Migration Strategies of Insects

Migration is an environmentally modified physiological syndrome adapted for dispersal and colonization.

Hugh Dingle

In recent years there has been a crystallization of new ideas concerning the nature of insect migration. These ideas have come from several sources and include physiology and behavior on the one hand and ecology, especially as it relates to strategies of colonization, on the other. On the face of it, these approaches seem complementary, but there have been until now no comprehensive attempts either to test their combined validity for any one species or to formulate a general theory of insect migration in which both an insect's physiology and behavior, and its population and life history statistics, are taken into account. In this article I have gathered data from studies of a variety of insect migrants; these data suggest that the holistic view arising from a synthesis of the various concepts does in fact provide a sound basis for future migration research, not only in insects but in other migrants, such as birds and fish, as well.

Migration in insects is a distinct behavioral and physiological syndrome (*1–3*). Kennedy defines it in terms of enhanced locomotory behavior which results in persistent, straightened-out movement (which need not be in any specific direction). At the same time "vegetative functions" associated with maintenance and growth, for example, feeding and reproduction, are inhibited. Following long-distance flight the thresholds for vegetative activity are lowered and further migration is inhibited (*1, 4, 5*). Kennedy has demonstrated (*2*) that in the aphid *Aphis fabae* migration involves a complex interaction between flight and feeding and depositing larvae. His definition of migration does not distinguish between active migration and passive dispersal by wind, considered separate phenomena by many older entomologists (*6*), because the latter usually requires active flight to attain altitudes permitting wind displacement and then sufficient wing beating to remain airborne.

Studies of female insects, summarized by Johnson (*3*), indicate that migration involves an "oogenesis-flight syndrome." The available evidence suggests that most migration takes place prior to egg development (oogenesis) and reproduction although some may be interreproductive. What is important is that the development of the reproductive system is minimized at a time when that of the flight system, including wings, wing muscles, and associated biochemistry, is maximized. Migration therefore occurs chiefly in young adults, and its ontogeny shows a distinct pattern. Its chief functions are to allow escape from unfavorable environments and dispersal over and colonization of all available habitats. This is in marked contrast to the older view that it represented a desperate attempt to relieve population pressure. Insect migrants are thus colonizers and not refugees.

It is the colonization aspect of migration that has received considerable attention from ecologists. Some time ago both Brown and Jackson (*7*) pointed out that there was a relation between migration and habitat; specifically, aquatic insect migrants were likely to be species inhabiting small ponds or ponds subject to periodic drying. More recently, Southwood (*8*) has explored the question further and has summarized an abundance of evidence indicating that migration occurs most often in denizens of "temporary" habitats or, in other words, habitats in early stages of ecological succession such as old fields, roadsides, waste areas, and ephemeral ponds. As old habitats deteriorate, new ones are colonized, although it should be emphasized that considerable migration takes place before the deterioration of the old habitat because of the tendency to exodus before reproductive maturation. Migration may also be abetted by responses to proximate stimuli such as photoperiod, crowding, or alterations in the physiology of a food plant; its function in adaptive dispersal is thus further indicated (*9*).

If a migrant insect is to be a successful colonizer upon arriving in a new habitat, it must of course be able to reproduce and leave descendants. In this situation evolution favors high productivity (*10*); in order to attain this, the migrant would be expected to modify its life history statistics, under the influence of either its environment or its genes, to produce a high rate of population increase. It can do this either by increasing fecundity or, more effectively, by reproducing earlier (*11*). Further, an individual should have a high "reproductive value" when it migrates. This value was defined by Fisher (*12*) as the expected contribution of an individual to population growth. Its computation is analogous to the computation of compound interest on a bank account (see below). Since young adults have their reproductive life ahead of them and at the same time have already survived the causes of juvenile mortality, their reproductive values are usually high relative to juveniles or older adults, indicating a high colonization potential. We would therefore expect evolution to favor dispersal in most species just prior to reproduction (*10*), and the evidence indicates that in insects this is exactly what happens (*3*).

Field Evidence for Insect Migration

Older studies on insect migration tended to concentrate on movements presumed to be long distance and to and fro (*4, 6*), and most information was gained from large insects, such as butterflies, often seen flying across the countryside in sizable swarms. By compiling observations of such swarms, Williams (*6*) succeeded in demonstrating that many insect species were migrants, and that migration was an important behavioral and ecological

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phenomenon. As data have continued to accumulate, however, it has become evident that many small species are also migrants whose movements are neither very far nor particularly spectacular (*3*). In fact, unless specifically looked for, their movements usually go undetected. Close study, however, reveals that in favorable weather there is a veritable rain of insects descending to the earth following migratory flight. Most of these insects, whether large or small, are transported across the countryside by the wind (*3*).

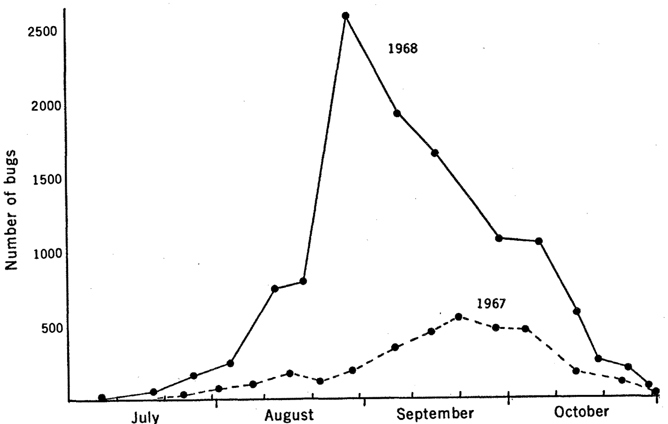
The role of meteorological factors in the transport of insect migrants was first clearly described by Rainey working on the African migratory locust *Schistocerca gregaria* (*13*). The gregarious phase of this species forms large migratory swarms traveling on winds which converge at the intertropical convergence zone. This zone moves back and forth across the equator once each year causing seasonal rains in much of tropical Africa. These rains promote greening and growth of the vegetation, and the locust swarms are thus deposited in areas suitable for breeding.

In North America several species migrate north in the spring, especially up the Mississippi Valley where they are aided by the southerly winds which blow consistently at that time. Three of the best studied species in this respect are the leafhoppers *Macrosteles fascifrons* and *Empoasca fabae* (Homoptera) and the harlequin bug *Murgantia histrionica* (Heteroptera) (*14*). Influxes of these species are correlated with the appropriate winds and weather fronts. Migrations into the valleys of California by another leafhopper *Circulifer tenellus* are also correlated with the winds (*15*). Perhaps the best known North American migrant is the monarch butterfly, *Danaus plexippus*, which has been shown from tagging experiments to migrate up to 1900 miles (1 mile = 1.6 kilometers) in the fall (*16*). The monarch may migrate independently of the wind although proof is lacking; the Florida salt marsh butterfly *Ascia monuste*, a short-distance migrant, almost certainly does so (*17*). Thus some insects may migrate without eolian transport, but present evidence suggests that they are the exception.

If they arrive in a suitable area, migrants begin a phase of rapid population growth. A good example is provided by studies of field populations of the milkweed bug *Oncopeltus fasciatus* (Heteroptera). This is a wide-ranging species occurring from Canada to Brazil (*18, 19*). It is a migrant that arrives in the northern parts of its range between spring and early summer, depending on latitude and temperature. The arriving migrants settle in patches of milkweed, mate, and lay eggs on the milkweed plant usually close to the developing seed pod. The egg is succeeded by five nymphal instars and after a few weeks by the adult. The population increases rapidly thereafter until it reaches its maximum in late summer. Numbers then decline because, with shortening days, the maturing adults leave. They presumably migrate south on the generally northerly winds of autumn, thus avoiding the oncoming winter. Four or more generations may occur in the southern United States during the course of a summer, while there may be only one in the north. If the weather is favorable, some nymphs and young adults can still be found in early November at the latitude of Iowa. Cold kills those unable to complete the adult molt before the first severe frost. The pattern of summer population growth and decline is given in Fig. 1 which indicates the numbers of *Oncopeltus fasciatus* in an Iowa field in the very cool summer of 1967 and the more unusual summer of 1968.

Age and Migration

A sufficient number of laboratory studies of migrants is now available to permit the general conclusion that migration occurs for the most part early in the life of the adult insect (*3, 20–23, 28*). Flight duration is measured with individuals tethered and either flying in place or on a movable flight mill. The results are the same whichever technique is used; the longest



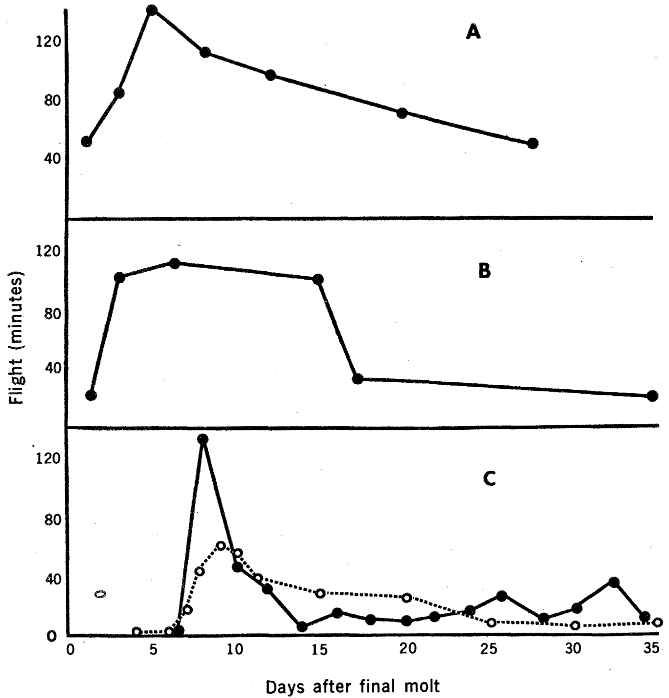


Fig. 1 (left). Growth and decline of *Oncopeltus fasciatus* in an Iowa field (approximately 1 acre) in the summers of 1967 and 1968. In 1967 (cool) there was one major generation with a few offspring from a second generation in early October. In 1968 (warm) there were three generations; the young of generation 2 constitute the sudden rise in late August, and the young of generation 3 account for the break in the population decline occurring in early October. Fig. 2 (right). Duration of tethered flight as a function of age in (A) the frit fly *Oscinella frit* (*20*), (B) the fruit fly *Drosophila funebris* (*21*), and (C) the milkweed bug *Oncopeltus fasciatus* (*22*). In (C) the dotted line indicates the flight of females tested only once during their lifetimes, and the solid line indicates females which flew for at least 30 minutes on day 8 and were flight tested every 2 days thereafter.

flights occur soon after the molt to adulthood with decreasing flight durations as the insects get older. These effects have been demonstrated for various species of bugs, flies, mosquitoes, aphids, moths, and grasshoppers, and there are some data for beetles which are suggestive of similar relationships (*3*). The decline in flight occurs concurrently with an increase in reproduction (the oogenesis-flight syndrome). Examples of the relation between age and flight activity for three species are given in Fig. 2.

In very young adults flight activity may be either nonexistent or very low. This is because flight cannot occur until the cuticle has hardened; the period during which hardening occurs is known as the teneral period, and flight is thus postteneral. In most insects (flies, mosquitoes, butterflies, and moths are apparent exceptions) the teneral period can be objectively defined by counting cuticular growth rings. These are laid down in the cuticle during the first days of adult life. The structure of the cuticle laid down during the day differs from that deposited at night; when viewed through a polarizing microscope, it is birefringent with one dark and one light ring for each 24 hours of growth (*24*). At the end of the growth period, which is a function of temperature (*25*), no further rings are deposited. In *O. fasciatus*, eight rings on the average are formed at 23°C; the teneral period is thus 8 days long, and the major migration flight occurs at the end of it (Fig. 2C). At 27°C six rings, broader than those at 23°C, are laid down, and migration begins 6 days after the adult molt rather than 8, and is again postteneral (*25–27*).

As insects age, a variety of biochemical changes occur. Included in these are declines in the amount of fuel used for flight and in the amount of enzymatic activity which makes the fuel available to the wing muscles (*21, 28*). Furthermore, because insects are flown to exhaustion while tethered, fuel consumption is commensurate with flight duration (*29*). As a result, there has been a tendency to assume that fuel limits migration. In the ultimate sense this may be so, but there are a variety of proximate stimuli, both internal and external, which trigger the changeover from migratory to other activities long before all fuel is consumed or age reduces enzymatic activity. Therefore statements that fuel limits migration, even though this may ultimately be true, are not particularly helpful (*2, 30*). In fact biochemical changes may themselves be initiated by the same stimuli that inhibit further migration (*2, 31*).

Migratory as Opposed to Vegetative Behavior

Kennedy's definition of migration, cited earlier, offers an objective and experimental test of whether or not flight is migratory (*1*); if it is, the insect should not be responsive to stimuli triggering vegetative behavior (for example, food or oviposition sites). The test has, unfortunately, seldom been applied, and in fact there is little information on the relation between locomotory and vegetative behavior in migrant insects. A notable exception is Kennedy's own work on the black bean aphid, *Aphis fabae* (*2*). In this species there is a reciprocal interaction between migratory flight and the postflight settling responses which include landing on a suitable bean leaf, probing with the mouthparts, and eventually feeding and depositing young. Stimuli which evoke flight inhibit settling, and conversely, stimuli which evoke settling inhibit flight. The two behaviors also have aftereffects on each other which can be either priming or depressing, depending on the respective excitatory states and on the strength of the incoming stimuli. The whole migration syndrome thus involves a complex integration of stimuli and responses.

The migration-settling sequence in aphids takes place in at most a few hours. A longer term interaction between migratory and vegetative behavior occurs in *O. fasciatus*. Oviposition in this species begins 13 to 15 days after the adult molt when the bugs are maintained on 16 hours of light and 8 hours of dark (LD 16 : 8) at 23°C; since peak flight occurs at 8 to 10 days under these conditions (Fig. 2), migration is largely prereproductive. The overlap between migratory flight and oviposition is therefore minimized. This is also interesting in another context. Both flight and oviposition show a daily periodicity with a peak at approximately midday (*27, 32*) as shown in Fig. 3. The two do not, however, come into conflict since they are temporally segregated in the life history. Mating also shows a circadian periodicity with a peak at the end of the daily light period (Fig. 3). In this instance, it is separated from flight not only in the life history but also in the day.

Analysis of daily periodicities reveals a separation of flight and feeding also. Females begin feeding a few hours after the adult molt. They continue at a high rate with little or no evidence of a circadian rhythm until day 7 when a rhythm becomes apparent; this rhythm is fully developed at day 8

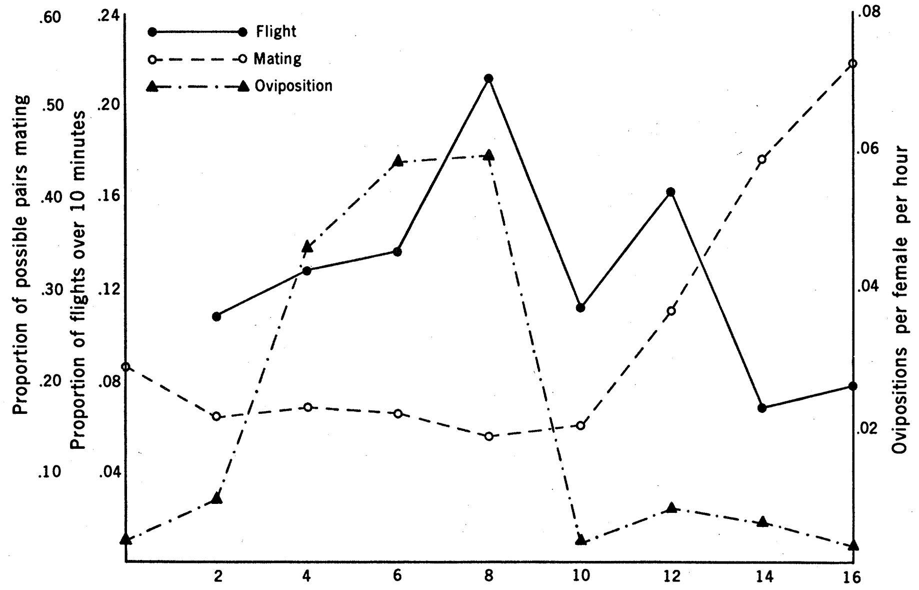


Fig. 3. Daily periodicities in flight, mating, and oviposition in *Oncopeltus fasciatus*. Flights lasting over 10 minutes were used to give a sufficient population size (*N*) at each interval (range, 36 at hour 12 to 304 at hour 4). Data for mating and oviposition are mean values for 40 pairs observed for 10 days. Temperature, 23°C. [After Caldwell and Dingle (*32*) and Dingle (*27*)]

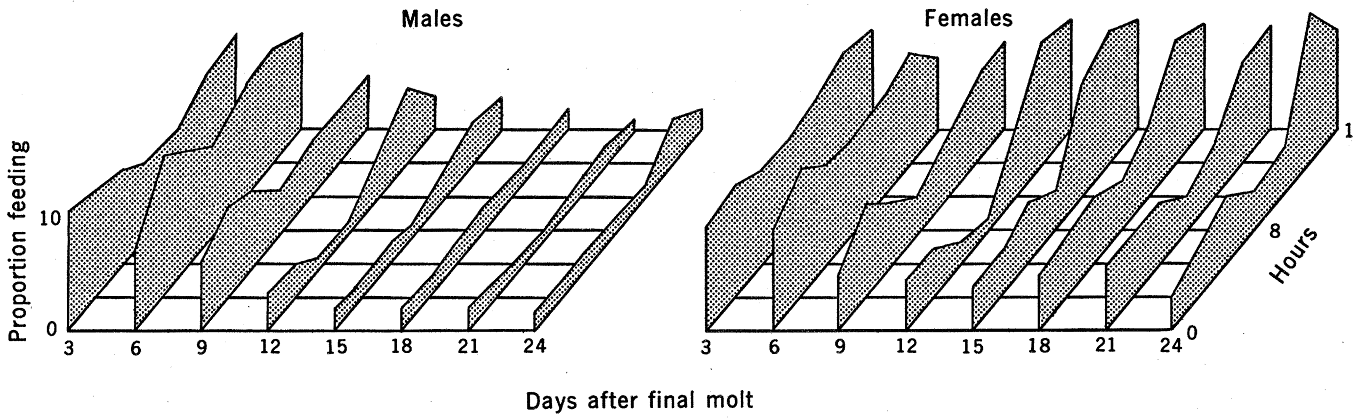


Fig. 4. Daily periodicities in feeding in *Oncopeltus fasciatus* as a function of age; data are averaged for each 3-day interval for 46 bugs of each sex. Hour 0 represents light on and hour 16, light off. Note that from day 9 feeding is low at midday when first flight and then oviposition are maximal. [After Caldwell and Rankin (*33*)]

when migration occurs (*33*). The peak of feeding activity, like mating, occurs at the end of the day (Fig. 3) so that at the time of longest flights, flight and feeding are temporally segregated by their daily periodicities. The maintenance of the rhythm from this point on in the life cycle also insures segregation of oviposition and feeding since the rhythm of the former peaks at midday. Mating proceeds simultaneously with feeding (*32*). In males, the overall rate of feeding falls markedly after day 6 and persists at a low rate throughout the remainder of life. Therefore, at the time of migration there is little feeding going on and indeed there is also more flight activity in older males than in older females (*22*). The relation between the feeding rhythms and the age of the insects is illustrated in Fig. 4.

It is evident from the foregoing that peak migration in the milkweed bug occurs at a specific time in the life history before reproduction occurs; these two activities, one locomotory and one vegetative, therefore do not conflict. Furthermore, there are also timing devices, based on daily periodicities, to assure nonoverlap between flight and feeding. The entire syndrome thus satisfies the physiological criteria defining insect migration.

Environmental Stimuli for Migration

Environmental factors can act directly to trigger migratory takeoffs or landings or can have longer term physiological effects, especially on reproduction, which determine the role of migration in the life history. Takeoff on a migratory flight requires the appropriate conditions of temperature, sunshine, and wind; populations can build up on the ground until conditions are favorable, whereupon a mass exodus may occur (*3*). Aphids provide good examples of this phenomenon as do the various migratory locusts. Locusts, the milkweed bugs *Lygaeus kalmii* and *Oncopeltus fasciatus*, and undoubtedly other migrants bask in the sun with bodies appropriately oriented to increase temperature to a point where flight can occur (*23, 34*); similarly, many butterflies, moths, and beetles increase body temperature by vibrating their wings or "pumping" the thorax (*35*). As flight proceeds, the insect becomes more responsive to stimuli which promote landing and subsequent vegetative behavior. Some aphids, for example, respond to blue wavelengths (of sky origin) on takeoff, but switch over to yellow wavelengths (from leaf surfaces) after a period of flight (*36*). Our knowledge of landing responses in other species is extremely meager.

Temperature can also have longer term influences on migration. At higher temperatures reproductive maturation is speeded, and the period of the life history available for migratory flight is correspondingly reduced (since migration is largely prereproductive). Temperature may also exert a more direct effect. In *O. fasciatus*, raising the temperature from 23° to 27°C results in a significantly smaller proportion of the population exhibiting tethered flights of 30 minutes or longer, the operational criterion for migration. This temperature is about optimal for population growth in *O. fasciatus*. Extrapolated to field situations, this result implies that once bugs find themselves in a thermally favorable environment, they will be inclined to stay there (*27, 37, 38*). Similarly, high temperatures tend to suppress the production of alate (migrant) forms in aphids (*39*).

In temperate regions photoperiod may exert a major influence on migration. Many temperate species of insect use the length of day as a cue to entering a state of suppressed development and metabolism known as diapause (*40*). This suspended state allows survival over the winter or any other set of unfavorable conditions. Diapause occurs in various species in all stages of the life history; when it occurs in the adult, it results in the arrest of reproductive development.

Since migration is largely a prereproductive phenomenon, prolonging the prereproductive period would be expected to prolong migration. This expectation was tested on laboratory populations of *O. fasciatus* and found to hold. At LD 12 : 12 and 23°C egg laying is delayed in this species until at least 45 days following the adult molt; at LD 16 : 8 it begins at around 15 days. Adult females 25 days past the adult molt were tested for duration of tethered flight. The LD 16 : 8 bugs were laying eggs and generally flew for only a few minutes or less; the LD 12 : 12 bugs showed no signs of reproductive development, and their performance was typical of prereproductive migrants (*27*). One of the possible consequences of this would be that in the autumn, females would be capable of migrating for much longer periods and therefore might have an improved chance of escaping the oncoming winter. Short photoperiods also suppress reproductive development in other known migrants such as the diamondback moth (*Plutella maculipennis*) and the red locust (*Nomadacris septemfasciata*), but the exact relationships remain to be defined (*41*). As these data indicate, diapause and migration are physiologically similar in that in both, growth and development are suppressed (*1*). They also both involve escape, the one in time and the other in space, and in many species they probably evolved together as parts of the same syndrome.

In addition to prolonging migration by suppressing oogenesis, short photoperiods increase the proportion of migrants in *O. fasciatus.* When LD 12 : 12 bugs were repeatedly tested between 8 and 30 days after the adult molt, a greater proportion of both males and females flew for a long period (at least 30 minutes, usually 2 to 3 hours) when compared to LD 16 : 8 bugs tested over the same interval (*42*). Especially interesting here are the results for the males which are not subject to the constraints of ovarian development. Photoperiod thus seems to have a direct effect on migration as well as an indirect one acting via the reproductive system.

In regions where it fluctuates sufficiently, photoperiod is an excellent proximate environmental cue signaling future conditions before they occur. Many species, however, especially those whose ranges span the equator where photoperiods are essentially constant, must rely directly on ultimate environmental factors. In particular they respond to the availability of food. When starved, the general pattern is for reproductive development to be delayed and migration prolonged; this is true of certain moths, for example (*43*). Three African cotton stainer bugs (*Dysdercus*) are especially interesting in this regard. Females of these bugs histolyze the wing muscles and produce eggs when fed; two species, *D. nigrofasciatus* and *D. superstitiosus,* show some flight activity before histolysis, but the third, *D. fasciatus,* never flies. When starved, there is no histolysis and no egg production, but rather migration in all three species. With food, flight ceases and egg production and muscle histolysis are initiated (*31*). Locusts (*Schistocerca*) delay reproduction when fed senescent leaves, but undergo reproductive development when fed fresh leaves. The active substance is apparently the plant growth hormone gibberellin A_3. They also mature more rapidly when in the presence of terpenoids from the young leaves of various aromatic shrubs. Since these grow young leaves after the rains, the locusts are more likely to mature reproductively in favorable habitats (*44*). At least some photoperiodically sensitive migrants also respond to food shortage. In *O. fasciatus,* for instance, starvation promotes takeoff in young adults, and prolongs migration while suspending reproduction in older individuals (*27*).

Stimuli from other individuals of the species can also be important environmental factors affecting migration. Outstanding examples are the various migratory locusts of which *Schistocerca gregaria*, *Locusta migratoria*, and *Nomadacris septemfasciata* are the best known. Here high population densities result in the development of a gregarious phase whose behavior is characterized by extreme restlessness and extraordinary migratory capability. It is also distinguishable morphologically, and in *Schistocerca* possibly also ecologically, with the gregarious form able, through its powers of dispersal, to exploit widely separated and only marginally suitable habitats (*45*). In the aphids *Megoura viciae* and *Aphis craccivora* crowding results in the production of winged individuals although the effect is modified by temperature and photoperiod (*39*). There is also some suggestion that other insects respond to crowding with increased migration, but the evidence, though tantalizing, is incomplete (*3*). In the milkweed bug *Lygaeus kalmii*, it is a stimulus from the opposite sex that is important, for following mating the amount of long-distance flight is significantly reduced. Mating apparently has a role in terminating the spring dispersal flights (*23*).

Heredity and Migration

Like all characteristics of organisms, migration has a genetic component. But the precise role of hereditary influences, especially their interaction with the environment, has received very little study. In locusts (*Schistocerca*) four generations of selection produces two lines differing significantly with respect to morphological characters defining the gregarious phase, but a single generation of crowding or isolation produces the same or greater differences. Gregariousness is also transmitted by a kind of maternal inheritance since crowding of females produces effects over more than one succeeding generation. The same is true of isolation although the magnitude and rates of change differ. The mechanism is not therefore a simple one (*45, 46*). When 30 minutes of tethered flight is used as the criterion for migration, about 25 percent of an Iowa population of *O. fasciatus* are migrants. Strong selection could increase this to just over 60 percent in one generation (*27*). Migratory capability in this species can thus be altered rapidly by selection.

Natural selection rapidly modifies populations of spruce budworms, *Choristoneura fumiferana,* and tent caterpillars, *Malacosoma disstria* and *M. pluviale.* These species are polymorphic for size. Smaller individuals mature more rapidly, lay fewer but larger eggs, are migrants, and are tolerant of environmental fluctuations. Larger individuals mature slowly, lay many small eggs, are generally sedentary, and survive only in favorable environments. Depending on both past history and current conditions, populations vary in the proportions of the two kinds of individuals. The polymorphism allows these species to deal with fluctuating environments; the large inactive forms exploit favorable conditions while the small migrants disperse and colonize new habitats. A model which assumes that the characters are transmitted by the X chromosome largely accounts for both experimental and field observations (*47*).

Migratory capability, however measured, is a continuous variable and can therefore be analyzed with the techniques of quantitative genetics where methods and theory are well developed (*48*). In only one case, however, have they been applied; this was in estimates of the heritability of the flight duration in the milkweed bug *Lygaeus kalmii* (*49*). Heritability is the proportion of the total variance in a trait resulting from the so-called "additive genetic variance," the variance contributing specifically to parent-offspring resemblance (in human height, for example) as opposed to the resemblance between all members of a species (as in the number of fingers, for example). Heritability is important because in combination with selection differential, it determines response to selection; since it is the ratio of additive genetic to total variance, it varies from zero to one (*50*). In *Lygaeus* the values were 0.20 when estimated from the offspring–male parent regression and 0.41 when estimated from offspring–female parent regression, indicating a possible maternal effect. There is thus sufficient additive genetic variance for selection to operate. In view of the results for *L. kalmii* and the behavioral differences between various migrants, quantitative genetic analysis could be a useful tool in studying dispersal strategies.

Migration and Populations

It is in the analysis of life history and population statistics with respect to migration that the complementarity of physiological and ecological parameters becomes evident. Since migration includes both escape from deteriorating habitats and the colonization of new ones, it is necessary to consider the physiological strategies which facilitate both. Such strategies involve varying reproduction either by varying the age at which egg laying starts or by altering fecundity itself (that is, the total number of eggs laid). As discussed above, many species prolong the prereproductive period with the result that the period in the life history given over to migration is also prolonged. Aphids are particularly interesting in this regard. The parthenogenetic apterous (vegetative) females have shortened the prereproductive period so much that larval development begins before the mother is born (that is, in the body of the grandmother) and a female begins giving birth to young almost as soon as she herself is born. The production of alate migrants (for example, by crowding) results in delaying births until after flight has taken place (*2, 39*). In some insects fecundity may also be reduced by migration, especially if there is a distinguishable migratory phase. This is true for the locust, *Locusta migratoria,* for example, where the gregarious phase lays fewer eggs and lays them later than the solitary phase. The same relationship holds for the "active" and "normal" forms of the beetle *Callasobruchus maculosus* (*1, 51*).

An interesting evolutionary outcome of the interactions between migration and reproduction occurs in females of three species of African cotton stainer bugs (*Dysdercus*) (*31*). These species appear to have modified a basic *Dysdercus* migration-reproduction strategy in which a short period of flight soon after the adult molt is followed by feeding, wing muscle breakdown, and egg development. In all three species, when no food is available, there is no breakdown of the wing muscles and no egg development; instead, flight continues until food is again encountered. Each species has modified the basic pattern to meet its own ecological requirements. *Dysdercus fasciatus* is the most opportunistic. It feeds on a few fruits which are abundant at certain times of the year, but absent at others. Females of this species do not fly at all in the presence of food; they reproduce early, and fecundity is highest of the three. *Dysdercus fasciatus* thus maximizes the dichotomy between locomotory and vegetative behavior. *Dysdercus nigrofasciatus* has adopted an intermediate strategy. It feeds on the seeds of a variety of annuals and perennials so that food is apt to be scattered but generally available. Females do fly for a short period before the wing muscles break down; reproduction is thus delayed for 2 to 3 days relative to *D. fasciatus*, but fecundity is almost as high. Finally, *D. superstitiosus* is a species which feeds on a far greater variety of host plants than either of the other two and thus faces fewer risks from the environment. Its females also undertake some flight before reproduction which begins at about the same time as in *D. nigrofasciatus.* Its fecundity, however, is considerably reduced indicating far less emphasis on reproductive opportunism, as is characteristic of species in more stable environments (*10, 11*).

Factors which affect reproduction also profoundly influence the rate at which a population grows (*11*). An effective measure of the rate of population growth is r, the so-called intrinsic rate of increase, which is usually expressed as growth per unit of time. It combines survivorship, fecundity, and developmental rate in a biologically meaningful way to estimate the growth potential of a population with unlimited resources, and has the particular advantage that it can be compared from one species to another without regard to generation times (*52*). A population of given size, N, growing in an unlimited universe will approach a stable age distribution and expand according to the relation $\mathrm{d}N/\mathrm{d}t = rN$. To determine r, one must solve for it in the equation

$$\int_0^\infty l_x m_x e^{-rx} \mathrm{d}_x = 1$$

where e is the base of natural logarithms, x is age, l_x is the proportion of individuals surviving to age x, and m_x is the birthrate defined as the average number of female offspring produced per female in the age interval $x - 0.5$ to $x + 0.5$. In practice r is approximated by trial-and-error substitution in the equation

$$\sum_\alpha^\omega l_x m_x e^{-rx} = 1$$

where α and ω are, respectively, the ages at first and last reproduction. Note that survival (l_x), fecundity (m_x), and rate of development (α) all enter into the solution of r.

The relation between r, life history statistics, and migration is illustrated by results from the milkweed bug *O. fasciatus* (*37*). In this species high temperatures and long photoperiods advance the age at which reproduction first occurs while low temperatures and short photoperiods delay it. The values of r for *O. fasciatus* at a density of 20 pairs per container under four different experimental conditions are given in Table 1 which also indicates the time it would take for the respective populations to double. On a long day (LD 16 : 8) at a high temperature (27°C) the bugs begin reproducing at 47 days after birth, and r, expressed as the rate of increase per individual per day, is 0.0810; this leads to a doubling of the population in 8.90 days. In contrast, a short day (LD 12 : 12) and a lower temperature (23°C) results in first reproduction at day 95, an r of 0.0369, and a doubling time of 19.13 days, about twice as long. Long days and high temperatures therefore produce much more rapid population growth; they do so by promoting earlier and more rapid reproduction. This is in fact the most effective way of increasing the value of r (*11*).

A high value of r (or more correctly the ratio r/m where m is the per capita birthrate) is of distinct advantage to a colonizing species (*10, 11*), for it allows such a species to increase its population rapidly when it invades a new environment. In the North American spring and summer *O. fasciatus* enters a previously empty universe, an environment which favors high productivity (*10*). The fact that long days and high temperatures promote rapid population growth means that this species can take maximum advantage of the habitat. There is thus

Table 1. Rates of increase for *Oncopeltus fasciatus.*

Photoperiod (light : dark)	Temperature (°C)	Age at first reproduction (days)	Increase per day (r)	Doubling time (days)
16 : 8	27	47	0.0810	8.90
12 : 12	27	61	.0593	12.03
16 : 8	23	63	.0499	14.24
12 : 12	23	95	.0369	19.13

a phenotypic modification of r which maximizes colonizing ability. The reduction in migration caused by high temperatures is apparently a still further adaptation to colonization since the bugs will tend to remain and reproduce where conditions are favorable.

In contrast the short days and cool temperatures of autumn delay reproduction and depress the value of r. In delaying reproduction, however, they lengthen the period during which migration can take place. Thus *O. fasciatus* under these conditions sacrifices the colonizing advantages of rapid population growth, but for alternative gain, namely, a longer time in which to migrate to a more favorable habitat. The time is apparently necessary because the winds of autumn, on which the bugs presumably travel, are less reliable than those of spring and because it is necessary to travel farther to avoid being overtaken by the oncoming winter. These insects, since they have their reproductive life ahead of them, are still potential colonizers; the extent to which they are actual colonizers is not known. Lack of knowledge of the reproductive fate of any southward migrating insect is one of the largest lacunae in our understanding of the whole migration process.

Maximization of growth potential under optimal conditions and some sacrifice of this potential under conditions promoting migration would seem to be a general strategy of migrant insects. The data from aphids, locusts, *Dysdercus*, and *O. fasciatus* all suggest that this is so.

Delay in reproduction is also interesting in relation to the other major escape mechanism of insects, diapause, in which reproductive delay occurs in adults or delayed growth occurs in immature stages. In both instances vegetative functions are suppressed, and diapause and migration are thus similar (*1*). As diapause allows escape in time, so migration allows escape in space. In many insects reproductive delay or diapause allows migration to a new environment and an escape from unfavorable conditions. In fact adult reproductive diapause may have evolved through delays in reproduction which allowed migration to new areas. The intimacy of the relationships between diapause and migration in adult insects is thus further emphasized.

The relation between life history statistics and colonizing ability is also brought out in the concept of reproductive value (*11, 12*). Because this is defined as the expected contribution of an individual of specified age to future population growth, it indicates at what age it is most likely to found a successful colony. The reproductive value, v_x, of an individual of age x in a growing population is defined mathematically relative to this value at birth, v_0. Thus where t is time and other terms are as previously defined

$$\frac{v_x}{v_0} = \frac{e^{rx}}{l_x} \int_x^\infty l_t m_t e^{-rt} dt$$

Since v_x is relative to v_0, we can set $v_0 = 1$. Rate of increase, survivorship, and fecundity all enter into the calculation of v_x and integration is from x to ∞ so that only future births are included.

What matters here is that since reproductive value indicates the chances of successful colonization, it is an important factor to consider when discussing a migrant insect. Accordingly, reproductive values were computed for *O. fasciatus* reared at LD 16 : 8 (high r) and at LD 12 : 12 (low r), both at 23°C, and for *Aphis fabae* (*22, 27*). In *O. fasciatus* at LD 16 : 8, v_x rises rapidly after the adult molt to reach a peak at day 20; since flight is maximal at 8 to 10 days, a migrant will reach its maximum v_x shortly after arriving in a new location and thus stands an excellent chance of founding a colony. At LD 12 : 12 the situation is more complex. In this case reproductive value does not reach a maximum until day 100 at the earliest or day 160 at the latest depending on density. Reproduction starts occasionally as early as 45 days after the adult molt, but more usually around days 60 to 70 which can thus be taken as the time most migration ceases. Bugs migrating under these conditions are therefore not so likely to be successful colonizers, for there is a time lag between maximum migration and peak reproductive value. Here the chances of successful colonization, although reduced, are still better than the alternative, which is death through failure to escape the approaching winter. Both high r and high reproductive value are sacrificed for the alternative gain of escape from unfavorable conditions. In *Aphis fabae* the adult molt occurs 4 to 5 days after birth, and migration follows within 24 hours; there is then a burst of reproductive activity. The latter is reflected in the reproductive value which peaks at day 5 indicating that the aphids have a high colonizing potential. In fact, physiological and ecological events are so tightly linked in these aphids that ordinarily flight is a prerequisite for settling and deposition of young (*2*).

Conclusions

Physiological and ecological results from a variety of species are consistent with what seem to be valid general statements concerning insect migration. These are as follows: (i) During migration locomotory functions are enhanced and vegetative functions such as feeding and reproduction are suppressed. (ii) Migration usually occurs prereproductively in the life of the adult insect (the oogenesis-flight syndrome). (iii) Since migrant individuals are usually prereproductive, their reproductive values, and hence colonizing abilities, are at or near maximum. (iv) Migrants usually reside in temporary habitats. (v) Migrants have a high potential for population increase, r, which is also advantageous for colonizers. (vi) Both the physiological and ecological parameters of migration are modifiable by environmental factors (that is, phenotypically modifiable) to suit the prevailing conditions. Taken together, these criteria establish a comprehensive theory and adumbrate the basic strategy for migrant insects. This basic strategy is modified to suit the ecological requirements of individual species. Comparative studies of these modifications are of considerable theoretical and practical interest, the more so since most economically important insects are migrants.

No satisfactory general statements can as yet be made with respect to the genotype and migration. Certainly we expect colonizing populations to possess genotypes favoring a high *r*, but genotypic variation in *r* depends on the heritabilities of life table statistics, and such measurements are yet to be made (*10, 53*). The fact that flight duration can be increased by appropriate selection in *Oncopeltus fasciatus*, and the demonstration of additive genetic variance for this trait in *Lygaeus kalmii*, suggest that heritability studies of migratory behavior would also be worth pursuing. Most interesting, of course, will be possible genetic correlations between migration and life history parameters. Also, migration often transports genotypes across long distances with considerable mixing of populations. An understanding of its operation therefore carries with it implications for population genetics, zoogeography, and evolutionary theory.

Finally, at least parts of the above general theory would seem to be applicable to forms other than insects. Bird and insect migrations, for example, are in many respects ecologically and physiologically similar. Birds, like insects, emphasize locomotory as opposed to vegetative functions during long-distance flight; the well-known *Zugenruhe* or migratory restlessness is a case in point. Further, many birds migrate at night at a time when they would ordinarily roost (vegetative activity). Because their life spans exceed single seasons, bird migrants are not prereproductive in the same sense that insect migrants are, and hence reproductive values do not have the same meaning (but note that some insects are also interreproductive migrants). The situation is complicated further by the fact that in many birds adult survivorship is virtually independent of age so that colonizing ability tends to be also (*10, 54*). Nevertheless, birds arrive on their nesting grounds in reproductive condition with the result that migration is a colonizing episode. It is also phenotypically modifiable by environmental factors, some of which, for example, photoperiod, influence insects as well (*55*). The similarities between birds and insects thus seem sufficient to indicate, at least provisionally, that the theory developed for insects applies also to birds with appropriate modifications for longer life span and more complex social behavior; comparisons between insects and fish (*56*) lead to the same conclusion. In birds especially, and also in other forms, various functions accessory to migration such as reproductive endocrinology, energy budgets, and orientation mechanisms have been studied extensively (*55, 56*). But there is need in vertebrates for more data and theory on the ecology and physiology of migratory behavior per se in order to better understand its evolution and its role in ecosystem function (*5, 57*). Migration in any animal cannot be understood until viewed in its entirety as a physiological, behavioral, and ecological syndrome.

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Visual Spatial Illusions: A General Explanation

A wide range of visual illusions, including geometrical distortions, can be explained by a single principle.

R. H. Day

Under specified conditions a consistent discrepancy occurs between the apparent and physical value of a property of an object, such as its size, shape, orientation, or movement. These differences are called spatial illusions and for over a century one group, the geometrical illusions, has remained unexplained despite intensive experimental analysis. Although there has been a resurgence of interest in explaining these effects, such as attempts to do so in terms of spatial constancy (*1*, *2*), no theory has yet gained general acceptance. I wish here to propose a general explanation that encompasses a wide range of effects, including the geometrical distortions and the effects which belong in the same class but are not usually treated as illusions. Whereas the following explanation is based on the processes that normally maintain perceptual constancy, it is more general than others and recognizes separate classes of illusion for size, shape, orientation, and movement. All classes are linked to a particular spatial constancy and explained in terms of the same principle. Size illusions have been singled out for detailed treatment because, in addition to containing the Müller-Lyer (*3*) and most of the other well-known effects, their analysis serves to elucidate the main principle on which the general explanation is based. However, I emphasize that there are *separate classes* of illusion derived from independent manipulation of the stimuli that normally preserve a particular form of perceptual constancy. Also, there is a much wider range of visual constancies, including those of orientation and movement, than is generally recognized.

Size Constancy and Distance Stimuli

As the distance of an object varies, the size of the retinal projection of the object (image), for all practical purposes, varies as an inverse linear function of distance (*4*). Departures from this function are slight as the object itself increases in size. Data show that with monocular viewing in a dark, featureless environment the apparent size of an object also varies as an inverse linear function of distance (*5*). However, with binocular vision in a normally illuminated, structured environment the apparent size of an object is nearly constant with distance. This relative stability, first described by Descartes (*6*) and studied quantitatively by Martius (*7*) and Thouless (*8*), occurs even when the observer and object are separated by more than 1000 meters (*9*). Because the retinal image of an object varies with distance but the apparent size remains constant, it has been assumed that size constancy is dependent on sensory information for distance. This assumption was tested and confirmed by Holway and Boring (*10*) in a well-known experiment in which information for distance was progressive-

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