Review

Migratory orientation in inexperienced and experienced avian migrants

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Massive bird migration across continents and seas is one of the most spectacular phenomena in nature, involving billions of birds annually. In the autumn, most birds on migration are juveniles migrating for the first time while adults are repeating their migrations. Migration syndrome in individual bird migrants involves multiple behavioural, morphological and physiological adaptations, and migration performance may improve with experience and age. In this review, we discuss in what ways young and adult birds differ with respect to migration performance and compass orientation during migration, how they respond to external information including topography and winds during migration, and what phenotypic characteristics related to migratory behaviour may change over a lifetime in individual birds. Here, we present the prevailing concepts of navigation, including compass mechanisms leading birds across the globe to predictable goals, and the underlying sources of variability within and between individuals and age groups. In particular, we focus on what changes in the endogenous migration program may lead to more efficient realizations of migration with age. We review our data combined with other data presented in the literature, based on different techniques to study the migration phenotype expression in caged and free-flying birds with different migratory adaptations. The widespread use of tracking technology to study birds in different environments and geographical areas has largely contributed to our current knowledge on how migration performance improves with age. Still, there is a need to understand in more detail how migration performance, timing and route choices develop across time in individual migrants, and what navigational information is used to guide birds across the globe from the first and following migrations.
**KEY WORDS:** compass orientation, circannual program, endogenous migration program, migratory adaptations, navigation.

**BACKGROUND**

Each year billions of birds engage in spectacular long-distance migrations across continents and seas (Hahn et al. 2009), enabling them to explore resources important for reproduction and survival. Long-distance migration has evolved repeatedly in animals (Alerstam et al. 2003), and may cover substantial distances in individual birds (e.g. Croxall et al. 2005; Gill et al. 2009; Stutchbury et al. 2009; Egevang et al. 2010; Åkesson et al. 2012; DeLuca et al. 2015; Sokolovskis et al. 2018). To successfully perform migration, birds have evolved morphological, physiological and behavioural adaptations, characterised as their individual species-specific migration phenotype (Åkesson & Hedenström 2007). In the autumn, most birds on migration are juveniles migrating for the first time while adults are repeating their migrations (Newton 2008). The ecological situation under which migration is performed varies substantially between bird species, where flock-living birds, typically swans, cranes and geese migrate together, and the juveniles can learn the migration route from their parents and other adults in the flock. For these species, there is scope for cultural learning of migration routes and stopover sites. Geese may even learn alternative stopover sites, depending on the expected disturbances, for instance, caused by hunting (e.g. Fox & Madsen 1997; Béchet et al. 2003).

Songbirds, on the other hand, primarily migrate on their own and often fly at night. Flying at night, they may free up more time for foraging during the daytime, reduce the risk of predation from diurnal predators, explore reduced wind speeds and turbulence in the airspace, and fly at lower temperatures and higher humidity, thereby reducing the risk of dehydration (Kerlinger & Moore 1989; Newton 2008; Alerstam 2009). Solo-migrating birds strongly rely on an endogenous migration program inherited by their parents (Berthold & Querner 1981; Gwinner 1986, 1996; Helbig et al. 1989; Helbig 1991, 1996; Berthold 1996; Liedvogel et al. 2011) to guide them during their initial migration. The endogenous programs provide scope for flexibility and adaptability on individual- to species-levels (Åkesson & Helm 2020), but the programs also provide strict internal circannual rhythmicity tuned to geophysical cycles, which enables timely movements between distant areas, as well as resetting to local diurnal light rhythms (Gwinner 1996). Long-distance movements may cause challenges in handling time on migration as transportation across latitudes and longitudes may be fast in birds, and may result in navigational errors if not corrected for (Åkesson et al. 2017). The ability to control time during migration and to set the internal time sense to external cues at different geographical locations can, thus, be expected to improve with experience and age.

Songbirds tend to follow inherited species- and population-specific migration routes (e.g. Helbig et al. 1989) which may involve complex directional shifts and intermediate stops (e.g. Willemoes et al. 2014; Brlík et al. 2018) and will lead individuals to suitable and species-specific stopover and wintering areas (Fransson et al. 2005; Newton 2008). The endogenous programs guiding young birds encode compass and space information in relation to the internal circannual clock (Able 1980; Berthold 1996; Gwinner 1996; Åkesson et al. 2014), with typical diel activity patterns specific for birds migrating at day or night (Fig. 1). The diel activity pattern as exemplified here for
two songbirds (Fig. 1), as well as the length of the migratory activity period within a season is species-specific and correlated with the length of migration (Berthold 1973). Occasionally during barrier crossings, however, nocturnal bird migrants may extend the nocturnal flight period outside the normal range, including some flight hours in the morning before landing for resting (Adamík et al. 2016). Across seasons for individual birds, we may expect changes in activity patterns associated with migratory intensity, including diurnal and seasonal periods lengths, to occur from first to later migrations as adult birds tend to perform migrations at higher speeds as compared to juvenile birds (Ellegren 1993).

In this review, we discuss in what ways young and adult birds differ with respect to migratory performance and compass orientation during migration, and what phenotypic characteristics may change over a lifetime for individual birds. Here, we focus our discussion on prevailing concepts of navigation, including compass mechanisms, leading birds across the globe to predictable goals, and underlying sources of variability within and between individuals and age groups. Several factors may contribute to changes in the endogenous migration program and more efficient realization of migrations with age (e.g. Sergio et al. 2014). Therefore, we first present the compass mechanisms, and the concepts explaining navigation during first and later migrations, and thereafter give examples of how adult and juvenile birds manage to find their suitable compass course and reach the migratory goal and how they perform the migrations.

A central question in migration ecology is in what way an adult migrant will improve its migration skills with time as compared to the first migration performed as a juvenile. Age effects on migratory orientation have been discussed by several authors

Fig. 1. — Actogram of 1st-year diurnal migratory dunnocks (Prunella modularis) and nocturnally migrating European robins (Erithacus rubecula) monitored under local daylength timing at a natural stopover site. Each color-coded horizontal line shows the mean time spent in flying mode by 12 birds per species from 12:00 hr of each day to 12:00 hr of the successive day. Dashed vertical lines indicate the time of sunset (19:00 hr both groups), and sunrise at local time (07:00 hr local time). Activity data are captured from automatic image analysis of captive birds held in individual cages following the procedure detailed in Ilieva et al. (2018).
in the past (e.g. Gauthreaux 1982; Moore 1984). Moore (1984) listed a number of ways that differences between young and adult birds may be predicted where experienced migrants would be expected to: (1) base their selection of a preferred migratory direction on less information as compared to juveniles (e.g. Keeton 1972; Wiltschko & Wiltschko 1975), (2) display greater flexibility in cue utilization (Wiltschko & Wiltschko 1975), (3) be able to switch more easily from one source of compass information to another (Able 1980), and (4) show less attraction to light sources on the sky such as the moon or the setting sun (Brown & Mewaldt 1968; Moore 1987). In addition to the list above, (5) adult experienced birds have been predicted to show less attraction to horizon glow from artificial light sources, such as sky glow visible around cities, during recordings of their activity in cages as compared to juvenile birds (Gauthreaux 1982; Gauthreaux et al. 2006). Here, we extend the list by adding the possibility of improving migration skills with respect to (6) speed of migration (Alerstam 2003), (7) ability to handle weather and winds on migration by adaptive timing of flight departures (e.g. Åkesson & Hedenström 2000; Sjöberg et al. 2015), (8) improved skills to cope with winds including drift on migration (Liechti 2006), (9) the ability to correct for enforced displacements (e.g. Åkesson et al. 2005; Kishkinev et al. 2015), and (10) efficient location of suitable and safe stopover sites providing good foraging conditions on migration (Alerstam & Lindström 1990; Lindström 2003), which all are predicted to improve with experience and age.

We provide examples from the literature in support of changes over time and present results from our experiments, including field-based tracking of migrations and evaluations of ringing recoveries, where behaviours of juveniles are compared with adult stages. The focus is on passerine migrants, but we also discuss our findings in light of work on other species of birds. We hope to help identify areas where future research on compass orientation and migratory performance in birds can fill the current knowledge gaps in how these features change over time and with experience in avian migrants.

COMPASSES

Migratory birds possess three biological compasses based on information from the sun and the skylight polarization pattern, stars and the geomagnetic field (e.g. Wiltschko & Wiltschko 1972; Emlen 1975; Able 1980; Schmidt-Koenig 1990; Åkesson et al. 2014). The use of compasses, especially those based on celestial information, is tightly connected to the diel and circannual time sense of the birds. The sun compass has a time-compensation mechanism enabling compensation for the apparent movement of the sun across the sky throughout the day (Schmidt-Koenig 1990; Schmidt-Koenig et al. 1991) while the stellar compass encodes direction towards the geographic north based on the rotation centre of the sky without changes due to time of day (Emlen 1967, 1970). The magnetic compass is expressed relative to the angle of inclination, providing directions along a north-south axis towards and away from the Poles (Wiltschko & Wiltschko 1972), with changes of course expressed at relevant times of year (e.g. Gwinner & Wiltschko 1978; Wiltschko & Wiltschko 1992). Compass interactions have been shown to lead to recalibrations during migration (e.g. Cochran et al. 2004; Muheim et al. 2006; cf. Åkesson et al. 2015) while during ontogeny a combined experience of geomagnetic information and a rotating star pattern is
crucial for birds to express a relevant population-specific migratory direction at the right time of year (Weindler et al. 1996).

CLOCK-AND-COMPASS VS GOAL NAVIGATION

It has been suggested that the endogenous programs guiding young birds during their initial solo-migrations encode compass and distance information in relation to the internal clock, and that young birds use a so-called “clock-and-compass” strategy during their first migration (Gwinner 1986, 1996; Berthold 1996). Experienced migrants may instead use “goal navigation” (Kramer 1957) to return to already known wintering sites as shown for adult European starlings (Sturnus vulgaris) by displacements of ringed birds (Perdeck 1958; cf. Piersma et al. 2020) (Fig. 2). The clock-and-compass model has been criticized (Rabøl 1978), as it may not explain how young birds handle wind drift during migration (Thorup et al. 2003; Klaassen et al. 2011) and how they reach intermediate sites used for fuelling at stopovers (Fransson et al. 2005). Instead, a model where birds are programmed to search for locations along the way, a so-called “moving goal area,” was proposed by Rabøl (1978) to be in place already during the first migration. Different species of songbirds have been shown to use nearby, but geographically distinct stopover sites already during their first migration (Fransson et al. 2005), suggesting the use of inherited stops along the route as proposed by Rabøl (1978).

AGE EFFECTS ON COMPASS ORIENTATION

Emlen and Emlen (1966) invented a method to record migratory restlessness and preferred migratory orientations in songbirds kept in circular cages, the so-called "Emlen-funnel," which has been a dominating tool in orientation research since then. The original method, including an ink-pad placed at the bottom of the cage and a white paper on the sloping walls, has been modified several times (Sandberg et al. 1988; Åkesson 1994; Mouritsen et al. 2009), and in recent years exchanged by digital versions where the behaviour of the birds is filmed by cameras (Muheim et al. 2014; Bianco et al. 2016). The recorded films can then be classified into different behaviours based on computer-vision methods (e.g. Ilieva et al. 2018; Bianco et al. 2019). Although modified Emlen-funnels are practical and widespread to record songbird orientation, there are still limited experiments focusing primarily on the behaviour of adults (e.g. Moore 1984; Åkesson et al. 2001, 2005) since most work involves studies of juveniles migrating for the first time (e.g. Sandberg et al. 1988; Åkesson 1994; Giunchi & Baldaccini 2004; Chernetsov et al. 2008a).

In a large-scale displacement experiment, the preferred orientations of both adult and juvenile white-crowned sparrows (Zonotrichia leucophrys), were investigated in the high Arctic (Åkesson et al. 2001, 2005). Birds were kept and tested in the breeding area while another group of birds was displaced across longitudes to the east by an icebreaker and the orientation of both groups was studied by repeated cage experiments (Åkesson et al. 2001, 2005). The experimental method build on a study of Northern wheatears (Oenanthe oenanthe) in Russia (Åkesson et al. 1996) and involves strictly comparable experiments (i.e. same type of cage and registration method and the same method to evaluate the data). Experiments with white-crowned sparrows
Fig. 2. — A visual representation of the predicted orientation responses investigated by Perdeck (1958) in displacement experiments with adult and juvenile starlings (A), and the distribution of the recoveries from three release points in Switzerland (adults: open circles; juveniles: filled circles) during the following autumn and winter periods (B). Both panels are based on Perdeck (1958), and have been modified from Newton (2008) and Piersma et al. (2020). Panel B reproduced with kind permission of Journal of Avian Biology.
generated some interesting findings, including differences in scatter and initial preferred orientation but similar responses to the displacement between the two age groups. First, the adults (n = 5) kept and repeatedly tested in the breeding area were very persistent in their preferred orientation, directed southeast towards the expected wintering area (Åkesson et al. 2005; Fig. 3). The juveniles kept indoors under the same conditions during the daytime as the adults and tested outdoors under clear skies at sunset as the adults, showed much higher scatter in their preferred mean orientation and more easterly courses (Fig. 3). Both groups of birds were captured in the breeding areas at the end of the breeding period and tested during the following autumn migration period in August and September. Still, the degree of scatter and preferred directions differed between the experienced adults and the juvenile sparrows migrating for the first time (Fig. 3; Åkesson et al. 2005). How can the differences in scatter and preferred orientation between age classes be interpreted? The limited degree of scatter in adults may be an effect of only successful birds being able to return to the breeding areas and repeat their migrations while individuals that may have been showing initial directions deviating more from the expected migration route may have selected against during previous migrations. In juveniles, a larger variation in genetically determined individually preferred migratory directions may still be present in the population (Helbig 1996), as no selection due to misorientation during migration has yet been realized. This scenario may be supported by an interesting finding by

![Fig. 3. — Mean orientation for adult (upper panels) and juvenile (lower panels) white-crowned sparrows (Zonotrichia leucophrys) captured and tested in modified Emlen-funnels under Clear sky and Overcast conditions at Inuvik (Control) and several sites on the high arctic tundra in Canada in autumn. Each symbol refers to the mean orientation of one individual bird. The symbols inside the circles indicate the grand mean orientation of the experimental birds as calculated for a number of tests at several sites West and East of the magnetic North Pole at Ellef Rignes Island. The calculated migratory directions along an initial great-circle route (i.e. shortest route between two sites, GC) and rhumbline route (i.e. constant compass course, RL) from the breeding site to the predicted wintering area are indicated outside the circle for the Control. For the birds displaced East of the magnetic North Pole, the range of initial GC directions are shown from the sites of experiment to the site of capture. The length of the arrow (r) is a measure of the scatter of the circular distribution, ranging from 0 to 1 and being inversely related to scatter (Batschelet 1981). Mean angle of orientation (given in degrees), vector length (r), 95% confidence intervals as broken lines, and significance levels (indicated as *P < 0.05; **P < 0.01; and ***P < 0.001) according to the Rayleigh test (Batschelet 1981) are given for the distributions outside the circles. Modified after Åkesson et al. (2005).]
a long-term tracking study in which juvenile black kites (Milvus migrans) were tracked across multiple migrations, and for which higher mortality occurred in birds with preferred migratory routes at the flanks of a distribution during the first migration, leading to more narrow spread around the mean with time (Sergio et al. 2014).

A larger scatter in preferred orientation in juvenile birds as compared to adults was reported for a nocturnal passerine migrant, the willow warbler (Phylloscopus trochilus) migrating from Fennoscandia to sub-Saharan Africa (e.g. Hedenström & Petterson 1987), demonstrating that the scatter is indeed expressed during an extensive autumn period. A long-distance tracking study of adult male willow warblers of the subspecies yakutensis breeding in Far East Russia has further confirmed similar route choice in adults (Sokolovskis et al. 2018). Here we show that recoveries of barn swallows (Hirundo rustica) ringed in Finland, Norway, and Sweden and migrating to sub-Saharan Africa, generate a different pattern, with no difference in scatter between age classes (Fig. 4). Barn swallows gather before migration and migrate in flocks, and there is a chance for cultural transmission of migration knowledge in this species as compared to solo-migrating passerine migrants, such as the willow warbler (Hedenström & Petterson 1987). Release experiments with European robins (Erithacus rubecula) and pied flycatchers (Ficedula hypoleuca), further revealed a larger scatter in departure orientation for juvenile solo-migrating birds as compared to adults, and the scatter was found to be larger under overcast as compared to clear night skies (Sandberg et al. 1991), suggesting an increased challenge to find the migration direction in juveniles when cues are limited (1–3, above). Bäckman and Alerstam (2003) explored a dataset collected by tracking radar for free-flying songbird migrants during the spring and autumn migration, which revealed a difference in the scatter of tracks between the seasons. When wind compensation corrected for in this study, there were only small differences in the spread of preferred heading directions between seasons, suggesting that the scatter was predominantly related to the effects of winds (Bäckman & Alerstam 2003). However, when low wind situations were evaluated separately, there was a tendency that the concentration of headings during the spring exceeds that of the autumn (Bäckman & Alerstam 2003), suggesting more concentrated goal-oriented behaviour in the experienced migrants (8 and 9, above).

ATTRACTION TO SUNSET, MOON AND ARTIFICIAL LIGHT SOURCES

It is well known that birds migrating at night attracted to fires and artificial light sources, such as lighthouses and cities, especially under overcast skies when the cloud base is low (Gauthreaux et al. 2006). Artificial night lighting may affect animals including birds in all parts of their life including breeding, foraging and migration, and might lead to higher mortality risks (Longcore & Rich 2004). Juvenile songbirds studied outdoors in cages have been shown to show higher responsiveness to elevated sky glows of the night sky associated with cities as compared to adults (Gauthreaux 1982; 5 above). Orientation coinciding with the sunset direction at night have further been observed in a large number of cage experiments under natural skies performed with songbirds in the high arctic (Åkesson et al. 1996; Sandberg et al. 1998), in temperate regions (e.g. Moore 1982; Åkesson 1994; Åkesson & Bäckman 1999; Muheim et al. 1999; Åkesson et al. 2015), and near the equator (Åkesson 1993), but also at day-time (Giunchi & Baldaccini 2004), suggesting that the behaviour is expressed by different species in widely different geographical regions and ecological
Fig. 4. — Distributions of recoveries of ringed adult (upper panels) and juvenile (lower panels) barn swallows (*Hirundo rustica*) ringed in Norway, Sweden and Finland and recovered within the same autumn migration season. Circles (red) denote site of ringing, and triangles (green) site of recovery. The circular diagrams show the mean direction for the recoveries presented separately for country and age class. The length of the arrow (r) is a measure of the scatter of the circular distribution, ranging from 0 to 1 and being inversely related to scatter (Batschelet 1981). Number of birds (n), mean angle of orientation (in degrees), vector length (r), 95% confidence intervals as broken lines and significance levels (indicated as *P < 0.05; **P < 0.01; and ***P < 0.001) according to the Rayleigh test (Batschelet 1981) are given for the distributions outside the circles. Ringing data (Norway: 32 ad., 22 juv.; Sweden: 12 ad., 7 juv.; Finland: 30 ad., 22 juv.) are from the European Union for Bird Ringing (EURING; du Feu et al. 2016).
situations (4 above). Studies on red-eyed vireos (*Vireo olivaceous*) (Sandberg & Moore 1996), and snow buntings (*Plectrophenax nivalis*) (Sandberg et al. 1998) in North America have revealed a higher attraction towards the sun in lean as compared to fat birds while the visibility of the lowest part of the sky leads to higher sunset attraction behaviour (Ottosson et al. 1990). We must conclude that both the view of the sky and physiological state may contribute to the preferred orientation of caged songbirds, resulting in a higher attraction to light sources in young (and lean) birds as compared to adults. Since the majority of bird migrants have to pass areas artificially illuminated at night (Cabrera-Cruz et al. 2018), attraction and induced delays may cause increased mortality in young as compared to adult bird migrants with important conservation implications for migratory birds (Backhurst & Pearson 1977; Van Doren et al. 2017; McLaren et al. 2018).

**EFFECTS OF DISPLACEMENTS ON ADULT AND JUVENILE BIRDS**

Displacement experiments have been used as a powerful tool to investigate differences in navigation capacity in birds (Åkesson 2003; Mouritsen 2003), demonstrating the use of clock-and-compass orientation in young birds migrating for the first time and goal navigation in adult birds (Perdeck 1958; Fig. 2). However, more recent displacement experiments with nocturnal passerine migrants have resulted in conflicting results, with some supporting the results by Perdeck (1958), reporting goal navigation in adult birds and clock-and-compass orientation in juveniles (Thorup et al. 2007; Chernetsov et al. 2008b; Kishkinev et al. 2015, cf. 2016) while others suggest that also young birds have an inherited capacity to correct for displacement during migration (Åkesson et al. 1996, 2005; Thorup et al. 2011, 2020; Willemoes et al. 2015). Most of the studies published so far have focused on one age class, or only on the behaviour of displaced birds. Both cage experiments (Åkesson et al. 1996, 2005; Chernetsov et al. 2008b; Thorup et al. 2011; Kishkinev et al. 2015) and tracking of free-flying birds (Thorup et al. 2007, 2020; Willemoes et al. 2015; Kishkinev et al. 2016) have investigated this question. Still, one of the few experiments designed to compare the behaviour of displaced birds with birds kept in the breeding area and tested simultaneously was performed with a North American nocturnal passerine migrant, the white-crowned sparrow, in high-Arctic Canada using an icebreaker for transportation (Åkesson et al. 2001, 2005; Fig. 3). In this strictly comparative cage experiment involving both adults and juveniles, the compass orientation of displaced and non-displaced birds recorded under both clear and simulated overcast skies (Åkesson et al. 2001, 2005). The experiments showed that although the juveniles showed increased scatter in their preferred orientation as compared to the adults, they could still detect that they were displaced and changed their orientation accordingly both under clear and overcast skies and similarly as the adults did (Fig. 3). An abrupt shift in orientation was associated with the shift of the magnetic declination associated with the passage of the magnetic North Pole (West and East of the magnetic North Pole, Fig. 3), and suggested that the birds may have used magnetic declination to determine their longitude (Åkesson et al. 2005). The results imply that the capacity to determine longitude after displacement is present in both juvenile and adult birds (Fig. 3). The use of declination to determine the longitude has later been investigated using simulated magnetic displacements of European nocturnal passerine migrants, the reed warbler (*Acrocephalus scirpaceus*), resulting in supportive results (Chernetsov et al. 2017),
which could, however, not be replicated in later experiments (Chernetsov et al. 2020). Deutschlander et al. (2012) showed that adult Australian silvereyes (Zosterops l. lateralis) could use the geomagnetic field to determine geographic position during migration by simulated magnetic displacements while juveniles did not suggest learning is important for successful geomagnetic navigation. The experiment by Åkesson et al. (2005) involved a gradual displacement by ship and repeated stops at tundra sites, at which time the inexperienced sparrows were provided the opportunity to learn important visual and magnetic cues. Although all displacement experiments have provided interesting insights into navigation capacities, the importance of declination for the determination of longitude of different bird migrants, as well as their use in different geographical areas, still remains to be resolved.

**TRACKING FIRST AND LATER MIGRATIONS**

*Seabirds*

Thanks to the technological tracking revolution, movements of animal migrants have been recorded at global scales for several decades, and by evaluating tracking data we may learn about navigation behaviours of inexperienced and experienced migrants (Guilford et al. 2011a). However, the tracking of the first and later migrations of individual birds is still limited while tracking of first-time migration by juveniles have been performed for a number of bird species, including several species of seabirds (e.g. Åkesson & Weimerskirch 2005; Weimerskirch et al. 2006, 2015; Guilford et al. 2011b; Péron & Grémillet 2013; Campioni et al. 2020). One of the first studies comparing migration behaviour and destination areas for adult and juvenile seabirds involved wandering albatrosses (Diomedea exulans) breeding in the Crozet Islands (Åkesson & Weimerskirch 2005, 2014; Weimerskirch et al. 2006; Fig. 5). The tracking data showed selective departures relative to winds in the juvenile birds and movements to sex-specific non-breeding ranges, which involved longer migrations in males as compared to females (Åkesson & Weimerskirch 2014; Fig. 5B–C). The navigation program leading the young albatrosses on their first journey must be based on an endogenous program (Åkesson & Weimerskirch 2014), but the sensory basis for open sea navigation in this challenging area remains unresolved (Åkesson & Alerstam 1998). The tracking data further have revealed it has taken up to 6 months for the young albatrosses to reach the daily movement speeds recorded for adults (Weimerskirch et al. 2006; 6 above; Fig. 5A), suggesting a learning phase to manage flight in strong winds including dynamic soaring (Wilson 1975; Pennycuick 1982). The necessary learning phase for improved flight performance in juvenile soaring birds has been shown for white storks (Ciconia ciconia), enabling higher climb efficiency, improved soaring/flapping flight ratios and faster migration speeds with increased experience (Rotics et al. 2016; 6 above). Increased capacity to compensate for wind drift has further been shown to improve with experience in juvenile great frigate birds (Fregata minor) (Wynn et al. 2020; 8 above).

Repeated tracking of migrating Cory’s shearwaters (Calonectris diomedea) has revealed consistency in routes followed both near coastal areas and in the open sea (Dias et al. 2013), suggesting a capacity to navigate and relocate stopover sites without direct contact with nearby landmarks. High inter-individual variation and within-individual consistency in timing and route choice have further been shown for Scopoli’s shearwaters (Calonectris diomedea), despite exposure to annual
Fig. 5. — (A) Change in average daily distance travelled with time since departure from the birthplace at Crozet Islands by juvenile wandering albatrosses (*Diomedea exulans*) tracked by satellite telemetry. Juvenile albatrosses attain a maximum speed of 600 km per day after 6 months, corresponding to a flight efficiency similar to that of adults. Panel A from Weimerskirch et al. (2006). (B) Locations of the centre of preferred ocean foraging zones for individual wandering albatrosses. Positions refer to different age and sex classes tracked by satellite telemetry during the migration from the breeding sites at Crozet Islands. Mean longitudes for each age category (JF and filled circles: juvenile females, AF and open circles: adult females, JM and filled triangles: juvenile males, AM and open triangles: adult males) are indicated by arrows. The grey triangle refers to an adult of unknown sex. The Crozet Island (staring point) is indicated by a star. The Sub-Tropical and Sub-Antarctic Fronts are indicated by light grey and dark grey lines, respectively. (C) and (D) Post-breeding foraging zones explored by juvenile and adult wandering albatrosses breeding at Crozet Islands during the post-breeding period as indicated by 75% kernel density zones. (C) Adult females (red, n = 3) and males (blue, n = 3). (D) Juvenile females (red, n = 7) and males (blue, n = 6). The location of Crozet Islands is indicated by a star in panel C. Panel A from Weimerskirch et al. (2006) and B-D from Åkesson and Weimerskirch (2014). Panel A reproduced with kind permission by Journal of Avian Biology.
environmental variations (Müller et al. 2014), suggesting the use of an endogenous program for the first and following migrations in individual birds, potentially involving some learning with age. Navigation by a bi-coordinate magnetic map (Wallraff 1990), has been proposed in the marine environment (Lohmann et al. 2001). Although this possibility has been supported by experimental evidence on sea turtles migrating in the Atlantic Ocean (Lohmann et al. 2001), there are geographical areas where navigation by a bi-coordinate magnetic map will be challenging because of nearly parallel gradients (Åkesson & Alerstam 1998; Boström et al. 2012; Fig. 6). In those areas and beyond we may expect birds to use additional cues based on visual and chemical information for navigation (e.g. Gagliardo et al. 2013; Wikelski et al. 2015). In the marine environment, an endogenous program combined with an initial exploratory phase enabling learning of navigation cues and movement skills seems necessary in seabirds to establish migration routes and stopover areas used in later migrations (Guilford et al. 2011b; Dias et al. 2013; Åkesson & Weimerskirch 2014). However, the complexity of the underlying cues and mechanisms used for long-distance navigation at sea remains to be resolved.

Terrestrial birds

Tracking terrestrial bird migration has revealed interesting adaptations, including differences in time and route consistency between species (Vardanis et al. 2011, 2016; Stanley et al. 2012; Conklin et al. 2013; Hasselquist et al. 2017), and improvements in route efficiency and speed with age (Sergio et al. 2014; 6 above). The circannual tracking of the Eurasian cuckoo (Cuculus canorus) has revealed highly stereotypical, but rather complex migration routes, involving multiple periods of residency and movement phases (Willemoes et al. 2014). The young cuckoos rely on an endogenous program leading them along similar routes as the adults during the autumn migration (Vega et al. 2016), but which also enables them to navigate back to those routes after enforced displacement (Willemoes et al. 2015; Thorup et al. 2020; 9 above). The use of an endogenous program leading juvenile migrants along the same routes as adults seems to be the case in most birds (see also, discussion on seabirds above), but this is not the case for the honey buzzard (Pernis apivorus). Juvenile honey buzzards perform their migration independently of adults with a ca 2-week later passage in southern Scandinavia during the autumn (Kjellén 1992), a time difference which remains in southern Europe (Agostini & Logozzo 1995). The juvenile buzzards migrate along highly varying routes across the Sahara Desert to their winter destinations in sub-Saharan Africa (Hake et al. 2003; Vansteelandt et al. 2017), including broad front passage of waterbodies (Agostini 2004), likely strictly guided by an inherited vector navigation program. Adult buzzards follow more similar routes across landmasses, providing many opportunities for soaring during migration, including minimization of passages across open water in the autumn (Hake et al. 2003; Agostini 2004; Vansteelandt et al. 2017). In a recent tracking study, it was shown that the longitude at which juvenile honey buzzards reached their individual wintering area was strongly dependent on winds experienced on migration and the resulting wind drift (Vansteelandt et al. 2017). Juvenile raptors have been shown to be less able to compensate for wind drift during migration (Thorup et al. 2003; 7 above), which can partly be the explanation of this migration pattern, and thus be a likely driver for the
large longitudinal spread of migration destinations in this species (Vansteelant et al. 2017).

EFFECTS OF EXPERIENCE ON MIGRATION PERFORMANCE

Experienced migrants may develop migration skills by learning, which could result in improved migration speeds (Ellegren 1993), reduced stopover times (Crysler et al. 2016), longer flight paths per day (Weimerskirch et al. 2006), faster fuelling at stopover (Lindström 2003) with reduced BMR and digestive capacity (McCabe & Guglielmo 2019), and more efficient handling of wind drift (Thorup et al. 2003) than juveniles. In addition, juvenile birds may more frequently be affected by topography on migration by coastal landings (Ralph 1971, 1978), including temporary reverse migration (Åkesson et al. 1996; Crysler et al. 2016) to search for safe and better foraging sites inland (Alerstam 1978; 10 above), and prolonged routes (Crysler et al. 2016; Fig. 7). Reverse migration seems to be strongly affected by physical conditions (Sandberg 2003) and has been shown to be expressed relative to the magnetic field (Sandberg 1994). The temporary course shift is likely part of a vector orientation mechanism and may contribute to reduced overall migration speeds in young birds (Ellegren 1993; McKinnon et al. 2014). Age-related differences in overall migration speed may further be related to flight performance, route length, and foraging
efficiency (10 above), which have been shown for the Eleonora’s falcon (*Falco eleonorae*) to differ along the route for juvenile and adult birds during the autumn migration (Mellone et al. 2013).

There is still limited understanding of how migration skills change in response to development, but a long-term tracking study of black kites (*Milvus migrans*) (Sergio
et al. 2014) has revealed in what way migration performance improves from first to later migrations. Individual kites were repeatedly tracked for up to 27 years of age, demonstrating that the migration development follows a consistent trajectory, but that the change is gradual and more prolonged than previously assumed (Sergio et al. 2014). The surviving birds were shown to improve migration speed, stopover length, and handling of wind drift during migration with age, leading to migration that is more efficient and has a longer life span. Selection was mainly found early in life and in birds with migratory directions at the flanks of the distribution (Sergio et al. 2014). The study shows that there is scope for improvements with experience, and that several factors contributing to efficient migration can change over a lifetime.

CONCLUSIONS AND FUTURE RESEARCH

Managing migration for the first time by strictly relying on an endogenous program encoding distance and spatial information without support from conspecifics, is one of the most complex phenotypic expressions one can imagine and which is regularly performed by migratory birds. There are several characteristics of the migration phenotype that need to be expressed at the right time of day and year, as well as at the right location to enable individuals to successfully reach the migration goal and to survive. The complexity of the program and how it is expressed in different species and populations of birds are still not fully resolved. Here we review the current knowledge on how young and adult birds may differ in their responses to environmental cues during migration, including the use of compass information and artificial light sources, as well as how they may differ in their ability to handle topography and winds during migration. We conclude that the recent development of tracking technology and the widespread use of this technique to study birds in different environments and geographical areas largely contribute to our current knowledge on how migration performance improves with age. Still, there is a need to understand in more detail how migration performance, timing and route choices change across time in individual migrants with different migration strategies, and what navigational information is used to guide birds across the globe from the first and following migrations. We suggest that the exploration of different experimental paradigms, including field-based tracking, may be a useful avenue to resolve the remaining open questions.

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AUTHOR CONTRIBUTION

S. Åkesson conceived the study and wrote the first draft of the manuscript, G. Bianco evaluated activity and ringing data and produced the graphics, H. Bakam evaluated ringing data, M. Ilieva and E. Martinez Hernandez collected data from caged birds with support from G. Bianco and S. Åkesson. All co-authors discussed the content and contributed to the writing of the manuscript.

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DATA ACCESSIBILITY

The ringing data presented in the manuscript was requested from the EURING database.

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