

PERSPECTIVE

From Individual Dispersal to Species Ranges: Perspectives for a Changing World

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Dispersal is often risky to the individual, yet the long-term survival of populations depends on having a sufficient number of individuals that move, find each other, and locate suitable breeding habitats. This tension has consequences that rarely meet our conservation or management goals. This is particularly true in changing environments, which makes the study of dispersal urgently topical in a world plagued with habitat loss, climate change, and species introductions. Despite the difficulty of tracking mobile individuals over potentially vast ranges, recent research has revealed a multitude of ways in which dispersal evolution can either constrain, or accelerate, species' responses to environmental changes.

From sticky seeds to efficient flight machinery with complex navigation systems, animals and plants have evolved an impressive variety of dispersal mechanisms. Through the simple act of moving individuals from one area to another, dispersal has important ecological and evolutionary consequences (1, 2), including the ability of species to change or expand their ranges (3). The distribution of species we observe today reflects a long history of alternating episodes of dispersal and isolation. Fluctuations in sea level that opened and closed land corridors, the splitting of continents, and the rising of mountain ranges and islands have all left their mark on the whereabouts of extant species. Nowadays, humans are creating new processes that isolate, connect, and shift landscapes at a much higher speed: Anthropogenic habitat fragmentation, transport of invasive species, and climate change are among them. How will species ranges react to them? How will their dispersal behavior change? Are physical barriers and open corridors all there is to explain species distributions?

To predict whether species can shift to new areas requires, on the one hand, understanding the colonization process at the expanding edge of the species range. On the other hand, the possible range contraction where habitat is deteriorating depends crucially on whether individuals simply leave poor-quality habitat or attempt to stay. Local adaptation to changing conditions is also possible, yet strong dispersal can swamp local genetic change and so prevent adaptation from happening (4). Current anthropogenic environmental changes

make the study of the evolution of dispersal a requirement for predictive ecology (5).

Dispersal is an important determinant of gene spread and is thus subject to strong natural selection (1, 2, 6). Even if dispersal is risky, it can evolve to avoid the detrimental effects of crowding and competing with kin (6). An evolved willingness of individuals to move about is an obvious prerequisite for the spread of a species to different parts of its fundamental niche. But how well do organisms actually achieve this? Evolutionary ecologists are increasingly aware that not only limitations of cognitive abilities, but also selective pressures themselves, can cause severe constraints on the habitat use of a given species. In other words, intrinsic spe-

cies properties, rather than just limitations imposed by the landscape, can have profound effects on the ability of a species to colonize new areas (3). Unraveling these mechanisms is important if we are to understand the evolution of species ranges and how they respond to environmental change.

Adaptation Does Not Predict Optimal Space Use

The ability to distinguish between suitable and less suitable habitats is an obvious first limitation to colonization of new areas. Dispersal and habitat settlement cues are often based on “rules of thumb” that can be breathtakingly simple. This can lead to ecological traps, where environmental change dissociates habitat quality from the cues and causes individuals to prefer suboptimal habitats (7). For example, dragonflies have been observed to patrol asphalt roads instead of rivers, which results from their use of polarized light as a cue for still water and can also lead to a strong preference for landing on oil (8). Another simplistic cue is conspecific attraction, where individuals use the presence of others as an indicator of good habitat: Playbacks of song attract young bobolinks *Dolichonyx oryzivorus* to settle in habitats of random quality (9). If individuals simply copy others' choices, one can envisage a self-reinforcing and intrinsically random component to habitat use.

But attraction to conspecifics can be more than just an easy cue indicating suitable habitat. In many species of animals, individuals directly benefit from living in groups; philopatry (i.e., staying in the natal patch) can be selected for, particularly if local habitats are worth clinging to



Fig. 1. Dispersing individuals are a nonrandom subset of the population. **(Left)** Dispersing females of the Glanville fritillary, *Melitaea cinxia*, have a higher flight metabolic rate and are more fecund than sedentary ones. [photograph: Anne Holma] **(Right)** In Siberian jays, *Perisoreus infaustus*, the subordinate individuals disperse, whereas the heavier and more dominant remain in their natal territories. [photograph: Hannu Siitonen] Differences in selective pressures on dispersal may have profound consequences for the stability of newly founded populations and, consequently, for the ability of the species to spread and react to environmental change.

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(10). The home advantage is particularly clear in social species, in which cooperative behaviors may enhance the value of home. When the natal patch has particular value, staying at home is often the privilege of the dominant offspring, and subordinates are forced to leave [e.g., the Siberian jay, *Perisoreus infaustus* (Fig. 1) (11)].

Regardless of the degree of sociality, the short-term fitness advantage of staying at home can contrast with the longer term ability of a species to colonize available patches (12). Thus, although some dispersal is always selected for, there is no guarantee that the evolving dispersal rate leads to the best possible persistence of a species. Similarly, improved cognitive abilities, while advantageous to the individual, do not necessarily lead to more efficient use of space. Computer simulations show that “blind” dispersal in a random direction can connect populations better than behaviors that allow habitat assessment to take place (13).

The consequences of such theoretical results are profound: It is even possible that a metapopulation (a set of populations connected by dispersal) evolves itself toward extinction. This can happen if dispersal becomes riskier, for example, because suitable patches have become scarce. In this case, individuals are selected to avoid the dangerous dispersal phase, yet the metapopulation cannot persist in the absence of a continuous influx of migrants (14). Predicting the direction of the evolutionary response is challenging, however. The failure of most dispersers in a scenario of risky dispersal will vacate much of the landscape, which can paradoxically enhance the fitness rewards for those lucky dispersers that survive. Under suitable conditions, this favors higher dispersal, potentially rescuing entire metapopulations—a scenario that has been shown to arise with parameters from populations of checkerspot butterflies, such as the Glanville fritillary, *Melitaea cinxia* (Fig. 1) (15).

Nevertheless, philopatry has its bright side too, which becomes visible when a species faces a different kind of change in its environment: the dissociation of cues and habitat quality that characterizes ecological traps. Philopatry dictates that wherever the production of young has been most recently successful is precisely where most individuals prefer to reside, and this may allow the species to track changing environments much faster than a genetic change in habitat choice cues would allow (16). Such population-level benefit of philopatry of course requires that at least some individuals have found the currently best habitats. This is ultimately dependent on dispersal, which, being the flipside of philopatry, highlights the complexity of population consequences of rules of movement.

Near the margin of a species' distribution, populations are precariously balanced on the edge between persistence and extinction, and ranges can easily become “pinned” to a fixed area by poor performance in marginal habitats or low densities (17). Such restrictions are important in a world in which shifts in climate will pose a dramatic

challenge to species persistence. Dispersal is a trait that often shows considerable phenotypic plasticity, responding to local density either positively or negatively (1). Cases where it occurs as a response to local crowding are highly relevant when predicting responses to habitat loss and shifting climates. Such shifts imply that locally declining populations could have better prospects elsewhere. Because the initial decline decreases local crowding, the result may be a decline in dispersal that prevents the population from finding the improved habitats elsewhere (18).

...Yet Space Use Can Accelerate Adaptation

Dispersing individuals take their genes with them. Thus, any genetic trait that influences the tendency or ability to disperse can easily cause spatial differentiation in the gene pool. Finding new habitats is an essential prerequisite for breeding in them, and thus, dispersal is a good example of a trait that can experience strong selection in marginal areas. Indeed, in Glanville fritillary (*Melitaea cinxia*) metapopulations, recently colonized patches are mainly composed of individuals with higher flight ability and fecundity than those found in old patches (19). Interestingly, allelic variation in a single gene can contribute significantly to this variation (20). Other species instead show trade-offs between fecundity and dispersal (21). Recent theoretical work shows that such differences can determine the stability of the species' range boundary and, consequently, play a decisive role in whether the species will expand its range (22).

Several recent examples suggest that evolution can be both fast and significant for the ability of a species to colonize new areas. The evolution of more dispersive individuals near species borders clearly creates a positive feedback that has potential to accelerate the expansion of a species. Marginal populations of bush crickets (*Conocephalus* and *Metroptera* spp.) expanding their ranges through the United Kingdom showed increased frequencies of long-winged dispersive individuals, which indicates evolutionary change (23). In an unfortunately spectacular example, cane toads, *Bufo marinus*, introduced into Australia are rapidly invading the continent, helped by fast adaptation that produces longer-legged individuals and enhances dispersal at the invasion front (24). Nevertheless, recent evidence suggests that invasions are not simple uninhibited traveling waves, but follow regulatory patterns analogous to the long-studied forms of density dependence within stationary populations (25). It will be interesting to examine the causes behind this apparent regulation and to find if different dynamics at range margins can be predicted depending on the determinants of dispersal behavior.

Future Perspectives

The above examples show great diversity in the potential responses of species to environmental change, determined by the constraints and selec-

tive pressures on dispersal. However, to get beyond a list of representative examples, we still need a comprehensive framework that links theoretical advances to empirical case studies. Without an understanding of why, for example, individuals of some species disperse from locally crowded habitats and others do not, we cannot make solid predictions on how species will react to new conditions.

There are empirical challenges too. It is not surprising that local population regulation is much better studied than the regulation of invasion fronts (25) or other dynamic aspects of dispersal: Tracking mobile individuals over potentially large distances presents obvious difficulties. Advanced techniques, such as stable isotope analysis or molecular methods, provide much insight, but to be truly useful, the results always need an ecological context (20, 26). An additional challenge is to understand the failure of some species to establish in new areas. The absence of populations requires explanation as much as their presence, and comparisons between populations or closely related species that differ in their ability to colonize new areas promise new insights into the question (23, 27). But to identify clearly the causal mechanisms behind dispersal, experiments will provide the most solid answers. This may seem challenging, yet there already exist examples of experiments conducted either in the field (9, 10, 28) or in artificial environments (29), demonstrating that one can move beyond correlational approaches for examining the causes of dispersal. Further work on model organisms with sufficiently short generation times promises an exciting way to test evolutionary responses of dispersal to environmental change.

We are surrounded by cases of unwelcome species introductions, as well as numerous failures of populations to persist in fragmented, human-disturbed habitats. This provides researchers with a unique large-scale experiment and valuable source of data to understand the evolution of dispersal. Ironically, such data are precisely what we need to better predict species reactions to change and to prevent the loss of biodiversity in an era of global warming, habitat loss, and invasive species.

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PERSPECTIVE

Conflicting Evidence About Long-Distance Animal Navigation

Thomas Alerstam

Because of conflicting evidence about several fundamental issues, long-distance animal navigation has yet to be satisfactorily explained. Among the unsolved problems are the nature of genetic spatial control of migration and the relationships between celestial and magnetic compass mechanisms and between different map-related cues in orientation and homing, respectively. In addition, navigation is expected to differ between animal groups depending on sensory capabilities and ecological conditions. Evaluations based on modern long-term tracking techniques of the geometry of migration routes and individual migration history, combined with behavioral experiments and exploration of the sensory and genetic mechanisms, will be crucial for understanding the spatial principles that guide animals on their global journeys.

Migration emerges and becomes suppressed among birds, fish, insects, sea turtles, bats, and sea mammals with apparent evolutionary ease. It has evolved numerous times without important phylogenetic constraints; closely related species or populations are often nonmigratory. Furthermore, post-glacial changes in travel patterns indicate a high degree of evolutionary flexibility in migration traits. Thus, as noted almost a century ago by the American ornithologist Joseph Grinnell (*1*), the evidence implies that migratory adaptations are rather simple extensions of capabilities that animals use for their everyday local life and movements. Yet after longstanding and intensive migration research, we are still far from a fundamental understanding of animal navigation, and the emerging picture is complex and intricate.

Linnaeus, in his treatise *Migrations Avium* (1757), appealed for field observations from all over the world that would reveal birds' migration routes. Over the next two centuries, banding of birds and fish produced a wealth of information, and displacement experiments revealed impressive homing performances. Orientation cage experiments proved to be powerful for discovering and exploring celestial as well as magnetic compass mechanisms. The map sense that is required in addition to a compass sense to explain the homing

capabilities of animals attracted increased attention (2, 3). Animal tracking studies have benefited during the recent decades from increasingly sophisticated techniques, such as radar registration, satellite-based radio telemetry, and electronic geolocation and data storage tags. However, current research is characterized by conflicting evidence and interpretations about several fundamental questions (Table 1).

Until recently, it was believed that juvenile birds (among species traveling solitarily) on their first journeys relied solely on an endogenous spatiotemporal program, defining the journey in terms of direction and distance along one or a few main legs (Table 1B). Adding successive travel steps for migrants guided by such a simple inherent clock-and-compass program, with some variation between each step, will lead to a geographic spread of a population of migrants that increases with distance as a parabola along the migratory axis. Ringing recovery distributions of some bird species fit nicely with this predicted pattern (4).

However, migration patterns converging toward narrowly defined species-specific passage or wintering areas can hardly be the result of such simple endogenous control (5, 6) (Fig. 1). Rather, these patterns indicate that migrants use external cues, such as geomagnetic coordinates (e.g., magnetic field strength and inclination). Thrush nightingales (*Luscinia luscinia*) that were experimentally moved in geomagnetic space (while retained geographically in Sweden) to their target stopover area in Egypt increased their fuel

deposition as expected when preparing to cross the Sahara desert (7). The best evidence for geomagnetic coordinates as regional markers comes from experiments with hatchling loggerhead sea turtles (*Caretta caretta*) (8). The turtles changed their orientation in relation to geomagnetic position so as to remain along the migration route at the North Atlantic gyre. However, inherent magnetic map guidance is not without complications. The current difference in magnetic coordinates between northern Florida and the northeastern gyre will be obliterated in less than fifty years because of differential geomagnetic secular changes at these two places. Geomagnetic coordinates at the thrush nightingale's target area, in 100 to 150 years time, will have changed to those that today are found at the target area of the blackcap (*Sylvia atricapilla*) (Fig. 1). How is it possible for evolutionary change in the animals' genetic migration program to keep pace with such secular changes in the Earth's magnetic field (Table 1H)?

Homing may be an important element in migration of experienced animals that return to favorable sites visited earlier, such as breeding and wintering destinations and goal areas along the route (Table 1C). If the geomagnetic field provides information for migration control, it may also be an important basis for the map sense used by homing animals, an idea that has been considered several times since the end of the 19th century (3). Recent experiments in which animals have been displaced in geomagnetic (but not geographic) space have provided support for this possibility among salamanders, spiny lobsters, and sea turtles (9–11). However, the hypothesis of homing based on a magnetic map sense is controversial. Supporting experiments have demonstrated homing responses to geomagnetic north-south displacements but not yet to east-west displacements, where the differential changes in geomagnetic parameters are more critical. It also remains to be shown whether geomagnetic gradients allowing unambiguous navigation are actually available within the local natural homing ranges of the experimental animals. An even more serious difficulty for the magnetic navigation hypothesis is the failure reported in several experimental attempts to disrupt homing success by attaching magnets to the animals (3). Sea turtles, petrels, and albatrosses equipped with disturbance magnets and recorded by satellite tracking show oceanic navigation performance similar to that of control individuals (12–15).

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