches have revealed astonishing stopover and winter site philopatry (Cantos & Tellería 1994, Merom *et al* 2000, Salewski *et al* 2000) as well as the basic mechanisms of stopover habitat selection and use (Bairlein 1981).

MIGRATION STRATEGIES

During migration, birds face a trade-off between locally-experienced performance at a site and the expected

performance at future sites (Weber *et al* 1999). Thus, understanding the migration strategy of a species requires detailed local single-site studies as well as, in particular, data over a wide geographical range in order to learn more about variation between sites in relation to large-scale geographical factors. Coordinated, collaborative and standardised projects at ringing sites where capture–recapture approaches are applied, together with multi-site comparisons, are especially useful in revealing migration strategies (for examples see Bibby & Green 1981, Bairlein 1991, Lindström *et al* 1996, Bairlein 1998, Grattarola *et al* 1999, Schaub & Jenni 2000, 2001, Dunn 2002, Delingat *et al* 2006, Schaub *et al* 2008). These studies have revealed species-specific and flyway-specific migration and fuelling strategies.

Length of stopover period: methodological challenges

In many studies of migratory fuelling at stopover sites, a minimum length of stopover period is estimated (*eg* Bairlein 1985, Biebach *et al* 1986). However, minimum stopover time might be a rather weak approximation for the real length of stopover periods (Schaub & Jenni 2001) because capture probability during stopover is often quite low. Therefore it cannot be assumed that the day of first capture is the arrival day and that departure immediately follows after the last capture. Probabilistic models help to overcome these difficulties (Schaub & Jenni 2001). Recently, the first model has been refined to relax the assumption that departure probability is independent of the time birds have already spent at the stopover site (Pradel 2009, Pledger *et al* 2009). Due to the statistical complexity involved in estimating stopover duration, very little is known about its variance due, for example, to seasonal effects, immediate environmental factors or physiological state. These statistical challenges are considerably reduced if real stopover times are measured by the use of techniques complementary to ringing, such as satellite or radio telemetry (*eg* Kjellén *et al* 1997, Nolet *et al* 2001, Bächler & Schaub 2007, Bolshakov *et al* 2007). However, the use of these techniques is often constrained by the size of the birds, feasibility, or funding to achieve adequate sample sizes.

PERSPECTIVES FOR FUTURE WORK

Despite considerable data on fattening rates, departure fat loads, and stopover behaviour of migrating birds, our understanding of the mechanisms of stopover and of migration strategies is still relatively poor (Lindström 1995). Many factors influence stopover, and the resulting overall migration schedules are complex. Therefore, we need many more-detailed studies to unravel this complexity. Despite

new technological tools for studying bird migration, such as satellite telemetry or geolocation loggers to retrieve migratory tracks of individual birds, ringing is still required as the key technique for facilitating our understanding of migration. However, we have to develop our methodology and techniques still further. Single-site studies should not just add another piece of fattening data but should focus in detail on the influence of food abundance and availability, of competitors and predators, and weather on fuel deposition, departure fuel loads and stopover behaviour, and they should compare autumn and spring passage. Wherever possible, these mostly descriptive studies should be complemented by field experiments, such as complementary feeding (Lindström & Alerstam 1992, Fransson 1998, Dierschke *et al* 2003, Delingat *et al* 2006) or predator experiments (Cimprich & Moore 2006). But even more important than single-site studies are multi-site comparisons in which the site protocols are standardised (Bairlein 1998). This kind of networking is the best approach for identifying migration strategies, and when and where different species prepare for their migratory flights, as well as their requirements en route for successful fuelling and migration. This is particularly important in the light of conservation needs. Several recent analyses clearly reveal that populations of long-distance, trans-Saharan migrating species are in decline, in contrast to resident species and species that migrate only within Europe. These declines are stronger in species wintering in dry, open African habitats than in species which winter in other habitats. Since most European trans-Saharan migrants winter in sub-Saharan savannas, this is of particular concern (Sanderson *et al* 2006, Ewing 2008, Heldbjerg & Fox 2008). Moreover, we must also bear in mind that most species rely on resting and fuelling sites during migration. Consequently, the identification and preservation of major stopover sites as well as stopover habitats are crucial for the conservation of migratory species, though this aspect is, as yet, almost neglected. There is evidence that migratory journeys are the phases with the highest mortality risks within the annual cycle of birds (Sillett & Holmes 2002), and thus the population dynamics of migrants might be strongly impacted by environmental conditions during their journeys.

Identification of the major stopover regions and habitats is also crucial for understanding the consequences of future global climate change on migratory landbirds (for reviews see Møller *et al* 2004, Jonzén *et al* 2007). Climate-change models predict considerable regional variation which will have different effects on migrating species due to variation in migratory routes and/or spatial variation of species-specific and even population-specific stopover sites. Networking is also crucial for elucidating and understanding carry-over effects between the conditions migrants face at their wintering grounds or stopover sites,

and subsequent breeding. Despite a few studies which have already emphasised the importance of carry-over effects between wintering sites and subsequent breeding (for example, Ebbinge 1989, Møller 1989, Marchant *et al* 1990, Bairlein & Henneberg 2000, Marra & Holmes 2001, Drent *et al* 2006), the subject is still very poorly investigated, and this is particularly true for carry-over effects between stopover sites and subsequent breeding or wintering, since stopover time can account for so much of the entire migration period. Consequently, this subject should receive increased attention in the future, and ringing will play a pivotal role in increasing our knowledge and achieving important conservation objectives.

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