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PERSPECTIVE

How and Why Do Insects Migrate?

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Countless numbers of insects migrate within and between continents every year, and yet we know very little about the ultimate reasons and proximate mechanisms that would explain these mass movements. Here we suggest that perhaps the most important reason for insects to migrate is to hedge their reproductive bets. By spreading their breeding efforts in space and time, insects distribute their offspring over a range of environmental conditions. We show how the study of individual long-distance movements of insects may contribute to a better understanding of migration. In the future, advances in tracking methods may enable the global surveillance of large insects such as desert locusts.

Large-scale movements of insects have enormous implications for human welfare (*1*), including catastrophic losses of crops (*2*), the spread of diseases to people and livestock (*3*), and the provisioning of essential ecosystem services such as crop pollination (*4*). In sheer numbers of individuals, insect migration far outweighs other migratory phenomena (*5*). Moreover, in terms of total moving biomass, the migrations of individual insect species rival and sometimes outstrip the largest extant herds and flocks of some well-known migratory mammals and birds (Table 1). And yet there is at least one fundamental difference between insect and most vertebrate migrations (*6*, *7*): As a rule, individual insects do not make a round-trip journey that returns them to the area from which they departed. Even in the case of the monarch butterfly (*Danaus plexippus*) (Fig. 1A), one of the best-studied migratory insects, few if any of the individuals wintering in Mexico return to their natal areas. Instead, monarchs repopulate northern latitudes through a process of intergenerational migration, whereby successive broods advance northward (*8*, *9*). Thus, return migration, the most common type of migration in birds and mammals (*7*), has yet to be documented in insects.

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Migration Strategies in Insects

Researchers accustomed to viewing long-range animal movements through the prism of classic return (i.e., round-trip) migration would likely categorize many so-called insect migrations as dispersal events (*6*). Entomologists, however, would disagree. Indeed, major reviews of this subject in the entomological literature have recommended abandonment of the term "dispersal" to describe insect movements; instead, all long-range movements of insects would be considered "migrations" (*1*, *7*, *10*, *11*).

Migration by vertebrates is often viewed as a mechanism for exploiting high-quality resources that are available during only a portion of the year [typically the breeding season (*7*, *10*)]. In the case of insect migrations, which we define here as repeated phenomena of directional movement that are cyclical in nature, the ultimate reasons are less clear. If insects are not able to return to a high-quality patch in a subsequent year, then why migrate at all? Although considerable progress has been made toward understanding patterns of insect migration (*1*, *11*), especially with respect to certain moths (*12*), the ultimate selection pressures resulting in these spectacular and ubiquitous movements remain mysterious. Intuitively, one expects migratory movements to evolve only when the fitness benefits exceed those of remaining in the current habitat (*13*). Whether this reasoning applies in the case of insect migrations is unclear. Because insects do not have to provide long-term care for their offspring, they can in theory reproduce in their natal area, along a migratory route, or in a discrete "winter range." This differentiates them from the classic vertebrate return-migration model. By spreading their breeding efforts both spatially and temporally, insects have the ability to "hedge their bets" by distributing their offspring across a range of areas and conditions that may be amenable for future reproduction (*14*).

To determine whether this bet-hedging hypothesis is a valid explanation for most (or any) insect migrations, one would need to know the reproductive output (and, ideally, success) of individual insects along their migratory route. Do

Table 1. Biomass of migrating animals.

Class	Species	Location	Size of herd, swarm, or flock	Biomass (tons)	Source (reference)
Insects	Darner (dragonfly), *Aeshna bonariensis*	Argentina	4–6 billion	4000	(*15*)
	Monarch butterfly, *Danaus plexippus*	Winter grounds in Mexico	100–200 million	40–80	(*39*, *40*)
	Desert locust, *Schistocerca gregaria*	Africa, Middle East, Asia	10^9–10^{11}	200,000	(*5*)
Mammals	Wildebeest, *Connochaetes taurinus*	Serengeti, Kenya and Tanzania, Africa	1.3 million	280,000	(*41*)
	Mexican free-tailed bat, *Tadarida brasiliensis mexicana*	Carlsbad Cavern, New Mexico, North America	20 million	300	(*42*)
Birds	Lesser sandhill crane, *Grus c. canadensis*	Platte River, Nebraska, North America	450,000	1440	(*43*)

individual insects simply continue to migrate until they die from exhaustion, or do they terminate their migration when reaching a suitable habitat? That is, do they simply move along a habitat cline and spread out their propagules, or do they search for a spatial peak in the reproductive landscape, as most long-distance migratory birds do (*6*)? For example, green darner dragonflies (*Anax junius*) engage in spectacular autumn migrations along the eastern seaboard of the United States (*15*). Many of the females captured in the fall are gravid, yet we do not know whether a given female is traveling to a particular site or region to lay its eggs, or whether it is slowly moving south and laying a portion of its eggs in suitable ponds along the way. There is no shortage of questions to challenge (or frustrate) researchers interested in insect migration.

Despite the importance of knowing the behavior of individual insects, the study of insect migratory movement in the field is usually only possible at the population level using radar observations (*16*), huge aerial samplers, and/or ground surveys (*17*). What seems to be emerging from several major research programs on agriculturally important pests [e.g., desert locust, *Schistocerca gregaria* (*18*) (Fig. 1B)] is that insects are often facultative migrants that respond to changes in habitat availability, quality, and level of crowding (*17*, *19*). A large majority of insects that migrate do so pre-reproductively, suggesting that such migration is in response to some indication that reproduction will be suboptimal in the natal area (*17*). This behavior may represent a multigenerational bet-hedging strategy that allows the offspring to avoid overcrowding or deteriorating environmental conditions. Spatial heterogeneity of the habitat—in particular, the existence of good and bad patches—may also select for migratory behavior as a bet-hedging strategy (*14*). However, too little is currently known about the strategies of individual insects to generalize about the ultimate factors responsible for the movements of megatons of insects within and between continents.

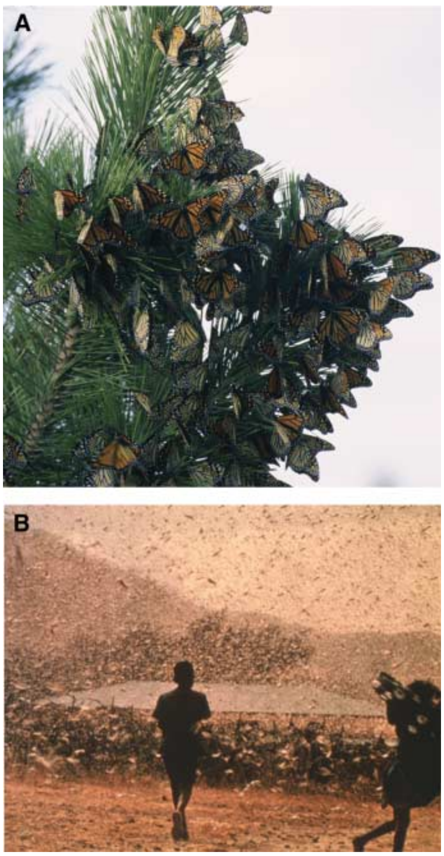

Fig. 1. Examples of large insects that migrate in swarms (see Table 1). (**A**) Monarch (*Danaus plexippus*); (**B**) desert locust (*Schistocerca gregaria*). [Credit: (A) U.S. Fish and Wildlife Service; (B) J. E. Estes (1939–2001), University of California Santa Barbara Geography Department]

Migration Mechanisms in Insects

At small scales, insect navigation is one of the best understood subjects in animal navigation (*20*). Far less is known about the orientation of migratory insects, however. In particular it is unclear how and whether insects decide to terminate migration, and what decision rules they employ during migration. In the case of migrating birds, a species-specific wintering ground is usually the goal, and it is located by an endogenous program of vector navigation in the first migratory journey, and possibly by "true navigation" based on experience in subsequent years (*21*). If migratory insects do not make round-trip journeys, then it is unlikely they develop navigational mechanisms based on experience (*22*). Yet, in the case of monarch butterflies, winter sites are highly localized year after year (*22*), suggesting some tight control of spatial movements across the 3000 km of North American landmass. To find their wintering sites, an environmental cue or a genetic vector engrained in an endogenous program similar to that used by juvenile migrating birds (*6*) is presumably employed.

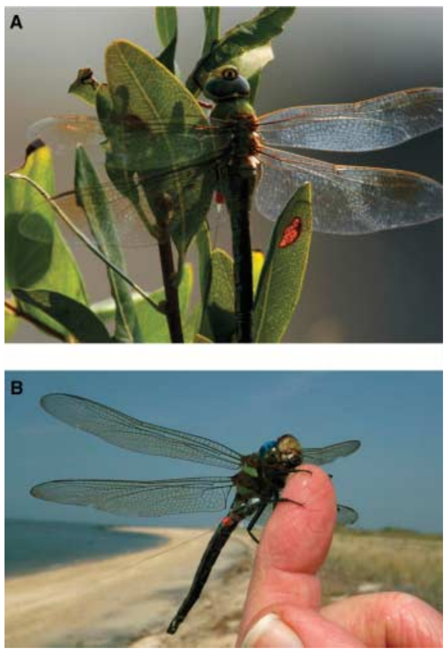

Fig. 2. Attachment of microtransmitters to migrating dragonflies (*34*). (**A**) Green darner resting on vegetation, with microtransmitter attached to ventral thorax. (**B**) Swamp darner warming up on finger before continuing migration along the Delaware Bay, New Jersey. [Credit: C. Ziegler]

Insects that migrate in the flight boundary layer (*23*), below the prevailing winds, must have a mechanism to maintain a heading. This has been proposed for monarch butterflies, with a 1° per day change accounting for the orientation of these animals through the course of a year (*9*). However, more recent data do not fully support this hypothesis (*24*). Geographical features may play an additional role in determining direction for monarchs (*24*). Orientation mechanisms to allow a migrating insect to maintain a heading have been investigated in a number of butterflies and moths and include a sun compass (*25*, *26*) and possibly a magnetic compass (*27*). Migrating butterflies and moths may also compensate for wind drift (*28*, *29*), and anecdotal evidence suggests that individuals are able even to compensate for large displacements (*30*), although this finding is controversial (*22*). The genetic control of insect migratory flight directions has yet to be confirmed.

Why We Don't Know More: The Future of Insect Migration Studies

The problems associated with studying insect migration are the same ones bedeviling anyone who wishes to study large-scale movements in a small flying animal, whether it is a bird, bat, or insect. Tracking the path of the animal over long distances has been the primary obstacle (*31*). Only recently have radio transmitters become small enough to attach to small birds and large insects (*32*) (Fig. 2), and the tracking of such animals has provided exciting new insights into migratory behavior (*31*, *33*). For example, radio tracking aided by small search planes has revealed that green darner dragonflies use falling nocturnal temperatures as a cue to initiate their southward migration (*34*). Individuals generally fly with the prevailing winds, but change or even reverse their migratory direction when encountering large geographical barriers such as ocean bays. Similar behavior in similar sites has been recorded in migratory songbirds, raising the possibility that both birds and dragonflies follow similar navigational rules (*6*).

We are entering an exciting new era for the study of insect migration. The genetic basis of insect migration can now be investigated using modern genomic methods (*35*). Ideally, lab-based experiments could be linked to field measurements of genetic polymorphisms of migratory potential that occur in certain insects; these polymorphisms, in turn, could be related to habitat heterogeneity, a result that could allow us to link ultimate and proximate aspects of insect migration (*14*, *36*). Such studies may also provide new insights into the genetic control of migratory flight decisions per se (*9*). Biomechanical models can be used to improve our understanding of the energetic costs of insect migration (*25*, *27–29*), and the trade-offs those costs impose on other aspects of an insect's life history (*37*). Most important, our ability to track small animals over large distances is improving steadily. Current systems for tracking animals globally are unsuitable for creatures smaller than ~500 g, which excludes the majority of birds and bats as well as all insects. However, the signals from transmitters now being used to track dragonflies could be received from space with the installation of a small-animal tracking satellite. Such a system is technologically feasible (*38*). The ability to follow individual insects throughout their migrations will be invaluable to understanding the selective forces behind insect migration. We also need data on individual insects to understand how migratory abundance changes with climatic cycles and with the use of pesticides on targeted and nontargeted species. Until the migratory behavior of individuals can be separated out from the behavior of populations, insect migration is likely to remain a poorly understood but immensely important phenomenon.

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REVIEW

Going East: New Genetic and Archaeological Perspectives on the Modern Human Colonization of Eurasia

Paul Mellars

The pattern of dispersal of biologically and behaviorally modern human populations from their African origins to the rest of the occupied world between ~60,000 and 40,000 years ago is at present a topic of lively debate, centering principally on the issue of single versus multiple dispersals. Here I argue that the archaeological and genetic evidence points to a single successful dispersal event, which took genetically and culturally modern populations fairly rapidly across southern and southeastern Asia into Australasia, and with only a secondary and later dispersal into Europe.

Research over the past 20 years has provided an increasingly clear picture of the way in which our own species (*Homo sapiens*) emerged and subsequently spread across the rest of the occupied world. DNA evidence and fossil skeletal remains indicate that human populations that were essentially "modern" both anatomically and in their mitochondrial and Y-chromosome lineages had emerged in Africa by at least 150,000 years ago, perhaps closer to 200,000 years ago (*1–11*). Studies of present-day world populations (especially those based on the maternally inherited mitochondrial DNA) strongly suggest that a small subset of these African populations made the crossing from northeastern Africa, probably over the mouth of the Red Sea, and subsequently dispersed into Arabia and southern Asia sometime before 50,000 years before present (yr B.P.) (*2*, *8*, *12–17*) (Fig. 1). Recent studies have suggested that these populations expanded rapidly along the coastlines of southern Asia, southeastern Asia, and Indonesia to arrive in both Malaysia and the Andaman Islands by at least 55,000 yr B.P., and conceivably as early as 60,000 to 65,000 yr B.P. (*12*, *18–21*)—though more recent estimates of mitochondrial DNA mutation rates (*8*) suggest that these figures may be overestimates. As Carl Sauer pointed out in 1962 (*22*), a strongly coastal pattern of dispersal would make good sense in ecological and demographic terms, because this would presumably have required only limited economic adaptations from one coastal location to another.

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