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Introduction

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Collective movement in ecology: from emerging technologies to conservation and management

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Recent advances in technology and quantitative methods have led to the emergence of a new field of study that stands to link insights of researchers from two closely related, but often disconnected disciplines: movement ecology and collective animal behaviour. To date, the field of movement ecology has focused on elucidating the internal and external drivers of animal movement and the influence of movement on broader ecological processes. Typically, tracking and/or remote sensing technology is employed to study individual animals in natural conditions. By contrast, the field of collective behaviour has quantified the significant role social interactions play in the decision-making of animals within groups and, to date, has predominantly relied on controlled laboratory-based studies and theoretical models owing to the constraints of studying interacting animals in the field. This themed issue is intended to formalize the burgeoning field of collective movement ecology which integrates research from both movement ecology and collective behaviour. In this introductory paper, we set the stage for the issue by briefly examining the approaches and current status of research in these areas. Next, we outline the structure of the theme issue and describe the obstacles collective movement researchers face, from data acquisition in the field to analysis and problems of scale, and highlight the key contributions of the assembled papers. We finish by presenting research that links individual and broad-scale ecological and evolutionary processes to collective movement, and finally relate these concepts to emerging challenges for the management and conservation of animals on the move in a world that is increasingly impacted by human activity.

This article is part of the theme issue 'Collective movement ecology'.

1. Introduction

The collective movement of animals is one of the great wonders of the natural world. Researchers and naturalists alike have long been fascinated by the coordinated movements of vast fish schools, bird flocks, insect swarms, ungulate herds and other animal groups that contain large numbers of individuals that move in a highly coordinated fashion ([1], figure 1). Vividly worded descriptions of the behaviour of animal groups feature prominently at the start of journal articles, book chapters and popular science reports that deal with the field of collective animal behaviour. These descriptions reflect the wide appeal of collective movement that leads us to the proximate question of *how* collective movement operates, and the ultimate question of *why* it occurs (*sensu* [2]). Collective animal behaviour researchers, in collaboration with physicists, computer scientists and engineers, have often focused on

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Figure 1. Collective movement is widespread in nature. Clockwise from top left: Wildebeest in the Serengeti, salmon in Alaska, godwits in The Netherlands and monarch butterflies in Mexico. Images by Daniel Rosengren (wildebeest), Jason Ching (salmon), Steven Ruiter (godwits) and Ingo Arndt (butterflies).

mechanistic questions [3–7] (see [8] for an early review). This interdisciplinary approach has enabled the field to make enormous progress and revealed fundamental insights into the mechanistic basis of many natural collective movement phenomena, from locust 'marching bands' [9] through starling murmurations [10,11].

Owing to the significant benefits of group living [12], the ecological role of collective movement has long been the subject of studies in animal behaviour [13–16]; however, there has recently been a resurgent focus on questions relating to *why* collective movement occurs and what its ultimate function is. Researchers have asked whether certain types of collective movement afford group members better survival probability [17], better access to information about the environment [18–20] and better abilities to make decisions [21], and even how different ecological conditions, such as different levels of predation, may act as selective drivers favouring specific collective movement 'rules' [22,23]. Increasingly, such evolutionary and ecological questions have appeared as essential complements to mechanistic accounts, and calls for more research in the area abound [24]. Thus, examining collective movement within its ecological context is a burgeoning field of study.

Similarly, within the field of movement ecology there is an increasing recognition of the importance of social dynamics on both fine-scale [25,26] and broad-scale processes [27–29]. Formalized by Nathan *et al.* [30] approximately a decade ago, movement ecology is a distinct paradigm for studying the *how* and *why* of movement, along with its consequences for individuals, communities and ecosystems. The expanse of research in this area has been driven in large part by technological advances that have revolutionized the collection of data on animal movement [31,32]. These advances have most notably involved biologging and remote telemetry which enable individual tracking, but also include advances in our ability to simultaneously collect environmental data, and analytical developments in mathematical models of movement [33] that enable statistical inference of cues and drivers [34]. As our knowledge of animal movement accumulates there has been an increasing appreciation that many movement processes must be considered and quantified within a social context. Even in species without stable social groups or high degrees of cohesion, the movements of one individual can influence the movement decisions of another, and often social cues are as important as environmental cues [35].

As an operational definition, we consider collective movement to be occurring when movements are modified by the interactions between animals, either directly (e.g. via visual cues) or indirectly (e.g. via trail formation). While collective movement is not restricted to intraspecies interactions, the movement decisions of individuals will typically share common drivers and/or motivations; thus we do not consider predator evasion by a single prey collective movement, whereas the escape of multiple prey making use of social cues is. Collective movement processes will often be characterized by social transmission of information, threshold responses to environmental cues, hysteresis and nonlinear behaviours that are the hallmark of complex systems. Increasingly the importance of social interactions is being recognized by researchers in the field of movement ecology [28,36–41]; hence while collective animal behaviour and movement ecology are two distinct fields, more and more researchers are operating at the interface between the two (figure 2). While it is clear that both disciplines are already beginning to integrate, in this theme issue we attempt to synthesize current results, identify key challenges common to research in collective movement ecology in a variety of study systems, and provide a road map for future directions.

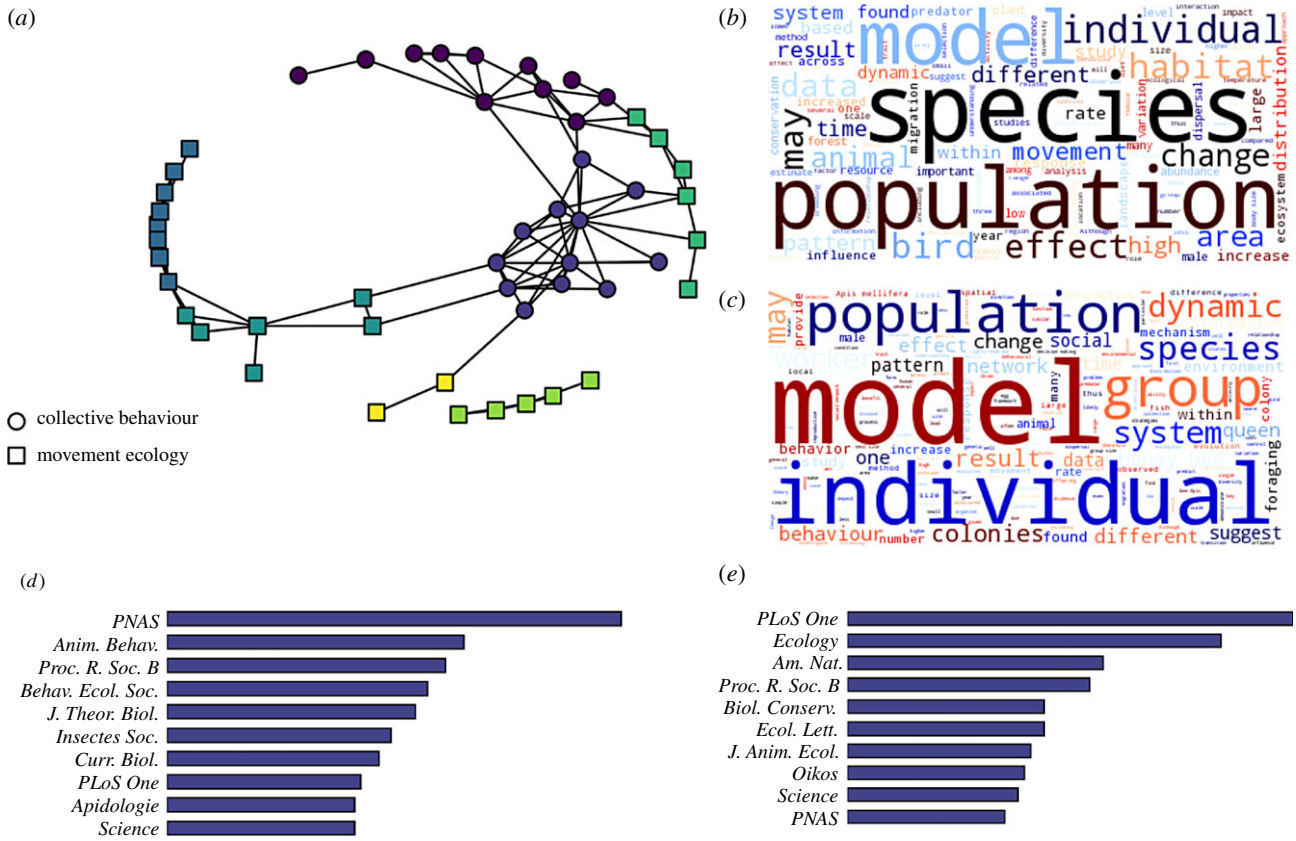

Figure 2. Current status of research in the fields of collective behaviour and movement ecology. (*a*) We examined the previous collaboration networks of all authors who participated in this theme issue and used a clustering algorithm to assign each author to a community. The algorithm detected seven distinct collaborative communities, indicated by different colours above. We then classified each of the seven communities determined by the algorithm as either 'collective behaviour' or 'movement ecology' based on which phrase appeared more predominantly in the abstracts and titles of all their published work. For each community, we then looked at the most common words that appeared in their previous articles. (*b*) The words most associated with contributors to the issue who were classified as movement ecologists. (*c*) Words associated with contributors from the field of collective behaviour. While highly qualitative, these results reveal the focus on population and species for movement ecology, whereas collective behaviour has a greater concentration on the individual. Further, we examined where researchers in each field publish. (*d*) Top 10 most common journals for contributors to the issue who were classified as collective animal behaviourists. (*e*) Top 10 most common journals for contributors to the issue who were classified as movement ecologists.

2. Aims of the themed issue

Recently, it was stated that for movement ecology 'understanding how social and interspecific interactions affect movement is the next big frontier' [31]. The overarching goal of this theme issue is to bring together researchers across disciplines in order to meet this challenge. Contributed articles span all facets of studying collective movement in ecology, from technological advances in tracking and data processing, through analysis of animal group behaviour and the population-level and ecological impacts of collective movement, to the implications of understanding such processes for the conservation of animal groups in their natural habitat. It is our intention that the issue will become a resource for scientists wishing to learn about methods and techniques in collective movement research, illustrate the importance of incorporating inter- and intra-species interactions into movement ecology, and act as a call to arms for researchers in the field to provide the impetus and expertise required to advance our understanding of animal movement patterns in nature.

3. Overview of contributed papers

While movement ecology has recently experienced a rapid increase in the availability of empirical data collected from free-ranging animals, the study of collective movement has largely relied on laboratory and simulation approaches. To investigate movement decisions in their social context, fine temporal resolution, simultaneous trajectories of multiple individuals are required. While there are several notable studies that explore collective movement *in situ* [10,42–45], recent technological advances are poised to dramatically improve our ability to collect data on the movements of animal groups. In this issue, Hughey *et al.* [46] review the advances that now permit data collection on the movements of, and interactions within, animal groups in the wild, from animal-mounted bio-loggers [47] to aerial video [48] and acoustic [49] field imagery. Moreover, technology such as GPS-enabled data loggers may turn animals themselves into environmental sensors that can be used to capture fine-scale physical data, such as detailed maps of airflow within complex thermal updrafts [47].

These new data sources create opportunities for rigorous new quantitative techniques to infer social interactions and the mechanisms behind the maintenance of group-level functioning in the wild. Strandburg-Peshkin *et al.* [50] propose a novel generalized framework that characterizes the distribution and consistency of individual influence on group decision-making processes, and review some of the analytical tools that can be employed to detect individual influence on group decisions. A continual challenge is to distinguish and

disentangle the influences of social and potentially co-occurring multiscale environmental drivers (reviewed by Torney *et al.* [51]). To address this issue, Calabrese *et al.* [52] present a stochastic model of correlated movement that quantifies the contributions of external forces and social dynamics. Through application of their model to barren-ground caribou (*Rangifer tarandus granti*) and khulans (*Equus hemionus*) of the Gobi Desert, the authors capture abrupt shifts from uncorrelated to correlated movement in caribou without incorporating external information. Khulans exhibit intermittent periods of correlated movement suggestive of shared tendencies to move from west to east following an unusually harsh winter. Using a factor analysis, Sumpter *et al.* [53] partition the influences of commonly measured traits (e.g. speed, group size, alignment) collected from tracks of guppies (*Poecilia reticulata*) into two key components of behaviour that the authors relate to sociability and activity. Their analysis suggests that these behavioural components differ between sexes and populations that experience divergent regimes of selection.

Together, new data from emerging technologies and novel quantitative techniques can reveal the behavioural processes at the individual level that drive collective group dynamics in the wild. Capitalizing on the advances in high-resolution GPS technology that allow the fine-scale tracking of individuals in flocks, Nagy *et al.* [47] explore how groups of migrating white storks (*Ciconia ciconia*) act as distributed sensor arrays when locating and climbing thermal updrafts. Sasaki *et al.* [54] use similar technology to investigate the link between individual heterogeneity and leadership during collective movement by homing pigeons (*Columba livia*). They find that 'bold' individuals tend to occupy higher ranks in the leadership hierarchy, and thus have more influence on the flock during flight, than do 'shy' birds. Berdahl *et al.* [55] review literature on collective animal navigation and highlight five mechanisms that can improve individuals' ability to find their way when travelling in groups, including emergent sensing [47] and leadership [54] discussed above. They go on to explore how social and collective learning can lead to the accumulation of navigational knowledge at the population level and thus to migratory cultures.

Early simulation-based studies of collective movement demonstrated that simple and intuitive local interactions between homogeneous individuals produced complex and realistic group-level patterns [56]. As empirical studies uncover the actual interactions between groups' members [10,44,47, 48,57], the importance of individual heterogeneity is being revealed [47,48,54]. In this issue, del Mar Delgado *et al.* [58] address this question directly and provide evidence that not accounting for individual variability currently impedes understanding of how group decisions are made and that predictions of collective movement that ignore individual variation are likely to fail. Through the use of aerial filming, Torney *et al.* [48] demonstrate how interaction rules and individual variation may be quantified, in this context examining the heterogeneous nature of social interaction of migrating caribou (*Rangifer tarandus groenlandicus* × *pearyi*). Taken together, many articles in this issue highlight the importance of individual heterogeneity for collective movement, suggesting that it is a current area of interest for the field, and likely to be a focus moving forward.

The main goal of this theme issue, and a unifying feature of many papers herein, is the illumination of the ecological and evolutionary consequences of collective movement. To that end, Torney *et al.* [51] explore the perennial problem of scale. An ultimate theory of movement ecology would be able to connect long-range movement (e.g. migrations) to their smallest constituent movements, taking into account the role of abiotic, biotic and social cues motivating these movements across scales. Berdahl *et al.* [55] tackle this in detail, by exploring how social interactions among individuals scale up to improved ability of groups to navigate when migrating or foraging. Yeakel *et al.* [59] investigate the interplay between ecology and evolution as a consequence of density-dependent dispersal consistent with collective navigation [60]. Their simulation based on a generic migratory salmon life history suggests that density-dependent dispersal can promote population robustness at the metapopulation level in the context of environmental change. In a social insect case study, Beekman & Oldroyd [61] use nest-site selection by two honeybee species (*Apis* spp.) to illustrate how a species' ecology may tune the decision-making processes underlying its collective movement. For example, whether suitable nest sites are more or less abundant in the environment may shape the extent to which the same ancestral decision-making algorithm is fine-tuned for accuracy to choose the best possible site. Beyond single-species collective movement, Sridhar & Guttal [62] argue that group benefits often cross species borders, and propose a new general framework for heterospecific sociality. At a broader scale, Hardesty-Moore *et al.* [63] undertake a general assessment of the state of the populations of a wide range of migratory species in the Anthropocene and find evidence that collective behaviour is associated with extinction risk for fishes and birds, but not for mammals. However, two studies highlight the importance of collective movement in mammals (wildebeest (*Connochaetes* sp.) [51] and Thomson's gazelles (*Eudorcas thomsonii*) [64]) in the Serengeti ecosystem. Focusing on trophic interactions, Fryxell & Berdahl [64] explore how group living may influence fitness and also reflect trade-offs. They speculate on how mechanisms such as the many eyes effect or increased competition can be captured in analytical models for population dynamics.

4. From cameras and collars to conservation and management

While the contributions to this issue are predominantly focused on fundamental research, the future of collective movement ecology is likely to be its application to conservation and the management of wild populations. In this section, we explore the linkages between group-level dynamics, ecological-level processes, and management implications. We conclude by discussing the potential adaptations and maladaptations of collective movement in a rapidly changing world.

(a) Ecological implications

The fact that collective movement is common across taxa, environments and contexts suggests that it improves individual fitness through a suite of anti-predatory and information-sharing benefits [12]. The social interaction rules that lead to group behaviour [10,42,44,47,48,57], and the mechanisms by which that group behaviour improves various metrics of performance, have both been relatively well studied [9,18,41,65,66]. By contrast, for the most part we are still missing an understanding of the influence of collective movement, and more generally collective behaviour, on ecological processes and patterns. However, there are a handful of

theoretical predictions of how collective behaviour might influence ecological dynamics along with some notable empirical demonstrations. For example, simple grouping is thought to influence trophic interactions and stabilize population dynamics [67], while reliance on sociality may induce Allee effects across a variety of contexts [27]. Specifically, collective navigation during breeding migrations has been predicted to cause analogous population collapse [29,68] and density-dependent dispersal [60] and to influence metapopulation stability [59]. Additionally, social interactions influence the timing of migrations [69,70]. Finally, fission–fusion dynamics allow ecologically relevant information to spread throughout populations [28,41,71]. A better understanding of collective behaviour, especially from rigorously quantified *in situ* observations and experiments, should allow us to better connect the resulting group dynamics to their ecological and evolutionary consequences.

(b) Management & conservation

How might a better understanding of collective behaviour and movement intersect with natural resource management and conservation? The collapse of the northern cod (*Gadus morhua*) fishery of Newfoundland and Labrador is a notorious failure of fisheries management. Virtually overnight in July 1992, approximately 40 000 people lost their jobs and way of life defined by a fishery that had been sustainable for over 500 years [72]. Political and economic influences notwithstanding, the schooling behaviour of northern cod undoubtedly contributed to their demise. As the stock collapsed in abundance, fish remained in dense aggregations that could be efficiently located and targeted by fishing boats equipped with modern navigation and sonar [73]. Catches targeting these aggregations of fish remained high in the years preceding the collapse, adding to the confusion of managers who relied on catch rates as indices of abundance. Schooling behaviour resulted in patterns of 'hyperstable' catches by harvesters that masked the true pattern of collapse and has led towards a recognition that catch rates, especially in socially aggregating fish schools, are a dubious index of abundance and should not form the core of stock assessments [74,75]. In general, drivers of collective behaviour that lead to spatial aggregation may cause range contraction and increase the risk of collapse or extinction [76].

Management that recognizes patterns of collective movement is already common for some species. For example, sockeye salmon (*Oncorhynchus nerka*) appear to form stock-specific groups in the final stages of their homeward marine migrations to the Bristol Bay region of Alaska, and managers and fishermen use this information to inform decisions about where and when to harvest nearly in real time [77]. Salmon management within river systems can similarly incorporate collective migration dynamics into decision-making frameworks. For example, on the Yukon River, Chinook salmon (*Oncorhynchus tshawytscha*) tend to migrate as large groups corresponding to genetic structure [78]. Perhaps not surprisingly, populations that are destined to spawning areas in the upper watershed, some as far as 3200 km from the ocean, tend to enter the river earlier than individuals from populations spawning lower in the watershed [79]. In general, salmon enter the river in discrete stock-specific pulses, which might be the result of social coordination [70], and by knowing the travel rates of individuals, managers can choose to target or avoid these groups by opening or closing different parts of the river system [80].

Management based on collective movement dynamics has, in fact, a long history. Traditional knowledge from Inuit people suggests that caribou migrations are led by a certain set of female caribou [81–83]. As a result, traditional hunting practices avoid harvesting the lead animals, since those cows are understood to be responsible for both ensuring a healthy migration and also leading the caribou to specific sites year after year, where they could be harvested [82,84]. Evidence is only anecdotal, but perhaps the recent shift in migration routes away from communities, which were established at traditional hunting sites, is in part linked to harvesting outside of these guidelines by less experienced hunters [82,83,85].

Consideration of such leadership by an informed subset of migratory individuals [55], be they older or more experienced, may generate important targets for management conservation and restoration more broadly. For example, it has been shown in whooping cranes (*Grus americana*) that the navigational performance of a group depends on that group's most experienced member [86], while restoration efforts employ ultra-light aircraft to *teach* migration routes to inexperienced migrants, in the hope that they will in time become tutors themselves.

Collective behaviour might also be an important consideration for management practices aiming to limit population growth or numbers in species that are pests or invasive. For example, migratory swarms of desert locusts (*Schistocerca gregaria*) cause extensive damage to crops, regularly leading to financial loss, food shortages and famine [87]. Outbreaks usually occur after locust density build-up, often due to a combination of increasing population and receding vegetation [88]. High densities of locusts trigger a physiological and behavioural switch from a solitary phase to a gregarious one where individuals are actively attracted to each other, which, combined with a tendency for locusts to align with their neighbours [9,89], eventually leads to migratory swarms [90,91]. By explicitly considering ecological and social factors leading to this behavioural shift, management practices may become more efficient and effective at preventing it [92]. Further, even after the shift has occurred, understanding locust collective behaviour can be key to improving control practices such as barrier spraying, because the efficiency of these methods relies on predicting the movement of locust hopper bands [93].

In species with complex and stable groups, optimal management approaches might take into consideration social structure, hierarchies and group dynamics. In species in which older members serve as informational repositories, such as elephants, the death of older animals has long-lasting effects. When culling elephants (*Loxodonta africana*), typically all of the older individuals in a group are killed and the younger individuals left [94]. However, even decades later, the remaining elephants do not respond appropriately to social cues [94]. In wolves (*Canis lupis*), in spite of compensatory dynamics, which support in general a high harvest rate, groups losing the alpha members may be more likely to skip a breeding season, alter group composition or break up altogether; so there may be some ephemeral behavioural and group-level responses [95–97]. Further work indicates that there may be a critical group size, below which reproduction rates are negative [98]. Some suggest that lethal population control efforts should target solitary individuals or territorial pairs [99].

(c) Collective movement in the Anthropocene

Across geographies and taxa, animals face new challenges in an era when humans are a dominant ecological and evolutionary force on the planet. Social animals face further challenges when the nature of their social interactions or group functioning is impacted by the changing environment. Pharmaceuticals and other synthetic chemicals are present in water in high enough concentrations to affect the behaviour of aquatic organisms such as fish [100], and in particular, such substances can affect social behaviour [101,102]. Similarly, anthropogenic noise pollution is thought to disrupt natural (social) behaviour in many marine and terrestrial organisms [103,104], and air and light pollution are likely to do the same. In all of these cases, social interaction rules may be finely tuned to optimize fitness [22,23,61,64] and altering these interactions would then lead to maladaptive behaviours. A similar mismatch between optimal collective behaviour and environmental conditions may occur when the social behaviours do not change, but the environmental conditions do. For example, fission–fusion dynamics may spread information about profitable foraging sites through a population, but if in contemporary, human-altered landscapes the environmental cues do not match the environmental quality, the same fission–fusion dynamics would spread maladaptive information through the population [28]. Similarly, it has been suggested that the strong social dynamics of matrilineal killer whale (*Orcinus orca*) pods may explain the continued use of habitats that are now polluted by chemicals and noise resulting from an increase in human activity [105]. A changing climate may alter the optimal destinations, routes and timings of animal migrations [106,107]. Thus, on the one hand, collective navigation and search strategies should help animals that migrate as groups adapt to this change, yet conversely, migratory culture could make current migratory tendencies more persistent and less adaptable to change [55,108]. Ultimately, it remains unclear whether collective movement may be a net promoter or inhibitor of survival in a world increasingly dominated by human activity [63].

5. Conclusion

It is our hope that this theme issue integrates collective movement with broader questions in ecology and evolution, provides a framework for future work, and by doing so takes a first step into the next big frontier proposed by Kays *et al.* [31]. Driven by the latest technological advances allowing us to simultaneously track many animals on the move, coupled with cutting edge analyses of behaviour at high resolution, we anticipate that social interactions will become a natural extension to the movement ecology paradigm [30]. Although there are major challenges on the horizon, such as how to integrate habitat heterogeneity and individual-level variation into analyses of collective movement, we are now closer to a comprehensive understanding of both *how* and *why* animals move together in nature. Just as conservation and management have increasingly acknowledged the role of evolution on ecological processes [109], we expect that the rules and potential trade-offs associated with collective movement will also be integrated into conservation efforts. Only by doing so may we expect to preserve the fascinating patterns of movement that have for so long captured our collective imagination.

Data accessibility. This article has no additional data.

Competing interests. We have no competing interests.

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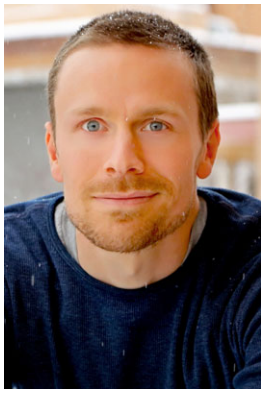

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