

## Collective animal migration

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Migratory movement is a strategy employed by a broad range of taxa as a response to temporally and spatially varying environmental conditions. Multiple factors can drive animal migration, including: movement to hospitable environments when local conditions become unfavourable (such as to reduce nutritional and thermoregulatory stress); movement to find mates and/or breeding sites; and movement to minimise competition, predation, infection or parasitism. Migrating animals can often be seen to move together (Figure 1), sometimes in vast numbers. Despite this, the social aspects of migration have, to date, received very limited attention. Synchronisation of migratory behaviour among organisms does not itself imply that migrants utilise social information: synchrony is inevitable if there are relatively short windows of opportunity in which to move, or if there exist sudden environmental changes to which a response is necessary. However, as will be outlined here in this Primer, there is growing evidence that many migratory animals do utilise social cues and that collective factors could shape migration in a variety of important ways.

### Information and collective migration

#### *Genetic and sensory information*

It is well-established that migratory timing (i.e. when to move), and at least the initial direction of travel, are in part genetically based in many seasonal migrants. In some species, there is evidence that individuals possess what is effectively a 'map-like sense', from which the target area of migration can be inferred (even from magnetic cues alone), and a 'compass sense' that is employed to steer in the appropriate direction en route. In addition, swimming or flying organisms exhibit mechanisms to exploit, and where necessary compensate for, the complex movement of the medium through which they move.

The sensory cues employed during migration are typically noisy, and thus individuals are inherently error-prone. Given the often life-or-death nature of migratory decision-making, many migrants have evolved to exploit a suite of sensory cues involving multiple modalities. This provides redundancy, allowing them to rely more heavily on some modalities (e.g. geomagnetic field cues) when others become unreliable (such as a sun compass on a heavily overcast day). While there has been considerable work on the sensory basis of individual migration, the informational benefits of social cues to migrants has been far less studied, despite the many potential benefits these cues can provide.

### ***Integrating personal and social information***

The genetic and sensory information upon which organisms must base 'personal' migratory decisions is subject to ambiguity. Thus, it should be expected that organisms evolve to exploit other sources of information, such as social cues, where they are available. It is known, across species, that the brain assigns different weights to individuals' personal and social information, according to their respective reliability, to make decisions. Utilising social cues, such as by observing movements of others (a proxy for their decisions), also allows individuals to integrate information that has been acquired over broader environmental scales (by others), thus reducing problems inherent with basing decisions only on their own, relatively local, experiences.

Social information could be relevant in a wide range of contexts, such as to reduce uncertainty with respect to migratory timing (when to migrate), as well as when and where to exploit stopover sites, and the local trajectory to be taken when on the move. Relevant social cues may be obtained both from conspecifics and, where informative, also from other species. In some circumstances, such as when personal information is very difficult or costly to obtain, there may even be selection for signalling among individuals (as may be the case for nocturnal flight calls in migratory birds, for example).



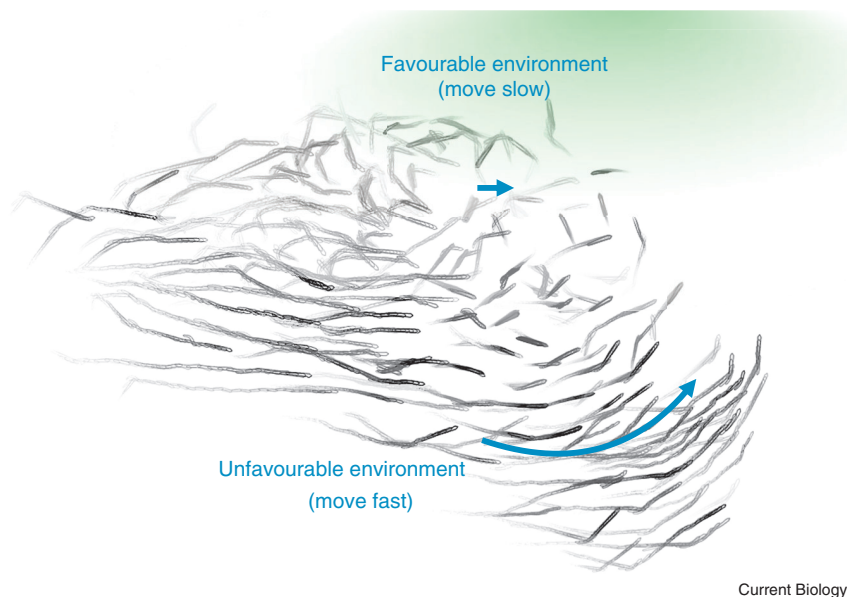
**Figure 1. Migrating caribou beginning their day.**

Many large herbivores, like caribou/reindeer, shown here, migrate many hundreds of kilometres during their seasonal migrations (Photo: Peter Mather).

Utilising both personal and social information on the move has been shown to improve the accuracy of navigation in several species of birds and fish (the range of species being limited by the small number of experimental studies conducted). A particularly effective strategy is for organisms to more heavily weigh social information when their personal information is unreliable, and as such we may expect a dynamic and changing exploitation of social cues throughout migrations. Theoretically, one may expect that accuracy will always increase with group size (or local population density) because, statistically, pooling many imperfect estimates ('many wrongs') is better than pooling few. This 'wisdom of crowds' argument assumes, however, that personal information is uncorrelated among individuals. In reality, this is probably rarely the case. Individuals in close proximity will experience similar (correlated) sensory cues (e.g. olfactory and visual cues), and the longer they remain together the more similar their experiences become. Since diversity of information is critical to the wisdom of crowds (averaging the same information gives no benefit), correlation of personal information among individuals will tend to

erode the informational benefits of traveling together and may even make decisions worse.

Two theoretical mechanisms have been suggested that could reduce the detrimental effects of information correlation. Firstly, individuals may change their local neighbourhood (e.g. by mixing within migratory groups/populations, and/or via fission–fusion dynamics among groups), ensuring that they take into account social cues from a diverse pool of others. In some cases, such as when individuals travel in relatively small close-knit family groups, such strategies may not be feasible. However, a second theoretical finding is that moving in small groups can, counterintuitively, maximise accuracy in environments where there exists correlated sensory information. This is because the noise inherent in such groups spontaneously allows individuals to escape an over-reliance on strongly correlated information, while simultaneously exploiting the benefits of collective decision-making. Although they appear to offer contrasting predictions, these mechanisms may, in fact, prove not to be mutually exclusive. Individuals in large groups may form subgroups and/or hierarchical internal social structures, allowing them to exploit



**Figure 2. Emergent sensing.**

Groups can exhibit an awareness of the environmental gradient, turning towards favourable regions (green), even though no individual within the group can detect the gradient. Organisms can simply modulate their speed as a function of their local environmental conditions, moving more quickly in unfavourable environments. Due to social interactions, however, a group-level responsiveness to the environmental gradient emerges spontaneously due to the speed differential created across the group, which causes turning (via emergent centrifugal social forces) towards favourable environments. The fish trajectories shown are courtesy of Colin Twomey.

both mechanisms simultaneously and thus to better cope with the complexities of minimising uncertainty in complex environments. Testing and further developing such theory will likely offer considerable new insights into collective migration.

#### ***Sparse, or weak, social interactions may be important***

A further theoretical prediction, and one that may also have broad consequences in the future study of migration, is that social factors can play a major role in the migratory strategies adopted by individuals even if such interactions are very rare, such as when the density of migrating organisms is very low. Thus, collective migratory strategies may exist among organisms that appear, to an observer, asocial. In addition, we may underestimate the social connectivity among migrating individuals. For example, there is growing evidence that the characteristic flight calls made by nocturnal migrant birds, previously thought to migrate alone, could play a vital role in a collective migratory strategy, despite the

relatively low density of individuals.

Such predictions set the scene for an urgently needed integration of experiment and theory in the study of migration, and highlight the importance of experimental studies of the relationship between the sensory basis of movement decisions, the dynamical structure of social interactions, and the speed and accuracy of decision-making in migrant animals.

#### ***Leadership***

The acquisition of personal information can be costly. For example, the sensory and cognitive machinery required to detect weak environmental cues may be energetically expensive, or there may be costs involved in venturing into areas where others are not present (due to increased predation risk, or the relative difficulty of locating a new thermal by migrant birds, for example). Under such circumstances, evolutionary models predict that 'frequency-dependent' strategies may emerge in which some individuals respond predominantly to personal

information (spontaneously becoming 'leaders') and others to social information (becoming 'followers'). The frequency dependence arises from the nature of information used: if the proportion of followers becomes too high, migrations can fail, and it pays individuals to obtain and utilise personal information (e.g. from a genetic program and/or environmental cues); whereas if a large enough proportion of individuals are utilising personal information, it can pay to exploit the social information they make available. As predicted by theory, experimental studies of fish, birds and mammals have shown that a small proportion of 'leaders' can strongly influence the motion of others. This suggests that in natural populations only a small proportion of individuals may 'know' where to go, and yet to an observer it would appear as if all do. In addition, depending on species and ecological context, 'leadership tendency' may be consistent among individuals (such as if it relates to individuals' previous experience) or may change dynamically as local conditions change.

#### ***Emergent sensing***

Some animal migrations appear to rely on individuals detecting and responding to long-range environmental (e.g. resource or thermal) gradients. Locally, such gradients are often extremely weak and subject to considerable, and unpredictable, fluctuations. Under circumstances where it becomes impossible for individuals to detect long-range gradients, it would appear that such migrations must fail. Experimental work on schooling fish, however, has demonstrated that nondirectional individual responses to the environment can, via social interactions, result in emergent collective sensing and gradient climbing at the group level (Figure 2). Thus, animal groups can climb long-range environmental gradients even if no individual is capable of estimating the local gradient. The minimal cognitive requirements and robustness of this strategy suggest that its role in aiding taxis may be widespread. For example, it is known that organisms like wildebeest detect

environmental gradients over length scales much, much greater than could likely be perceived by any individual within the group. Furthermore, evolutionary models demonstrate that this group- or population-level awareness of the environment can readily evolve, even in populations of completely unrelated (and thus genetically selfish) individuals.

### **Social learning and 'culture'**

Another factor that can strongly influence leadership in migratory groups (and populations) is individual experience. It has long been supposed that experienced individuals may lead naive individuals and that, by learning environmental cues en route, followers can become informed about suitable migratory routes. For many species (even when a 'map-like' capability is thought to be present), experience appears to play a considerable role, with animals learning meaningful cues en route (which can be employed to calibrate map-like representations). In this way, uninformed (e.g. less experienced) individuals will tend to experience similar environmental cues as those who are more experienced, and thus they can learn similar routes. This allows route information to be transferred among individuals and across generations, a form of animal 'culture'.

### **Energetics, food and collective migration**

Long-distance migrants exhibit a suite of mechanisms to minimise energetic costs. These include strategies to minimise heat loss, and the tendency for aquatic and airborne animals to utilise the flow properties of the medium in which they live (currents and winds, respectively), including, in some cases, exploitation of energy from flows and vortices created by other group members. Terrestrial migrants often minimise locomotory costs by following in the footsteps of those ahead, thus benefiting from taking a less-resistive path through vegetation or snow.

In addition, many migrants are on the move to find suitable food. Thus, migratory distances moved by large herbivores (ungulates and elephants), for example, are associated with

broad spatial scales of resource availability, which relates to seasonal weather patterns. Similarly, swarming insects, like migratory or desert locusts, tend to follow the rains and the corresponding new vegetation growth, and they do so over successive generations across vast, continental scales. Nutritional demands also define locust migrations at a local scale, with fierce competition for essential nutrients (particularly protein, salt and water) driving flightless juveniles to cannibalism (conspecifics being a perfect pre-packaged source of these nutrients). Locusts are most vulnerable to attack from the rear, and it is the constant avoidance of approaching individuals from behind, and the attraction to others ahead, that results in the formation of vast mobile swarms. These insects are effectively on a forced march. The highly directed collective motion that results from these local social interactions enables insects to more effectively leave nutrient-poor areas, and turning on others can give (some) insects the nutritional sustenance they need to make it across barren environments in their search for vegetation.

### **Lost migrations**

Locust migrations were once a common sight in North America, with vast swarms formed by the red-legged locust and the now extinct Rocky Mountain plague locust. On the same continent, squirrels too once migrated in multitudes, as Audubon and Bachman reported in 1845, "the Squirrels congress ... Onward they come, devouring on their way every thing that is suited to their taste, laying waste the corn and wheat-fields of the farmer; and as their numbers are thinned by the gun, the dog, and the club, others fall in and fill up the ranks, till they occasion infinite mischief". The most iconic lost mass migration, however, was that of the passenger pigeon. Audubon wrote of these now extinct birds in 1813, "The air was literally filled with Pigeons; the light of noon-day was obscured as by an eclipse ... I cannot describe to you the extreme beauty of their aerial evolutions, when a hawk chanced to press upon the rear of the flock. At

once, like a torrent, and with a noise like thunder ... they darted forward in undulating and angular lines, descended and swept close over the earth with inconceivable velocity, mounted perpendicularly so as to resemble a vast column, and, when high, were seen wheeling and twisting within their continued lines, which then resembled the coils of a gigantic serpent".

These migrations have all been lost due to urbanisation, deforestation, commercial agriculture and hunting. Today, across the globe many species of migrants, and especially those that move over long distances, are in sharp decline. Species that rely on social cues may be especially at threat when populations, and thus the capacity for social interactions, decrease; consequently once lost, it is expected that collective migrations will be difficult, and in many cases practically impossible, to recover. The contribution of migratory species to many ecological processes is disproportionately strong, and the loss of these species is likely to have cascading negative effects on ecosystem services and health. Despite the considerable scientific effort devoted to migration biology, little research has considered collective behaviour. Consequently, we lack essential information that will be required to develop a general and predictive science of animal migration.

### **Outlook**

Tremendous possibilities lie ahead in the study of collective animal migration. With today's rapidly accelerating pace of technological change there are especially prescient opportunities to tag large numbers of migrant animals with miniature loggers to obtain information about their fine-scale movements and locomotory activity (e.g. from GPS and inertial measurement units). Increasingly, it is also possible to integrate this information with genetic, physiological (e.g. heart rate and blood pressure), neural (e.g. implanted electrodes and electroencephalography), acoustic, and video information. Advances in remote sensing, airborne (e.g. drone) imaging, as well as on-animal



recording of local environmental parameters offer to provide complementary streams of extremely valuable information that will allow researchers to obtain an increasingly accurate picture of how migrating animals make movement decisions, and to do so across species boundaries. It is vital, therefore, that we bring together researchers from diverse disciplines to gather and integrate the knowledge that will prove essential if we are to conserve migratory populations in the face of increasing anthropogenic pressures.

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