Evolving migration

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Mass migrations of wildebeest, caribou, song birds, sting rays, and monarch butterflies are among the wonders of the natural world (Fig. 1). At a very different scale, the coordinated migration of cells within the body is central to embryological development, immune responses, and wound healing. Although the scale, functions, and mechanisms may differ, these examples share one key feature: they are the product of local interactions among individual agents (wildebeest, butterflies, or cells). The proximate mechanisms where collective behavior arises from local interactions between individuals have become a fertile area of research, founded on models from statistical physics in which interacting agents are modeled as self-propelled particles (1–4). Guttal and Couzin (5) take such analyses to the next level and ask how and under what ecological circumstances might collective migration have evolved.

Collective migration is a group level phenomenon, but its underlying mechanisms are at the level of individuals. What, then, are the individual level traits that might be subject to selection, and how might the collective level phenomena arising from these traits feed back to affect the fitness of the individuals involved? Guttal and Couzin (5) model a situation where two traits are subject to selection. The first is the capacity of an organism to respond to a gradient or some other external cue, indicating the correct direction of migration. Real examples of cues used by migrating organisms include magnetic fields, sunlight, wind direction, temperature, and chemical gradients. The second evolvable trait in the model is the sociability of an organism: specifically, its tendency to be attracted to and align with moving neighbors. Examples include the visually guided responses of starlings and locusts or physical adhesion and chemical signaling among bacteria. Various combinations of traits values in the model could result in a spectrum of population level outcomes, including individuals moving randomly (low gradient detection and low sociability), migrating independently of one another (high gradient detection and low sociability), forming aggregations but not migrating (low gradient detection and high sociability), migrating together along the gradient (high gradient detection and high sociability), or forming filamentous groups that split and fuse again as they move along the gradient (high gradient detection and intermediate sociability).

Fig. 1. Caribou migration: a spectacular annual event in the Arctic. (Photograph courtesy of Ryan K. Brook.)

As grist for evolution in the model, cost functions were specified for each of these variable traits: the greater the gradient detection ability and level of sociability, the higher the cost to the individual. Costs of detecting and following a gradient might include reduced vigilance to predators and the energetic costs of maintaining gradient detection mechanisms, whereas the costs of sociability could include increased competition for food, disease transmission, or greater visibility to predators (6). On the positive side of the evolutionary ledger, fitness benefits were gained according to how far and precisely organisms migrated in the direction of the gradient.

Having set their agents free to evolve, Guttal and Couzin (5) find that populations typically evolved two coexisting and equally fit individual strategies: a minority of individuals evolved to become leaders, and the rest were highly sociable followers. Leaders assiduously followed the environmental gradient and largely ignored other individuals, whereas sociable individuals were attracted by one another but had little or no ability to detect the gradient. As a consequence, the entire group tracked the gradient together, with leaders showing the way and sociable individuals tagging along and freeloaded on the gradient-following ability of the leaders.

Couzin et al. (1) had previously shown in an agent-based simulation how a small number of informed individuals can direct a large group of naive individuals to a resource site, as seen, for example, in the way that a small number of informed scout honey bees directs a large swarm of ignorant insects to a new nest site (7). In the model by Guttal and Couzin (5), such a situation evolved spontaneously.

Distinct groups of leaders and sociable individuals arose under a wide range of scenarios in which population density and cost functions were varied. However, other outcomes were possible under certain conditions. At very low densities with low gradient-following costs, most individuals were leaders, resulting in individuals migrating independently rather than collectively. Conversely, at extremely high population densities when gradient following costs were high, stationary aggregations resulted. Nevertheless, collective migration in which a majority of sociable followers exploited the gradient-following abilities of a minority of leaders was observed over the vast majority of the parameter space explored.

The process by which the two stable strategies arise and coexist reveals the central role of information structure and collective dynamics in affecting the fitness payoffs to individual group members. Under most conditions, all individuals in a population that initially lacks both gradient detection and sociability rapidly evolve the ability to detect a gradient because of the associated fitness benefits of migration. At the same time, individuals who also acquire a mutation to become sociable gain an additional fitness advantage because of the increased migratory accuracy accrued through the many wrongs principle of group navigation (8). Thus, individuals with both strong gradient detection and sociability parameters initially come to dominate the population. It is at this point that the information provided within the group facilitates some surprising evolutionary dynamics. Individuals can achieve higher relative fitness by relaxing their gradient detection ability while obtaining the benefits of migration through increased social attraction to gradient-detecting group members or their followers. As a result, an overall decrease in gradient detection ability is observed, whereas the strength of sociability increases. The stage is now set for a split in strategies. Some individuals achieve higher relative fitness by further reducing the

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costs of gradient detection and increasing their sociability, thereby exclusively becoming followers. In other individuals, mutations that increase gradient detection ability but reduce sociability become favored; they evolve as leaders that gain a fitness advantage through increased individual migratory benefits and relaxed costs of sociality. The net result is a frequency-dependent balance of the two alternative strategies with equal fitness in the population. The population exhibits collective migration but is actually comprised of two sets of individuals following very different rules.

Many behavioral strategies are conditional: the animal exhibits one strategy under some circumstances and another strategy in a different set of conditions. Variation among individuals in migratory strategies is well known in nature (9). To model a scenario in which individuals with a high gradient detection ability might either avoid exploitation by sociable individuals or exploit the gradient detection ability of others, they were allowed to turn their gradient detection on or off, depending on the density of local neighbors. The ability to switch was allowed to evolve without cost and mediated by reaching a threshold local neighbor density, determined through a quorum-sensing ability (10). A facultative strategy might be predicted to be advantageous at intermediate costs of gradient detection; however, this did not evolve. Rather, a balance of invariant leaders and followers was observed in the population. Sociable individuals evolved with either a very low neighbor density threshold value and therefore did not use their gradient detection ability or a sufficiently high threshold that they always used their gradient detection ability to migrate.

What might the model tell us about variation in strategies among individuals in naturally occurring populations that exhibit collective migration? One intriguing possibility is that individuals that fail to migrate in an otherwise collectively migrating population are simply sociable individuals who failed to get the message and did not experience sufficient stimuli from leaders whom they otherwise would have followed. Alternatively, there are, of course, many other ways in which an organism's state, developmental stage, and environment could mediate its expression of migratory behavior. Extensions of individually based modeling platforms such as the one used here hold considerable promise for exploring these possibilities in conjunction with their ecological and evolutionary consequences at the group level (11).

Collective migration can arise even in very sparse populations, when individuals rarely interact.

Another insight arising from the model is that collective migration can arise even in very sparse populations, when individuals rarely interact. This suggests that collective processes might be involved in migrations of some species in which individuals are thought to behave independently (e.g., dragonflies or Monarch butterflies) (12, 13). Even some seemingly passive directional migrations, such the seasonal movements of moth populations, are now thought to be influenced by active navigation, with individuals selecting specific air columns within which to fly (14). What remains to be determined in such cases is the level of social influence on movement decisions, the scale at which such stimuli can be detected, and the frequency at which conspecifics encounter each other during migration.

It is well known that populations may lose or gain migratory behavior (9). A clever aspect of the model by Guttal and Couzin (5) is that they used the shape of migration benefit function as a surrogate for increasing habitat fragmentation to examine the potential impact of anthropogenic changes on migratory patterns. Using a simple nonlinear function, they could adjust how far individuals needed to migrate before enjoying increased benefits. As habitat fragmentation along the migratory route increases, for example, through loss of stop-over sites, migration is gradually lost because of the higher costs of reaching more distant destinations. However, restoring the habitat does not simply restore migration. This is because minor mutations that only slightly improve gradient detection do not increase fitness enough to overcome the increased costs of migrating greater distances. The major mutations in gradient detection required to do so may be rare over typical ecological timescales, thereby resulting in the observed hysteresis effect in the loss vs. gain of migratory behavior.

As with all models, the ultimate test of their generality comes with empirical validation. The authors offer an abundance of techniques, study systems, and approaches that could be used to test the model's predictions about the role of social information in the ecology and evolution of migration (5). Research into the mechanisms of collective behavior has been distinguished in recent years by the productive interplay between theory and experiment. Guttal and Couzin (5) add evolutionary dynamics to the mix and set the scene for a new generation of experimental tests and applications.

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