

# What Is Migration?

HUGH DINGLE AND V. ALISTAIR DRAKE

*We outline a general scheme for migration that applies across taxa, incorporates the several varieties of migration, and includes all levels of biological organization, from genes to populations. The scheme links the environment, pathways, traits, and genes, and highlights the selective forces that shape and maintain migratory adaptation. We endorse an individual-based behavioral definition of migration that allows an objective distinction between migration and other forms of movement. We recognize migration as an adaptation to resources that fluctuate spatiotemporally either seasonally or less predictably, and note that it is often preemptive. Migration plays a central role in the spatial dynamics of mobile populations, and is largely distinct in both form and function from the within-population mixing arising from postnatal dispersal and from the interpatch movements characteristic of metapopulations. We call for more interaction between biologists studying different taxa and different forms of movement, and between behaviorists and population ecologists.*

*Keywords:* animal movement, migration, behavior, population, natural selection

**F**or the public and for many biologists, the word *migration* evokes visions of “heroic” movements of whole populations over long distances. When barn swallows (*Hirundo rustica*) appear over an English village in April, when Pacific salmon (*Oncorhynchus* spp.) leap the rapids of an Alaskan river, or when southern right whales (*Eubaleana australis*) come to the Great Australian Bight to calve, both lay observers and biologists recognize that what is occurring is a special type of animal movement, and one that forms an essential component of the life history and ecological niche of the organism. Migrating animals are found in all major branches of the animal kingdom, their journeys take place in a variety of media, and they move by flying, swimming, walking, or drifting. Despite this variety, however, it is apparent that we are dealing with a single biological phenomenon that transcends taxon, form, and environment but that relates directly to one of the most universal and defining traits of animals: their mobility.

If one looks across taxa, it is apparent that the term *migration* is also used to describe movements that differ considerably from the seasonally synchronized relocations of populations between the “two worlds” (Greenberg and Marra 2005) of breeding grounds and wintering area (Rankin 1985, Dingle 1996). Insects of the same or different generations may migrate several times within a breeding season, and fish such as herring may move in circuits between breeding, feeding, and wintering sites (Dingle 1996). Entomologists engaged in quite a vigorous debate in the early 1980s about the nature of migration (Kennedy 1985, Taylor 1986). An important point that emerged from this dialogue was that migration involved two levels, the behavioral applying to individuals and the

ecological applying to populations. Thus a broad conceptual understanding of migration encompasses both its mechanism and its function. Biologists studying various taxa have developed rich insights into individual (physiological, behavioral, genetic) and population (ecological, evolutionary) aspects of the phenomenon. This is perhaps particularly evident in work on birds, fish, and insects. Their visibility and their often spectacular journeys have made birds favorite subjects, while the economic value of species like herring and salmon has been a driving force in studying fish migration. The economic impact of pest species has fostered studies of insects, and their short life spans and the relative ease with which laboratory cultures can be maintained make this group especially suitable for experimental work, including genetic investigations using artificial selection and crossing (Dingle 2001, 2006). Our principal aim here is to illumine and distinguish the various aspects of the migration phenomenon and to draw together from different taxa and levels of analysis a common viewpoint that takes into account the diversity of migration and provides a framework for further analysis of its proximate basis, its ecology, and its evolution.

Hugh Dingle (e-mail: rdhdingle@ucdavis.edu) is a professor emeritus in the Department of Entomology and Center for Population Biology, University of California, Davis, CA 95616. He is currently an honorary research consultant in the School of Integrative Biology, University of Queensland, Brisbane, Queensland 4072, Australia. V. Alistair Drake (e-mail: a.drake@adfa.edu.au) is a senior lecturer in the School of Physical, Environmental, and Mathematical Sciences, University of New South Wales at the Australian Defence Force Academy, Canberra, ACT 2600, Australia. © 2007 American Institute of Biological Sciences.

## The scope of migration

Drawing on dictionary definitions (Taylor 1986, Gatehouse 1987) and the biological and natural history literature, we suggest that the word *migration* (as applied to animals) can evoke four different but overlapping concepts: (1) a type of locomotory activity that is notably persistent, undistracted, and straightened out; (2) a relocation of the animal that is on a much greater scale, and involves movement of much longer duration, than those arising in its normal daily activities; (3) a seasonal to-and-fro movement of populations between regions where conditions are alternately favorable or unfavorable (including one region in which breeding occurs); and (4) movements leading to redistribution within a spatially extended population.

These interpretations encapsulate some significantly different perspectives about what migration entails. First, types 1 and 2 relate to individual organisms, while types 3 and 4 explicitly concern populations. Second, type 1 describes a process, whereas the remaining three types describe outcomes (for individuals or populations) of locomotory activity by individuals. Third, types 2 and 3, but not 1 and 4, invoke a time or spatial scale. The process-versus-outcome distinction lies at the heart of the debate among entomologists about whether migration should be defined for individuals (“behaviorally”) or for populations (“ecologically”; Kennedy 1985, Taylor 1986, Gatehouse 1987). The former approach appears more compatible with our contemporary understanding of the mode of action of natural selection, namely, that it acts principally on individuals (and their genes). In contrast, the population perspective reveals the *function* of migration and the source of natural selection. The “two worlds” viewpoint, derived largely from birds, has tended to draw attention especially to questions concerning function. In the insect literature, the equivalent focus has been on travel between “temporary” habitats, such as ephemeral ponds, early successional habitat stages, or successively senescing host plants (Southwood 1962, Denno et al. 1991). In both cases, migration is implicitly recognized to be an adaptation driven by the transitory availability and changing location of resources. (We note in passing a renewed interest in selection at higher organizational levels than the individual [Wilson 1997] and also modeling results linking such selection to spatially extended populations [Werfel and Bar-Yam 2004], and we recognize that some migration is undertaken in social groups and involves communication [van Noordwijk et al. 2006], but our perspective here remains focused on individual selection.)

The behavior-versus-ecology dichotomy can now be recognized as one part of a broader spectrum extending both across processes occurring in individuals and across those occurring in populations. Much research has been undertaken on the underlying morphological and physiological adaptations that make migratory behavior possible (McKeown 1984, Dingle 1996, Berthold et al. 2003, Ramenofsky and Wingfield 2007) and on the adjustments migrants make to complete their journeys successfully (Åkesson and Hedenström 2007). There has been some investigation of the genetic

basis that underlies these adaptations (Han and Gatehouse 1993, Dingle 2001, van Noordwijk et al. 2006, Pulido 2007, Roff and Fairbairn 2007). The questions of how migration systems have evolved (and perhaps led to some instances of speciation; Helbig 2003, Jahn et al. 2004, Irwin and Irwin 2005) and how current systems are subject to natural selection (Dingle 2001) take us beyond the scope of a strictly ecological viewpoint. Following Rogers (1983), we note that migration, like other biological phenomena, can be viewed at a series of organizational levels, from the molecular to the evolutionary, and that while we can describe events occurring at one level, such as the behavior of the individual migrant, in terms of lower-level attributes, we must seek explanations for them by identifying their functions at higher levels. The hierarchy of viewpoints is in fact closed, as the highest level—natural selection—acts directly on the lowest—the genes underlying the migratory adaptations.

In areas of biology outside behavior and ecology, the term “migration” has been used in contexts involving a longer (usually) time frame. Thus biogeographers often refer to the range expansions of faunas or individual species as migration, an example being the northward extension of ranges following the retreat of glaciers at the end of the ice ages. Population geneticists incorporate the term *m*, indicating “migration,” into their equations to describe gene flow—the exchange of genes among populations by whatever means, including but not limited to migration as we consider it here. These interesting phenomena fall outside the scope of this article, which is concerned with the movements of individuals and the short-term consequences of these movements for populations.

## Varieties of migration

Migration can take a number of forms and has been described by biologists in different ways. We list many of these migratory patterns in table 1, classifying them by whether the focus is on the organism, the spatial or temporal attributes, or the medium in which migration takes place. Migrants are often classified as either *obligate* or *facultative*, depending on whether they always migrate or do so only in a proximate response to current deterioration of local conditions. In practice, however, the distinction is often blurred. In *partial* migration, a fraction of the population remains either in its breeding or its nonbreeding area while the remainder moves away (see Jahn et al. 2004 for some variants), while in *differential* migration there are differences in the migration patterns of older and younger individuals or of the two sexes.

**Table 1. Variation in patterns of migration.**

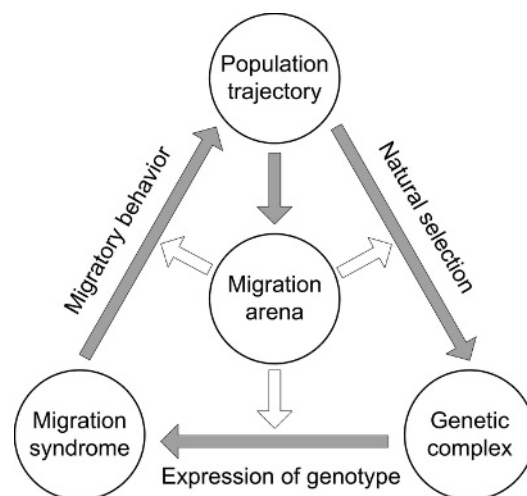
Category	Pattern
Organism	Obligate, facultative, partial, differential
Space	To-and-fro, round-trip (loop), one-way, altitudinal, nomadic
Time	Seasonal, irruptive
Medium	Diadromic, drift (including devices)

*To-and-fro* migration is what we call here “two worlds”; *round-trip* migration is a variant of this in which animals return to the general breeding area from which they originated but may stage their movements through a succession of non-breeding areas, and perhaps follow different paths on the outward and return journeys (*loop* migration). *One-way* migrations, found mainly in insects and marine larvae, carry animals from a location where they were produced to another where they breed and produce the next generation (or generations) before dying; a succession of such one-way movements through a series of breeding areas may form a multiple-generation round trip. *Vertical* migrations occur between different water depths (and are actually a form of what we term “commuting” [see below] rather than migration), and *altitudinal* migrations occur between different terrestrial elevations. In *nomadism*, migration does not follow a regular pattern or route but links temporary breeding sites that are located where conditions are ephemerally favorable.

*Annual* migrations are round trips synchronized with the annual cycle, and *seasonal* migrations are particular stages of these annual journeys. *Irruptions* are occasional, irregular movements of a significant proportion of a population beyond its usual breeding or nonbreeding area. *Diadromic* migrations take fish (and some crustaceans) between fresh and salt water. Another distinction is between movements achieved primarily by transport on a wind or current (sometimes referred to as *drift*) and those resulting essentially from locomotion *through* a medium. Special evolved devices, such as the ballooning threads of spiders and some larval insects, are sometimes employed to promote drift (Dingle 1996).

### A holistic view of migration

Recognition that the various phenomena comprising migration occur across a series of organizational levels helps greatly to distinguish them, refine our separate knowledge of each, and develop both descriptive and explanatory understandings by drawing from lower and higher levels (Rogers 1983). Nevertheless, migration is a single phenomenon, and we should aim to recognize its unitary structure. This has been attempted by Drake and colleagues (1995) in the form of a conceptual model of what they termed a “migration system” (figure 1). The model incorporates both components and processes (the changes in and linkages between components) and explicitly considers the environment in which the migrant population survives as well as the migrants’ responses and adaptations to it. The four system components are as follows: (1) A *migration arena* comprising the environment (including biotic elements) to which the migrants are adapted; (2) a *migration syndrome*, which is the suite of traits enabling migratory activity—this suite comprising both locomotory capabilities and a set of responses (or nonresponses) to environmental cues that schedule and steer the locomotory activity; (3) the *genetic complex* that underlies the syndrome; and (4) a *population trajectory* (or its long-term average, the *population pathway*) comprising the route followed by the migrants, the timing of travel along it, the points along it where



**Figure 1. Holistic conceptual model of a migration system.** Circles indicate the four primary components, gray arrows the principal processes that connect them, and open arrows the primary modes of environmental influence. The short process arrow represents the impact of the population on its habitat, including exhaustion of resources and introduction of pathogens. Natural selection occurs through differential mortality and through the process of spatial partitioning, in which different phenotypes steer individuals (and the genes they carry) to different destinations. Adapted from Drake and colleagues (1995).

migration temporarily ceases, and the times when these points are occupied for breeding and other key life stages.

The model incorporates the ultimate (selective) and proximate factors acting on migration (the arena), the response to natural selection in the phenotype and genotype of migrants (the syndrome and its genetic complex), and the population consequences in terms of both selection and current conditions (the trajectory and pathway). Its aim was to identify and describe qualitatively how a migratory adaptation functions by employing movement to exploit a changing and spatially extensive environment, and how a capacity for appropriate movements is maintained within a population. A demonstration of the model was the examination of migratory adaptation in a relatively well-researched moth species, the oriental armyworm (*Mythimna separata*) (Drake and Gatehouse 1996). Gauthreaux (1980) provides both a comprehensive list of the geophysical factors, short- and long-term, that contribute to the migration arena and numerous examples of migrant species and their arena-specific adaptations.

### Migration as a form of individual movement

Although the outcome of migration can be viewed as a population process, it is useful to focus first on the migratory behavior of individuals, as this underlies the collective aspects. Further, because natural selection acts primarily on individuals, understanding the function of migration, and how migration systems are maintained and evolve, will ultimately

concern the genotypes and phenotypes of individual migrants (Dingle 2006).

**Movement and resources.** Animals employ movement for a variety of purposes, but probably most frequently in connection with the use of resources. These include food, shelter, and mates, all of which are included within an individual's home range, which is in turn located—along with many others—within a habitat that provides the necessary requirements for breeding or maintenance (or both). Movements can be divided into those that occur generally within the home range and those that take the individual more or less permanently beyond it (Dingle 1996). The former include several types of behavior that have been called “station keeping” (Kennedy 1985, Dingle 1996), the most prominent of which is foraging. Foraging is concerned with finding and appropriating resources (a food item, say, or a mate) and is characteristically meandering and repetitive on short timescales and small spatial scales, the animal changing course frequently as it finds and moves between items. It has an extended form, which we term “commuting,” in which longer to-and-fro or round-trip journeys are made regularly (often daily) to spatially separated resource patches, roost sites, and other localities where specific activities occur. Dramatic examples include the mass daily vertical movements of plankton and the several-thousand-kilometer foraging round trips extending over several days made by albatrosses (*Diomedea* spp.) and other seabirds between nesting islands and food locales.

Two types of movement take the individual “permanently” beyond the home range; these are *ranging* and *migration*. Ranging implies an exploratory component and takes the organism beyond the current home range to settle eventually in a new one. We define the behavior as one that ceases once a suitable new home range (a resource) is found, and a large literature (Gandon and Michalakis 2001, Bullock et al. 2002) suggests it is characteristic especially of young birds and mammals that must find space away from their parents to avoid competition and inbreeding. Migration is movement away from the home range that does not cease, at least not initially, when suitable resources or home ranges are encountered. Eventually, however, the migrant is primed to respond to appropriate resources. This sequence of inhibition and then priming of response assures that the migrant escapes from a region of deteriorating habitats, as would occur for temperate-zone birds in the autumn, for example, and extends its movement to a region where habitats will remain or are becoming favorable (Kennedy 1985, Dingle 1996; see the discussion of preemption, below). In short-lived insects, the abandonment of home range by migrants is in fact permanent; in long-lived vertebrates, migrants with strong philopatric tendencies (i.e., tending to stay in or return to their native territories or regions) may return to the home range the following season. Thus repeat migrations are often a consequence of long life spans. Ecologically, migration occurs between habitat *regions*, whereas ranging occurs between habitat units within a habitat region. There will most likely be cases

where the distinction between migration and ranging is not obvious, and these may repay careful examination from both behavioral and ecological perspectives.

The qualitative characterization of movement behaviors draws on both form and function, but it seems probable that objective distinctions could be made from observations of the organism's *lifetime track*, the time series of its successive locations (Baker 1978). With modern tracking technologies, such an analysis is increasingly practicable, at least for larger vertebrates (Kenward et al. 2002). Foraging, ranging, and migration might appear as separate (probably broad) peaks in a spectrum of the track's straightness, or the two longer range movements (or just migration) might give the spectrum a “fat tail.” As an alternative to relying on observations of the organism's location (an “outcome” perspective), it is at least in principle possible to telemeter observations of the organism's ongoing behavior—including its responses or lack of response to the resources it encounters—and obtain an objective characterization based on a “process” viewpoint.

The distinctions between foraging/commuting, ranging, and migration are most easily recognized when a home range is readily identifiable. When an animal is nomadic, and home ranges and breeding areas and times are unpredictable, the trajectories of the three types of movement may overlap to some degree. In any case, the distinctions are to be recognized from the *patterns* of relocations or behaviors and not by their absolute scale: One species's ranging may be as extended (temporally, spatially, or both) as another's migration. The scale characteristic of migration is more apparent when considered in relative terms. The spatial extent of an animal's migrations is generally greater than that of any other type of movement it makes, and its periodicity is generally that of one or the other of the two longest timescales most animals experience, the annual cycle and the animal's lifetime. Animals that complete only a single migration cycle (or only part of one) include almost all insects, Pacific salmon, and the African black oystercatcher (*Haematopus moquini*). For example, in the latter species, newly fledged young migrate from their birthplace on the south coast of South Africa to lagoons on the west coast of Namibia, where they remain for two to three years before returning to their natal area to breed without ever migrating again (Hockey et al. 2003).

**Migratory behavior and the migration syndrome.** Because individuals manifest their capacity for migration through behavior, it is through behavioral traits in particular (although not exclusively) that natural selection will act to shape migration. Of the various organizational levels, the behavioral is the highest that concerns individuals. Behavior is also observable, although in wild populations where migration is high in the atmosphere, at night, or over or within oceans, the challenge is considerable. In insects, laboratory studies using wind tunnels (Hardie and Powell 2002) or flight mills or balances (Cooter 1983, Han and Gatehouse 1993) are more practicable and allow experimentation as well as observation. It is now possible to study birds in wind tunnels as well



(Pennycuik et al. 1997). On the basis of a pioneering study of the aphid (*Aphis fabae*), in which he monitored locomotory activity and responses to resources in a laboratory flight chamber, J. S. Kennedy developed a characterization of the special nature of migration (summarized in Kennedy 1966 and Dingle 1996) and defined it as follows: “Migratory behavior is persistent and straightened out movement effected by the animal’s own locomotory exertions or by its active embarkation upon a vehicle. It depends on some temporary inhibition of station keeping responses but promotes their eventual disinhibition and recurrence” (Kennedy 1985, p. 8).

The “vehicle” refers to transport on the wind or in water currents. As with many insects, *A. fabae*’s movements are primarily windborne, but Kennedy emphasized that the aphids nevertheless had to fly actively to get into the airstream and to keep themselves aloft. The sentence about station-keeping responses summarizes Kennedy’s experimental findings that at the initiation of migratory flight, and during its early stages, the aphids would ignore an environmental cue (a young bean leaf) to which they would normally respond by settling and starting to feed, but that after some period of flight they would again become responsive (even hyperresponsive) to this. This is a refined expression of the frequent observation, made for a variety of taxa from butterflies to African ungulates, that migratory movement is characteristically *undistracted* (Dingle 1996). Kennedy stressed that because the inhibition of station keeping is temporary, it can be repeatedly switched on and off. Thus a migrant may switch between migration and foraging while en route, as in the well-known stopovers of migratory birds. Further emphasis on the distinction between the two types of behavior was noted in Kennedy’s (1985) definition of foraging as “reiterative locomotory activity that is readily interrupted by an encounter with a resource item of one particular kind.”

As we have noted, migratory behavior itself relies on adaptations at lower levels, especially adaptations of physiology and morphology (Åkesson and Hedenström 2007, Ramenofsky and Wingfield 2007) resulting in differences—sometimes obvious, sometimes subtle—between similar migrant and nonmigrant species. As well as responses to cues for initiating and terminating locomotion, the migration syndrome includes endogenous mechanisms for priming and inhibiting these responses, and metabolic and hormonal shifts necessary to prepare the migrant for its journey (Dingle 2006). These traits are integrated into the organism’s life history; for example, it is not only feeding that is inhibited but also maturation and reproduction (Kennedy 1985, Ramenofsky and Wingfield 2007). Morphological traits that increase power and efficiency, such as increased wing lengths in migratory birds and insects and enhanced streamlining in fish, are also considered part of the syndrome (Dingle 2006, Åkesson and Hedenström 2007). It is interesting that migration syndromes have evolved repeatedly and across many taxa. Phylogenetic studies fail to reveal a deeply embedded ancestral pattern (Piersma et al. 2005); rather, syndromes appear to arise as

needed from traits that already exist to serve other contexts, a classic example being flight.

Underlying the migration syndrome is a genetic complex (figure 1) that incorporates both genes and genetic architecture (van Noordwijk et al. 2006, Pulido 2007, Roff and Fairbairn 2007). This too is accessible to experimentation through artificial selection and crossing trials, mostly in insects (Han and Gatehouse 1993, Dingle 2001) but also in birds such as the black-cap warbler (*Sylvia atricapilla*; Pulido and Berthold 2003). Such experiments have demonstrated correlations between migration-related traits and between migration and reproduction, both indicative of a coadapted suite of traits. Other expected properties of syndromes, such as trade-offs and the suboptimal adaptations that these imply, are discussed by Sih and colleagues (2004), Pulido (2007), and Roff and Fairbairn (2007).

### The function of migration

Southwood (1962) showed that in insects migration is associated with impermanent habitats. When resources are temporary in relation to generation time, migration and/or dormancy are required strategies (Southwood 1962, 1977, Dingle 1996). Southwood (1977) and Solbreck (1978) later made clear how changes in habitat favorability in both time and space (now versus later, and here versus elsewhere) drive the evolution of migration and dormancy. Migration can be viewed as an adaptation specific to arenas in which changes in habitat quality in different regions occur asynchronously so that movement allows a succession of temporary resources to be exploited as they arise. It thus involves both escape and colonization.

At a minimum, a habitat must enable survival; better-quality habitats will allow development, physiological sequestering of resources, and breeding. Individuals unable to locate a sequence of such habitats will fail to produce offspring. The members of a migrant population are therefore directly subject to natural selection by the arena through which they travel. Selection will arise from the pattern and timing of the development and decline of favorable habitats, from the incidence of inclement conditions, and, for weak flying and drifting migrants especially, from the incidence of winds and currents in appropriate directions. Selection for locomotor capabilities adequate for traversing potentially lethal intervening spaces—for example, deserts and oceans for terrestrial organisms—and for appropriate responses to directional and timing cues is likely to be intense (Åkesson and Hedenström 2007). Population pathways can be expected to match those features of the arena that affect the migrants in essentially all their properties, including spatial and temporal scale, direction and seasonality, and degree of variability. At high latitudes, the migratory adaptation will be primarily to the predictable warm–cold seasonal variations; pathways can be expected to show little spatial variance and to be closely synchronized with the annual cycle. Temperate-zone bird migrants are the classical example (Newton and Dale 1996). If climate changes, timing of migration and resource availabil-

ity may become mismatched and the population may decline (Both et al. 2006). At the other extreme, in semiarid regions, where erratic rainfall is the main determinant of habitat favorability and temperatures are rarely limiting, trajectories may vary greatly; examples include desert locusts (*Schistocerca gregaria*), quelea birds (*Quelea quelea*; Cheke and Tratalos 2007), and Australian bird migrants (Griffioen and Clarke 2002).

As noted above, one key component of a strategy for surviving in a spatiotemporally varying arena is *preemption*, in which habitats are abandoned before their quality has declined too seriously. Preemptive departure may be adaptive for at least three reasons: (1) If an animal waits until quality is poor, it may not be able to accumulate fuel for migration, or habitats at locations within its range may also have deteriorated; (2) if it starts a new breeding attempt, its offspring may be insufficiently developed to depart before conditions become lethal; and (3) early departure may provide it with the advantage of being an initial colonizer of a habitat that is just becoming favorable rather than a late arrival facing established competitors. Preemption requires precisely the temporary inhibition of station-keeping responses observed by Kennedy (1985) in his aphid experiments and incorporated into his definition of migration. In appropriate circumstances, the advantages conferred by preemptive departure will favor migration over extended foraging or ranging as an adaptation. Preemption cannot rely on proximate cues, such as low temperature or food shortage, to initiate migration, and selection therefore acts on the migrants' responses either to surrogates that forecast habitat deterioration (such as photoperiod or increased population density) or to endogenous rhythms or "internal clocks" (Ramenofsky and Wingfield 2007).

## Migration and populations

For much of its history, ecology has focused more on population dynamics over time than on changes in spatial distributions. In this perspective, changes in population size arise both through births and deaths and through emigration and immigration to and from external sinks and sources (Thomas and Kunin 1999). By recognizing the spatial dimensions and adding movement to the dynamics, it becomes evident that a cohort of individuals and their descendants form a population regardless of where they are, and follow a trajectory through both space and time (Taylor and Taylor 1977, Solbreck 1985, Taylor 1986, Drake et al. 1995). Viewed from this perspective, emigration and immigration fuse, and the movements of individuals maintain the structure and cohesion of populations and determine their connectivity (Webster and Marra 2005, Cheke and Tratalos 2007). Movement is now seen as a key process in its own right and not just an alternative mechanism contributing to effective birth and death rates. Depending on the extent of spatial variation and of developmental desynchronization, temporarily distinct subpopulations may form and remain isolated for one or more generations. The population trajectory then consists of a number of strands that may split and merge through

space and time, and when mapped, the resulting three-dimensional pathway forms a tangled reticulum that has been analogized to a fern stele (Taylor and Taylor 1977).

Analysis of population trajectories reveals the processes leading to a reticular form. Classic examples are various species of locust and any of several species of nomadic and seminomadic birds (Cheke and Tratalos 2007). Population trajectories of such nomads typically differ between years as resources vary, but often an overall to-and-fro trend in the pathway can be discerned (Griffioen and Clarke 2002, Deveson et al. 2005). The distributions of aphids and other insects over the British Isles display reticular patterns over seasons and years, and populations are resupplied each spring by infusions from the continent (Taylor 1986). On a smaller scale, migration allows the milkweed bug (*Lygaeus equestris*) to exploit isolated habitat islands of a few square meters each on limestone outcrops in Sweden (Solbreck 1985). With migration, accompanied by temporary suppression of reproduction, the bugs track resources (including single milkweed plants), avoid intraspecific competition, and overwinter in microclimatically suitable diapause sites among the rocks.

The case of *L. equestris* raises interesting questions concerning the role of movements in the dynamics of subdivided populations or *metapopulations*. Metapopulations are the subject of a large literature (Hanski 1999, Ovaskainen and Hanski 2004) that concerns populations spread over an ensemble of separated habitats in which colonization and extinction of subpopulations occur, with connectivity between subpopulations maintained by movement. The principal application to conservation in fragmented landscapes is easily appreciated. While movements between fragments are often referred to as "migration" in the metapopulation literature (e.g., Ovaskainen and Hanski 2004), most are probably what we call ranging. Although it is unlikely that migration (in our sense) contributes to structure in most metapopulations so far studied (but see Cheke and Tratalos 2007), it would be interesting to know how frequently migratory behavior occurs within metapopulations in nature. It may be worth considering "migratory metapopulations" as a special case; this would be compatible with characteristics of nomadic migrants such as locusts and quelea birds (Cheke and Tratalos 2007). In any event, the focus has usually been on the outcomes of movements in the form of colonizations and the contribution of departures to local extinctions, and field data are usually based on mark-recapture methods or surveys rather than direct observation of movement behavior. We agree with Thomas and Kunin (1999) that studies of spatiotemporal population dynamics need to examine behavioral processes as well as patterns and outcomes.

In "two worlds" and other round-trip migratory pathways in which migrants return repeatedly to a breeding area, population-genetic and demographic processes may be little different from those of a resident population. Both distant and local environments will of course determine year-to-year variation in mortality and breeding condition. Young that have not bred previously will most likely seek a breeding site by

ranging over suitable habitat either before departing or after completing their round-trip annual migration (Winkler 2005), but the behavior of settling is not well studied. In some species, animals from different parts of the breeding range occupy different nonbreeding areas, either in a “leapfrog” pattern across latitudes or in a “chain” pattern that may be either latitudinal or longitudinal; there may also be movements within the nonbreeding range (Bell 2005). The adaptation that steers the migrants along their pathways is presumably coded genetically, so offspring of crosses between members of different subpopulations may be poorly adapted to find either parental breeding site and therefore selected against. Such processes may help to maintain subspecies or even lead to full speciation (Irwin and Irwin 2005). Alternatively, extensive mixing may limit the development of complex or differentiated migration pathways, as seems to be the case with monarch butterflies (*Danaus plexippus*; Brower and Boyce 1991, Shephard et al. 2002) and Mexican free-tailed bats (*Tadarida brasiliensis mexicana*; Russell et al. 2005).

In addition to describing their dynamics in time and space, populations can be characterized by the mean distance among the individuals within them (Southwood 1981). When animals are attracted to each other, they congregate; if they gather in the same habitat, they aggregate. In either case, the mean distance among individuals decreases, at least on a local scale. In contrast, behavioral responses can result in animals in a population moving apart, in which case they disperse. Foraging or commuting, ranging, and migration can all be processes causing either aggregation/congregation or dispersal (Kennedy 1985, Taylor 1986, Dingle 1996). However, the term “dispersal” is also used in the rather different sense of leaving one’s place of birth to breed elsewhere (“postnatal dispersal”) and of movements between successive breeding places (“breeding dispersal”; Greenwood and Harvey 1982, Bullock et al. 2002). These movements are probably in most cases what we term “ranging,” but they could also be migration (e.g., as in Kennedy’s [1966] aphids). Although they increase the distance between young and their parents, and between the young of a clutch or litter if departures are in different directions, the movements of unrelated young will cross, and young that end up in a particular locality will have arrived from different directions—an example of convergent movement. Overall, the population experiences little change in the mean distance between individuals; it therefore does not exhibit dispersal in the original sense. The functions of these movements appear to be reoccupation of vacant habitat units, readjustments to local changes in habitat quality, and avoidance of kin competition and inbreeding (Gandon and Michalakis 2001). At the population level, they result in *mixing*, the internal redistribution of individuals that leaves the location and spatial extent of the population unchanged. Population mixing can also occur with migration (e.g., monarch butterflies, bats), but it need not do so (e.g., some “two worlds” bird migrations); with migration, however, there is displacement as well as mixing.

## Conclusions: What is migration, and what studies are needed?

We note first that a definition of a trait or syndrome in biology should provide clear indication that it can respond to natural selection. With few exceptions, that means the definition must be couched in terms of individuals. This is no less true for migration. Selection has produced specific behaviors and responses to the environment to solve common problems that distinguish migration from other forms of movement (Kennedy 1985, Dingle 1996). At the same time, it is equally clear that migration is an important population phenomenon. Individual behaviors produce a population outcome, and that outcome provides the selection acting back on individuals. Although migration can be *defined* only for individuals (behavior, syndromes), it can be *described* in terms of population outcomes (dynamics, trajectories, displacements; table 1; Gatehouse 1987). The answer to the question “What is migration?” thus includes all aspects of a multilevel syndrome (Rogers 1983), its consequences for the dynamics of populations, and the relationships between them (figure 1).

A great advantage of the definition of migration from Kennedy (1985) cited above is that it invites direct empirical investigation at behavioral and lower organizational levels, potentially leading to several productive lines of research. There are explicit hypotheses to test using, for example, straightforward (at least in principle) experiments of a stimulus–response type. Although not all aspects of the syndrome may be present in any one migrant, experiments should still distinguish migratory from other types of movement behavior by revealing the suppression of responses to resources. An obligate migrant will continue moving and bypass breeding sites or food while on its trajectory. Well-known migrants, such as arctic terns (*Sterna paradisaea*) and salmon (*Oncorhynchus* and *Salmo* spp.), have been observed to do just that (see table 17-1 in Dingle 1996), and, interestingly, so have some young rodents (called “innate dispersers” by Howard 1960). Like any good hypothesis, Kennedy’s definition identifies means by which it can be falsified. Thus it can be modified, improved, or replaced, but to accomplish these, any proposed alternative must distinguish individual migrants from those undertaking other kinds of movement and provide clear means, at least implicitly, by which empirical observation or experiment can make the distinction. If definitions are too narrow, we need to know what characteristics should be included to broaden them. What is obvious is that analyses of migration as an explicit behavioral syndrome are all too rare. We do not minimize the methodological difficulties in performing such analyses, but neither do we apologize for the complexities presented by migration.

Our second observation is that studies of animal movements, including migration, need to be more broadly based. Students of migration need to focus more on migration as a behavioral, ecological, and evolutionary phenomenon rather than as an event that occurs in a particular taxon. The use of movement to exploit separated and ephemeral habitats and resources transcends particular species and taxonomic groups,



and its investigation should do likewise. Much could be learned and heuristic approaches developed from a comparative view. There is also little linkage between migration research and bodies of work on foraging, dispersal, and spatially extended populations or metapopulations. Such isolation does not appear defensible. Each field of study has strengths that can contribute to others. For example, as already noted, flight-mill and selection-experiment approaches to studying migratory behavior, pioneered by entomologists, are now being employed on birds. A behavioral viewpoint might broaden perspectives in fields (e.g., postnatal “dispersal,” metapopulations) in which trajectories and populations are currently the focus. Research on insect migration would in turn benefit from an infusion of population-level theory and modeling, as entomologists now rarely venture into these areas. One obstacle to such cross-disciplinary interactions will surely be differing terminologies. Our third observation is that imprecise and ambiguous terminology—including the core terms “migration” and “dispersal”—is systemic across this field and is hindering the development of the conceptual frameworks needed to advance understanding and to design revealing experiments and fieldwork.

Our final observation is that the field needs to recognize that there may be different kinds and degrees of migration. We suspect that “classic” examples of migration may be extreme cases and the exception rather than the rule (even for birds). Investigations of migratory adaptations that seem less complete than these (or in which migration is facultative rather than obligatory) might prove particularly revealing. Such studies might, for example, allow examination of trade-offs between migration and alternative strategies. Can migration be combined with other strategies, or is it always categorically distinct? A case in point is the integration of stopovers into migratory trajectories. Are there species or populations in which the types of outcome normally associated with migration are achieved through some sort of directed foraging or ranging? How distinct are the boundaries between migration and ranging, or between behavioral adaptations leading to dispersal as opposed to aggregation? These questions are applicable to a range of organisms; to answer them will require the ecumenical approach we advocate.

## Acknowledgments

H. D. wishes to thank Meron Zalucki for support, discussion, and suggestions; Matt Watts for technical support and assistance; and the University of New South Wales for travel funding in support of manuscript preparation. H. D.’s long-term research on migration has been funded by the US National Science Foundation. V. A. D. acknowledges funding support from the Australian Research Council.

## References cited

Åkesson S, Hedenström A. 2007. How migrants get there: Migratory performance and orientation. *BioScience* 57: 123–133. doi:10.1641/B570207  
 Baker RR. 1978. *The Evolutionary Ecology of Animal Migration*. London: Hodder and Stoughton.

Bell CP. 2005. Inter- and intrapopulation migration patterns. Pages 41–52 in Greenberg R, Marra PP, eds. *Birds of Two Worlds: The Ecology and Evolution of Migration*. Baltimore: Johns Hopkins University Press.  
 Berthold P, Gwinner E, Sonnenschein E, eds. 2003. *Avian Migration*. Berlin: Springer.  
 Both C, Bouwhuys S, Lessells CM, Visser ME. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* 441: 81–83.  
 Brower AVZ, Boyce TM. 1991. Mitochondrial DNA variation in monarch butterflies. *Evolution* 45: 1281–1286.  
 Bullock JM, Kenward RE, Hails RS, eds. 2002. *Dispersal Ecology: The 42nd Symposium of the British Ecological Society*. Oxford (United Kingdom): Blackwell.  
 Cheke RA, Tratalos JA. 2007. Migration, patchiness, and population processes illustrated by two migrant pests. *BioScience* 57: 145–154. doi:10.1641/B570209  
 Cooter RJ. 1983. Studies on the flight of black-flies (Diptera: Simuliidae). II. Flight performance of three cytospecies in the complex of *Simulium damnosum* Theobald. *Bulletin of Entomological Research* 73: 275–288.  
 Denno RF, Roderick GK, Olmstead KL, Dobl HG. 1991. Density related migration in planthoppers (Homoptera: Delphacidae): The role of habitat persistence. *American Naturalist* 138: 1513–1541.  
 Deveson ED, Drake VA, Hunter DM, Walker PW, Wang HK. 2005. Evidence from traditional and new technologies for northward migrations of Australian plague locust (*Chortoicetes terminifera*) (Walker) (Orthoptera: Acrididae) to western Queensland. *Austral Ecology* 30: 928–943.  
 Dingle H. 1996. *Migration: The Biology of Life on the Move*. New York: Oxford University Press.  
 ———. 2001. The evolution of migratory syndromes in insects. Pages 159–181 in Woiwood LP, Reynolds DR, Thomas CD, eds. *Insect Movement: Mechanisms and Consequences*. Wallingford (United Kingdom): CABI.  
 ———. 2006. Animal migration: Is there a common migratory syndrome? *Journal of Ornithology* 147: 212–220.  
 Drake VA, Gatehouse AG. 1996. Population trajectories through space and time: A holistic approach to insect migration. Pages 399–408 in Floyd RB, Sheppard AW, De Barro PJ, eds. *Frontiers of Population Ecology*. Collingwood (Australia): CSIRO.  
 Drake VA, Gatehouse AG, Farrow RA. 1995. Insect migration: A holistic conceptual model. Pages 427–457 in Drake VA, Gatehouse AG, eds. *Insect Migration: Tracking Resources through Space and Time*. Cambridge (United Kingdom): Cambridge University Press.  
 Gandon S, Michalakis Y. 2001. Multiple causes of the evolution of dispersal. Pages 155–167 in Clobert J, Danchin E, Dhondt AA, Nichols JD, eds. *Dispersal*. Oxford (United Kingdom): Oxford University Press.  
 Gatehouse AG. 1987. Migration: A behavioral process with ecological consequences? *Antenna* 11: 10–12.  
 Gauthreaux SA. 1980. The influences of long-term and short-term climatic changes on the dispersal and migration of organisms. Pages 103–174 in Gauthreaux SA, ed. *Animal Migration, Orientation, and Navigation*. New York: Academic Press.  
 Greenberg R, Marra PP, eds. 2005. *Birds of Two Worlds: The Ecology and Evolution of Migration*. Baltimore: Johns Hopkins University Press.  
 Greenwood PJ, Harvey PH. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13: 1–21.  
 Griffioen PA, Clarke MF. 2002. Large-scale bird-movement patterns in eastern Australian atlas data. *Emu* 102: 97–125.  
 Han E-N, Gatehouse AG. 1993. Flight capacity: Genetic determination and physiological constraints in a migratory moth *Mythimna separata*. *Physiological Entomology* 18: 183–188.  
 Hanski I. 1999. *Metapopulation Ecology*. New York: Oxford University Press.  
 Hardie I, Powell G. 2002. Video analysis of aphid flight behaviour. *Computers and Electronics in Agriculture* 35: 229–242.  
 Helbig AJ. 2003. Evolution of bird migration: A phylogenetic and geographic perspective. Pages 3–20 in Berthold P, Gwinner E, Sonnenschein E, eds. *Avian Migration*. Berlin: Springer.



- Hockey PAR, Leseberg A, Loewenthal D. 2003. Dispersal and migration of juvenile African black oystercatchers *Haematopus moquini*. *Ibis* 145: E114–E123.
- Howard WE. 1960. Innate and environmental dispersal of individual vertebrates. *American Midland Naturalist* 63: 152–161.
- Irwin DE, Irwin JH. 2005. Siberian migratory divides. Pages 27–40 in Greenberg R, Marra PP, eds. *Birds of Two Worlds: The Ecology and Evolution of Migration*. Baltimore: Johns Hopkins University Press.
- Jahn AE, Levey DJ, Smith KG. 2004. Reflections across hemispheres: A system-wide approach to New World bird migration. *The Auk* 121: 1005–1013.
- Kennedy JS. 1966. Nervous coordination of instincts. *Cambridge Research* 2: 29–32.
- . 1985. Migration: Behavioral and ecological. Pages 5–26 in Rankin MA, ed. *Migration: Mechanisms and Adaptive Significance*. Contributions in Marine Science 27 (suppl.). Austin: Marine Science Institute, University of Texas.
- Kenward RE, Rushton SP, Perrins CM, Macdonald DW, South AB. 2002. From marking to modelling: Dispersal study techniques for land vertebrates. Pages 50–71 in Bullock JM, Kenward RE, Hails RS, eds. *Dispersal Ecology: The 42nd Symposium of the British Ecological Society*. Oxford (United Kingdom): Blackwell.
- McKeown BA. 1984. *Fish Migration*. London: Croom Helm.
- Newton I, Dale L. 1996. Bird migration at different latitudes in eastern North America. *The Auk* 113: 626–635.
- Ovaskainen O, Hanski I. 2004. From individual behavior to metapopulation dynamics: Unifying the patchy population and classic metapopulation models. *American Naturalist* 164: 364–377.
- Pennycuik C, Alerstam T, Hedenström A. 1997. A new low-turbulence wind tunnel for bird flight experiments at Lund University, Sweden. *Journal of Experimental Biology* 200: 1441–1449.
- Piersma T, Pérez-Tris J, Mouritsen H, Bauchinger U, Bairlein, F. 2005. Is there a “migratory syndrome” common to all migrant birds? *Annals of the New York Academy of Sciences* 1046: 282–293.
- Pulido F. 2007. The genetics and evolution of avian migration. *BioScience* 57: 165–174. doi:10.1641/B570211
- Pulido F, Berthold P. 2003. The quantitative genetic analysis of migratory behaviour. Pages 53–77 in Berthold P, Gwinner E, Sonnenschein E, eds. *Avian Migration*. Berlin: Springer.
- Ramenofsky M, Wingfield JC. 2007. Regulation of migration. *BioScience* 57: 135–143. doi:10.1641/B570208
- Rankin MA, ed. 1985. *Migration: Mechanisms and Adaptive Significance*. Contributions in Marine Science 27 (suppl.). Austin: Marine Science Institute, University of Texas.
- Roff DA, Fairbairn DJ. 2007. The evolution and genetics of migration in insects. *BioScience* 57: 155–164. doi:10.1641/B570210
- Rogers D. 1983. Pattern and process in large-scale animal movement. Pages 160–180 in Swingland IR, Greenwood PJ, eds. *The Ecology of Animal Movement*. Oxford (United Kingdom): Clarendon Press.
- Russell AL, Medellín RA, McCracken GF. 2005. Genetic variation and migration in the Mexican free-tailed bat (*Tadarida brasiliensis mexicana*). *Molecular Ecology* 14: 2207–2222.
- Shepherd JM, Hughes JM, Zalucki MP. 2002. Genetic differentiation between Australian and North American populations of the monarch butterfly *Danaus plexippus* (L.) (Lepidoptera: Nymphalidae): An exploration using allozyme electrophoresis. *Biological Journal of the Linnean Society* 75: 437–452.
- Sih A, Bell AM, Johnson JC, Ziemba RE. 2004. Behavioral syndromes: An integrated overview. *Quarterly Review of Biology* 79: 241–277.
- Solbreck C. 1978. Migration, diapause, and direct development as alternative life histories in a seed bug, *Neocoryphus bicrucis*. Pages 195–217 in Dingle H, ed. *Evolution of Insect Migration and Diapause*. New York: Springer.
- . 1985. Insect migration strategies and population dynamics. Pages 641–662 in Rankin MA, ed. *Migration: Mechanisms and Adaptive Significance*. Contributions to Marine Science 27 (suppl.). Austin: Marine Science Institute, University of Texas.
- Southwood TRE. 1962. Migration of terrestrial arthropods in relation to habitat. *Biological Reviews* 37: 171–214.
- . 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology* 46: 337–365.
- . 1981. Ecological aspects of insect migration. Pages 196–208 in Aidley DJ, ed. *Animal Migration*. Cambridge (United Kingdom): Cambridge University Press.
- Taylor LR. 1986. Synoptic ecology, migration of the second kind, and the Rothamsted Insect Survey. Presidential Address. *Journal of Animal Ecology* 55: 1–38.
- Taylor LR, Taylor RAJ. 1977. Aggregation, migration and population mechanics. *Nature* 265: 415–421.
- Thomas CD, Kunin WE. 1999. The spatial structure of populations. *Journal of Animal Ecology* 68: 647–657.
- van Noordwijk AJ, et al. 2006. A framework for the study of genetic variation in migratory behaviour. *Journal of Ornithology* 147: 221–233.
- Webster MS, Marra PP. 2005. The importance of understanding migratory connectivity and seasonal interactions. Pages 199–209 in Greenberg R, Marra PP, eds. *Birds of Two Worlds: The Ecology and Evolution of Migration*. Baltimore: Johns Hopkins University Press.
- Werfel J, Bar-Yam Y. 2004. The evolution of reproductive restraint through social communication. *Proceedings of the National Academy of Sciences* 101: 11019–11024.
- Wilson DS. 1997. Introduction: Multilevel selection theory comes of age. *American Naturalist* 150: S1–S4.
- Winkler DW. 2005. How do migration and dispersal interact? Pages 401–413 in Greenberg R, Marra PP, eds. *Birds of Two Worlds: The Ecology and Evolution of Migration*. Baltimore: Johns Hopkins University Press.

doi:10.1641/B570206

Include this information when citing this material.