11-2022

Viewing Animal Migration Through a Social Lens

Ellen O. Aikens

Iris D. Bontekoe

Lara Blumenstiel

Anna Schlicksupp

Andrea Flick

Trends in
Ecology & Evolution

Review

Viewing animal migration through a social lens

Ellen O. Aikens [1,2,5,*] Iris D. Bontekoe, [2,3,4] Lara Blumenstiel, [2,4] Anna Schlicksupp, [2,4] and Andrea Flack [1,2,4,@,*]

Evidence of social learning is growing across the animal kingdom. Researchers have long hypothesized that social interactions play a key role in many animal migrations, but strong empirical support is scarce except in a few unique systems and species. In this review, we aim to catalyze advances in the study of social migrations by synthesizing research across disciplines and providing a framework for understanding when, how, and why social influences shape the decisions animals make during migration. Integrating research across the fields of social learning and migration ecology will advance our understanding of the complex behavioral phenomena of animal migration and help to inform conservation of animal migrations in a changing world.

Highlights

Social influences (i.e., social information use, social learning, and culture) are often assumed to play a role in animal migration, but studying social aspects of migration remains a challenge.

We evaluate support for predictions from the social learning literature within the context of migration, and suggest that social influences during migration are likely more widespread than previously recognized.

To study social migration, future research can leverage next-generation tracking techniques and experimental manipulations of the social environment.

Movement diversity constitutes the building blocks of migration culture, and thus warrants further consideration in conservation and management of migratory species.

Studying social influences during migration is a grand challenge in movement ecology

A long history of research on **animal migration** (see Glossary) has revealed the widespread importance of migration across all levels of ecology, from individual fitness and population dynamics [1] to community ecology and ecosystem services [2]. Researchers have also gained important insights into the physiological, cognitive, and behavioral strategies that animals employ to migrate successfully [3]. Despite these impressive adaptations, many migratory populations are in decline [4]. Migrants frequently face challenges from predation and environmental variability that generate uncertainty and risk during migration [5,6]. Furthermore, these challenges are exacerbated by barriers to movement from human development along **migratory routes** [7], and habitat loss on **seasonal ranges** and **stopover sites** [8]. Additionally, climate change is altering the phenology and distribution of resources, which may force migrants to alter their annual schedules and shift space-use patterns in unprecedented ways [9,10].

Migration involves many choices about whether, where, and when to migrate [3,11], and often these choices are made with imperfect **information**. For example, successful migration may be especially difficult for young individuals because they must decide upon schedules, routes, and destinations with limited previous experience. Even for adults, migration is often the riskiest part of the annual cycle [12,13], and carryover effects from the migratory period can strongly impact reproductive success [14]. Given these risks and uncertainties, migrants may not simply rely on their own experiences to make decisions during migration. Instead, the reliance on **social influences** – which we define as **social information use**, social **learning**, and **animal culture** – could be adaptive for many migratory species. Despite the potential importance of social influences on migration, most research occurs at the individual level, and social interactions during migration are rarely quantified, or only inferred indirectly [15]. Social influences can occur in many forms and at various temporal and spatial scales during migration (Box 1 and Figure 1), but it is largely unknown to what extent social information use goes beyond immediate, short-term benefits to establish long-term memories and affect future decision-making. Thus, understanding social influences during migration represents a key knowledge gap in the field of migration ecology, with important implications for the conservation of migratory populations in a rapidly changing world.

[1]Center for the Advanced Study of Collective Behavior, University of Konstanz, 78468 Konstanz, Germany
[2]Collective Migration Group, Max Planck Institute of Animal Behavior, 78315 Radolfzell, Germany
[3]Department of Migration, Max Planck Institute of Animal Behavior, 78315 Radolfzell, Germany
[4]Department of Biology, University of Konstanz, 78457 Konstanz, Germany
[5]Current address: U.S. Geological Survey, South Dakota Cooperative Fish and Wildlife Research Unit, Department of Natural Resource Management, South Dakota State University, Brookings, SD, 57007, USA.

*Correspondence:
eaikens@usgs.gov (E.O. Aikens) and aflack@ab.mpg.de (A. Flack).
[@]Twitter: @anflack

Box 1. The many scales of social influence during migration

Animals obtain information about their environment to adjust their behavior. Learning is the process of using information to improve performance of a task [79]. Migrating animals process and store spatial information such as the distances and directions between relevant locations [92]. Yet, to migrate successfully, animals not only need to find their way or locate suitable sites for foraging and breeding, but they also must learn about the temporally dependent properties of each spatial location [93]. Some of these skills may be inherited genetically, like compass directions in the form of 'signposts' that trigger certain navigational responses [80]. Alternatively, learning can enable animals to obtain, store, and retrieve different types of information. Individuals can gain information through trial and error interactions with the environment, or by observing and copying the behavior of others [94].

In ecological contexts, information flow is often hard to quantify. We propose to distinguish three sources of social information: (i) indirect cues, (ii) observational interactions, and (iii) collective interactions (Figure IA). We also predict that an individual's reliance on these different types of social information use will differ depending on the social organization of the species (Figure IB). Specifically, larger groups of unrelated individuals should be more likely to benefit from collective interactions [95], whereas solitary species, such as many large carnivores, may profit from indirect cues when locating resources or suitable habitats [59]. Moreover, in stable, moderately sized family groups, juveniles can directly copy the behavioral repertoire of their kin and maintain traditional migration features across multiple generations (i.e., migration culture) [96] through observational interactions. Thus, the temporal scales at which these sources of social information impact migration traits vary from seconds to generations (see Figure 1 in main text). On short timescales, collective sensing allows animals to avoid predation [97] or detect the best conditions [60]. In contrast to these transient effects, social information use can have longer-term impacts when this information is retained through memory formation and used to improve migratory performance via social learning [16].

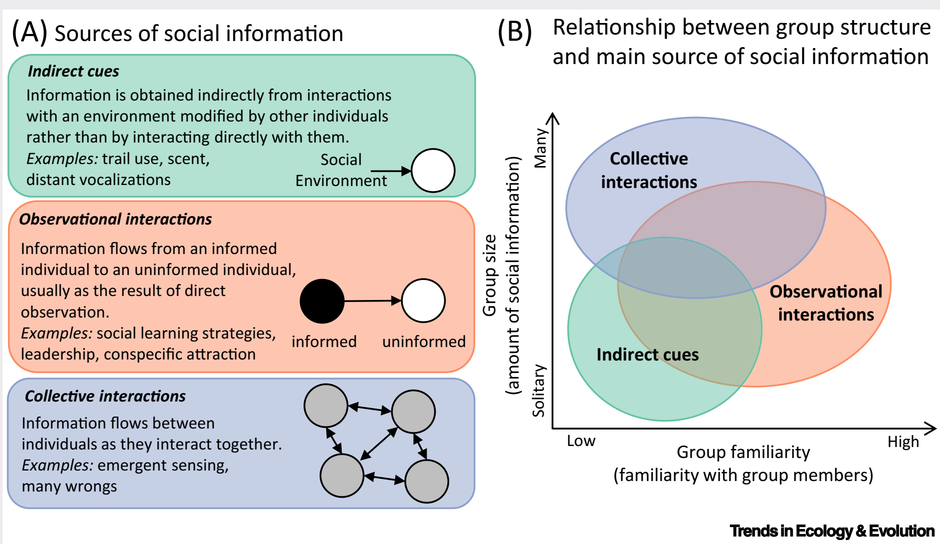

Figure I. Sources of social information. (A) Definitions and examples of three main sources of social information, which include indirect cues, observational interactions, and collective interactions. (B) Predictions about how group structure (i.e., group size and group familiarity) influences the main source of social information.

When, how, and why do social influences shape migration?

Social influences allow migrants to obtain information from conspecifics and heterospecifics, which can reduce uncertainty during migration and enhance migratory performance [16,17]. However, the importance of social influences may not be uniform across the diverse taxa and systems where migration has evolved [18,19]. Here, we propose a general framework to predict when, how, and why social influences shape migration. To do so, we borrow three key predictions from the social learning literature [20,21] and we link each prediction to a different question (i.e., when, how, and why) within the framework. We also explore each prediction across the diverse life histories and social structures of migratory taxa [20].

Glossary

Animal culture: distinct behavioral phenotypes shared by group members that are transmitted across generations through social learning.
Animal migration: directional movement of animals between a minimum of two nonoverlapping seasonal ranges to exploit spatiotemporal variability in resources.
Collective sensing: the ability to detect and respond to environmental cues, achieved by many individuals pooling their local information and acting as a distributed sensor network over larger spatial scales.
Corridor/flyway: the spatial area used by multiple individuals, usually from the same population, during migratory movements.
Cumulative cultural evolution: the multigenerational refinement of a behavior, which occurs when a culturally transmitted behavior (i.e., a socially learned behavior that is transmitted over generations) is improved by successive generations.
Group cohesion: the degree to which group members stay together. Group cohesion can range from highly stable groups that remain together for long periods of time to fission-fusion groups that experience frequent changes in group size and composition through merging (fusion) and splitting (fission) events.
Information: anything that helps to improve decision-making or reduce uncertainty.
Leadership: guidance of a group by a single individual or a small minority of the entire group.
Learning: using previous experience to improve performance of a task. This previous experience may be acquired asocially (individual learning), by observing others directly or indirectly (social learning), or by acting together with others (collective learning).
Migration culture: elements of migratory behavior (e.g., routes, stopover locations) that are passed from one generation to the next through social learning. Typically, these elements of migratory behavior are distinct between different groups, populations, or regions. Migration culture is a form of animal culture.
Migratory route: the spatial path used by an individual during migration.
Next-generation tracking: merging animal tracking techniques with novel

When? Social information is favored when personal information is difficult to obtain

During migration, there are many situations where personal information (i.e., information acquired individually through direct interactions with the environment) is difficult to obtain. Previously obtained personal information can quickly become outdated when migrants move through dynamic or unpredictable environments. For example, marine and terrestrial herbivores track dynamic foraging patches during migration [22], and migratory birds use variable wind support or uplift for energy-efficient flight [5]. Dynamic changes in resources, variability in weather, and rapid environmental change are commonplace in migratory systems, making personal information frequently unreliable. Likewise, young individuals have limited opportunities to explore and obtain personal information before performing their first migration. Practicing migration outside the typical time window exposes migrants to risks and inhospitable conditions [23], and is also infeasible when the journey is long or energetically expensive [24]. Furthermore, once an individual reaches sexual maturity, opportunities for exploration during migration are likely reduced. For example, many migrants experience pressure to arrive early at their migration destinations to secure key resources or territories needed for breeding [25]. Other migrants must time reproduction appropriately within a narrow window when key resources are abundant [26]. As a result, the time available to explore during migration can be reduced as migrants move into the reproductive phase of their life, creating selective pressure for migrants to quickly learn beneficial behaviors early in life through social information use and social learning. Alternatively, social information may not be favored when personal information already exists (e.g., an experienced individual [27]) or when information is easily obtained individually (e.g., when resources are predictable or exploration is not costly).

The life-history strategies of migratory species should influence both when and which social influences are most beneficial in mitigating these difficulties associated with obtaining personal information during migration. The number of migratory trips performed over a lifetime could influence the relative importance of genetics versus learning (including individual learning, social learning, and collective learning). Short-lived species may rely more on genetically inherited migration patterns because their limited lifespan does not provide opportunities for exploration or learning [28]. Nevertheless, even in the multigenerational migrations of butterflies, which have a strong genetic underpinning, social cues that facilitate communal roosting help to reduce predation risk [29]. Similarly, many anadromous fish, like Pacific salmon (genus *Oncorhynchus*), migrate once to their natal hatching grounds to spawn and then die. Yet, there is growing evidence to suggest that collective navigation plays an important role in migration timing and accuracy for salmon [30]. Together, these examples suggest that shorter-lived species may mitigate the difficulties associated with obtaining personal information by relying on social information during migration over their entire lifespan. By contrast, long-lived species with overlapping generations and extended family care are often assumed to learn their migrations directly from their parents during early life (e.g., ungulates, cetaceans) [31,32]. Evidence of vertical transmission of navigational techniques comes from a study of simultaneously tracked mother and pup Egyptian fruit bats (*Rousettus aegyptiacus*), which found that pups learn navigational landmarks from their mothers [33]. Likewise, juvenile Caspian terns (*Hydroprogne caspia*) appear to learn where to migrate by following their fathers [34]. In long-lived species, social information may be most important for juveniles, but as individuals consolidate socially obtained information into memories, older individuals may rely less on social information [22].

How? Social interactions occur during sensitive developmental periods, facilitating social information use and learning

Migration increases the opportunities for social interactions because migratory movements are more synchronized in space and time than movements during other phases of the annual cycle

study designs to refine movement ecology studies. Examples of next-generation tracking include lifetime tracking, multigenerational tracking, group tracking, and hotspot tracking.

Seasonal ranges: the seasonal destinations of migration, which are often characterized as breeding/nonbreeding ranges for birds, winter/summer ranges for temperate migrants, or wet/dry season ranges for migrants inhabiting tropical or dry climates.

Social influences: the social processes that influence behavior, including social information use, social learning, and culture.

Social information use: information that is obtained socially from direct observation, indirect cues, or collective interactions.

Stopover site: location that is used to rest or refuel during migration.

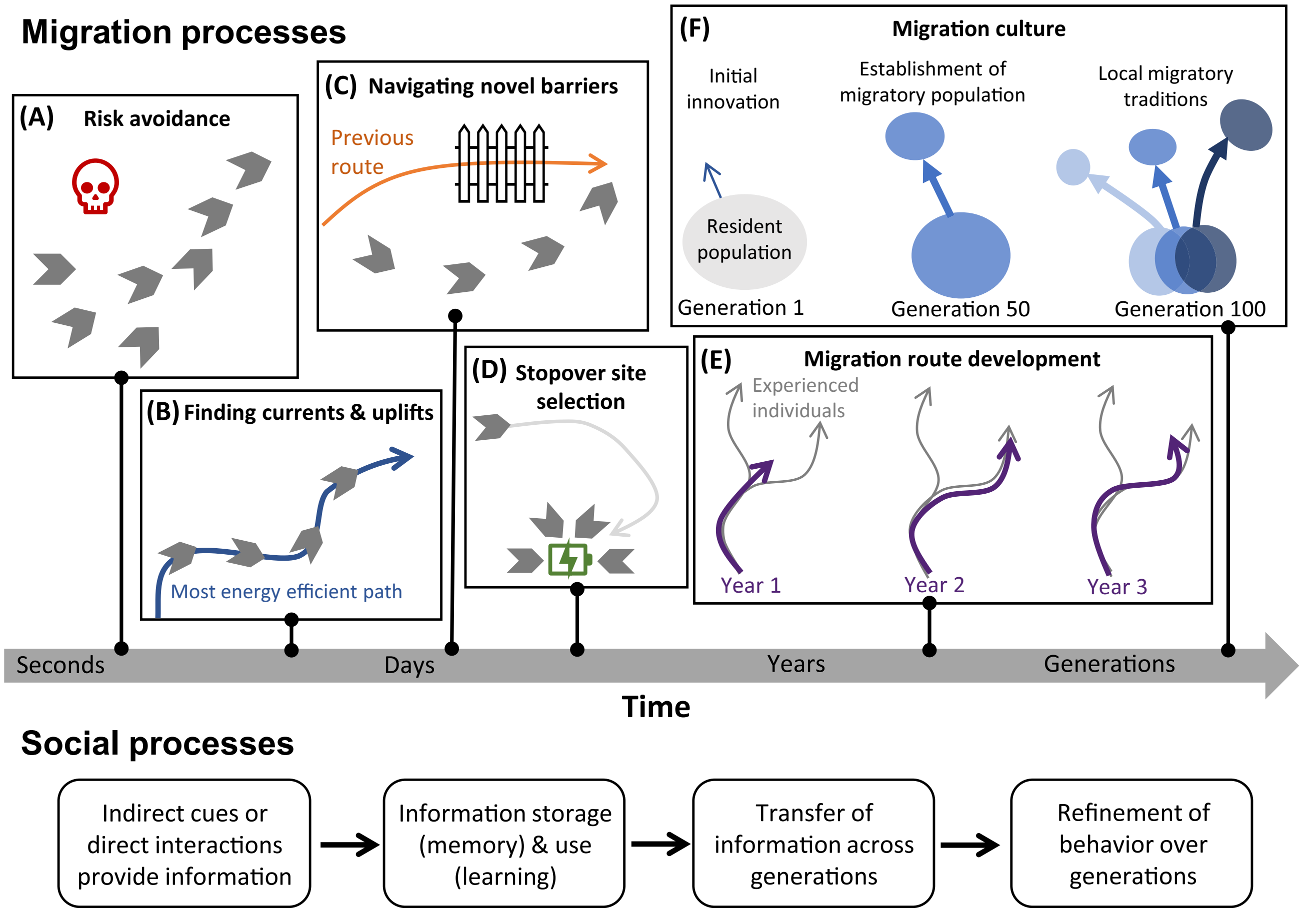

Figure 1. Examples of the temporal scales at which different social influences affect migration. Gray chevrons correspond to individuals with their movement directions; lines with arrows represent movement paths of individuals or groups. At the finest temporal scale, moving animal groups can act as distributed sensor networks for risks (A) or resources (B), such as ocean or atmospheric currents, by enabling animals to sense the environment outside of their perceptual range (i.e., collective sensing). Animals may follow more experienced leaders around obstacles and barriers (C), or may simply be attracted to stopover sites by conspecifics or heterospecifics who may signal favorable environmental conditions (D). During route development, individuals may balance the use of social information from experienced individuals with the exploration of new areas when establishing their own routes, territories, and seasonal ranges (E). Finally, over the course of generations, migration culture can develop through cumulative refinements of learned behaviors from previous generations (F).

[35]. Overlaps in time and space along migration **corridors** or **flyways** are often the result of behavioral responses to the environment [36]. Nevertheless, the synchronized nature of migration in taxa as diverse as insects [37] and marine mammals [35] increases encounters among individuals and may facilitate the transmission of information through social interactions. Many songbirds are thought to migrate solitarily at night. However, because of the synchronized nature of migration, these ‘solitary’ songbirds often migrate at the same time and in the same direction as thousands of other migratory birds [38,39], providing chances for information exchange (Box 2). Furthermore, migration provides opportunities for individuals from different groups, populations, and even regions to interact and share information [17,40]. In fact, many typically territorial or solitary animals modify their social behavior during migration to form large groups [35].

The synchronized nature of migration creates an environment where individuals are more likely to experience social interactions, which may be particularly important for young individuals. Many

Box 2. Rethinking songbird migration

Songbirds are a key model system in migration research. In particular, songbird migration research over the past several decades has investigated the navigational mechanisms underlying migration. Classical studies with Emlen funnels suggest that many inexperienced songbirds have a genetically inherited migration direction [98]. And displacement experiments that manipulate magnetic, celestial, or solar cues provide insights into the many sources of information migratory animals can exploit to orient themselves [80]. But the results of these experiments are often mixed [80], leading researchers to conclude that multiple layers of orientation information are likely integrated to avoid issues arising from unreliable cues (e.g., magnetic cues are favored on a cloudy day when solar cues are less prominent) [15]. However, the possible use of social cues as an additional and complementary source of navigational information is often ignored in the songbird migration literature, possibly because of prevailing theory about the role of genetic determination in songbird migration. Yet, some researchers have questioned the interpretations of classical displacement experiments that are often cited as providing evidence of an innate genetic program, arguing that individual and social learning from conspecifics (or even heterospecifics) could explain key anomalies in the data [99].

It is often argued that many songbirds migrate solitarily, precluding the possibility of social influences during migration. However, there are numerous anecdotal accounts of otherwise solitary songbird species aggregating en masse at migratory bottlenecks (e.g., along alpine passes, peninsulas, and islands), suggesting that these 'solitary' species may modify their social behavior during migration. Furthermore, although nocturnal songbirds are often more widely dispersed than diurnal migrants, groupmates appear to fly in a coordinated manner in the same direction [38]. Likewise, birds may use calls to coordinate movement [58] or adjust their movement based on the direction and altitude of other calls. As a result, highly dispersed individuals that coordinate movement through contact calls may benefit because this group structure likely samples a more diverse range of environmental conditions [15]. Although studies that quantify group dynamics of long-distance migratory birds over their entire annual cycle are rare, one study in a nonpasserine highlights that stable groups do indeed exist [51]. Thus, it may be time to revisit songbird migration to reconsider whether and how social information shapes migration in this iconic model system.

migratory animals conduct their first migration in their early lives (the period of juvenile development before the onset of reproduction). Early life stages of migrating animals are often characterized by high mortalities [41,42], generating strong selection pressure to quickly learn migratory behaviors that improve performance and survival. Migrants are therefore likely to improve their migration skills early in life during 'sensitive' developmental periods using individual and social learning.

Together, the increased social interactions during sensitive developmental periods create many opportunities for migrants to improve their performance through social information use. For example, juvenile soaring birds expend more energy during flight compared to older conspecifics [43], but social information allows soaring birds to exploit the dynamic thermal environment more efficiently [44]. Likewise, visual and auditory cues from both conspecifics and heterospecifics can influence stopover selection in birds [45–47]. In many cases, this reliance on social cues changes with site familiarity and experience [45–47], which suggests that social learning shapes stopover site development during early life. Experiments with pigeons (*Columba livia*) suggest common mechanisms whereby navigational information can be socially learned and consolidated into spatial memories. Specifically, inexperienced pigeons have a sensitive period during route learning in which they are more likely to follow and learn the paths of conspecifics [48,49]. Similar mechanisms may be at play for juvenile migrants traveling in families [50] or groups of unrelated individuals [51]. Older and more experienced individuals may serve as repositories of navigational knowledge that benefits younger individuals in the group, as in white-fronted geese (*Anser albifrons*) parents that lead their offspring during migration [50], or groups of whooping cranes (*Grus americana*) that navigate more efficiently when an older individual is present [16]. Furthermore, displacement experiments suggest that social interactions are essential for many young individuals when navigating to their destination [52], and the reliance on social influences changes as individuals develop their own navigational memories with experience [53].

Why? Social learning can outperform individual learning

From **collective sensing** to **cumulative cultural evolution**, there are many examples of social interactions improving migration performance in comparison to what an individual could accomplish alone [15]. Migrating animals exhibit a diverse range of social structures, which likely influences the social mechanisms used to improve migratory performance. Highly dispersed migrants, which are often assumed to be solitary, may rely on indirect cues and long-distance communication. For example, blue whales (*Balaenoptera musculus*) appear to use long-range acoustic communication to appropriately time migration [54,55] and improve resource sensing in their highly dynamic ocean environment [56]. Both theoretical work and empirical evidence suggest that long-range communication can enhance foraging efficiency [57] and navigation during long-distance movements [58]. Visual and olfactory cues, such as game trails or scent trails made by previous migrants, can improve navigation [59]. By contrast, large migratory groups could benefit from collective sensing [15,18], because gradient sensing ability often increases with group size [60]. For instance, collective attention in flocks of homing pigeons appears to enhance predator detection and improve navigation [61]. In addition to enhanced risk detection and predator dilution, large groups that migrate together to shared calving or spawning grounds might also benefit from collective sensing of forage resources, as hypothesized in wildebeest (*Connochaetes taurinus*) [62] and caribou (*Rangifer tarandus*) migration [15,63]. Similarly, collective sensing in massive flocks of passenger pigeons (*Ectopistes migratorius*) may have helped birds locate spatially and temporally unpredictable food patches [64]. Fish migrating at high density were able to navigate fishways at dams more quickly, suggesting benefits of collective navigation [65]. Together, 'solitary' migrants likely rely on indirect cues while large groups likely benefit from collective sensing, both of which allow individuals to gain information outside of their perceptual range to make more accurate or efficient decisions during migration.

Another key aspect of social structure that should determine which social mechanisms influence migration is **group cohesion**, which can range from highly stable to dynamic fission-fusion groups. Groups that are cohesive over extended time periods, such as family groups, may benefit from older, more experienced individuals serving as repositories of ecological knowledge. For example, matriarch killer whales (*Orcinus orca*) and African elephants (*Loxodonta africana*) were found to lead the group during periods of resource deficiency [66,67]. In these types of social organizations, younger, less experienced individuals benefit from the knowledge of older individuals, while matriarchs yield an inclusive fitness benefit [66,67]. By contrast, individuals in fission-fusion groups must balance social cues and their own personal information. For example, when choosing between different foraging patches, bison (*Bison bison*) followed the majority when they were unfamiliar with local forage conditions [68]. Associating with individuals that possess different knowledge or experiences may enhance the transfer of innovations, as shown in foraging experiments with great tits (*Parus major*) [69]. Likewise, pairs of pigeons that were incrementally replaced with a naive individual innovated more efficient routes in comparison to stable pairs [70]. Thus, we expect fission-fusion migratory groups to exhibit faster rates of information transfer and faster refinement of migration behaviors in comparison to stable migratory groups.

Emerging approaches for studying social influences in the wild

Animal migration creates situations where personal information is difficult to obtain, where social interactions occur during sensitive developmental periods, and where social learning outperforms individual learning. As a result, social influences during migration are likely beneficial and more widespread than current research suggests. However, studying social influences during migration remains a challenge, and empirical data to validate theoretical models are often lacking. To advance the study of social migrations, we suggest leveraging technological advancements by creatively merging different data sources with novel study designs.

Traditional tracking studies, which often occur at the individual level, can be modified in their design to provide insights into social influences during migration, an approach we call **next-generation tracking** (Box 3). Furthermore, combining next-generation tracking with data from long-term ecological studies provides opportunities to understand how individual features – such as age, relatedness, and reproductive outcome – influence the transfer of migratory information among group members. For example, group tracking of a well-studied pod of killer whales revealed the important role of older individuals as leaders [66]. Furthermore, even if tracking studies are infeasible, pairing long-term ecological studies with strategically placed camera traps or overhead video footage (e.g., from drones) can quantify group composition and **leadership** at key bottlenecks along migration corridors and flyways, especially if the long-term study uses visible individual identifiers (e.g., color-coded tags) or individuals are easily identifiable (e.g., zebras, whales). Such studies can reveal how long parent-offspring bonds last during migration or could detect the emergence of leadership behavior as an individual ages and gains more experience. Even without long-term identity data, important insights can be gained for species with age and sexual dimorphism. For example, drone footage from migrating caribou herds revealed differences in interaction rules across age and sex [71].

Technological advances can provide new insights into how visual and auditory communication influences information spread in moving animal groups. Proximity loggers could estimate encounter rates in species that may be too small to be tagged with GPS devices or live in habitats with poor satellite coverage (e.g., under dense canopy) [72]. Beyond simply estimating proximity and inferring an interaction, emerging technology can provide more nuanced information about the visual and auditory cues used during migration. The role of visual perception can be estimated

Box 3. Next-generation tracking

Technological advances that reduce the size, weight, and cost of tracking devices are providing opportunities to tag entire groups, while new techniques that extend the lifetime of tags and enable remote data download are facilitating long-term data collection. Next-generation tracking merges these advances in tracking technology with novel study designs to quantify social interactions of mobile groups (Figure I). These approaches include the following:

(i) Lifetime tracking: tracking the movements of an animal over its entire lifetime, beginning at its juvenile stage, which is the developmental stage when learning is most likely to occur. Lifetime tracking can provide insights into route development, responses to phenological and environmental changes, and the importance of early life experiences.
(ii) Multigenerational tracking: tracking the movement of parents and offspring, ideally over long timescales that include multiple generations. This approach can provide insights into migration culture and modes of social learning, such as vertical transmission of migration routes.
(iii) Group tracking: tracking the movements of an entire group of individuals. Groups can be defined on the basis of social organization (e.g., harems), relatedness (e.g., family groups), or location of origin (e.g., breeding site). Linking group tracking with information about individual identity within the group – such as relatedness, social status, or age – can provide key insights into group decision-making, leadership, and conflict resolution in migrating groups.
(iv) Hotspot tracking: tracking a large proportion of a group captured during a transitory phase of migration (e.g., at a stopover site or along a migration bottleneck). This approach can help answer questions about group dynamics and migratory connectivity during migration. Hotspot tracking can also be extended to mixed-species groups to study social information use among heterospecifics.

Although next-generation tracking techniques provide exciting opportunities to advance movement ecology, each approach has logistical and technical challenges. In lifetime and multigenerational tracking studies, high juvenile mortality requires large tagging (and redeployment) efforts to obtain adequate sample sizes. Therefore, lifetime tracking studies are better suited for species where juveniles are easy to locate, handle, and tag (e.g., large birds that nest at high densities). Tagging juveniles may require specially designed tags or attachment methods that accommodate juvenile growth. Advances in remote data download and solar-powered tags extend the lifetime of tags to better match the lifespan of the study species. Furthermore, group and hotspot tracking require the development and improvement of methods to catch entire groups of different migratory species safely. At the same time, decreases in tag costs allow an increase in the number of individuals or groups that are feasible to track, while decreases in tag sizes and weights will increase the range of species that can be tracked.

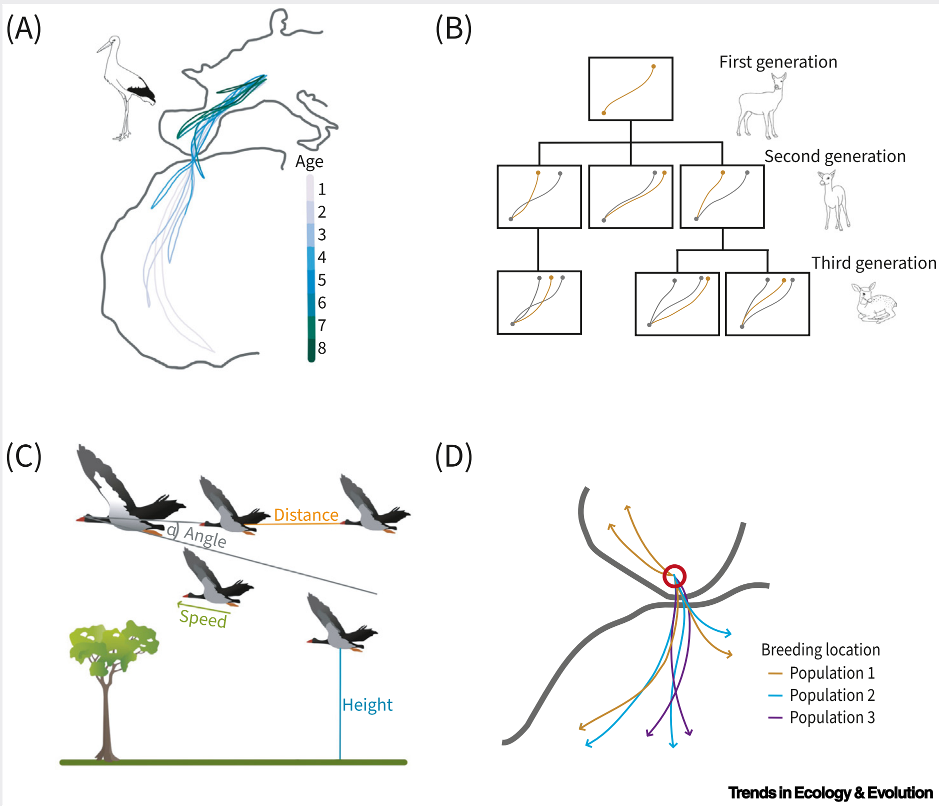

Figure I. Empirical and hypothetical examples of next-generation tracking techniques. (A) Lifetime tracking of a white stork (*Ciconia ciconia*) from birth onwards [42], showing that migration routes become shorter as the individual ages. (B) Multigenerational tracking of a deer family, with the current generation shown in orange and the previous generations shown in gray [100]. (C) Group tracking of geese flying in a V-formation allows researchers to measure the distance and angle between the geese, the height above the ground, and flight speed [50]. (D) A hypothetical example of hotspot tracking at the Strait of Gibraltar. Birds are captured at a migration hotspot (circled in red) and released with tracking devices to estimate group cohesion and migratory connectivity. The different colors of routes represent different breeding populations. Individuals from the same breeding population may not all travel to the same overwintering location. The geese and tree icons are from the Integration and Application Network (ian.umces.edu/media-library), which is licensed under Attribution-ShareAlike 4.0 International (CC BY-SA 4.0). All other icons are drawn by Anna Schlicksupp.

using head movement and gaze direction from video footage [73], or through specialized sensors like accelerometers and magnetometers [74]. In addition, acoustic communication is an essential form of information exchange in many species. Animal-borne sound recorders can be used to quantify and characterize vocalizations [75] and can reveal how auditory signals mediate group cohesion or enable group decision-making during migration [56,58]. Social network analyses can characterize the social organization of groups [76] and estimate the spread of information across space and time [77]. Combining methods that quantify animal communication with tracking data and social network analyses can provide insights into how changes in migration behavior spread through groups.

Despite these technological advances, quantifying the social environment over the large spatial and temporal scales that are relevant to migration remains one of the largest methodological challenges associated with studying social migration. One important tool that can help to address this issue is pairing tracking technology with experimental manipulations of the social environment [78,79]. Experimental approaches can also help to disentangle the role of genetics versus individual and social learning [32,80]. For example, migrants could be moved into an area they are unfamiliar with, or released with other individuals with which they have no previous experience; techniques that are commonplace in navigational experiments with homing pigeons [70]. Importantly, experimental manipulation requires special attention to ethics and animal welfare [81]. However, the social environments of animals are sometimes manipulated by management actions, including the long-distance translocations of animals to mitigate human–wildlife conflicts [82], reintroductions of locally extinct migratory populations (e.g., [16,32]), and release of rehabilitated individuals into the wild. We encourage researchers to take advantage of these management actions to gain insights into social influences during migration.

Implications for conservation and management of migratory species

A key challenge facing conservation and management is understanding if and how animals will adjust to rapid environmental change. Individual and social learning provide opportunities for animals to adjust to environmental change within their lifetime, while cumulative cultural evolution provides a second inheritance system, in addition to genetics, where beneficial behaviors can be transferred across generations [83]. For example, barnacle geese (*Branta leucopsis*) from a rapidly growing population discovered a stopover site that became more suitable due to rapidly increasing temperatures [47]. This behavior quickly spread to other geese in the population through social learning [84]. Thus, social information, learning, and culture likely shape the ability of many migratory animals to adjust to environmental change, yet these factors are rarely incorporated into conservation policy or management plans [85].

In contrast to the potentially underappreciated role of social learning, the role of genetic diversity has long been recognized as a key component of a population's ability to thrive and adapt to environmental change. The concept of the extinction vortex highlights the importance of genetic diversity for small populations that often face a high risk of collapse due to negative feedbacks between genetic and demographic processes [86]. A loss of behavioral diversity may have similar negative consequences. Specifically, populations with diverse life histories and behaviors are hypothesized to be more robust in the face of environmental change, a phenomenon known as the portfolio effect [87]. For example, the diverse range of spawning sites and migration routes used by individual salmon in Bristol Bay (AK, USA) scaled up to reduce fluctuations in salmon abundance across the entire watershed [87]. Likewise, bird species with greater diversity in migratory behavior were more resilient to climate change and less likely to experience population decline in comparison to species with a more limited portfolio in migration behavior [88]. As a result, conserving movement diversity, including **migration culture**, is likely to enhance population resilience and reduce the risk of local population extinction. Just as protecting genetic diversity is employed to avoid species extinction, the protection of diverse movements and migration culture should help to avoid the loss of migrations that can take generations to relearn [18,32].

Approaches to conserve threatened migratory populations rarely consider behavioral diversity and migration culture, although there are efforts underway to change this [85]. One critically important approach to conserve migratory species is through corridor and flyway conservation, where high-use areas are identified and protected [89]. However, as human development expands, the creation of protected corridors within a matrix of human development may erode movement diversity and increase population synchrony by funneling mobile species through limited movement corridors on the landscape [90]. Future research could investigate whether and how corridor and flyway conservation efforts protect diverse movement behaviors – including socially learned migration routes used at low densities – that contribute to a population's migration culture and migration portfolio.

Partnerships between managers and researchers continue to advance science, while also improving conservation and management of migratory populations. In fact, some of the best examples of social learning in migratory species arose from research on reintroduced whooping cranes [16,27,91] and bighorn sheep (*Ovis canadensis*) [32], which were facilitated by strong collaborations between researchers and managers. Another promising area for collaboration between researchers and managers involves the development and improvement of methods to monitor migratory populations. Specifically, researchers can help develop protocols, tools, and technologies to facilitate long-term monitoring of migration culture by tracking changes in routes, stopover sites, seasonal ranges, and migration schedules.

Concluding remarks and future directions

It is an exciting time to tackle the grand challenge of understanding the role of social influences during migration (see Outstanding questions). As we have illustrated in this review, the three predictions about when, how, and why social information use and learning should be favored are often met in many migratory species and systems. Thus, social influences are likely to be widespread across a range of migratory taxa. Yet, most empirical research integrating social learning and migration occurs in only a few well-studied systems, likely because of the difficulties associated with quantifying social interactions over the appropriate spatial and temporal scales. The technological revolution that allows better data collection on both animal behavior and the environments that animals are moving through provides new opportunities to study questions that a decade ago were nearly impossible to address.

Acknowledgments

This work was supported by the German Research Foundation (DFG, Emmy Noether Fellowship to A.F.: 463925853) and by the Max Planck Society. A.F. acknowledges support by the Hans und Helga Maus-Stiftung, and the James Heineman research award of the Minerva Stiftung. E.O.A. was supported by the German Research Foundation under Germany's Excellence Strategy EXC 2117-422037984. I.D.B. was supported by the International Max Planck Research School (IMPRS) for Organismal Biology and by the IMPRS for Quantitative Behaviour, Ecology and Evolution from lab to field. Feedback from Martin Wikelski, Katherine Snell, Joshua Stafford, and four anonymous reviewers helped to improve earlier versions of this review. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

Declaration of interests

No interests are declared.

References

1. Fryxell, J.M. *et al.* (1988) Why are migratory ungulates so abundant. *Am. Nat.* 131, 781–798
2. Bauer, S. and Hoye, B.J. (2014) Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science* 344, 1242552
3. Dingle, H. (2014) Migration: The Biology of Life on the Move. Oxford University Press
4. Harris, G. *et al.* (2009) Global decline in aggregated migrations of large terrestrial mammals. *Endanger. Species Res.* 7, 55–76
5. Nourani, E. and Yamaguchi, N.M. (2017) The effects of atmospheric currents on the migratory behavior of soaring birds: a review. *Ornithol. Sci.* 16, 5–15
6. Sabal, M.C. *et al.* (2021) Predation landscapes influence migratory prey ecology and evolution. *Trends Ecol. Evol.* 36, 737–749
7. Wyckoff, T.B. *et al.* (2018) Evaluating the influence of energy and residential development on the migratory behavior of mule deer. *Ecosphere* 9, e02113
8. Marques, A.T. *et al.* (2020) Wind turbines cause functional habitat loss for migratory soaring birds. *J. Anim. Ecol.* 89, 93–103
9. Horton, K.G. *et al.* (2020) Phenology of nocturnal avian migration has shifted at the continental scale. *Nat. Clim. Chang.* 10, 63–68
10. Kubelka, V. *et al.* (2022) Animal migration to northern latitudes: environmental changes and increasing threats. *Trends Ecol. Evol.* 37, 30–41
11. Xu, W. *et al.* (2021) The plasticity of ungulate migration in a changing world. *Ecology* 102, e03293
12. Sawyer, H. *et al.* (2019) All routes are not created equal: an ungulate's choice of migration route can influence its survival. *J. Appl. Ecol.* 56, 1860–1869
13. Lok, T. *et al.* (2015) The cost of migration: spoonbills suffer higher mortality during trans-Saharan spring migrations only. *Biol. Lett.* 11, 20140944
14. Norris, D.R. (2005) Carry-over effects and habitat quality in migratory populations. *Oikos* 109, 178–186

Outstanding questions

How do migratory animals gain information from other species? Reintroduced whooping cranes can learn to migrate from humans piloting ultralight aircraft, but the role of learning from heterospecifics in the wild is rarely considered and warrants further investigation.

How does the resource landscape shape social interactions during migration? Can the resource landscape shape where individuals interact by creating bottlenecks in movement?

How do we distinguish between different types of learning (i.e., individual, social, collective) and the relative role of each in migration?

Does reliance on individual experience versus social information shift over a migrant's lifetime? If so, when does this shift occur?

To what extent do solitary migrants (i.e., those species that do not obviously migrate in groups) use direct interactions and indirect social cues during migration?

When do life-history traits, such as lifespan, constrain learning periods? How might this differ across migratory and nonmigratory populations or species?

How do characteristics of migration (e.g., distance, complexity, dynamism) affect reliance on social information? For example, is social information more important in long-distance migrations, or migrations that require flexibility in timing or location?

What are the evolutionary implications of social influences during migration? For example, does social structure favor the evolution of different modes of information transfer? Across taxa, how do animals balance the costs and benefits of social migrations?

How can research on social influences be better integrated into practical applications for conservation and management? For example, could indirect cues be used to help migrants learn the location of a newly constructed highway or dam-crossing structures, or the location of suitable

15. Couzin, I.D. (2018) Collective animal migration. *Curr. Biol.* 28, R976–R980
16. Mueller, T. *et al.* (2013) Social learning of migratory performance. *Science* 341, 999–1002
17. Cohen, E.B. and Satterfield, D.A. (2020) 'Chancing on a spectacle:' co-occurring animal migrations and interspecific interactions. *Ecography* 43, 1657–1671
18. Guttal, V. and Couzin, I.D. (2010) Social interactions, information use, and the evolution of collective migration. *Proc. Natl. Acad. Sci. U. S. A.* 107, 16172–16177
19. Foss-Grant, A. *et al.* (2018) Social transmission of migratory knowledge: quantifying the risk of losing migratory behavior. *Theor. Ecol.* 11, 257–270
20. Aplin, L. (2016) Understanding the multiple factors governing social learning and the diffusion of innovations. *Curr. Opin. Behav. Sci.* 12, 59–65
21. Hoppitt, W. and Laland, K.N. (2013) Social Learning. Princeton University Press
22. Abrahms, B. *et al.* (2021) Emerging perspectives on resource tracking and animal movement ecology. *Trends Ecol. Evol.* 36, 308–320
23. Kauffman, M.J. *et al.* (2021) Causes, consequences, and conservation of ungulate migration. *Annu. Rev. Ecol. Evol. Syst.* 52, 453–478
24. Hein, A.M. *et al.* (2012) Energetic and biomechanical constraints on animal migration distance. *Ecol. Lett.* 15, 104–110
25. Nilsson, C. *et al.* (2013) Differences in speed and duration of bird migration between spring and autumn. *Am. Nat.* 181, 837–845
26. Laforge, M.P. *et al.* (2021) Tracking snowmelt to jump the green wave: phenological drivers of migration in a northern ungulate. *Ecology* 102, e03268
27. Abrahms, B. *et al.* (2021) Ontogenetic shifts from social to experiential learning drive avian migration timing. *Nat. Commun.* 12, 7326
28. Merlin, C. and Liedvogel, M. (2019) The genetics and epigenetics of animal migration and orientation: birds, butterflies and beyond. *J. Exp. Biol.* 222, jeb191890
29. Calvert, W.H. *et al.* (1979) Mortality of the monarch butterfly (*Danaus plexippus* L.): avian predation at five overwintering sites in Mexico. *Science* 204, 847–851
30. Berdahl, A. *et al.* (2016) A collective navigation hypothesis for homeward migration in anadromous salmonids. *Fish* 17, 525–542
31. Whitehead, H. (2017) Gene–culture coevolution in whales and dolphins. *Proc. Natl. Acad. Sci. U. S. A.* 114, 7814–7821
32. Jesmer, B.R. *et al.* (2018) Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *Science* 361, 1023–1025
33. Goldshtein, A. *et al.* (2022) Mother bats facilitate pup navigation learning. *Curr. Biol.* 32, 350–360
34. Byholm, P. *et al.* (2022) Paternal transmission of migration knowledge in a long-distance bird migrant. *Nat. Commun.* 13, 1566
35. Cote, J. *et al.* (2017) Behavioural synchronization of large-scale animal movements – disperse alone, but migrate together? *Biol. Rev.* 92, 1275–1296
36. He, P. *et al.* (2019) The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity. *Behav. Ecol. Sociobiol.* 73, 9
37. Hu, G. *et al.* (2016) Mass seasonal bioflows of high-flying insect migrants. *Science* 354, 1584–1587
38. Larkin, R.P. and Szafoni, R.E. (2008) Evidence for widely dispersed birds migrating together at night. *Integr. Comp. Biol.* 48, 40–49
39. Van Doren, B.M. and Horton, K.G. (2018) A continental system for forecasting bird migration. *Science* 361, 1115–1118
40. Bauer, S. *et al.* (2016) Timing is crucial for consequences of migratory connectivity. *Oikos* 125, 605–612
41. Sergio, F. *et al.* (2014) Individual improvements and selective mortality shape lifelong migratory performance. *Nature* 515, 410–413
42. Cheng, Y. *et al.* (2019) "Closer-to-home" strategy benefits juvenile survival in a long-distance migratory bird. *Ecol. Evol.* 9, 8945–8952
43. Rotics, S. *et al.* (2016) The challenges of the first migration: movement and behaviour of juvenile vs. adult white storks with insights regarding juvenile mortality. *J. Anim. Ecol.* 85, 938–947
44. Flack, A. *et al.* (2018) From local collective behavior to global migratory patterns in white storks. *Science* 360, 911–914
45. Mukhin, A. *et al.* (2008) Acoustic information as a distant cue for habitat recognition by nocturnally migrating passerines during landfall. *Behav. Ecol.* 19, 716–723
46. Németh, Z. and Moore, F.R. (2007) Unfamiliar stopover sites and the value of social information during migration. *J. Ornithol.* 148, 369–376
47. Tombre, I.M. *et al.* (2019) Northward range expansion in spring-staging barnacle geese is a response to climate change and population growth, mediated by individual experience. *Glob. Chang. Biol.* 25, 3680–3693
48. Pettit, B. *et al.* (2013) Not just passengers: pigeons, *Columba livia*, can learn homing routes while flying with a more experienced conspecific. *Proc. Biol. Sci.* 280, 20122160
49. Flack, A. *et al.* (2012) What are leaders made of? The role of individual experience in determining leader–follower relations in homing pigeons. *Anim. Behav.* 83, 703–709
50. Kölzsch, A. *et al.* (2020) Goose parents lead migration V. *J. Avian Biol.* 51, e02392
51. Dhanjal-Adams, K.L. *et al.* (2018) Spatiotemporal group dynamics in a long-distance migratory bird. *Curr. Biol.* 28, 2824–2830.e3
52. Chernetsov, N. *et al.* (2004) Migratory orientation of first-year white storks (*Ciconia ciconia*): inherited information and social interactions. *J. Exp. Biol.* 207, 937–943
53. Willemoes, M. *et al.* (2015) Flexible navigation response in common cuckoos *Cuculus canorus* displaced experimentally during migration. *Sci. Rep.* 5, 16402
54. Oestreich, W.K. *et al.* (2020) Animal-borne metrics enable acoustic detection of blue whale migration. *Curr. Biol.* 30, 4773–4779.e3
55. Oestreich, W.K. *et al.* (2022) Acoustic signature reveals blue whales tune life history transitions to oceanographic conditions. *Funct. Ecol.* 36, 882–895
56. Cade, D.E. *et al.* (2021) Social exploitation of extensive, ephemeral, environmentally controlled prey patches by supergroups of rorqual whales. *Anim. Behav.* 182, 251–266
57. Martínez-García, R. *et al.* (2013) Optimizing the search for resources by sharing information: Mongolian gazelles as a case study. *Phys. Rev. Lett.* 110, 248106
58. Winger, B.M. *et al.* (2019) Nocturnal flight-calling behaviour predicts vulnerability to artificial light in migratory birds. *Proc. Biol. Sci.* 286, 20190364
59. Noyce, K. and Garshelis, D. (2014) Follow the leader: social cues help guide landscape-level movements of American black bears (*Ursus americanus*). *Can. J. Zool.* 92, 1005–1017
60. Berdahl, A. *et al.* (2013) Emergent sensing of complex environments by mobile animal groups. *Science* 339, 574–576
61. Kano, F. *et al.* (2021) Collective attention in navigating homing pigeons: group size effect and individual differences. *Anim. Behav.* 180, 63–80
62. Holdo, R.M. *et al.* (2009) Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *Am. Nat.* 173, 431–445
63. Gurarie, E. *et al.* (2021) Memories of migrations past: sociality and cognition in dynamic, seasonal environments. *Front. Ecol. Evol.* 9, 7429920
64. Bucher, E.H. (1992) The causes of extinction of the passenger pigeon. In *Current Ornithology* (Power, D.M., ed.), pp. 1–36, Springer
65. Okasaki, C. *et al.* (2020) Collective navigation can facilitate passage through human-made barriers by homeward migrating Pacific salmon. *Proc. Biol. Sci.* 287, 20202137
66. Brent, L.J. *et al.* (2015) Ecological knowledge, leadership, and the evolution of menopause in killer whales. *Curr. Biol.* 25, 746–750
67. McComb, K. *et al.* (2001) Matriarchs as repositories of social knowledge in African elephants. *Science* 292, 491–494
68. Merkle, J.A. *et al.* (2015) To follow or not? How animals in fusion–fission societies handle conflicting information during group decision-making. *Ecol. Lett.* 18, 799–806

stopover habitats? Can we alter the flow of information between individuals to reduce human–wildlife conflicts?

69. Chimento, M. *et al.* (2021) Population turnover facilitates cultural selection for efficiency in birds. *Curr. Biol.* 31, 2477–2483 e2473
70. Sasaki, T. and Biro, D. (2017) Cumulative culture can emerge from collective intelligence in animal groups. *Nat. Commun.* 8, 15049
71. Torney, C.J. *et al.* (2018) Inferring the rules of social interaction in migrating caribou. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 373, 20170385
72. Rutz, C. *et al.* (2012) Automated mapping of social networks in wild birds. *Curr. Biol.* 22, R669–R671
73. Graving, J.M. *et al.* (2019) DeepPoseKit, a software toolkit for fast and robust animal pose estimation using deep learning. *eLife* 8, e47994
74. Wilson, R.P. *et al.* (2020) An "orientation sphere" visualization for examining animal head movements. *Ecol. Evol.* 10, 4291–4302
75. Lynch, E. *et al.* (2013) The use of on-animal acoustical recording devices for studying animal behavior. *Ecol. Evol.* 3, 2030–2037
76. Farine, D.R. and Whitehead, H. (2015) Constructing, conducting and interpreting animal social network analysis. *J. Anim. Ecol.* 84, 1144–1163
77. Aplin, L.M. *et al.* (2015) Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* 518, 538–541
78. Fagan, W.F. *et al.* (2013) Spatial memory and animal movement. *Ecol. Lett.* 16, 1316–1329
79. Lewis, M.A. *et al.* (2021) Learning and animal movement. *Front. Ecol. Evol.* 9, 681704
80. Alerstam, T. (2006) Conflicting evidence about long-distance animal navigation. *Science* 313, 791–794
81. Sikes, R.S. *et al.* (2016) 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *J. Mammal.* 97, 663–688
82. Viljoen, J.J. *et al.* (2015) Vocal stress associated with a translocation of a family herd of African elephants (*Loxodonta africana*) in the Kruger National Park, South Africa. *Bioacoustics* 24, 1–12
83. Whiten, A. (2021) The burgeoning reach of animal culture. *Science* 372, eabe6514
84. Oudman, T. *et al.* (2020) Young birds switch but old birds lead: how barnacle geese adjust migratory habits to environmental change. *Front. Ecol. Evol.* 7, 502
85. Brakes, P. *et al.* (2019) Animal cultures matter for conservation. *Science* 363, 1032–1034
86. Blomqvist, D. *et al.* (2010) Trapped in the extinction vortex? Strong genetic effects in a declining vertebrate population. *BMC Evol. Biol.* 10, 33
87. Schindler, D.E. *et al.* (2010) Population diversity and the portfolio effect in an exploited species. *Nature* 465, 609
88. Gilroy, J.J. *et al.* (2016) Migratory diversity predicts population declines in birds. *Ecol. Lett.* 19, 308–317
89. Sawyer, H. *et al.* (2009) Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecol. Appl.* 19, 2016–2025
90. Haddad, N.M. *et al.* (2014) Potential negative ecological effects of corridors. *Conserv. Biol.* 28, 1178–1187
91. Teitelbaum, C.S. *et al.* (2016) Experience drives innovation of new migration patterns of whooping cranes in response to global change. *Nat. Commun.* 7, 12793
92. Kashetsky, T. *et al.* (2021) The cognitive ecology of animal movement: evidence from birds and mammals. *Front. Ecol. Evol.* 9, 724887
93. Shamoun-Baranes, J. *et al.* (2017) Atmospheric conditions create freeways, detours and tailbacks for migrating birds. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* 203, 509–529
94. Danchin, E. *et al.* (2004) Public information: from nosy neighbors to cultural evolution. *Science* 305, 487–491
95. Berdahl, A. *et al.* (2017) Social interactions shape the timing of spawning migrations in an anadromous fish. *Anim. Behav.* 126, 221–229
96. Harrison, X.A. *et al.* (2010) Cultural inheritance drives site fidelity and migratory connectivity in a long-distance migrant. *Mol. Ecol.* 19, 5484–5496
97. Ioannou, C.C. *et al.* (2012) Predatory fish select for coordinated collective motion in virtual prey. *Science* 337, 1212–1215
98. Emlen, S.T. and Emlen, J.T. (1966) A technique for recording migratory orientation of captive birds. *Auk* 83, 361–367
99. Piersma, T. *et al.* (2020) Rethinking classic starling displacement experiments: evidence for innate or for learned migratory directions? *J. Avian Biol.* 51, e02337
100. Nelson, M.E. (1998) Development of migratory behavior in northern white-tailed deer. *Can. J. Zool.* 76, 426–432