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Dispersal strategies in terrestrial insects

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Terrestrial insects frequently disperse and/or migrate, either through their own self-directed actions or via other vehicles. Here, the following recent advances in the study of insect dispersal are highlighted: (1) components of classic hypotheses (marginal value theorem and inbreeding avoidance via sex-specific dispersal) have found varying degrees of recent support; (2) modern genetic tools have uncovered several candidate dispersal genes; (3) dispersal syndromes vary in their genetic and/or physiological constraints; and (4) common laboratory techniques may not accurately reflect dispersal in the field. A common theme is the tendency for breakthroughs to be concentrated in species with extremely well-defined dispersal phenotypes (e.g., long-distance migrants, wing polymorphic insects), suggesting the need for increased focus on species exhibiting less self-directed modes of dispersal.

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Introduction

Class Insecta is known for two of the greatest evolutionary milestones in Animalia: (1) it contains, by far, the largest number of species (approximately 5.5 million) [1]; and (2) it is the first lineage to have evolved powered flight (possibly during the Early Devonian) [2]. An evolutionary advantage of the latter is increased capacity for dispersal and/or migration (see **Box 1** for discussion of the distinction between the two terms), which can yield substantial adaptive benefits such as avoidance of environmental stressors and access to seasonally-available habitats [3]. Dispersal is, of course, also critical to the study of extant insect populations via its importance in predicting their establishment, seasonality of occurrence, and rate of spread [4–6].

As with all behaviors, there is value to studying both the proximate and ultimate causes of insect dispersal strategies (**Figure 1**). This brief review utilizes this approach to highlight recent advances, with specific reference to (1) classic hypotheses of how dispersal may be optimized via natural selection; (2) the genetics behind dispersal, which determines its evolutionary potential; and (3) the evolution of suites of life history traits ('syndromes') correlated with dispersal by flight. Finally, I will address the more practical issue of whether or not laboratory techniques commonly employed by entomologists accurately reflect insect dispersal in the field.

Optimization of dispersal decisions in insects

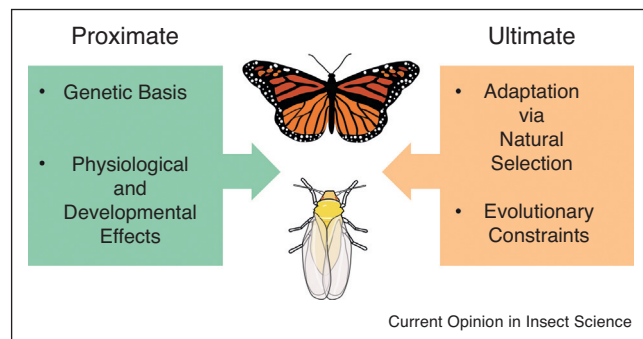
Optimality models of dispersal commonly emphasize the following benefits of leaving a site, weighed against the safety risks [7]: (1) increased habitat sampling, and (2) avoidance of inbreeding depression at the natal site. With respect to the former, the marginal value theorem (MVT) posits that an optimal forager adjusts patch residency time based on resource richness and time costs [8,9]. For the MVT to be realistic, however, insects must be able to gather information on these variables. Although host location cues have received considerable attention in insects, recent studies of parasitoid wasps by Parent and colleagues [10,11] have confirmed their ability to measure time while foraging. First, the egg parasitoid *Trichogramma euproctidis* appears to measure time by remembering the duration of the pre-oviposition host assessment period (the 'initial transit duration') [10]. Female *T. euproctidis* lay more eggs on hosts for which the initial transit duration was longer, an effect that is independent of host egg size. Another parasitoid species, the braconid *Microplitis croceipes*, is able to associate time intervals with odors [11]. In this study, female parasitoids

Box 1 The distinction between dispersal and migration.

Dispersal and migration are related concepts that often have similar effects on gene flow in populations. Although recognizing the myriad definitions and population-level outcomes of migration [40], migration is defined here as a characteristic of individuals and contains the key attributes noted by Kennedy [41]: (1) inhibition of responses to typical 'station keeping' cues used to locate resources; (2) abandonment of the home range via this extended movement; and (3) as a behavior, it is 'persistent and straightened out', occurring regardless of whether the animal is using its own locomotory apparatus or not (e.g., using a current). Dispersal has been defined in two ways [40], the latter of which is emphasized in this review: (1) an increase in distance between members of a population; or (2) behaviors leading to displacement from the natal habitat or movements between breeding habitats. Here, it is recognized that migration produces movements that may (or may not) result in dispersal according to each sense of the word.

2 Behavioral ecology

Figure 1



Dispersal and migratory behaviors have both proximate and ultimate causes. Proximate mechanisms include a behavior's genetic basis, as well as its potential regulation through physiological (neuronal, hormonal, or cell signaling pathways) or developmental processes (e.g., learning). Ultimate mechanisms explain the evolution of a behavior, both in terms of optimization via adaptation and evolutionary constraints due to life history trade-offs or phylogenetic history. The two migratory insect species pictured differ greatly in the degree to which we understand this aspect of their biology, illustrating the need for more research on non-traditional insect models (see text). Top: North American populations of the monarch butterfly (*Danaus plexippus*) exhibit seasonal, transgenerational migrations on a continental scale [42]. There are clear signs of a dispersal syndrome in this species; migratory individuals possess significantly larger forewings [27], and reproductive diapause is coupled with increased longevity (modulated by juvenile hormone) during the migratory period [43]. Furthermore, the molecular and genetic basis of monarch migration has been the subject of extensive study [e.g., 41]. Bottom: The sweet potato whitefly (*Bemisia tabaci*) exhibits migratory behaviors during vertical flight chamber assays, with approximately 6% of the population ignoring a green light vegetative cue in favor of sustained, positively phototactic climbs [45]. The genetic basis of this behavior has not been studied, and the species appears to exhibit only weak signs of a dispersal syndrome (i.e., subtle differences in wing morphology and mixed evidence for an oogenesis-flight syndrome) [45-47].

were trained by offering them caterpillar hosts after 5 min (short) or 30 min (long) intervals, each associated with a different odor cue (strawberry or vanilla). Successful conditioning was measured using a 'choice test' of trained parasitoids placed downwind of both odor sources following either a short or long interval since host exposure. Wasps in this assay consistently preferred the correct pairing of time interval experienced and its associated odor, with no biases connected to chamber position of the odor, training-test order, or the odor itself. Interestingly, restraining the parasitoid during training interferes with this process, suggesting that energy expenditure may also play a role in time measurement.

A common trend in insects is the tendency for one sex to exhibit higher dispersal rates [12,13]. Such sex-biased dispersal has long been considered an adaptation for inbreeding avoidance [14], especially in hymenopterans with complementary sex determination (such as all known members of Formicidae) [15-17]. Here, low

fitness diploid males (rather than normal haploid males) can be produced from fertilized eggs if homozygosity (which is expected to increase with inbreeding) exists at one or more sex determination loci. An extensive recent study with the ant *Formica exsecta* suggests that, despite substantial evidence of male-biased dispersal (twice the distance on average of queens), neither male nor female natal dispersal distance correlated with a reduction of homozygosity in workers [18]. Detailed studies that thoroughly test long-held hypotheses under field conditions are important for understanding the adaptive basis of sex-biased dispersal in insects, which may also have maladaptive consequences (e.g., increased risks of Allee effects) [5,19].

The genetic basis of insect dispersal strategies

Although the most famous candidate 'dispersal gene' is *foraging (for)*, with its 'rover-sitter' polymorphism first discovered in *Drosophila melanogaster* [20], there have been several recent studies searching for additional ones. Perhaps the most pivotal of these combined measurements of tethered flight (i.e., behaviors measured while the insect is attached to a flight mill; see the section on laboratory measures of dispersal below) with genomic analysis, revealing several candidate genes for migratory activity in the cotton bollworm (*Helicoverpa armigera*) [21**]. In this species, short and long-distance flight activity is associated with the differential expression of approximately 1.26% of the genome, with a considerable proportion of the 215 genes associated with physiological factors classically related to insect migration: lipid mobilization (presumably for flight fuel, although not all insect taxa use lipids for this purpose [22]), reduction of oxidative stress in highly active tissues, flight muscle structure, and juvenile hormone regulation. Another approach involves direct genetic manipulation to study flight-related traits. In one example, RNA interference in the *nub-Gal4* gene of *D. melanogaster* can produce wing shapes that increase in-flight maneuverability in laboratory arenas [23]. Perhaps more germane to long-distance movement, the gene editing technologies TALENs and CRISPR/Cas9 have recently been employed in the monarch butterfly (*Danaus plexippus*). Here, mutagenesis of the *clock* gene disrupts the circadian clockwork of this species, which is predicted to have strong effects on this seasonal migrant [24].

The recent advances outlined above are critical steps toward understanding the genetic architecture of insect dispersal, especially in long-distance migrants with well-defined phenotypes (see the discussion of dispersal syndromes). Terrestrial insect species vary greatly, however, in the degree to which they control potentially substantial movements through the environment. This certainly limits our ability to generalize from these important case studies. Some species disperse passively through

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