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Review

New frontiers in bird migration research

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SUMMARY

Bird migrations are impressive behavioral phenomena, representing complex spatiotemporal strategies to balance costs of living while maximizing fitness. The field of bird migration research has made great strides over the past decades, yet fundamental gaps remain. Technologies have sparked a transformation in the study of bird migration research by revealing remarkable insights into the underlying behavioral, cognitive, physiological and evolutionary mechanisms of these diverse journeys. Here, we aim to encourage broad discussions and promote future studies by highlighting research fields that are characterized by major knowledge gaps or conflicting evidence, namely the fields of navigation, social learning, individual development, energetics and conservation. We approach each topic by summarizing the current state of knowledge and provide a future outlook of ideas and state-of-the-art methods to further advance the field. Integrating knowledge across these disciplines will allow us to understand the adaptive abilities of different species and to develop effective conservation strategies in a rapidly changing world.

Introduction

The migratory lifestyle is an ancient behavioral trait of many bird species that enables them to track changes in climate and habitat conditions across the globe[1,2]. As such, migration behavior is remarkably common among birds, producing many amazing examples of migration feats. Billions of individuals perform regular cyclical journeys every year[3], seabirds and shorebirds literally circumvent the globe[4,5], tiny songbirds navigate across continents using their diverse navigational senses[6] and some species impress by staying airborne throughout most of their migration cycle[7]. These migrants make numerous decisions regarding the timing, routes and destinations of their movements, each of which affects the costs, benefits and risks of their journeys[8,9]. Refining these decisions results in complex spatiotemporal migration strategies that often vary between individuals and species, depending on life stages and goals. Given the complexity of these patterns and their underlying decisions, research on bird migration commonly formalizes frameworks that generate testable predictions for, for example, navigational mechanisms[10] or strategies on the optimization of energy or time during migration[11]. Yet, over the years, simplified frameworks and limited questions may have constricted migration research by creating theories with narrow viewpoints, often neglecting the behavioral diversity and flexibility of bird migration. With recent technological advances, we are now able to investigate individual decisions and their consequences in unprecedented detail[12]. These novel approaches, in combination with a comprehensive research framework that systematically addresses temporal and functional aspects of bird migration[13], will allow us to explore the full diversity of behaviors across various stages of migration and also to scrutinize prevailing theories on the ontogeny, costs, and adaptability of bird migration.

Over the last 120 years, bird migration research has advanced together with technology, to build our understanding of birds in their natural habitats (Figure 1). Classical monitoring schemes, such as long-term observations at migration hotspots (e.g. straits, mountain valleys), to monitor phenological patterns[14] have a long history. In recent years, they have been complemented by large-scale weather surveillance radar networks[3]. Although these techniques are essential for understanding long-term, large-scale macroecological patterns, they are less suited to draw conclusions at the species or individual level. In contrast, bird ringing (i.e. marking birds with unique numbers) provides detailed records of individual movements through time. Over 3 million ring recoveries

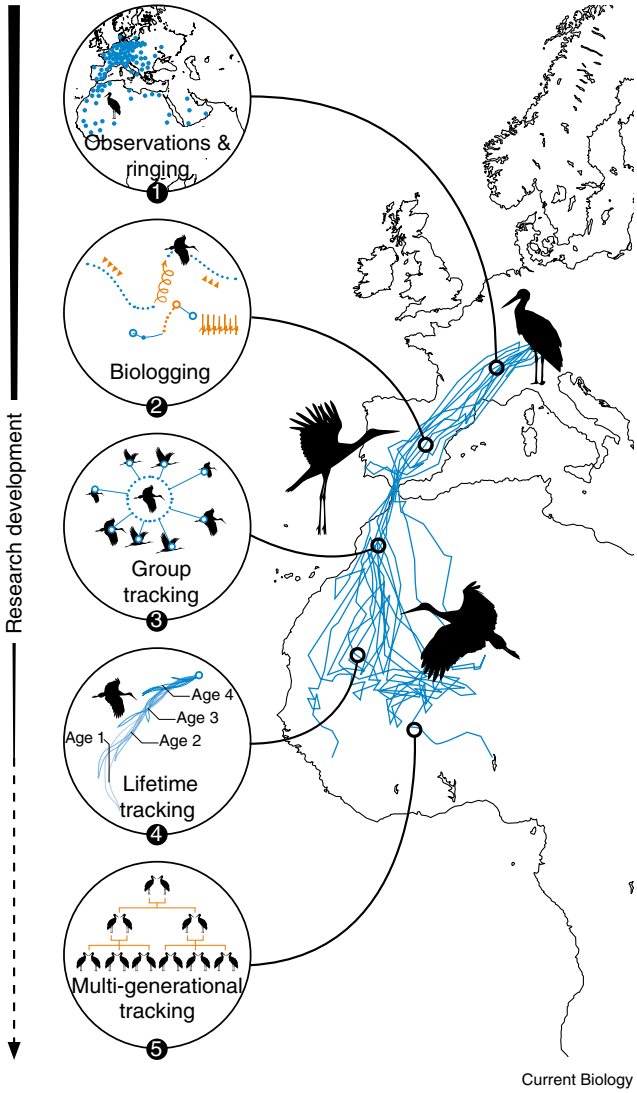


Figure 1. Technology-driven bird migration research.
Developments in migration research follow those of animal tracking technology, illustrated with empirical examples from white storks (*Ciconia ciconia*). From ring recoveries and large-scale banding efforts providing the first glimpse into the migration patterns of migratory birds, to the combined use of biologging and innovative study design for entire group tracking, lifetime tracking and multi-generational tracking. Researchers are able to collect ever more detailed data on the movements, activity patterns, and behavior of free-flying birds in their natural environments.

since the beginning of bird ringing have provided detailed knowledge on the migratory behavior of many species[15], including long-term monitoring of how migration changes over time[16]. However, regional biases in ring recovery rates can influence data analyses and scientific findings[17]. Tracking devices, such as geolocators, radio, satellite or GPS transmitters, have overcome these limitations and extended the traditional monitoring methods[18]. These tools may influence the birds' behavior due to the added weight or drag[19], but the scientific community continuously discusses and adjusts ethical standards for the use of biologgers. Also, miniaturization is progressing rapidly, decreasing the impact on behavior and increasing the number of species that can be tracked ethically[12]. In addition to the classical positional data that can be recorded at a sub-second resolution, biologgers commonly house accelerometers, magnetometers, gyroscopes and pressure sensors to resolve behavior and orientation, and to provide proxies of energetics or performance[20]. With multiple sensors combined, we can reconstruct fine-scale bird movements[21], measure local environmental conditions[22] and social interactions[23], and relate physiological measurements to migration decisions[24] (Figure 1). Given the vast distances migrants cover, remote data transmission has been a limiting factor in migration research. Yet, nowadays, satellite (Argos, ICARUS) and ground-based (MOTUS, GSM, IoT) networks provide nearly global data readout and transmission[25–27]. In addition, solar-powered tracking devices provide the capacity for lifetime tracking[9], as the batteries are constantly being recharged. These technological innovations drastically increased the amount of collected data, highlighting the need for standardized methods for data storage, management, analysis, and exchange.

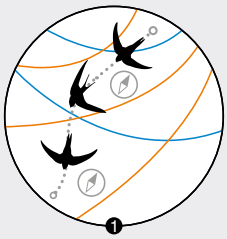
Various platforms and tools to track, store and analyze migratory behavior (e.g. Movebank[28,29]; UvA Bird Tracking System, www.uvabits.nl; Birdlife International, http://seabirdtracking.org; EURING Migration Mapping Tool[15]) are enabling us to study bird migration at unprecedented scales and resolutions. As a result, studies reveal novel records in migration performance, such as the Arctic Tern (*Sterna arctica*) for the longest migration circuit (~ 50,000 km)[5], the Bar-tailed Godwit (*Limosa lapponica baueri*) for the longest non-stop flight (~8 days)[4] and the Great Reed Warbler (*Acrocephalus arundianceus*) for its extreme flight altitudes[30]. In addition, research increasingly sheds light on the diverse behavioral and physiological adaptations that allow birds to cope with the energetic demands of their journeys, such as flying in groups, or tracking beneficial environmental conditions[31–33]. These tools have sparked transformations in various areas of bird migration research as recent innovative findings provide new insights into long-standing questions in a diverse range of topics including navigation[34], social learning[35], individual development[36] and energetics[37]. Critically, filling these gaps in migration research will allow us to improve the protection and conservation of bird migrants[38]. Here, we aim to encourage discussion and new studies by closely scrutinizing research areas that are characterized by major knowledge gaps or conflicting evidence and that now can be approached from new angles thanks to technological advances. In the following sections, we focus on five key research areas in bird migration research — navigation, social influences, individual development, costs and the environment and conservation. We center each section around supporting and contradicting findings on traditional views in this area, and then provide an outlook on innovative ideas and methods that will allow us to transform some of these long-standing theories (Box 1) and with it our understanding of bird migration.

Navigation

Birds are remarkable navigators, crossing regularly entire continents and oceans. For example, the Northern Wheatear (*Oenanthe oenanthe*) navigates across the entire Asian continent

Box 1. Future research path.

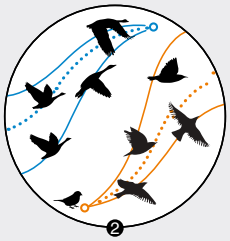
Here we present outstanding questions for each of the five research areas. Within each research line, we order the questions by our assessment of feasibility (from most to least feasible). However, we highlight those questions (arrows pointing toward them) that require the integration of multiple research themes such that answering these question may be a hierarchical process (e.g. to understand how different resource landscapes are integrated during migration, we need to first understand the sensory input and other environmental dependencies).



Navigation

What causes vagrancy? Is straying off course or inhabiting atypical areas maladaptive or a form of bet-hedging? What broader role do vagrants play in the distribution and adaptability of the population?

How do birds integrate different information and sensory cues when performing navigational tasks? Does the importance of these different cues vary between contexts?



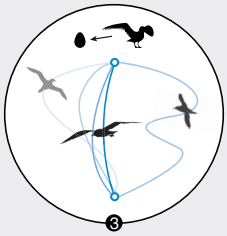
Social influences

To what degree do birds that do not obviously migrate in flocks (e.g. nocturnal migrating passerines) use social influences during migration?

How do heterospecific interactions influence migratory decisions?

How do inviduals navigate to their breeding grounds for the first time and during subsequent journeys?

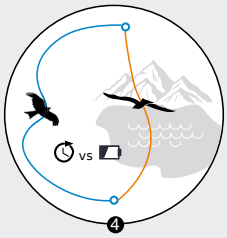
How does a reliance on individual experiences or social information develop throughout a bird's life?



Development of strategies

How do small-scale environmental properties (e.g. fine-scale variability in uplift, forage resource density) and physiological responses (e.g. flapping/gliding ratio, search effort) act or interact to influence migratory decisions? To what degree and over what spatial and temporal scales can migrants respond physiologically to variability in risks and resources?

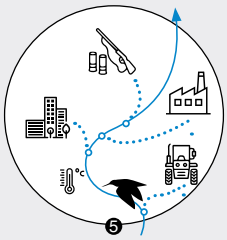
To what extent could biologging on birds (or drones) provide environmental sensor platforms to build relevant landscape layers or critical environmental data to better understand and model movement on migration?



Cost balance and environment

How can we integrate different resources (atmospheric, social, foraging) into species-specific energetic/decision landscapes, also for marine environments which are relevant for swimming migrants (e.g. penguins)?

Besides anthropogenic threats, what are the main drivers of mortality during migration? How do these relate to navigation and energetics?



Anthropogenic threats

How can bird migration research be better integrated into practical applications for conservation and management? What types of analytical tools and datasets do managers need for on-the-ground decision-making (e.g. data synthesis, long-term monitoring, real-time alarm systems, population modeling)?

How do we quantify and disentangle the multiple stressors that migratory birds face during migration to prioritize conservation action?

when leaving their breeding grounds in Siberia to overwinter in sub-Saharan Africa. Birds truly are globetrotters, making the question of 'how do they find their way?' one of the most intriguing in migration research. In the last two decades, we have expanded our knowledge on established navigational theories such as the 'clock-and-compass' model that enables first-time migrants to follow an inherited navigational vector towards their wintering regions[39–41]. According to this model, birds follow inherited seasonally appropriate compass directions to their destination[42] or to stopover sites along the way[43]. However, navigational research has generally been subject to strong observational biases towards those individuals that are returning to the locations where they have previously been observed, compared to those that disperse to novel regions or habitats. Likewise, most navigational experiments have been carried out in laboratory conditions and, thus, may not reveal how birds make decisions during natural migration. Many of these experimental studies explore whether migrants can correct for experimental displacements by returning to their expected routes and wintering grounds[39,44]. Based on navigational theories that distinguish between the migratory behavior of juveniles and adults, young birds are expected to be unable to compensate for experimental displacements while adults are able to do so using navigational information gained from previous experience[45]. However, different studies have created ambiguous results that cannot be universally interpreted. For example, experiments have found that even young first-time migrants can compensate for displacements during migration[41,46,47], or that displaced adults do not always do so[48]. In addition, some species exhibit high flexibility when navigating toward goal areas[49], suggesting that their experiences with dynamic environmental conditions allow them to adjust their migratory patterns[50,51]. There is increasing evidence that birds can continually integrate navigational cues from their previous experiences[52,53] to create either a bi-coordinate map (i.e. mental representation of navigational factors along two spatial dimensions)[54] or even just a uni-coordinate stop sign[55]. Navigational cues are very diverse, including olfactory[44], celestial[56] and geomagnetic cues[54]. This multi-modal navigation has led to conflicting results regarding the relative importance of different sensory cues[57]. However, these may also stem from a prevalent unawareness of species' life-history demands. Some species may be more or less flexible in their navigational decisions owing to the degree of flexibility in their habitat requirements[53,58]. In addition, migratory species may have evolved differently due to the demands of diverging migratory behavior. This can be commonly observed as morphological differences, for example in the flight apparatus of resident and migrant species, or between long- and short-distance migrants of the same species[59]. These differences may also apply to behavioral adaptations or sensory abilities, such as the magnitude of olfactory capabilities[60]. Similarly, species originating from, or migrating to, areas with salient geographic features, such as mountains or coastlines, may have adapted to rely more on temporary visual guidance compared to other species[61].

Despite years of navigation research, we are still far from answering the question of 'how do birds find their way'? However, innovative, interdisciplinary techniques in tracking and data analyses are now allowing us to explore hypotheses that were generated by traditional experimental studies. For example, machine learning approaches enable us to perform automated comparative trajectory analyses which can identify features of recorded tracks that are characteristic of inexperienced and experienced or social and solitary individuals[62]. Furthermore, by extending full annual cycle tracking to smaller species, such as songbirds[12], we will address questions, such as how navigational strategies develop, by comparing outgoing and homecoming migration. Likewise, extending lifetime tracking to songbirds and other species lacking longer-term tracking data allows for the comparison of first and subsequent migratory journeys (see below). In addition, when combined with experimental manipulations, long-term tracking allows us to test hypotheses regarding sensory cues (e.g. olfactory navigation[44]), or age-dependent navigational strategies[47]. These experiments could build upon traditional approaches, such as displacement, delays, cross-fostering or sensory manipulations, and be advanced by employing temporary manipulations of single or multiple sensory cues onboard, in-flight and in real-time during navigational tasks. These manipulations could include the use of electromagnets, noise cancellation technology and other drop-off mechanisms. Future observations of natural or experimental navigation decisions need to be accompanied by real-time assessments of the local environment, such as wind, pressure, temperature and magnetic field changes. Another very informative approach will be to study individuals that do not reach their expected target areas[63]. Such individuals include vagrants that are either outliers in large population tracking studies or are specifically tracked from a place where they typically show up, such as offshore islands[64]. It is almost completely unknown whether such vagrants have impaired navigation[64] or are simply highly exploratory individuals[65] potentially engaged in a bet-hedging strategy[66]. Tracking their ongoing exploration, return migration, survival and breeding success may provide insights into the navigational skills of these individuals and the fitness consequences of their behavior. In general, studying the mechanisms underlying navigational mistakes and navigational variability would require the deployment of advanced multi-sensor biologging devices recording the availability of environmental cues in real-time (Figure 2).

Social influences during migration

Migratory flights are rarely undertaken in isolation — as is generally assumed for many nocturnally migrating songbirds — but rather in collectives of individuals. Thus, no solid conclusions about individual navigational decision-making can be reached without taking the action of and the communication with other birds into consideration as movement decisions and social interactions are often linked[67,68]. There are many examples of social influences shaping stopover site selection[69], migration timing[70], navigation and route development[71] and the mitigation of costs and risks during migration[23]. Although we are aware that social influences must play a role in bird migrations, we are far from understanding the mechanisms involved and the scales at which they act. Addressing this knowledge gap is not trivial as it requires the recording of social interactions in flight, understanding how social information is sensed and quantifying its influence on migratory decision-making (e.g. step selection, route choice, energetics or timing).

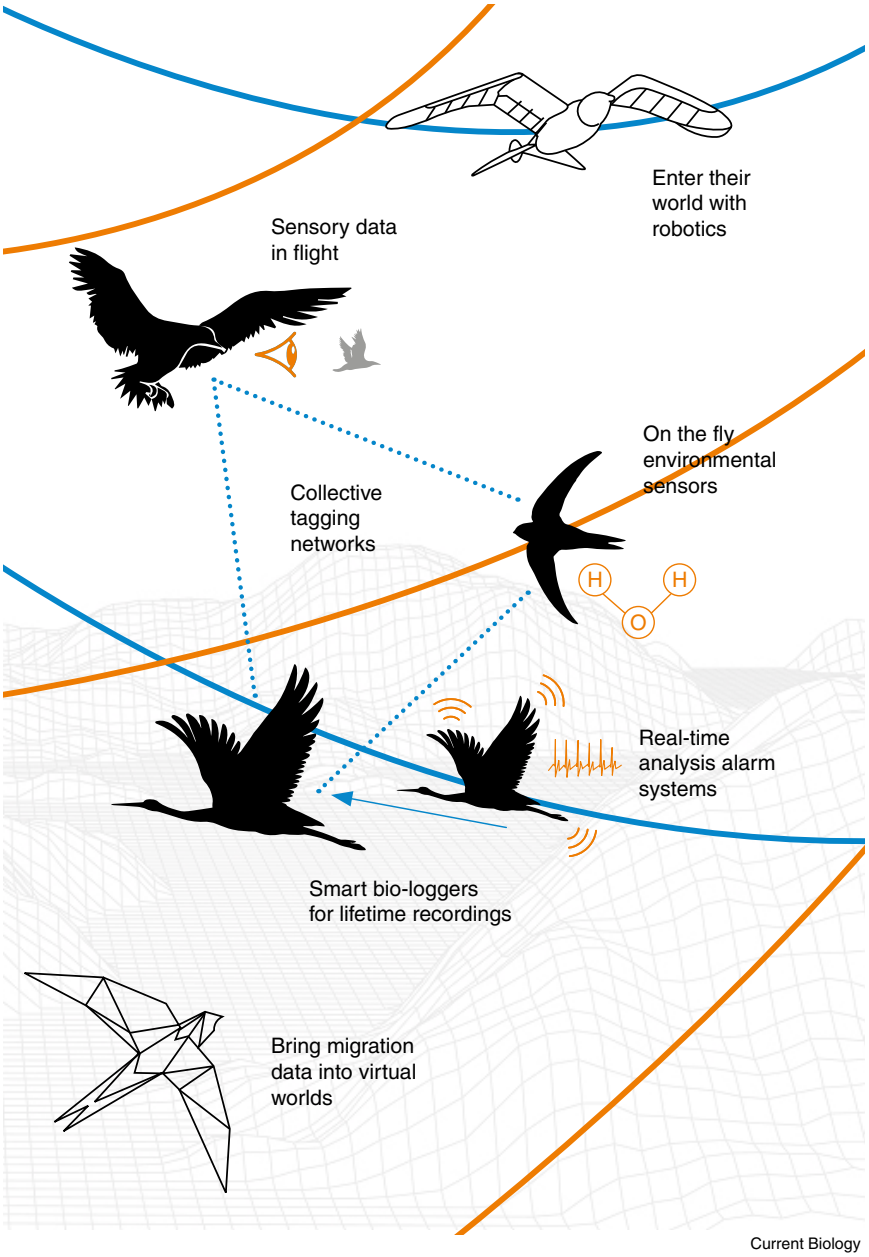


Figure 2. The future of technology for bird migration research.
Innovative engineering and application of current technologies could provide the data required to challenge dogmas. For example, by: sensing what they sense for improved understanding of navigation mechanisms; equipping numerous animals/species with biologgers that behave as a collective network of sensors to work at the interaction level rather than with each individual separately; using smart recording devices that record flexibly (in physical or data recording properties) to extend the monitoring duration for lifetime tracking; to sample volatiles in the environment at the scale at which movement decisions are made; developing 'on the fly' behavioral recognition and alarm signals for conservation; and introducing experimental manipulation during free flight with the use of virtual reality and robotics.

In general, migration behavior requires decision-making based on imperfect information, due to limited experience and the dynamics of environmental conditions[72]. As a result, migrating birds are likely to benefit from social influences that help to reduce uncertainty and improve migratory performance[35,72]. Additionally, moving as a group can improve the search for resources such as nutritious vegetation or supportive wind conditions. For example, soaring birds, such as White Storks (*Ciconia ciconia*) and Andean Condors (*Vultur gryphus*), benefit from the social information provided by nearby conspecifics to locate and exploit favorable flight conditions[23,31]. Yet, most migration research focuses either on the movements of single individuals[73] or captures group movements only at fixed points in space and time[3]. Only a few recent studies have successfully recorded social interactions directly by monitoring the behavior of entire migratory groups[31,74,75]. These cases rely on well-studied systems and have created a taxonomic bias in our understanding of social migration towards large and long-lived species (e.g. cranes[71], storks[31] or geese [75]). However, the highly synchronized nature of migration[3] often results in large multi-species aggregations of individuals moving together, and evolutionary evidence suggests these provide benefits, such as collective navigation[76]. Thus, it is to be expected that migratory single- and multi-species aggregations provide opportunities for information exchange across a diverse range of life histories including species that may be typically solitary during non-migratory periods[77]. Social interactions may even occur between different species[78], especially when multi-species assemblages are brought together by shared resources or stopover sites[69].

Social influences can shape decision-making at many scales, ranging from short-term, direct use of social information for navigation and energy saving in flight to a long-term integration of socially obtained information via social learning and animal culture[72,79]. Thus, increased opportunities for social interactions are likely to be particularly important during early life stages when individuals are performing their first migration. For example, social information has been hypothesized to influence route development and navigation in juvenile migratory raptors[80] and other long-lived species[70,75]. However, to date some of the best evidence of social learning in early route development comes from research on Caspian terns (*Hydroprogne caspia*), a species that is often assumed to migrate solitarily[35]. In addition, songbirds provide some of the best evidence for animal culture outside of migration[81], but it is often assumed that because of their short lifespan, culture cannot

play a role in learning to migrate. Lifetime and multi-generational tracking may provide the means to examine the role of vertical and horizontal transmission of social information on key elements of migratory behavior[35,72].

To achieve a more complete understanding of social influences on migration, the development of onboard technology for small short-lived species is key, as well as increased tagging and observation efforts *en route*, to explore group dynamics during migration. In addition to continuous positional monitoring, recording relative orientation or the sensory framing of individuals can characterize social cues and their direct influence on migratory decision-making. Recording vocalizations or other sensory inputs can help investigate, for example, the role of flight calls in mixed-species flocks[82]. There are already technologies available that, if deployed innovatively as a collective network in data recording and transmission[25], could revolutionize the study of social behavior in migratory flight. Using bio-logging devices that record acoustics, proximity, and orientation (Figure 2), we could explore the social aspects of flight formations by recording air movements and analyzing air dynamics in relation to the locomotion of others within the same formation, or by exploring the perception of social information in flight[67,83]. We can even manipulate the availability of social information in flight experimentally using virtual reality or robotics[84] to simulate conspecific or heterospecific migrants (Figure 2), or similarly to disentangle the effect of social and environmental mechanisms that bring animals onto the same migratory routes[85] (see 'The effect of the environment on migration costs and strategies').

The ontogeny of migration strategies

Migration is a complex behavior in that individual strategies and performances can vary enormously between individuals of the same species and for a single individual over its lifetime[36,86]. It is well known that birds of all life stages migrate, often starting shortly after they have fledged from the nest. Yet, our understanding of how migratory strategies and capabilities develop with age is still in its infancy, owing mainly to the lack of knowledge of the first year of life. The majority of tracking data comes from adult individuals; and although more juvenile birds are ringed compared to adults, ring recoveries can be rare during immature years for some bird groups, such as seabirds. Moreover, the transition from juvenile to experienced adults is unexplored as naturally high mortality rates for juveniles and poor recapture rates mean complete lifetime tracks are often lacking[87] (but see[88]).

Ontogenetic studies of migratory behavior have focused on specific aspects like timing, routes, and direction. These works have revealed that young birds can migrate based on genetically inherited information[89–92] but that some species rely on social information transmitted between flock members that can potentially override innate information. Thus, juvenile migratory behavior is often described as either inherited or socially learned. However, these categories are just two extremes on a continuum, and it is largely unknown where most species fall on this scale. Such dichotomous thinking neglects that the development of an individual represents a continuous interaction between internal, organismic, and external, environmental 'causes'. For example, species that do not migrate in flocks may still benefit from social influences[80]. In addition, migration patterns of some first-year migrants can be highly flexible[93], indicating that inherited information alone cannot explain migratory phenotypes. This variability may be due to the compensation against wind drift and displacement[47,49,94] and a response to stochastic environmental conditions[67] (see 'The effect of the environment on migration costs and strategies').

In general, migratory strategies are often highly diverse across species, populations, and individuals, but while some species show considerable variation in their migratory routes and timing[93], others seem highly conserved[95]. This diversity hinders clear-cut predictions on how migration strategies evolve with age. Navigational abilities appear to change as birds become more experienced. Yet, in addition to navigational skills, a bird's priorities or constraints also change throughout its lifetime. This means that potentially fitness-relevant currencies for migration, such as time, energy and information, may differ between initial migration and those in the reproductive phase of life[52,96]. Additionally, young and old individuals are likely to differ in their ability to exploit environmental conditions to conserve movement energy[86,97].

Long-term tracking allows us to explore the ontogenetic trajectories of migratory behavior in individual birds and has enabled us to move beyond the dichotomy of social learning or genetic inheritance. Various hypotheses, such as the 'arrival time hypothesis', according to which males benefit more from early arrival to breeding ranges, or the 'differential habitat preference hypothesis', according to which differences in physiological tolerance across body size or sexual dimorphism result in differential habitat use, may explain variation in migratory strategy within a population[96]. Intuitively, the 'exploration-refinement hypothesis' suggests that in long-lived species with deferred breeding, juveniles have the opportunity to explore their environment and refine their migratory behavior[52,88]. Thus, large inter-individual variation in juveniles is being refined with age, leading to more stable patterns[36,98]. In addition, this concept also applies to migration phenology and efficiency, as experience allows birds to adjust their fine-scale movements and circannual cycle according to environmental conditions[94,99,100]. This development can even involve a shift from relying on social information to more individual experience-based reinforcement learning and decision-making[70].

What remains to be uncovered are the mechanisms of learning. To achieve that, we need to move beyond the famous flagship species (e.g. Arctic Terns, Bar-tailed Godwits, Cuckoos (*Cuculus canorus*), White Storks, Blackcaps (*Syliva atricapilla*)) and study migration across the full range of taxonomic diversity. Tracking entire groups, flocks or cohorts, including juveniles, immatures and adults, over their lifetime will enable us to quantify not only individual learning curves but also to discern how much of learning is through expertise accumulation and how much is facilitated socially[12,21,101]. This knowledge, together with the advances in our understanding of the role of genes in regulating migratory behavior[89], are paving the way for disentangling the role of genetics and experience in migratory behavior in general[92,102] and ontogeny of migration in particular.

The effect of the environment on migration costs and strategies

Movement from one location to another is generally costly in terms of energetic investment in locomotion, time spent and

mortality risk[9,11,103]. Bird migration in particular often involves extreme movements over great distances, or across varied environments that present physiological challenges[7,30]. Hence, migration has generally been considered an energetically costly phenomenon that animals undertake to ensure access to required resources and to avoid harsh conditions that would otherwise incur a far greater cost than the movement itself. With a growing understanding of small- and large-scale environmental properties that influence travel costs (i.e. the energy landscape determined by aerodynamic turbulence and varying wind dynamics[104]) and migration benefits (e.g. availability and quality of food resources), it is becoming increasingly clear that the 'cost' of migration is complex[105]. Thus, decisions about when and where to move are vital given their significant impact on overall migration costs and performance. For example, while flying thousands of kilometers to a destination requires energetic investment, navigating the energy landscape effectively can reduce this investment substantially[24,106].

Variation in how individuals travel between migration sites can be explained on a broad scale using general atmospheric phenomena and the underlying geography. For example, large bodies of water, mountain ranges and deserts seemingly present an ecological barrier to migration for landbirds that have not evolved for sustained flight in such aerial environments[107]. However, developments in biologging and the availability of fine-scale environmental data have opened up the possibility of detailed investigations into how birds negotiate the physical environment to achieve cost-efficient movements when faced with ecological barriers[21,33,108]. We know that birds of all sizes and shapes can reduce the energy and time spent on migration by flying with supportive winds[24,109–111]. In fact, we are becoming increasingly aware that the smallest movement steps may be affected by dynamic fine-scale properties of media flows, causing variation in movement costs at scales of seconds and meters[112]. Using this knowledge, studies have shown that many landbird species are able to cross the open sea, with the support of wind[4], uplift[107,113] or by flying at high altitudes, highlighting that these routes do not present as much of a barrier as previously assumed. Adjusting flight height over seas and deserts may reduce the risk of hyperthermia and dehydration, and allows birds to save energy by benefiting from supporting wind[30]. However, adopting these strategies still poses a risk of mortality[103,114], the full extent of which remains unclear.

In addition to flight costs, migratory decisions regarding timing of departure, travel speed, or route choice impact the opposing end of the payoff in the value of stopovers or destinations. For example, synchronizing stopovers with spring vegetation greening provides advantages through peaks in nutritional quality (i.e. 'green wave hypothesis') for primary[115] and secondary consumers[116,117]. Thus, adjusting schedules to maximize food intake during migration may also influence the movement costs animals are able or willing to forgo. Depending on species-specific constraints, various environmental conditions can influence these decisions, including wind conditions[118], temperature[119], the onset of frost[120]or vegetation phenology[121]. Thus, migration strategies need to integrate the energetic cost–benefit of these different environmental variables[121,122], but we are just at the beginning of understanding the mechanisms involved. Only by simultaneously considering multiple resource landscapes within a decision landscape are we able to quantify the trade-offs that shape migration. This extends to all spatio-temporal landscapes that influence movement costs, including mortality, which can be shown as a landscape of different mortality risks[67,123]. To assess this, tracking technology needs to record not only the position of the animal but also a diverse set of environmental variables and behavior 'on the fly' and at high frequency at each decision step (Figure 2). Onboard environmental sensors that record humidity or temperature can be used to estimate thermal updraft quality, turbulence, or updraft–downdraft velocities. In addition, recording atmospheric gasses (e.g. oxygen sensors) can provide measures of air quality and altitude to reveal fine-scale behavioral strategies for energy saving, such as migrating at extreme altitudes to exploit supportive wind conditions or reduce water loss[30,32]. Finally, we can develop current techniques to measure movement costs more accurately in response to the environment and to pair these costs with the benefits of access to resources. Physiological variables, such as blood gases, glucose levels or body temperature, are key to understanding the proximate causes of a movement decision, but also measures of food intake that can be balanced with energetic output[124], both of which can be recorded with the innovative use of onboard sensors[20].

These sensors can measure the variables that determine a movement decision at the most relevant scale for migratory decision-making, but this approach cannot tell us what the animal chose not to do, an insight that would be extremely valuable in predictive models and defining migration limits. Spatial modeling of energy landscapes[22] could, however, be informed by the use of drones (passively moving or developed to emulate a bird's flight behavior; Figure 2) to record high-frequency environmental data where the birds are not recorded roaming or decide not to go. These energy landscapes need to be tailored to the species' specific requirements for flight. Thus, when studying large soaring birds, we need environmental data to estimate for example updrafts, while, for smaller birds, we may need to measure wind support at different altitudinal layers. Considering this approach may also provide the data we often lack from the unsuccessful individuals and, for example, determine the cause of mortality. We tend to assume that extreme weather events lead to high mortality but obtaining data on the conditions that lead to mortality is extremely rare (although some datasets have captured such events[125,126]), owing mainly to issues in remote data transmission and retrieval, which could be improved with transmission infrastructure or onboard algorithms to send a final burst of data from a device if mortality is detected using the remaining battery capacity.

Threats to bird migration

Migratory bird populations are threatened by numerous direct and indirect human-related actions that differ in their immediate impact and complexity[38,127]. One major but relatively simple direct threat is illegal hunting or poaching, which kills millions of migrant birds every year[128,129]. Over the last centuries, predation by non-human species has also increased dramatically[130], due to a decrease in alternative prey as well as an increase in introduced, non-native predators[131]. In addition, collisions with

human-made structures, such as windows, power lines and wind turbines, cause enormous numbers of casualties[132–134]. Major indirect threats to migratory birds include light and noise pollution[135,136], the use of pesticides on cultivated lands[137], emerging diseases[138], habitat degradation and climate change[139]. These indirect, more complex and severe threats often lead to unpredictable changes in food availability and the loss of suitable habitats for nesting, stopover, molting or overwintering[140,141]. The growth and intensification of agricultural and urban areas reduce suitable habitats for many migratory species[142]. In addition, climate change alters temperature, precipitation and wind regimes across the globe, affecting the availability of resources for foraging, breeding and cost-efficient movements, while altering disease risk[143–146].

However, are migrants exceptionally threatened by anthropogenic changes? It has been argued that migratory birds are more strongly affected by these threats than non-migratory species[127,147] because they depend on resources in several, often distant regions throughout their annual cycle[38,103,148]. Their often long-distance movements increase the chances of encountering novel threats and of being adversely affected by inferior conditions (the 'multiple jeopardy hypothesis'[149]). In addition, climatic conditions between these different sites are becoming increasingly de-synchronized[150] because of differential changes in climate and habitat conditions at the various sites along the migratory cycle. These unequal changes are disrupting the interdependencies between the cues that migratory birds use to adjust their schedules, leading to unpredictable resources and phenological mismatches[151,152]. For example, mistimed arrival at the breeding grounds can cause reduced reproductive outcomes because of a mismatch between food availability and offspring requirements[100,153,154]. Additionally, climatic changes appear to be favoring a rise in non-migratory strategies and a shortening of migration routes across the temperate zones[155]. However, their mobile lifestyle allows migrant birds to gain experiences in response to the conditions of the many regions along their migratory flyways. This knowledge can enable them to react dynamically to environmental changes and novel threats[149,156–158]. High innate levels of plasticity to cope with dynamic environmental conditions might enable migrants to adapt their temporal and spatial routines efficiently[100,149,159]. Various avian species exhibit temporal or spatial shifts in their migratory patterns due to anthropogenic effects[160]. Some species arrive earlier at their breeding grounds, others breed closer to their wintering areas[161,162], and yet others cease to migrate altogether[163]. However, for such behavioral changes to be adaptive, the benefits of temporal changes need to be maintained throughout the migratory cycle[164], and in large enough areas to ensure adequate levels of survival and reproduction for the population to persist[165]. Furthermore, adjustments in migration behavior due to one threat could lead to conflicts with other species (including humans) at other locations or time points[166]. Thus, given the intensity and magnitude of human-related changes, the protection of avian migrants requires concerted effort and rapid implementation of innovative conservation actions to ensure the long-term survival of many migratory species[147].

To design effective conservation plans, we need to fully understand the tightly interwoven consequences of the different threats and conditions along the routes. Only a full annual cycle approach can identify the periods of the migratory cycle that are most limiting[167], and those effects with delayed fitness consequences (e.g. carry-over effects)[168–170]. Using this knowledge, researchers, managers, and policymakers can determine where and which conservation interventions will lead to the greatest demographic impact[171] and how they will affect the ecosystems involved[166]. International collaborations and long-term monitoring, including citizen science projects, will be key to reaching this goal[172]. The most promising way to gain an understanding of the year-round temporal-spatial whereabouts, timing, behavior, and demographic rates of migratory birds is individual tracking[12,101]. This technology is continuously improving and is presently reaching the capacity to track smaller vertebrate species (i.e. most threatened avian migrants), in large numbers, and through their complete life cycles[26], including their death[103,162]. Combining state-of-the-art analysis methods[173] with real-time alarm systems based on movement tracks can inform and enhance direct conservation actions[174]. These tools will provide novel insights into the behavior and ecology of migratory birds, allowing us to continuously update our knowledge in the fields of navigation, ontogeny and learning, environment interactions, and social influences (Figure 2; Box 1). Integrating our understanding across these disciplines is essential for understanding the adaptive capacities of different species and populations to develop effective conservation strategies for bird migrations in a rapidly changing world.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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