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Insect Flight

Dispersal and Migration

Edited by

W. Danthanarayana

With 62 Figures

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Preface

This volume is based on a Symposium entitled "Insect Flight: Dispersal and Migration" held at the XVIIth International Congress of Entomology in Hamburg, Germany in August, 1984. An earlier similar Symposium was held at the XVth International Congress of Entomology in 1976 in Washington DC, USA ("Evolution of Insect Migration and Diapause" edited by Hugh Dingle, Springer-Verlag, 1978). It is, therefore, appropriate that the present Symposium was held 8 years later in view of the intensified interest and developments in this field, particularly in the areas of evolution, genetics, endocrine/neuroendocrine influences, orientation, navigation and nocturnal flight activity.

It was intended that the Symposium should have a fairly representative, albeit non-complete, coverage of the various aspects of its topic, and the Congress facilitated the gathering of many specialists in the field, enabling the presentation and discussion of 18 papers. Fifteen of these are presented in this volume, mostly as modified and expanded versions. Also included is a contribution by Roger Farrow who presented his paper at another section of the Congress, and one by Wolfgang Stein who could not attend the Congress; an additional paper, by myself and Stuart Dashper, is included with the intention of supporting my presentation at the Congress. One of the most interesting contributions was that by Rudiger Wehner on "The role of polarized skylight in insect navigation". Much of what he said has been published elsewhere under the title "Astronavigation in Insects" (*Annual Review of Entomology* 29:277–298, 1984). Two of the papers presented at the Symposium, one by Christer Solbreck and Brigitta Sillen-Tullberg entitled "Role of migration in exploiting patchy and time-varying resources: dynamics of a seed-predator system" and the other by Robert F. Denno entitled "Wing polymorphism and migration in plant hoppers: the role of host plants" are not included in this volume, as their research is still in progress. The reader is referred to the Congress Abstract volume, pp. 344 and 345, for synopses of these works.

The majority of chapters in this volume give accounts of original research; these and the review articles include developments over the last several years. This material indicates that at least *some* of the older concepts are being questioned and new ones proposed. This indeed is a reflection of the dynamism and progress of the subject, and fulfils the primary aim of the Sym-

posium. Chapters in this book have not been grouped into sections because of the overlapping nature and the broad range of topics covered, but the order followed after the Introduction is to begin with the opening address by Hugh Dingle on "Evolution and Genetics of Insect Migration" followed by those on physiology, behaviour, genetics/ecology, pest insects, and methodology respectively. A number of colleagues in Australia, Britain, and the USA to whom I extend my sincere thanks, kindly assisted in reviewing the papers.

I was very fortunate and privileged in obtaining the services of two distinguished and eminent researchers in the field, Hugh Dingle and Roy Taylor to give the opening and closing addresses respectively, and also to Chair the four sessions. I am very grateful to them for doing this onerous work, as well as for the encouragement given to me during the organization of the Symposium and the preparation of this volume. I also thank all those who participated in the Symposium and contributed to this volume, and to Springer-Verlag and especially Dr. Dieter Czeschlik for undertaking the task of publication so enthusiastically. Tacit support given by my wife, Sunimal, during the preparation of this work and the considerable typing assistance given by Rhonda McLauchlan are greatly appreciated. Financial support provided by the Alexander von Humboldt-Stiftung for my attendance at the Entomology Congress at Hamburg is gratefully acknowledged. L.R. Taylor holds an Emeritus Research Fellowship from the Leverhulme Trust and wishes to acknowledge their support.

Armidale, Spring 1986

W. Danthanarayana

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1 Introductory Chapter

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Major aspects of insect dispersal and migration by flight have been discussed in detail in several books (Baker 1978; Dingle 1978; Johnson 1969; Rabb and Kennedy 1979; Rainey 1976a; Williams 1958) and a large body of review papers (e.g. Dingle 1972, 1980; Johnson 1974; Kennedy 1975; Schneider 1962; Southwood 1962, 1975, 1981; Taylor L.R. and Taylor R.A.J. 1983). The purpose of this introduction is, therefore, mainly to draw attention to advances in this field over the last few years, in the light of work presented in this volume. In doing so an attempt is made to highlight areas in which more research effort is desirable. In an introduction such as this, it is necessary to emphasize the obvious in order to present an intelligible perspective of the topics covered and discuss their implications.

There have been many attempts to arrive at acceptable definitions for the terms dispersal and migration (e.g. Andrewartha and Birch 1954; Elton 1930; the references listed above). This has led, on occasion, to confusion and contention largely due to attempts to provide all embracing definitions covering the entire animal kingdom. Life-cycle strategies of insects in comparison to, say, vertebrates are often very different reflecting the vast differences between the two groups in their body size, generation times and longevity. Primarily because of the short life span, bicoordinate navigation does not occur in insect migrations except perhaps to a limited extent in a few (apparently rare) examples such as the monarch butterfly (Urquhart and Urquhart 1977, 1978, 1979). Also, homing associated with migration and based on memory, in the sense of that found in higher animals, is yet to be demonstrated for insects. Nevertheless, there is now a consensus on the terminology applicable to insect movements. Although none of the papers presented at the Symposium considered the definitions of terms, the question was raised in discussion, and a re-iteration of definitions appears to be appropriate at the outset.

'Dispersal' refers to scattering of a population, leading to an increase in the mean distance between individuals (Andrewartha and Birch 1954; Southwood 1962, 1981; Schneider 1962), and encompasses two types of movements: migratory and non-migratory. Non-migratory movements involve travel within the habitat associated with such activities as feeding, mating, and oviposition, and have been referred to as 'appetitive' (Provost 1952), 'vegetative' (Kennedy 1961a, 1975) or 'trivial' (Southwood 1962) movements. In contrast, migratory movements take insects beyond the habitat for the purposes of colonizing new habitats, re-colonizing old ones, aestivation or hibernation (Johnson 1969; Southwood 1962; Dingle 1972). Migration is thus an evolved adaptation for survival and reproduction (Johnson 1960), so promoting genotypic fitness.

The genetic ('gene flow') and ecological (colonization, escape from inhospitable environmental conditions) consequences of migration will in turn lead to the evolution of a range of migratory behaviours and the associated physiological and morphological characteristics. In the final analysis it is difficult to separate sharply the ecological, behavioural, physiological, and morphological factors of insect migration. Integration of genetics with the above factors is, therefore, of fundamental importance. Dingle (Chap. 2) deals with this aspect, and emphasizes that little is known of the genetics underlying migratory behaviour. He stresses the need to comprehend the genetic variance and genetic correlation so that evolutionary processes that connect migration to important life history and fitness components can be understood. Understanding of the genetics of migration is expected to make a significant contribution to modern evolutionary biology because of the polygenic nature of most migratory traits, the evolutionary implication of genetic variation, phenotypic expression, selection of life history patterns and the involvement of migration in maintaining life cycle flexibility. Dingle's overview is supported by Rankin, McAnelly, and Bodenhamer (Chap. 3) on some physiological aspects and Gatehouse (Chap. 9) on ecological aspects of migration. The above workers use clear-cut physiological and morphological characteristics to distinguish migrants from non-migrants, and the adaptive roles of the migratory traits under varying environmental conditions are then examined. Rankin and colleagues show that the individual cost of migration has been previously overestimated, for in populations where migration is a major life-history strategy selection maximizes the product of reproduction and flight, rather than acting on either of these parameters; the physiological mechanism involved is juvenile hormone (JH) stimulation of both migration and reproduction. Gatehouse considers the ecological factors that determine the migratory capacity of the African armyworm. These act via a density-dependent phase polymorphism that ensures rapid re-dispersal of dense populations resulting from meteorological disturbances. The resulting low densities are achieved by seasonally cycling selection acting on genetically determined variability in potential flight capacity. It is suggested that this strategy is shared by many other oligophagous and polyphagous tropical and subtropical noctuids which do not undergo diapause, and depend on ubiquitous host plants.

The behavioural factors of insect migration include: persistent, undistracted locomotor activity (i.e. increased ortho-kinesis) that becomes straightened out, in the sense of traversing new ground instead of frequent changes in direction (i.e. decreased klinokinesis), temporary depression of vegetative responses, special take-off and alighting patterns (Kennedy 1961a, 1975) and temporarily dominating phototaxis (Johnson 1969) which takes the insects right out of their 'boundary layer' (Taylor 1958, 1960, 1974). The term 'boundary layer' refers to the relatively shallow layer of air immediately above the earth's surface in which the wind speed is less than the flight speed of the insect. Within this layer the insect can control its movement to a large extent, and control its course and track. The depth of the boundary layer is variable depending on the species' size and flight speed, the strength of the prevailing wind and the terrain. Above the boundary layer upwind flight is difficult, and the insect's course and track are to a large extent influenced by wind direction.

For many years it has been known that insects flying at night rise through a temperature inversion with no help from convection and attain high ceilings ranging from a few hundred metres to 1-2 km (Kennedy 1975). Typical ground tracks of these insects

are downwind, but rather than being merely carried by the wind, insects actively fly upwards and show a common orientation even under dark and completely overcast conditions (Johnson 1969; Kennedy 1975; Farrow, this volume; Riley 1975; Reynolds and Riley 1979, this volume; Schaefer 1976; Waloff 1972). In considering this riddle of orientation of night-flying insects, Kennedy (1975) stated that "we must, as C.B. Williams believed, start looking into some sensory guidance mechanism not yet considered for insects". Although an unambiguous answer to this question has not been found, there has been a considerable body of work during the last several years on insect orientation. It has been shown that insects use one or several cues available in our celestial system, something considered to be highly unlikely several years ago! These include: the use of the earth's magnetic field (Arendse 1978; Baker and Mather 1982; Dyer and Gould 1981; Gould 1980, 1982; Gould et al. 1978; Kirschvink 1983; Martin and Lindauer 1977), time-compensated stellar navigation (Sottibandhu and Baker 1979), celestial skymarks (Wehner 1983, 1984), infra-red energy perception (Evans and Kusher 1980; Meyer 1977) and moon-compass reaction (Sottibandhu and Baker 1979). Riley and Reynolds review the nocturnal orientation problem in Chap. 6 and by a process of elimination conclude that time-compensated stellar navigation and perception of the terrestrial magnetic field might be used by the compass navigators, and accelerative anisotropies in the air motion could provide the necessary cues for the wind navigators, as both types of navigation have been detected by radar in high-flying nocturnal migrants. They expect nocturnally migrating insects to adopt wind-related cues or compass orientation in an hierarchical manner depending on wind conditions and on their individual flight strategies. The stage is now set for further experimental work on nocturnal orientation, preferably under natural conditions, for the elucidation of the circumstances under which insects use the various navigational strategies available to them.

The influence of the moon on flight and migratory activities are covered by Danthararyana in Chap. 7. It is shown that there is lunar periodicity in these activities in two experimental insects and that this may extend to other species also. Lunar periodicity appears to be rhythmic, but it is not yet known with certainty whether insect lunar rhythms are of endogenous or exogenous origin, although the available evidence tends to support the former (Neumann 1981). Naylor (1982) and Cloudsley-Thompson (1980) point out that endogenous lunar rhythms in the behaviour and physiology of insects and other organisms, as well as the mechanism of the internal lunar clock have presumably been selected for and inherited. It is perhaps in this context that lunar periodicity of insect activities needs to be examined. Also there is a remarkable similarity between the pattern of lunar periodicity of insect flight described in this volume and the semi-lunar cyclicity of cardioactive neurotransmitterlike substances found in the central nervous system of the cockroach, human and mouse blood as well as in leaf extracts of several plant species (Rounds 1975, 1981, 1982). It has been proposed that some of these substances may be involved in "system" modulating organismic response to lunar-related forces (see Rounds 1982). As an operating hypothesis, Rounds suggested that these cardioactive materials are "modulators" or "enablers" and are released into the blood or tissue fluid to act on "excitability" of cells in general and make the target tissues more or less responsive to other triggers. This "general response system" is presumed to be responding, directly or indirectly, to the gravitational force changes associated with variations in the position of the moon, the sun, and the earth. There is

thus a need to investigate whether the neurophysiological and hormonal activities that influence insect flight and migration are affected by lunar periodicity.

The influence of polarized light on some night-flying insects is the topic of Chap. 8 (Danthanarayana and Dashper). Waterman (1981) points out that with the exception of Wehner's work on *Cataglyphis* (Wehner 1972, 1976) and Wellington's observations on mosquito flight (Wellington 1974a,b, 1976), there are few recent field experiments on polarization sensitivity. He goes on to stress that experiments are needed not only to establish the adaptive utility of polarization sensitivity, but also to define the specific functions of the relevant detecting and processing mechanisms, and that "the rather elegant hypotheses of sensory mechanisms currently being elucidated or postulated, therefore, may seem a bit top heavy for the field's somewhat makeshift foundation!" (Waterman 1981). Work reported in this volume provides a modest, but significant, contribution to our knowledge of polarization sensitivity of several nocturnally active insects as it relates to species other than the social Hymenoptera. The significance of further research on these lines need not be stressed.

As migration involves specialized behaviours and sustained travel, the process is extremely demanding and requires considerable changes in the insect's physiology. Physiological factors involved in migration include: the control of movement (flight) and the utilization of fuels mediated by the neuroendocrine system and the "oogenesis flight syndrome" (Johnson 1963, 1969). In the oogenesis flight syndrome the locomotor drive is optimal in young pre-reproductive adults with the metabolism switched to increased flight muscle growth and fat accumulation, and as the ovaries mature the locomotor drive disappears, the flight muscle apparatus autolyses and migration terminates (Danthanarayana 1970; Johnson 1969, 1976). These migratory and reproductive changes are closely coordinated by the JH-system in response to environmental cues (Caldwell and Rankin 1972; Rankin 1974, 1978). In Chap. 3 Rankin et al. reconsider the oogenesis flight syndrome. They point out that in species of highly migratory insects, JH stimulates both flight and oogenesis, although in some species JH can cause flight-muscle histolysis or have no effect on flight behaviour. They see the JH control of migratory behaviour as a mechanism evolved in response to selection associated with colonizing life-styles in which, ideally, both flight and reproductive parameters would be maximized. The implications of the stimulation of both flight and oogenesis are considered in their discussion.

In addition to the key role played by JH, several other hormone systems, those that are essential for the mobilization of fuels, are part and parcel of the physiology of insect flight and migration. At the onset of flight the energy requirements are met by the breakdown of the endogenous fuel (glycogen and proline) found in the flight muscle. Thereafter trehalose from the blood is the main fuel, and the sugars from the crop may also contribute; most of the energy required during long-term and sustained flights is obtained from the main stores of glycogen in the fat body and intestinal wall (Mordue et al. 1980). Mobilization of stored fuel reserves in the fat body has received much attention during the last several years. In Chap. 4 Goldsworthy and Wheeler discuss fuel mobilization via adipokinetic hormones and octopamine and the coordination of the fuel supply and its utilization in locusts. They compare the chemical nature and actions of the two known adipokinetic peptides, and discuss the actions of octopamine on the fat body and flight muscle, suggesting that it may play a vital role in maintaining the oxidation of glucose in the early stages of flight.

A form of energy transfer that happens during flight, but not quite linked to the process of migration and dispersal is that small part of the energy transmitted to the wings that gets converted into sound. In Chap. 5 Belton covers this aspect and considers the effects of the major environmental factors that influence wing-beat frequency. The value of wing-beat sounds to insects is for sexual attraction as in the case of female biting Diptera using wing-beat sounds to attract males. These sounds have been of value in radar studies of migration because wing-beat frequencies of individual insects or swarms can be detected by radar using the Doppler effect or differences in intensity of the echos (Buchan and Stelle 1979; Riley and Reynolds, this volume; Schaefer 1976).

Turning to the ecological factors of insect migration, the primary ecological characteristic of migration is the displacement of the insect from one habitat (breeding site) so that it arrives at another (Johnson 1960, 1969). Simultaneous pre-reproductive flights are characteristic of most migrants, but there are species that migrate between bouts of oviposition (Johnson 1969, 1974). Since migration is linked closely to habitat variations, the evolution of the migratory capacity has reached its climax in species living in impermanent habitats (Southwood 1962) and is a characteristic life-cycle strategy among *r*-selected species (Dingle 1972, 1974, 1981a). The initiation of migration is evoked by extrinsic and intrinsic mechanisms that can anticipate the arrival of adverse conditions. Intrinsic timing mechanisms such as lunar rhythms will not only permit initiation of migration, but synchronize settlement of individuals at points of termination. Extrinsic environmental cues also have similar roles, and selection will favour those individuals that can develop such timing mechanisms (Lidicker and Caldwell 1982).

Where alternate habitats are geographically distant and their suitability is seasonal and predictive as in temperate environments, photoperiod provides a very precise cue for the initiation of migration (Dingle 1972, 1980; Johnson 1969; Vepsäläinen 1978). In situations where the geographical separation of habitats varies from short to long distances and the time factor is less relevant, as in migrations of tropical insects or within-season migrations of temperate ones, cues other than photoperiod may be used. These include temperature, food availability and quality (Danthanarayana 1976; Dingle 1972, 1981a,b; Dixon and Howard, this volume; Vepsäläinen 1978), rainfall, natural enemies, and disease pressure (Dingle 1981b, Gatehouse, this volume) and intraspecific density effects (Taylor L.R. and Taylor R.A.J. 1977, 1983). The seasonal synchronization of insect life histories by migration and diapause, evoked by the various environmental cues in different geographical situations has been discussed by Dingle (1981b). Intraspecific population pressure may operate through social behaviour as in locusts where crowding induces the migratory phase transformation (Kennedy 1956, 1961b; Uvarov 1966) and the development of the alate morphs in aphids (Dixon 1973, this volume; Hughes 1963, 1974; Kennedy 1972). Similar social effects are known to occur even at very low densities as in some Lepidoptera where mutual interference between even two individuals resulting from low-density larval crowding will make one individual develop into a more flightworthy adult (Danthanarayana et al. 1982). The impact of migration as a density-dependent process for population regulation has been stressed recently by Taylor and Taylor (Taylor L.R. and Taylor R.A.J. 1977, 1983; Taylor R.A.J. and Taylor L.R. 1979). Their concept is encompassed in a mathematical model, the Δ -model, the components of which are migration (or repulsion) and congregation (or attraction) which produces the Δ -response in a negative feedback loop,

and a quantitative assessment of migration potential is possible because the model can be simulated. In their purely spatial concept, animal movement is not sub-divided into categories other than migration and attraction. In this balancing of the association between density-dependent aggregation and migration, all movements of animals in space have the common function of regulating populations by constant re-distribution of populations in space and time. This allows the colonizers and re-colonizers to exploit the shifting heterogeneity of habitats as exemplified by the movements of East African armyworm populations (Gatehouse, Chap. 9). In Chap. 10 Dixon and Howard show that the variability in reproductive investment between individuals within an aphid clone is programmed. This intraclonal tactical diversity in reproductive investment, characteristic of the Aphidinae, is shown to be associated with differential dispersal which is an adaptation to living in, rather than developing in, a heterogeneous environment. This, they say, may account for the success of most members of this sub-family.

In most insect species distance travel is achieved rapidly and economically by supplementing their own powers of flapping flight with the energy freely available from the wind (Johnson 1969; Pedgley 1982; Rainey 1951, 1976b; Taylor 1974). Mikkola, in Chap. 11, gives numerous examples of wind-dependent migrations into Finland. He shows that even among boundary-layer migrants wind seems to play a role in keeping the track of the migrant straight. Butterfly migration, often thought to be carried out without any wind assistance (Baker 1978; Walker and Riodan 1981), is shown to have an "above-country and resource-independent long-range flight" dependent on winds in addition to the frequently observed "cross-country progress" during which feeding and reproduction occurs. This is very evident from the work of Gibo (Chap. 12) on monarch butterflies, which use energy-saving mechanisms of soaring in thermals and flying at high altitudes. This enables them to escape from high latitudes as quickly as possible before they become trapped by the onset of deteriorating weather. It is suggested that selection will tend to favour energy-efficient displacement and rapid escape in the southern Ontario populations. Many insect migrations are thus synchronized to annual climatic cycles and the resulting seasonal changes in weather. Meteorological aspects of insect migrations have been well reviewed recently by Gauthreaux (1980), Pedgley (1982), and Rainey (1976b, 1982). Farrow (Chap. 13) shows that a net southward displacement of micro-insects in the temperate latitudes of Australia is caused by the characteristic pattern of synoptic weather, and the rotation of winds' trajectories with the passage of weather systems ensures extensive re-distribution of aerial populations in all directions over inland Australia. The greatest potential for this displacement occurs in northerly airflows at night above the planetary boundary layer. Farrow says that this type of displacement and re-distribution of aerial populations obviates the necessity of requiring specific 'return' migrations in autumn to compensate for the poleward migrations of spring and at other times. Such partly misdirected and wasteful products of migration can also have beneficial effects on the ecosystem. Edwards (Chap. 14) shows how arthropod fallout on the snowfields of Pacific Northwest volcanoes plays a role in the establishment of vegetation, and thus in the diversification of the ecosystem. In this rare example of 'primary succession in reverse', the initial colonizers are scavengers and predators subsisting on wind-borne arthropods. This arthropod fallout also yields suitable nutrients for primary plant colonists, contributing to further diversification.

Papers by Gatehouse (Chap. 9), Raulston et al. (Chap. 15), and Wolf et al. (Chap. 16) also emphasize the significance of weather transport systems in insect migrations, par-

ticularly the spread of pest species in the African and North American continents. Pheromone trap sampling and monitoring of population build-up in corn fields (Raulston et al. Chap. 15) show that initial populations of the fall armyworm, the corn earworm and the tobacco budworm migrate from south (north-eastern Mexico) to north (north and west Texas) in the spring. Synchrony of weather systems with the emerging populations in the south is conducive to these migrations. Wolf et al. (Chap. 16), with the aid of blacklight traps on offshore oil platforms and radar observations, show that insects could move significant distances over water and pest species such as the fall armyworm can cross the widest part of the Gulf of Mexico with favourable winds. These studies thus improve our increasing knowledge (e.g. Dingle 1981b; Greenbank et al. 1980; Gunn and Rainey 1979; Joyce 1981; Rabb and Kennedy 1979; Rainey 1976a) of migrant agricultural pests. Stinner et al. (Chap. 17) stress the desirability of predicting pest outbreaks. Two mathematical models are presented, one based on a highly mobile species and the other on a species with limited mobility. In Chap. 18 Stein reviews the occurrence of dispersal among arthropods of public health importance and the influence of biotic, abiotic, and trophic factors on dispersal. He points out that the amount of published work on the dispersal of public health pests is scanty, particularly on Siphonaptera, Hemiptera, and Acarina. Finally, in Chap. 19 Lingren et al. provide information on night-vision equipment and its use in observing nocturnally active insects which constitute a greater portion of the pest types. In the concluding chapter (Chap. 20) Taylor discusses the meaning of the word migration with respect to different animal taxa. He proposes an interesting new classification that defines four different kinds of migration and provides an acceptable rationale for its adoption.

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2 Evolution and Genetics of Insect Migration

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1 Introduction

The last few decades have seen the firm establishment of the notion that insect migration represents an adaptive syndrome. It was not always so. In the decade before the Second World War most entomologists thought large-scale movements of individuals between populations were rare. If such movements did occur, they were usually regarded as pathological attempts to relieve population pressure (see Lidicker and Caldwell 1982). There were of course exceptions which did not pass unnoticed, such as the spectacular movements of locusts and butterflies (Williams 1958), but on the whole most movement was thought to be a "rather quiet humdrum process" resulting from "the normal life of animals" (Elton 1927, p. 148). The perspective has changed dramatically with migration now seen as a fundamental element in the framework of an insect's life history and ecology (Johnson 1969; Taylor and Taylor 1983; Dingle 1984a).

There is enormous variation both within and among species in the way that natural selection has shaped this relation between migratory behavior and the structure of life histories. But running through the diversity is a common thread of adaptation to shifting environments (Southwood 1962, 1977; Vepsäläinen 1978; Dingle 1979, 1980, 1984a). As habitats deteriorate or become overcrowded, insects leave and move to new areas so that there is a shifting mosaic of departure from and invasion of habitats through time - the now famous "fern stele" of Taylor and Taylor (1977). Further, as Kennedy (1985) has again recently emphasized, these movements often involve specialized behavior that renders migrating individuals physiologically distinct from their nonmigrating counterparts. During migration, feeding and reproduction are suppressed by locomotory activity, but this suppression simultaneously primes them for action at the termination of migration. The ultimate relation between migration and life histories is that migratory behavior allows the individual choice of both place and time of breeding and so is a major component of fitness (Dingle 1984a).

We are thus beginning to grasp the critical features of the environmental "templet" (Southwood 1977) which mould the evolution of migratory patterns. What we need to fully understand this evolution, however, and what we have only just begun to assess, is information on the genetic basis for migration. The influence of genes is of fundamental importance, for if the templet of natural selection is to result in the evolution of migration and its appropriate "fit" to habitats and life histories, there must be a

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genetic basis for differences among individuals. But beyond simply knowing whether genes are involved, we need to know what sorts of genetic structure are available for selection and hence what the potential response to selection might be, and what constraints might derive from genetic correlations among traits or from genotype x environment interactions within traits across environments (Via 1984). All are important to comprehending the “substructure of fitness” (Istock 1978) with respect to migration. I shall explore these issues here and attempt to summarize briefly what we know of the genetic mechanisms underlying migratory behavior itself and of the genetic correlations between migration and suites of life-history traits. In doing so, I shall consider both theory and data and briefly discuss some of the methods available from genetics for analyzing continuous characters such as migratory behavior.

2 Genetic Variance and Genetic Correlation

In some cases that I shall discuss, gene influences on migration can be attributed to alleles at one or a few loci behaving in Mendelian fashion. In most cases, however, the relevant traits are polygenic and continuously varying and so do not segregate according to Mendel’s classical laws. Rather, the appropriate analyses of such traits require the techniques of quantitative genetics. These are covered lucidly and in detail in Falconer (1981), so I shall briefly summarize here only some of those necessary to understand the particular cases I shall review.

The basic model of quantitative genetics assumes that individual differences in metric traits are the result of both genetic and environmental influences which can be expressed as

$$V_P = V_A + V_N + V_E ,$$

where V_A is the polygenic or additive genetic variance, V_N is the non-additive genetic variance, and V_E is the environmental variance. V_A arises from the average influences of all genes contributing to a character and is the variance involving specifically the resemblance between offspring and their parents (as distinct from resemblance to other members of the population); because of this, it determines sensitivity to selection and, hence, the maximum rate at which evolution can occur. V_N includes effects due to dominance and epistasis as well as effects resulting from the fact that genes can behave differently in different environments (genotype X environment interaction). V_E is the variance due to environmental fluctuations. If one is trying to estimate genetic variances in the laboratory, one usually attempts to maintain a constant environment so that $V_E = 0$ (and there are no G x E interactions). All of these variances sum to V_P which is the total or phenotypic variance in the population being considered.

We are particularly interested in V_A because of its bearing on rates of evolution. The relation between V_A and V_P is usually expressed as the heritability (h^2) of the trait, where $h^2 = V_A/V_P$. Estimating h^2 gives us an estimate of V_A and can be done in several ways. One is to take advantage of the fact that V_A involves offspring-parent resemblance and to estimate h^2 by offspring on parent regression, where the slope of the regression is a good estimator of h^2 . Similarly one can estimate h^2 by selection where, again because of offspring-parent resemblance, the response to selection (R) is