

Flight Behavior in Migrating Insects^{1, 2}

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ABSTRACT Definitions of migration can be couched in behavioral or ecological terms which are not necessarily inclusive. Long-distance movement can be achieved by insects showing a behavioral migratory phase during which they ignore cues associated with resource items. It can also be achieved by insects actively seeking a resource item(s) which is not apparent or if directed flight is overtaken by climatic conditions (e.g. winds) that they cannot counter. The behavioral distinction between migratory and non-migratory behavior can be detected under exacting laboratory conditions which provide sensory stimuli for both free flight and cues associated with resource items. The interaction of these opposing stimuli is crucial to measurement of behavioral migration. This paper reviews some of the recent work on behavioral migration in insects with particular emphasis on aphids.

KEY WORDS Behavior, flight, migration, aphids.

In 1985, J. S. Kennedy emphasized the dichotomy in the understanding of the term migration. To an insect ecologist it is 'a population re-distribution by movement, whether or not the movement is controlled by the animal through some specialized migratory behavior' (Kennedy 1985, after Taylor and Taylor 1983). On the other hand, to an insect physiologist migratory behavior can be more precisely defined as 'persistent and straightened-out movement effected by the animal's own locomotory exertions or by its active embarkation on a vehicle. It depends on some temporary inhibition of station keeping-responses, but promotes their eventual disinhibition and recurrence' (Kennedy 1985, 1992). The latter definition allows for insect movement effected by, for example, wind but such movement is actively initiated by take-off. It also allows for the possible alternation between, for example, movement and feeding which may occur during long-distance displacement while the station-keeping responses may be associated with particular requirements as diverse as food and diapause sites.

From the ecological view, migration is defined at the population level and it is not possible to identify those individuals displaced by accident or very localized movement from those displaced after specialized migratory behavior (Taylor and

¹ Dedicated to the late Professor J. S. Kennedy.

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Taylor 1983). From the behavioral perspective migration rests with the individual, although unless a readily definable marker can be found, it will be impossible to categorize a field-flying insect as behaviorally migrating or not. Flight behavior that is not migratory is described as foraging, defined as a 'reiterative locomotory activity that is readily interrupted by an encounter with a resource item of one particular kind' (Kennedy 1985). The resource item is again not restricted to food. There is a spectrum of behaviors that runs from migration through extended foraging, where there is a shorter inhibition of station-keeping responses than involved in migration, to local foraging. However, it is feasible to have long-distant displacements during a foraging flight if the resource items are widely separated or if climatic conditions prevent directed flight and access to the resource.

Laboratory Investigations of Migratory Flight Behavior

1. Tethered flight. The behavior of flying insects, with respect to migration, has been investigated by laboratory scientists over many years. Such studies have aimed to define migratory flight in behavioral terms as no laboratory flights would be considered migratory from the ecological sense as there is little or no displacement. Many studies have concerned flight capability or duration and have used tethered flight approaches. It is recognized that this represents a crude approximation to field flight as the mechano-sensory and visual cues perceived are very different (Dingle 1985). For the most part, tethered flight experiments have attempted to equate long flight durations with migratory behavior, although the readiness to take off has also been considered where this has been effected by the insect rather than the experimenter. There are a number of recognized problems with this approach including the effects of insect manipulation although this can be minimized by, for example, attaching the insect to a suitable holding device prior to the final molt and subsequent suspension from the flight apparatus (e.g. Gatehouse and Hackett 1980). The flight apparatus has ranged from stationary holder to the flight mill, which allows forward progression but with the flight path forced upon the insect. A more sophisticated device was designed by Gatehouse and Hackett (1980) which allowed for landing and re-take off with some provision for forward movement, yaw and pitch. The initial experiments also included a head wind but still-air conditions were later considered equally satisfactory (Parker and Gatehouse 1985).

Despite these inadequacies, the correlation between behavior on a laboratory flight apparatus and observed field behavior lends support to the idea that experimental manipulation is minimally intrusive. Thus take-off rates of the nutgrass (African) armyworm, *Spodoptera exempta* (Walker), were similar in the laboratory and the field (Gatehouse and Hackett 1980). In addition, long-duration flights were more frequent in convergent ladybeetles, *Hippodamia convergens* Guérin-Ménéville, field-collected during times of population movement to and from aggregation sites (Rankin and Rankin 1980) and in grasshoppers, *Melanoplus sanguinipes* (Fabr.), taken from known migratory populations than those taken from sedentary populations (Rankin et al. 1986). These results indicated that there was correlation between long-duration flights and migratory flights. Indeed, there could well be a relationship between flight potential and migratory behavior as energy reserves and flight mechanisms may be better developed (see Fescemyer 1993).

Nevertheless, extended flight duration is not strictly a measure of migratory behavior, as defined above, because in the majority of cases the minimal sensory cues are presented to the insects in order to entice them to fly. These conditions of semi-sensory deprivation cannot distinguish between foraging and migratory flight as the possible termination of flight on the presentation of a suitable resource item is overlooked. This latter point is crucial as the introduction of a calling female, a food plant or a suitable oviposition site may well terminate flight and, if it did, would indicate a foraging flight. The choice of resource item and the sensory cues that represent it would, of course, require some experimentation. However, such tethered flight experiments have continued (e.g. Sappington and Showers 1992) despite the demonstration, over 20 years ago, that male bark beetles, *Dendroctonus pseudotsugae* Hopkins and *Trypodendron lineatum* (Olivier), ceased tethered flight in response to frass odor indicating females and food (Bennett and Borden 1971). These beetles showed an initial period of flight, when these odor cues were ignored, that was equivalent to a migratory phase.

2. Free Flight. The potential for using free-flying insects and presenting them with visual cues which mimicked their host plants was recognized by Kennedy in the 1960's (Kennedy and Booth 1963). Those studies utilized the phototactic response of winged aphids that induces them to fly skywards in the field. In the laboratory a bright white light source has a similar effect, but the insect's upward progress can be countered by a downdraft of air. The evolution of aphid flight chamber design in Kennedy's hands culminated in the study of 'migratory' and 'targeted' flight in winged summer forms of the bean aphid, *Aphis fabae* Scopoli (Kennedy and Ludlow 1974). To standardize flight history only aphids on their maiden flight, just after the teneral period, were used for experiments. In that paper, 'migratory' flight referred to flight oriented towards the large overhead light source and targeted flight was oriented towards a yellow leaf-shaped card periodically presented to one side of the flying aphid. The changes in the rate of climb of the flying aphid were countered by manually altering the speed of the down-flow of air. The air speed was recorded, and it was shown that orientation to the artificial leaf was accompanied by a change in rate of climb so that the wind speed record also indicated the insect's response to the target. Targeted flight was thus indicative of a foraging flight but landing was prevented by removal of the target. These studies showed that the longer an aphid had flown, the more persistent was its attraction to the target and the more depressed was its rate of climb. Nevertheless, the target leaf often initiated targeted flight even in the first minute of maiden flight, indicating foraging behavior during the initial period of maiden flight and excluding migratory behavior.

The definitions of 'migratory' and 'targeted' flight used by Kennedy and Ludlow (1974) did not strictly separate migratory and foraging behavior. The association of targeted flight as part of foraging flight, albeit based solely on the response to visual cues, is tenable, but the description of all flight oriented towards the overhead light as 'migratory' is flawed. If when the target leaf was presented the insect showed targeted flight, then the periods of flight to the overhead light immediately adjacent to that targeted response were also part of foraging flight. The difference was that the plant-like stimulus was not presented. Foraging flight, therefore, includes targeted flight and the periods of upwardly directed flight between approach-provoking target presentations. The definition of Kennedy and

Ludlow (1974) does not adhere to the criteria for migration proposed by Kennedy (1985; see above).

Utilizing the basic concepts of the Kennedy designs, an automated aphid flight chamber was developed in the late 1980's (David and Hardie 1988). The advantages were automated operation and automated collection of data on the aphid's flight path. The latter allowed computer analysis of flight coordinates. The plant-like visual target was a circular, translucent target screen in one side wall of the chamber which was back-illuminated by a green light; this was computer controlled and presented once per minute of flight for a few seconds. Movement towards this green target could be monitored directly, rather than via a change in the rate of climb. In addition to the summer winged aphid forms flown by Kennedy and Ludlow (1974), other winged female forms were flown. In the annual life cycle of host-alternating aphid species, winged females (spring migrants) fly from the winter host plants, usually bushes or trees, to the summer, herbaceous hosts. A number of winged and wingless generations then occur when stimuli such as nutrition and crowding induce the formation of the summer winged forms. The short days of autumn induce another winged female form, the autumn migrants, which fly from the summer to the winter host plant where they give birth to the sexual female generation. During spring and summer, and under long-day conditions in the laboratory, aphids reproduce parthenogenetically and individuals form part of a genetic clone. Any differences between the adult forms, as diverse as winged or wingless, is phenotypic.

The three different winged forms, from two aphid species, *A. fabae* and the bird cherry-oat aphid *Rhopalosiphum padi* (L.), were flown in the automated flight chamber and their responses to the green target were investigated (David and Hardie 1988, Hardie et al. 1989, Nottingham and Hardie 1989, Nottingham et al. 1991). The spring forms were field-collected, and therefore not clonal, but the summer and autumn forms, of each species, were from the same cultured clones. The aphids were selected for maiden flight, just after the teneral period, and it was found that there was an initial period of migratory behavior during which the green target was ignored. During this time there was persistent flight towards the overhead light. The end of behavioral migration was judged as being when the insect consistently responded to the intermittent green target. The autumn females demonstrated a prolonged period of behavioral migration (Table 1), significantly longer than the summer forms. The range of migratory periods was also revealing in that all autumn forms required a period of flight before they were responsive to the green target and it appears that, behaviorally, they are obligatory migrants. Not all spring and summer forms showed behavioral migration, some responded to the target during the first minute of flight indicating that in the field they would only undergo a foraging flight. However, even in these forms the variation in duration of migratory flight was large, indicating phenotypic plasticity (at least in the summer forms which were clonal) which would undoubtedly spread the risk for survival should fresh host plants prove difficult to find (see Loxdale et al. 1993). In addition, the rate of climb of the autumn migrants was greater than the summer forms in *A. fabae* (25 ± 1 vs. 16 ± 0.4 cm/sec [$n = 10$; $t = 7.76$, $df = 18$, $P < 0.001$]; David and Hardie 1988).

It is possible to manipulate the migratory flight behavior of the autumn migrant of *A. fabae* (Hardie et al. 1989). In this species treatment with juvenile

Table 1. Durations of the migratory phase in the initial period of maiden flight in three winged, female forms of the black bean aphid, *Aphis fabae*, and the bird cherry-oat aphid, *Rhopalosiphum padi*.^a

Aphid form	Mean duration and range of migratory behavior (min)			
	<i>Aphis fabae</i> ^b		<i>Rhopalosiphum padi</i> ^b	
	Mean \pm SE	Range	Mean \pm SE	Range
Spring migrant	19 \pm 7	0 - 110	72 \pm 3	4 - 360
Summer migrant	15 \pm 4	0 - 99	36 \pm 8	1 - 93
Autumn migrant	184 \pm 20	41 - 384	110 \pm 23	14 - 345

^a From Nottingham and Hardie 1989, Nottingham et al. 1991.

^b n = 25 for *A. fabae* and 15 for *R. padi*.

hormone has effects that mimic long days and induce parthenogenetic reproduction, effects normally associated with the summer forms. Similarly treatment just before the final molt, but not after it, induces the early development of targeted flight. It also appears that a period of flight may not be necessary for these forms to enter the foraging phase of flight, since holding them for extended periods after adult molt (24 h without food and in darkness, to prevent flight) will induce the early appearance of targeted flight (i.e. 102 \pm 19 [n = 25] vs. 36 \pm 11 [n = 15] min; Mann-Whitney U test; U = 81, P < 0.05; Hardie in press).

Similar vertical chambers have also been used to study the free flight behavior of male and female dried fruit beetles, *Carpophilus hemipterus* (L.) (Blackmer and Phelan 1991). In these conditions the majority of flights lasted less than 15 min but all flights were readily interrupted by the introduction of a food odor (apple cider vinegar). Such interruptions involved a marked reduction in the rate of climb and often landing. Takeoff and flight could be reinitiated by removal of the food odor. The influence of this olfactory cue indicates that beetles undertake only foraging flights which are readily interruptible by resource (in this case food) stimuli. The dried fruit beetle results appear to contrast with the behavior of smaller European elm bark beetle males, *Scolytus multistriatus* (Marshall), which needed a period of flight (intermittent flight in a well lit cage) before they would respond to the aggregation pheromone by upwind flight (Choudhury and Kennedy 1980). Recent experiments with odor cues in the aphid flight chamber indicate interactions between the visual and olfactory senses but rate of climb was not affected by host or nonhost plant volatiles (Nottingham and Hardie in press).

Indications of Migratory Behavior in Field Aphids

Behavioral differences between summer and autumn aphid fliers have also been reported in the field. Thus *A. fabae* and the green peach aphid, *Myzus*

persicae (Sulzer), have been reported to fly higher in the autumn than in the summer (see Kennedy et al. 1959). Using live trapping techniques and host choice bioassays, to separate the forms when they overlapped, Tatchell et al. (1988) showed that summer forms of *R. padi* flew lower than the autumn forms. The greater rate of climb and the initial period of maiden flight during which plant visual cues are ignored (Nottingham et al. 1991) may explain these field differences. The intense readiness of the autumn migrants to migrate ensures that they leave the summer host plant, if they did not the life cycle would break down. It may ensure genetic mixing in the host-alternating species, and Tatchell et al. (1988) also suggest that the higher altitude may aid location of the taller, winter host trees. This is not to say that all host-alternating autumn fliers show an obligatory migratory behavior. For example, field reports of the hop aphid, *Phorodon humuli* (Schrunk), indicate that distance flights are not required prior to settling on the winter *Prunus* host (Eppler 1988). Preliminary observations in the automated flight chamber also indicate that these aphids are target responsive shortly after first take-off (J. Hardie and C. A. M. Campbell, Horticultural research International, Kent, U.K., unpublished data).

In summary, the detection and measurement of a behavioral component that elicits long-distance movement in insects is probably impossible to achieve in the field. The recorded long-distance travelers may or may not have undergone a behavioral migration. In the laboratory it has been possible to distinguish the migratory behavior that inhibits landing and short, foraging flights in individuals. Continued attention should be paid to introducing stimuli that are associated with resources present under natural conditions, which will eventually lead to station-keeping behavior, and to examine the response of laboratory flying insects to such stimuli. Only then can migratory flight behavior be distinguished from foraging flight behavior.

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