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# Slaves of the environment: the movement of herbivorous insects in relation to their ecology and genotype

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The majority of insect species do not show an innate behavioural migration, but rather populations expand into favourable new habitats or contract away from unfavourable ones by random changes of spatial scale. Over the past 50 years, the scientific fascination with dramatic long-distance and directed mass migratory events has overshadowed the more universal mode of population movement, involving much smaller stochastic displacement during the lifetime of the insects concerned. This may be limiting our understanding of insect population dynamics.

In the following synthesis, we provide an overview of how herbivorous insect movement is governed by both abiotic and biotic factors, making these animals essentially 'slaves of their environment'. No displaced insect or insect population can leave a resource patch, migrate and flourish, leaving descendants, unless suitable habitat and/or resources are reached during movement. This must have constrained insects over geological time, bringing about species-specific adaptation in behaviour and movements in relation to their environment at a micro- and macrogeographical scale. With insects that undergo long-range spatial displacements, e.g. aphids and locusts, there is presumably a selection against movement unless overruled by factors, such as density-dependent triggering, which cause certain genotypes within the population to migrate. However, for most insect species, spatial changes of scale and range expansion are much slower and may occur over a much longer time-scale, and are not innate (nor directed).

Ecologists may say that all animals and plants are figuratively speaking 'slaves of their environments', in the sense that their distribution is defined by their ecology and genotype. But in the case of insects, a vast number must perish daily, either out at sea or over other hostile habitats, having failed to find suitable resources and/or a habitat on which to feed and reproduce. Since many are blown by the vagaries of the wind, their chances of success are serendipitous in the extreme, especially over large distances. Hence, the strategies adopted by mass migratory species (innate pre-programmed flight behaviour, large population sizes and/or fast reproduction), which improve the chances that some of these individuals will succeed. We also emphasize the dearth of knowledge in the various interactions of insect movement and their environment, and describe how molecular markers (protein and DNA) may be used to examine the details of spatial scale over which movement occurs in relation to insect ecology and genotype.

**Keywords:** insect; herbivores; migration; dispersal; molecular ecology; spatial scale

## 1. INTRODUCTION

For most insects, true behavioural migration, i.e. innate genetically programmed and prolonged active flight versus dispersal by various means, is the exception rather than the rule. Normally, animal populations expand into favourable new habitats or contract away from unfavourable ones by random movement over different spatial scales (Andow *et al.* 1993). The importance of these two modes of movement seem to have been confused and therefore, whilst dispersal and migration are often described in titles of general texts, insufficient emphasis has been placed on their relative occurrence in nature. The fascination with long-distance mass migratory events has, over the past 50 years, tended to overshadow the more universal mode of population displacement and may be limiting our understanding of population dynamics.

In insects, this dichotomy between dispersal and migration is clearly alluded to (e.g. Williams 1958; Johnson 1969; Taylor & Taylor 1983; Kennedy 1985; Dingle 1984, 1986, 1991). However, what has not been highlighted is whether or not the phenomena are just behavioural continua over different geographical scales or are the response of different genotypes. This article does not seek to untangle the Gordian knot of this complex subject (c.f. Drake & Gatehouse 1995; Gatehouse 1997). Instead we wish to establish that spatial displacements

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(dispersal) rather than migration *sensu stricto*, are the 'norm', and that in some instances these patterns of movement determine genetic variability and gene flow in natural populations.

### (a) *Dispersal*

Dispersal is defined as 'the process by which individuals escape from the immediate environment of their parents and neighbours, and become less aggregated; dispersal therefore relieves local congestion' (Begon *et al.* 1990). However, 'dispersal is not always just "escape"; it can also often involve a large element of discovery' (Begon *et al.* 1990). In short, 'individuals go to the patch where their rewards are highest' and this involves sampling and/or testing and learning (Sutherland 1996). Hence dispersal of individuals and populations over different spatial scales (e.g. Loxdale *et al.* 1993) does not necessarily involve a predisposition to movement.

### (b) *Migration*

The various types of classical migration have been discussed at length (Taylor 1986*a*,*b*; Drake *et al.* 1995; Sutherland 1996). For example Taylor (1986*a*) refers to: (i) passive migration or one-way projected immigration; (ii) dynamic migration, one-way single migration; (iii) homeostatic migration, two-way migration; and (iv) social migration, i.e. the collective movement of individuals within a population. First-instar coccids demonstrate the first criterion when they are carried downwind from their plant hosts like inert particles (Hanks & Denno 1998). Host-alternating flying aphids may be used to represent the second category as different generations return to the overwintering woody host from their summer hosts (Hardie 1993). The monarch butterfly, *Danaus plexippus* of North America, approximates to the third category in its generation that migrates to, and overwinters in, southern California (western population), the Gulf coast states and Mexico (eastern population) returning north to Canada by midsummer (Urquhart & Urquhart 1977; Eanes & Koehn 1978). The last category (iv) is exemplified by migratory locusts (Lecoq 1995). The intricacies of diurnal foraging activity, for example in bees, wasps and ground beetles, are not considered here.

Kennedy (1985) has emphasized the behavioural aspect of migration as 'a 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 reoccurrence'. Some of the aforementioned migration categories (ii and iii) represent unique specialized phenomena limited to certain species which produce a seasonal protracted movement. Such movements are not only innate, i.e. can occur over several generations, but also involve a return to an established niche in the same or another generation (Neigel 1997). Categories (i) and (iv) are different in that they still involve innate behaviour that overrules environmental stimuli, but they do not involve two-way movement either seasonally or from year to year. Although most insect orders have winged stages, the dispersal activity discussed here is usually, but not necessarily, by flight.

### (c) *Gene flow*

In population genetics circles, migration and gene flow are in many ways seen as being synonymous. Gene flow may be strictly defined as the 'change [in gene frequency] due to movement of gametes, individuals, or groups of individuals from one place to another' (Slatkin 1987). With sexually reproducing, vagile species, these tend to migrate after a teneral period, sometimes involving feeding and maturation (Johnson 1969). Their genes leave the original population (gene pool) and are introduced into the new gene pool established or contributed to, on arrival at the destination. In other words, gene flow may be said to occur when animals reproduce successfully and leave descendants following displacement between two or more populations (Daly 1989). Even in cyclically parthenogenetic insects such as aphids, which have an alternation of asexual and sexual phases (Dixon 1998), gene flow can occur between populations. Thus genes are contributed from one population to another when the pre-sexual females (gynoparae) and males move from the secondary, herbaceous summer hosts to the primary, woody hosts where mating takes place and overwintering eggs are laid (Dixon 1998). However, in the case of obligate asexual aphid morphs found in some species (Simon *et al.* 1996*a*) or wholly asexual species (e.g. the shallot aphid, *Myzus ascolonicus*; Blackman & Eastop 1984), migration and gene flow may then be considered to be decoupled from each other (see Simon *et al.* 1996*a*).

In the following discussions of delineating movement, we briefly consider the most important aspects of environmental constraints (abiotic and biotic factors) with respect to the herbivore genotypes that govern the displacement of insects from one region to another. Together these various factors allow the exploitation of new habitats with concomitant range expansion, sometimes involving host adaptation and ultimately speciation, thereby making insects so versatile in the great game of life. This synthesis emphasizes the use of molecular markers to elucidate the genetic aspects of the continua of insect population movement in relation to their ecology.

## 2. MOVEMENT: PATTERNS OF DISPLACEMENT

In insects showing migratory behaviour, definite regular patterns of spatial and temporal displacement are observed. The few examples of these are well documented because of their remarkable nature. These include mass movements over large geographical areas: the monarch butterfly tracking its host plant milkweed, *Asclepias* spp. (Uqhuart 1960; Brower 1977); the long-distance movements of aphids in India (Riley *et al.* 1995) and across middle America (Irwin & Thresh 1988); the annual coastal migrations of dragonflies in North America (Shannon 1916, 1926); the movements of plant hoppers in south-east Asia, including journeys across the sea (den Hollander 1989; Kisimoto & Sogawa 1995); the movement of hoverflies across the Pyrenees (Lack & Lack 1951); and the mass movements of grasshoppers and armyworm moth (*Spodoptera exempta*) in Africa (Riley & Reynolds 1983; Riley *et al.* 1981, 1983) and budworm moths (*Helicoverpa* spp.) in Australia (Gregg *et al.* 1995; Walden 1995).

Like the monarch butterfly, a few other insect species have also been found to show a bidirectional migration between breeding and overwintering sites, i.e. butterflies, the red admiral, *Vanessa atalanta* (Benvenuti *et al.* 1996) and the large white, *Pieris brassicae* (Spieth & Kaschuba-Holtgrave 1996). However, in contrast to the monarch, the bidirectionality is restricted solely to different generations.

Distinct from these classic and dramatic movements the more prevalent dispersal patterns followed by insects involve both individual movements as well as mass displacements. Whiteflies, aphids and thrips display large-scale movements but these are normally affected by air masses above the boundary level because of their small size (Johnson 1969). Even so, they exhibit diurnal periodicities in response to temperature and photoperiodic cues (Johnson 1954; Lewis & Taylor 1965) and in the case of whiteflies and aphids, much greater control over their flight orientation (Blackmer & Byrne 1993*a*,*b*, 1995; Hardie 1993). These large-scale patterns in movement observed in small insects are generally random, although periodic changes in wind direction and conventional currents, pressure changes etc. influence the distribution and deposition of these airborne masses (Johnson 1969; Loxdale *et al.* 1993).

In larger insects, which show displacement, movements may be governed by habitat corridors, such as has been found with some butterfly species (Dover 1991). In these linearized movements (Taylor & Taylor 1983), the rate of displacement is variable and driven along by the distribution of suitable resources and their depletion. These niche corridors have been shown to maintain species populations and richness in fragmented systems (Gilbert *et al.* 1998). Similar work on metapopulation structure in butterflies has emphasized the importance of habitat fragmentation (size and distribution of habitat patches) on the dynamics of local population recolonization and extinction (New *et al.* 1995; Thomas 1994; Thomas & Hanski 1997). In localized populations of the silver-spotted skipper butterfly, *Hesperia comma*, long-term studies of patterns of colonization have revealed that there is a high probability of colonies from big patches recolonizing nearby extinct patches; however, the probability of recolonization declines after a kilometre to within a limit of 9 km. Work on several butterfly species indicates reduced rates of dispersal with increased distance (Thomas & Hanski 1997). It appears that in these species, although the insects themselves are capable of dispersal over many kilometres, their behavioural traits ensure habitat fidelity; for example, they show patch-restricted foraging (Costa 1998). Here the patchiness of the environment constrains the pattern of distribution, although this is species dependent, often with a temporal component (Veith *et al.* 1996).

In some insects, such as the cereal leaf beetle, *Oulema melanopus*, in North America (Andow *et al.* 1993), patterns of population distribution during their dispersal can be described by classical modes of range expansion, i.e. from focal points of establishment going outwards in concentric waves of increasing diameter. Similarly, the Knopper gall wasp, *Andricus quercuscalicis*, whose host which alternates between pedunculate oak, *Quercus robur* and Turkey oak, *Quercus cerris,* has tracked the artificial plantation of the latter host across Europe since the 17th century in a concentric pattern of colonization (Stone & Sunnucks 1993) (see below). Sometimes, as in the lupin aphid, *Macrosiphum albifrons*, which has also shown a radiating pattern of distribution and colonization since its initial discovery at Kew, London in 1981, the initial focus of population appears to represent a founder event, possibly a single parthenogenetic female (Carter *et al.* 1984; Piron 1987). Similar founder events are proposed for the arrival and dispersal of the Russian wheat aphid, *Diuraphis noxia*, in North America (Araya *et al.* 1987) and the 'Africanized honeybee', *Apis mellifera scutellata,* invasion into the Americas (Hall 1992), both in historically recent times. On a geological time-scale, the movement and adaptive radiation from a founder event(s) by drosophilid flies in the Hawaiian Islands (Carson *et al.* 1970) may have followed similar patterns.

## 3. MOLECULAR MARKERS AND MOVEMENT: SPATIAL SCALE AND RESOLUTION USING GENETIC MARKERS

The advent of molecular markers (protein and DNA) has allowed greater insights into the structure and dynamics, gene flow, and by inference, movement of insect populations (Menken & Raijmann 1996; Loxdale *et al.* 1996; Carvalho 1998). A plethora of molecular markers (Hoy 1994; Clapp 1995; Loxdale 1994; Loxdale & Lushai 1998)—allozymes and DNA markers: mitochondrial DNA (mtDNA) as well as nuclear DNA (nDNA) (ribosomal DNA, microsatellites, intron markers, random amplified polymorphic DNA (RAPD), restriction-fragment length polymorphisms, amplified-fragment length polymorphisms), have been used to examine population structure and dynamics at various spatial and temporal scales, including across physical barriers (Liebherr 1988; Napolitano & Descimon 1994).

With allozyme and nDNA markers, the distribution of allele frequencies between populations may be examined, with drift, selection, mutation and local extinction being likely to perturb homogeneity existing in populations in genetic equilibrium (Slatkin 1985; Luikart *et al.* 1998; Peterson & Denno 1998*a*,*b*). Mitochondrial genetic markers, because of their predominantly maternal inheritance, lack of recombination and fast rate of evolution (Avise 1994), have been employed especially in studies where genetic bottlenecks may have had a role in shaping population structure (Loxdale *et al.* 1996; Carvalho 1998). Daly (1989) and Slatkin (1985, 1993) discuss how estimates of gene flow derived from allele frequency data (contingency $\chi^2$ tests, $F$-statistics, $Nm$ (effective population size, $N \times$ migration rate, $m$), Slatkin's (1985) methods, etc.) can be directly related to the extent of movement. Sampling methods adopted for molecular ecology studies by Shufran *et al.* (1991) and De Barro *et al.* (1995*a*,*b*) have involved collecting insect samples (here aphids) at local and geographical scales over a growing season to see spatial and temporal trends. Mark–recapture studies carried out in conjunction with molecular markers by Lewis *et al.* (1997) have also provided effective ways of mapping genetic variation over different spatial and temporal scales. However, for more accurate spatial sampling, a concentric collection approach from a fixed point spreading out at exponential distances would be optimal, but technical considerations often limit such sampling.

At the geographical scale, studies of the noctuid cotton bollworm moth, *Helicoverpa armigera*, in eastern Australia have revealed population genetic homogeneity. This is considered to be a consequence of long-range movements in this well-known pest (Daly & Gregg 1985). In Californian fruit flies, *Drosophila pseudoobscura*, long-distance movements by individuals (up to 15 km over unfavourable habitats) lead to interpopulation allelic homogeneity (Jones *et al.* 1981; Coyne *et al.* 1982). However, in *Drosophila willistoni* there are implications that such homogeneity found among populations across Florida, Mexico, the West Indies, and Central and South America results from locally differentiating selective forces, i.e. stabilizing selection at the macrogeographical scale (Ayala *et al.* 1972).

In the Knopper gall wasp, whilst spatial changes of population distribution appear concentric, a more 'step wise' dispersal has been determined using genetic (allozyme) markers (Stone & Sunnucks 1993). In addition, with each successive movement and colonization by founders from the initial genetically diverse stock in central Europe, the level of diversity observed has declined so that the peripheral populations only contain a limited amount of genetic heterogeneity compared with the refugia (Stone & Sunnucks 1993). A similar conclusion is drawn from work on the rose grain aphid, *Metopolophium dirhodum* recently introduced into New Zealand, compared with supposed source populations in Scotland (Nicol *et al.* 1997).

In the November moth, *Epirrita dilutata*, a woodland species, the generally high level of homogeneity (low heterogeneity) observed in population allele frequencies over a large geographical area in Britain was thought to be associated with movement and gene flow counteracting the effects of drift, selection etc. and thereby reflecting the historical genetic pattern of colonization (Wynne 1997). However, this pattern was not found when large sample sizes were examined over small spatial scales ($< 2$ km) over a number of consecutive years. In this study, significant genetic heterogeneity was observed even at the commonest alleles, suggesting a lack of movement, and these results were supported by mark–release–recapture methods (Woiwod & Wynne 1994; Wynne 1997). This is an example where spatial scale and interpretation of allele frequency data have a very important influence on the conclusions drawn from temporal genetic studies. In localized butterfly populations, e.g. checkerspot butterflies (*Euphydryas editha*), allelic homogeneity was generally observed throughout the species range in North America, despite great differences in morphology and ecology. This was attributed to a combination of historical patterns of distribution, gene flow and parallel selection (Baughman *et al.* 1990). Examples where significant genetic heterogeneity is observed over small spatial scales have been attributed to restricted interpopulation movements, for example as found in some species of aphids (Loxdale & Brookes 1990; Loxdale *et al.* 1998; De Barro *et al.* 1995*a*,*b*).

Peterson & Denno (1998*b*) have extensively reviewed the relationship between the dispersal ability of insects as well as diet breadth on population genetic structure. They examined the allozyme data versus estimated isolation by distance (IBD) for 43 phytophagous insect species and races. They tested the opposing hypotheses that (i) the IBD slopes in plots of log gene flow ($Nm$, $y$-axis) versus log distance (km, $x$-axis), are unchanged by distance yet the intercepts increase with mobility, and (ii) that IBD slopes vary with dispersal ability (see fig. 1 in Peterson & Denno 1998*b*). Mobility trends tended to fit with the second hypothesis rather than the first. Thus in sedentary and highly mobile species, IBD was weak over distances ranging from tens of kilometres to 1000 km; both species categories had shallow slopes, and markedly different intercepts. However, the relationship was more pronounced in moderately mobile species, i.e. comparatively steeper slope and higher $y$-axis intercept (see fig. 5 in Peterson & Denno 1998*b*). From these data it was deduced that: (i) genetic divergence among most populations of sedentary species found over the distances tested is due to limited gene flow; (ii) the genetic homogeneity found in intermediate dispersers over small spatial scales results from adequate gene flow, whereas the heterogeneity seen at larger spatial scales is due to a restriction of gene flow; and (iii) the homogeneous genetic structure of highly mobile species at all spatial scales is a consequence of high gene flow. The hypothesis that IBD increases with decreasing diet breadth was also tested, although no clear patterns were detected. In both gene flow and diet-breadth trends, the number of populations tested was a more crucial component than the number of polymorphic loci surveyed (Peterson & Denno 1998*b*).

## 4. CONSTRAINTS OF THE ENVIRONMENT

The constraints of the environment include both abiotic and biotic factors. These interact with the herbivorous insect population (ultimately the genotype) to the extent that their negative influences direct population expansion, i.e. in favourable conditions dispersal would not occur unless the insect concerned is an innate migrant. The examples below demonstrate all the various factors involved and how they have, and could be, investigated using molecular markers.

### (a) *Abiotic factors affecting redistribution*

It is well known that many insect species undergo aerial movements in response to seasonally induced changes in habitat, physiology and climatic cues (Drake & Gatehouse 1995). This is well exemplified in aphids which display phenologies involving alternation of hosts (Miyazaki 1987; Dixon 1998). Such phenological changes involving flight periods have a *latitudinal* basis, i.e. tend to occur relatively later in the spring further north (Smith & MacKay 1989, 1990). In addition, the timing of first flight in some aphid species is directly correlated to preceding mean winter *temperatures* (in January and February) (Harrington *et al.* 1995). The sporadic mass movements of locusts in Africa, rice planthoppers in Asia and the mustard aphid, *Lipaphis erysimi* in India, are known to be influenced by large-scale *weather* movements, often related to storm fronts (Pedgley *et al.* 1995; Johnson 1995; Kisimoto & Sogawa 1995; Riley *et al.* 1995). Similarly, the apparent large-scale movements of cereal aphids across mid-west North America are associated with the *jet stream* as winged forms are carried up by convection currents to *ca.* 900 m (Irwin & Thresh 1988).

The periodic mass movements of Lepidoptera into the UK from Europe during the spring and summer are associated with unusually favourable winds and weather conditions (e.g. *Laphygma* (=*Spodoptera*) *exigua*; French 1969), as are similar movements in the Middle East (Pedgley & Yathom 1993). It is also known that some insects fall out of *air masses* during transportation as a result of down draughts and precipitation, especially small insects such as thrips and aphids (Taylor 1965; Bowden & Johnson 1976; Drake & Farrow 1989; Peck 1994*a*). With small insects borne on the wind above their flight speed, a level of orientation persists below the boundary layer (Taylor 1965, 1986*c*; Gatehouse 1997) enabling host orientation in response to visual and olfactory stimuli (Blackman 1990). *Climatic and/or biogeographical* zones are major factors influencing species geographical distribution (Kimura & Beppu 1993; Ayres & Scriber 1994), such zones sometimes being limited in extent. An example is the Glanville fritillary butterfly, *Melithea cinxia*, which in Britain is confined to cliffs on the south side of the Isle of Wight, probably due its dependency on warm temperatures (Thomas & Lewington 1991). It is thus on the edge of its geographical range in Britain, yet elsewhere in Europe it is widely distributed and frequents a range of habitats as far north as Scandinavia (Saccheri *et al*. 1998). The influence of spatial and temporal habitat heterogeneity is central to insect dispersal and has been reviewed extensively (Kim & McPheron 1993; Wilson 1995).

Sometimes, insects may be *inertly* carried long distances on floating vegetation and debris by water currents (Peck 1994*b*), while others are transported over different spatial scales, sometimes great distances, by human agencies including ships, aeroplanes and motor vehicles (Johnson & Bowden 1973). Examples are the median wasp, *Dolichovespula media* and the Saxon wasp, *Dolichovespula saxonica*, which were previously confined to the continent of Europe. Since the 1980s both have established themselves in southern Britain, possibly as a result of inadvertent importation, and are continuing to expand their range (Else 1992, 1994) (note that Mikkola (1984), however, observed active dispersal of wasp and bumble-bee queens across large bodies of water). Either way, this successful expansion may relate to large-scale climatic factors, i.e. the generally warmer weather conditions experienced in Britain during the mid-1980s and the 1990s. It is also possible that insecticide resistant strains of the mosquito, *Culex pipiens,* have been transported around the world by ships and aircraft (Raymond *et al*. 1991).

There are very few entomological examples where molecular markers have been used to track gene flow resulting from transport by abiotic media. These include small herbivores of the suborder Homoptera—aphids using ribosomal DNA markers (Shufran *et al*. 1991), psyllids using allozyme markers (Unruh 1990)—along with movement by human agency of the medically important mosquito, *C. pipiens*, as mentioned above, tracked using esterase markers (Raymond *et al*. 1991).

### (b) *Biotic factors affecting redistribution*

#### (i) *Energy resources*

The success of all animal species populations is determined fundamentally by food resources. All insects, regardless of their type of displacement, leave a suitable resource patch at their peril. Therefore, displacement is often as a consequence of the carrying capacity of the habitat resources being exceeded (Taylor 1986*b*; Hedrick & Gilpin 1997). Whatever the exact cause of departure, usually resource depletion or its predicted depletion by the insect, the extent of displacement is critically influenced by the energy reserves within the insect (e.g. Liquido & Irwin 1986). This can involve trade-offs between biosynthesis of fuels (e.g. triglycerides) and reproduction (Zera & Denno 1997). Either way, these factors are highly correlated with the likelihood of finding a suitable host and habitat that is better than the one left behind. In aphids, the balance of energy costs of such movement is probably related to ovariole number, gonad size, lipid reserves and nutritional threshold levels in continuous changes between host–herbivore interactions (e.g. Dixon *et al*. 1993; Kindlmann & Dixon 1994).

As far as molecular ecological studies are concerned, there appear to be no published accounts correlating energy constraints (i.e indicators such as ovariole number, gonad size, lipid reserves), movement and genotype together. However, there are many accounts of two out of these three variables being tested. Hence to date, investigators must presume that the dispersing population is genetically similar and therefore have not addressed all these factors simultaneously.

#### (ii) *Host: range and persistence*

All herbivorous insects are also limited in their distribution by their host range (Bradley 1993) and/or availability (Dempster 1989). With monophagous insects, the limits of distribution may be critical in determining range, although this may well be less of a problem with polyphagous insects. Some insects can get around the problems of limitations of host range by adapting to a new host or a greater selection. As well as range, host phenology (such as bud burst) is another determining factor (see § 4b(v)). Wherever insects migrate to, they have ultimately to land on suitable hosts and habitat. Habitat stability *per se* may influence the success of insect establishment and patterns of colonization. Habitat changes, whether they be natural such as drought or man-made, influence host availability and hence successful colonization.

A good example of herbivore distribution related to host range is seen in Idaho where the distribution of various sage brush aphid species, monitored using a network of 8 m high suction traps, was found to be correlated with that of their host plants (Halbert *et al*. 1995). The cinnabar moth, *Tyria jacobaeae* is an example where distribution is related to its host abundance, i.e. females only laid eggs on dense clumps of its food plant ragwort, *Senecio jacobaea*, thereby relieving herbivory on less-dense clumps (Van der Meijden 1979). There are also examples where the insect distribution is tightly bound to host-plant distribution as well as other ecological parameters. Thus the distribution of the heath fritillary butterfly, *Melithea athalia*, in south-eastern England is limited by the distribution of its host, cow-wheat, *Melampyrum pratense*, as well as the correct habitat requirements, i.e. recent woodland clearings (Thomas & Lewington 1991; New *et al*. 1995). With the British subspecies of the large copper butterfly, *Lycaena d. dispar*, drainage of the fens in eastern England beginning in the early 17th century, reduced the availability of habitat as well as the food plant, great water dock, *Rumex lapathum*, on which the larvae of this fine butterfly fed. This, along with over-zealous taking of specimens by collectors, marked the death knell for this insect, which became extinct in around 1848 (Thomas & Lewington 1991).

Local adaptations may cause behavioural changes which restrict certain populations to specific habitats. In the North American goldenrod ball gallformer fly, *Eurosta solidaginis,* which is partially genetically adapted to the goldenrod species, *Solidago altissima* and *Solidago gigantea*, the insect shows host-plant fidelity and assortative mating along with a geographical element in the distribution of the insect races (Itami *et al.* 1998). In these cases, the ecotypes become intimately associated with particular host niches and thereby constrained in their distribution.

However, there are instances where such constraint is lifted by exploitation of a broader range of host resources, which may increase the distribution of a given ecotype. Some examples of this include (i) the comma butterfly, *Polygonia c-album* in Britain, which seems to have changed from predominantly colonizing commercial hops (*Humulus lupulus*) up to 1914 to mainly the stinging nettle (*Urticae dioica*) today after passing through a population bottleneck (Pratt 1987; Thomas & Lewington 1991); (ii) the expansion of the Russian wheat aphid, *Diuraphis noxia* from its central Asian source in the 1800s where it had a limited host range to economically important cereal hosts both in Eurasia (Kovalev *et al.* 1991) and more recently, North America among other continents (Araya *et al.* 1987); (iii) the expansion of the Colorado beetle, *Leptinotarsa decemlineata*, from its original refugia in the foothills of the Rocky Mountains where it fed on buffalo bur (*Solanum rostratum*) prior to its colonization of cultivated potatoes in North America and later Europe (Jacobson & Hsiao 1983); and (iv) the host range expansion of angiosperm-feeding moths introduced into Britain (Fraser & Lawton 1994).

Where insects show polyphagy, their potential with respect to range expansion may be greatly increased by the greater availability of suitable hosts (Quinn *et al.* 1997). However, the evolution of host diversification may have a genetic basis entailing fitness costs in terms of performance (Futuyma & Peterson 1985), while differences in host preference, including that for oviposition, determine the transition to, and success on, new hosts (Lushai *et al.* 1997*a*; Thomas & Singer 1998). Sometimes selective pressure, such as the introduction of insect-resistant crop genotypes, can lead to the evolution of biotypes which then have close host-related distributions (Powers *et al.* 1989). In some sympatric planthopper (*Nilaparvata lugens*) populations, host-plant adaptations have been reinforced by behavioural differences, i.e. song pattern, thus promoting reproductive isolation without morphological dimorphism and leading to speciation (Claridge *et al.* 1997; Henry 1994).

Even monophagous species can have a large range by tracking a suitable host through its growing season. The highly migratory monarch butterfly tracks its milkweed hosts over several generations to and from its goal (overwintering site) (Brower 1977; Eanes & Koehn 1978). Similarly, in the armyworm moth, the movement of the population is closely linked to the flush of growth of vegetation following frontal weather patterns in train with tropical rainstorms (Rose 1979). Where migration is related to seasonality, and subsequent physiological changes in the individual are synchronized to local habitat deterioration, the expected displacement is likely to be dramatic both in terms of timing and spatial scale (Gatehouse & Zhang 1995). Sometimes, habitat disturbance encourages new colonization events from adjacent habitats (Pimentel 1993). There is possibly less environmental resistance (e.g. low parasitism, parasitoid or predator levels) in such habitats compared with those that have achieved a stable state. (Note that the 'push' effect of predators, etc., that is to say the direct influence or causation of insect dispersal, has been described in relation to drift effects of stream-dwelling insects (Sih & Wooster 1994), although this biotic factor has apparently not been documented for terrestrial dispersing insects; however, see Moran *et al.* 1996.)

Herbivore genotypic variation across a given host has been revealed by several studies. In the grain aphid, *Sitobion avenae*, populations colonizing gramineous hosts have been found using DNA fingerprinting methods to show local genetic heterogeneity and host adaptation early in the field season (De Barro *et al.* 1995*b*,*c*). This apparent adaptation breaks down later in the season, probably as the frequency of local movements increases, both within a field and between fields leading to a lowering of the distinction between the host-adapted clones. However, within a field, certain genotypes (clones) can colonize greater areas, possibly because of increased adaptive performance, and hence clonal variation declines (De Barro *et al.* 1995*a*). Shufran *et al.* (1991) also using a method of DNA fingerprinting, showed that populations of the cereal aphid, the greenbug, *Schizaphis graminum*, in the USA had numerous genotypes but none was unique at any spatial scale from field to county level. Even so, a similar decline in genetic diversity was noted within fields as the season progressed.

In aphids, movement between hosts can greatly affect patterns of genetic diversity. In the bird-cherry–oat aphid, *Rhopalosiphum padi*, scarcity of the principal primary overwintering host (bird-cherry, *Prunus padus*) in southern Britain (Tatchell *et al.* 1983) appears to be correlated with low aphid genetic variation and for those loci displaying polymorphisms, high genetic homogeneity (Loxdale & Brookes 1988). This pattern may arise because the overwintering host is effectively acting as a genetic bottleneck eliminating rare alleles and fixing some loci, whilst the high level of migration of this aphid tends to homogenize the frequency of the remaining polymorphic variants. In extreme cases such as *M. persicae*, whose principal primary overwintering host (peach, *Prunus persica*) is generally very restricted in its distribution in Britain, most of the loci surveyed are fixed for one allele, again possibly due to a bottleneck effect related to host abundance (Brookes & Loxdale 1987). In gall-forming aphid species, the pattern of heterogeneity observed suggests low levels of intergall dispersal and gene flow (Hebert *et al.* 1991).

### (iii) *Physiological and behavioural*

The main difference in insects with innate behavioural responses (such as locusts and aphids), compared with dispersing insects, is that the migratory persistence before stimulation and the spatial area covered during the migratory phase is usually much greater in the former group. Hence migratory insects will continue to fly and not settle on patches of suitable resources (energy sources and potential mates) (e.g. Kennedy & Booth 1963). However, after a 'threshold' level has been reached, the innate influence (migratory mode) is superseded by other behaviours, e.g. mating and breeding, which may involve various physiological changes. Such behaviours may often be induced by seasonal change as well, often being intimately linked with the sequence of reproductive events. Insects in migratory mode generally show delayed and depleted reproductive potential, hence fitness, as a consequence of the demands of flight metabolism (Gatehouse & Zhang 1995). There are a few examples of greater distances being flown post-mating, e.g. *Helicoverpa armigera*, but these were in the presence of abundant food resources (Armes & Cooter 1991).

In some insects, especially in Hemiptera, the autolysis of flight muscles occurs post-migration (Johnson 1957; Tanaka 1993, 1994) or there are changes in the total area occupied by myofibrils preventing further flight (Blackmer *et al.* 1995). In aphids, the stimulus to produce winged forms capable of dispersing is related to crowding and/or tactile responses or the nutrient quality of the host (Dixon 1998). After dispersal, successive parthenogenetic generations of some aphid species produced by a winged colonizer are unable to form wings until a period of time has elapsed, and which involves a biological clock-based control mechanism (Sutherland 1970). In the cowpea weevil, *Callosobruchus maculatus*, a pest of stored legumes, production of winged morphs capable of dispersal is density dependent, with strain differences occurring in the propensity to produce winged morphs under high-density conditions (Dingle 1991). Here, the genetic polymorphism seems to be polygenic with a maternal bias (Dingle 1991). In all these examples, such changes may be under hormonal control (Dingle & Winchell 1997; Zera & Denno 1997). Synchrony in migratory behaviour may also be mediated by pheromones. Examples here include the change from solitary to gregarious phases in the desert locust, *Schistocerca gregaria* (Deng *et al.* 1996) and the attraction of male aphids and hymenopterous parasitoids to 'calling' female aphids (Pickett *et al.* 1992). Alternatively, alarm pheromones produced by aphids as a response to attack or disturbance cause members of the colony to be displaced from the host plant (Pickett *et al.* 1992).

There has been some work to demonstrate subtle genetic components related to various dispersal behaviours. For instance in *D. plexippus*, a relationship with a sexual dimorphic component has been found between heterozygote frequencies at the enzyme locus, phosphoglucose isomerase in relation to flight at low temperatures (Hughes & Zalucki 1993). In the field, higher frequencies of heterozygotes were recorded among late-day compared with early-day fliers. In comparison, in *Colias* butterflies (clouded yellows) such heterozygotes have been shown to be at a selective advantage because they can sustain flight over a wider temperature range (Watt 1983). Either way, the activity of these glycolytic enzymes is intimately associated with flight behaviour in these highly dispersive fliers. Selection pressures on such loci appear to be independent of other genetic traits, but as the genetic traits all parallel each other, the selection on one reflects 'the summation of similar selective pressures on all of them' (Watt *et al.* 1983).

When an insect with a particular adaptive trait, such as tolerance to insecticides, is displaced to a region of pesticide usage, it may have a competitive advantage. In the case of the highly insecticide resistant ($R_3$) strains of the peach–potato aphid, *M. persicae,* some mutations which confer pesticide resistance affect the physiology and behaviour directly. Such cross-resistant insects, which are detectable as a consequence of their elevated carboxylesterase E4 enzyme activity, also have a pyrethroid resistant 'knockdown' mechanism which affects their nervous system via a structural change in the sodium channels. This in turn induces a reduced propensity for insects to move from deteriorated leaves, a lower sensitivity to alarm pheromone, whilst such animals are also less likely to form winged morphs (Foster *et al.* 1996, 1997). As above, independence of genetic mechanisms must account for highly resistant *M. persicae* incurring no fitness costs (Crow 1957), even when the amplified carboxylesterase E4 genes are unexpressed, i.e. kept in the population as 'revertants' (cf. Foster *et al.* 1996).

### (iv) *Competition*

As mentioned earlier, direct competition can lead to physiological changes in insects such as crowding effects, etc. (Lees 1967). These influence displacement events, thereby reducing the impact of intraspecfic competition for resources leading to competitive exclusion (Taylor 1986*b*). In some instances, intraspecific redistribution of populations will also relieve the predator–parasitoid pressure on individuals that have moved (Hanks & Denno 1998) and such 'enemy-free space' (Jeffries & Lawton 1984; Hopkins & Dixon 1997) may lead to the establishment of subpopulations (Mopper & Strauss 1998).

When insects adapt to a new resource (Pashley 1993), assortative mating can occur and in a few rare instances, sympatric species evolve. The most celebrated study concerns the apple-maggot fly, *Rhagoletis pomonella*, which has morphologically similar but genetically distinct forms infesting hawthorn and apple (Feder *et al.* 1998). Host preference is strongly correlated with genotype and reinforced by significant allochronic isolation brought about by asynchrony between fly eclosion and host phenology. Further entomological examples include hymenopterous parasitoids of the genus *Aphidius* (*A. ervi sensu lato*) attacking pea and nettle aphids in the same locality (Atanassova *et al.* 1998), and introgression between sister species of the cereal aphid *Sitobion* spp. producing wild grass-adapted clones (Sunnucks *et al.* 1997). Where a species complex exists, e.g. *M. persicae*, chromosomal changes associated with translocation and gene mutation and/or duplication may produce new strains or species in a short time (Blackman 1987; Blackman & Peterson 1986; Blackman *et al.* 1995). Such change has the evolutionary advantage of reducing intraspecific competition. The evolution of host-adapted strains may allow movement onto new resources as shown by *Bemisia tabaci* (Legg 1996), and tephritid fruit flies

(Aluja & Birke 1993), but may also prevent such specialized adapted strains from returning to the original host, which is perhaps more widespread in its distribution. In this circumstance, specialization can lead to an adaptive 'dead end' (Moran 1988).

There is very little reported evidence for the genetic components of intraspecific competitive interactions between herbivores on a host plant and the influence of this interaction and subsequent population displacement. One conclusive experiment using phenotypic (colour) and allozyme markers (esterases) involving Canadian populations of the rose aphid, *Macrosiphum rosae,* showed genotypes that fluctuated dramatically over the season within local habitats with certain successful clones dominating (Rhomberg *et al.* 1985). From these data, the authors speculate that clonal competition followed by extensive dispersal (not tested for) purged most genetic diversity within the population.

Even the hypothesis of predator-free space as a component of dispersal has not been investigated using a molecular marker approach to determine whether there are changes in genetic diversity as a result of lifting such constraints. These approaches need to be examined further.

### (v) *Life cycle*

When an individual or population arrives in a new habitat it may be unsuitable and the emigrants may thus perish. With persistent insect populations established over many generations and which are sexually reproducing, both sexes have to be present for founder events to occur. Such occurrences may be infrequent when the arrival site is geographically distant or isolated, such as in the remote island species complexes of *Drosophila* founded from a few individuals (Carson *et al.* 1970). Asexuals clearly have a greater chance of establishment in new locations and habitats since only a few select founder clones are required (Blackman 1981; Hughes 1989; Wellings 1994; Sunnucks *et al.* 1996).

In some insects like the Mexican bean beetle, *Epiachna varivestis*, the sex ratio is influenced by the quality and age of host plant eaten (Saks 1993). This influence differs with life stages and has an effect on the flight behaviour of the beetle such that there tends to be a bias towards more mature adult males in a migrating population. This is likely to increase male–male competition for mates and intensify the sexual selection of traits which increase male fitness (Saks 1993). In several insect taxa such as Orthoptera, Hemiptera and Lepidoptera, the physiological differences between the sexes that influence flight behaviour show pre-reproductive migration with an inhibition of reproductive organs (Gatehouse & Zhang 1995). However, where resources are abundant, mated females have been reported to fly greater distances compared with unmated individuals (Armes & Cooter 1991) and certainly in some species, e.g. the monarch butterfly, both sexes mate before migration (Herman 1985).

In tropical environments that are more stable, multivoltinism in insect life cycles is more prevalent compared with temperate systems, where more variable resource availability induces a facultative voltinism, often univoltinism (Pullin 1988). In the univoltine orange tip butterfly, *Anthocaris cardamines*, a close synchrony has been found to occur in southern Britain between egg laying and the availability of flower heads of the principal woodland host *Cardamine pratensis* (Dempster 1997). This type of phenological association may limit range expansion into northern areas where the plants are delayed in their flowering. Such associations are also noted in the synchrony of hatching in the winter moth, *Operophtera brumata*. Here, there are fitness consequences related to adult size in relation to synchrony with budburst of the host tree oak, *Quercus robur* (VanDongen *et al.* 1997).

Some molecular ecological studies highlight life-cycle strategies in relation to demography, but no genetic correlation have been alluded to describing life-cycle synchrony and dispersal in concomitant studies. (NB. One study has genetically related egg hatch to plant host bud burst synchrony in a non-migratory aphid species; Komatsu & Akimoto 1995). In aphids, the geographical distribution of certain life-cycle strategies (obligate asexual and sexual) has been correlated with climatic conditions in French populations of *R. padi* (Simon *et al.* 1996*b*). Using allozyme markers, sexual populations were found to be polymorphic early in the season, whereas asexual populations were relatively less varied, and possibly monoclonal in origin. On analysis with mtDNA markers, sexuals could again be differentiated from asexuals: the former all had one of two mtDNA haplotypes (II or III) in contrast to the latter which were predominantly found to be of another haplotype (I) (Simon *et al.* 1996*a*). Other studies indicate that the genetic differences between these two life-cycle types have a divergence of around 0.4–1.4 million years (Martinez-Torres *et al.* 1996). All these trends indicate relative genetic invariance in asexual populations (but see Lushai *et al.* 1998). If true, this would link with the trends shown by *R. padi* in North America. Here, genetic heterozygosity is low on the grass hosts compared with aphids on the woody hosts colonized by the pre-sexuals and sexuals, and is correlated with invariant dispersants arriving from southern areas (Simon & Hebert 1995). These are most likely to be asexual, but this has to be evaluated with the asexual–sexual differentiating mtDNA markers developed in later studies.

Another example where population genetic structure and life cycle have been correlated using allozyme markers is seen in North American populations of the large heath butterfly, *Coenonympha tullia* (Wiernasz 1989). In recent years, the butterfly has dispersed southwards from its original 'univoltine' range in Canada, becoming bivoltine with concomitant greater genetic diversity. It may be that two flight–mating periods allow for enhanced genetic heterogeneity, although Wiernasz (1989) suggested that there is weak selection maintaining the differentiation between the life-cycle forms in the face of restricted gene flow.

### (vi) *Morph adaptations*

An individual animal species or population may have the physiological ability to traverse a particular distance, but lack the behavioural response. In a given population, there may be some individuals that make migratory flights whereas others within the same species show a behaviour more readily classed as dispersal. A good example of this phenomenon are the apparent phenotypes of the whitefly, *Bemisia tabaci*, which appear to have differential flight behaviour. Only a small proportion (*ca.* 6%) of the insects in a vertical flight chamber displayed a response indicative of migration, i.e. did not settle on the host cue presented for a longer period than the general population tested (Blackmer & Byrne 1995). Males flew longer than females (Blackmer & Byrne 1993*a*), whilst those engaged in longer flights had smaller wing dimensions compared with those engaged in short flights (Blackmer & Byrne 1995).

Similarly in the aphid, *R. padi*, the autumn form which seeks the sparsely distributed overwintering host *Prunus padus* where it produces sexual females, has a very different flight behaviour (including duration and height) than the summer forms seeking grass hosts (Tatchell *et al.* 1988). Wind tunnel experiments have shown these two phenotypes to have differential flight behaviours in response to host stimuli represented by a green light (Hardie 1993), the autumn forms flying for longer. The black bean aphid, *Aphis fabae* shows similar behavioural dimorphism (Shaw 1970, 1973; Kidd & Cleaver 1984, 1986).

As well as interphenotype differential displacements, intraspecific differences in flight behaviour are known. Thus, the British subspecies (ssp. *britannicus)* of the European swallowtail, *Papilio machaon* is confined to small colonies living on milk parsley (*Peucedanum palustre*) in low-lying fenland in eastern England (the Norfolk Broads). In contrast, the continental form (ssp. *gorganus*) is polyphagous on a range of umbellifers in diverse habitats throughout mainland Europe (Thomas & Lewington 1991). Interestingly, despite its strong flight and apparent ability to traverse large geographical distances, the continental subspecies is rarely found in Britain (Thomas & Lewington 1991), suggesting that the Channel or climate is a sufficient barrier (cf. Napolitano & Descimon 1994). This phenomenon should not be confused with that which occurs with the North American checkerspot butterfly, *E. editha*, which is restricted in its dispersal by resource patchiness (Britten *et al.* 1995; Thomas & Singer 1998). It would appear that within a species, strategies for resource seeking can be differentiated into various levels of adaptive behaviours, often related to complicated life-cycle strategies, e.g. oviposition host preference in butterflies (Wiklund 1975, 1981; Thomas & Singer 1998).

In a range of insect taxa (Orthoptera, Psocoptera, Thysanoptera, Hemiptera, Coleoptera, Diptera, Lepidoptera and Hymenoptera), there are forms with reduced wing sizes (brachypterous) whilst others have done away with flight apparatus altogether (apterous). These species are said to show dispersal polymorphism (Zera & Denno 1997). Morphological polymorphism associated with differences in flight behaviour can also determine intraspecific dispersal. For example, in the saltmarsh planthopper, *Prokelisia marginata*, wing length polymorphism is found in the adult, with both long-winged forms capable of flight and flightless short-winged forms occurring (Denno *et al.* 1996). In the wing-length polymorphic Mediterranean lygaeid bug, *Horvathiolus gibbicollis*, morph production seems to be under single locus control, yet there is a correlation between wing length and female reproductive performance, with a peak of oviposition followed by muscle autolysis in the winged forms (Dingle 1991).

The stability of habitats appears to determine the proportion of the different morphs found within populations, unstable habitats tending to have much higher proportions of the long-winged forms than habitats which can be occupied all year round (Denno *et al.* 1996). The type of habitat also affects genetic heterogeneity. Thus populations of *P. marginata* comprising predominantly short-winged forms and living in persistent habitats have reduced gene flow and more genetic differentiation compared with similar populations with a preponderance of long-wing forms living in unstable habitats, which show enhanced levels of gene flow (Peterson & Denno 1998*a*; Zera & Denno 1997). Similar patterns of genetic heterogeneity occur intraspecifically in wingless versus winged water striders, *Gerris* spp. (Zera 1981), and this may be a widespread phenomenon in many insect orders involving physiological changes in flight muscles. In such forms, there appears to be a trade-off between dispersal capability and fitness components, including reduced fecundity or delayed age at first reproduction in the fully flighted forms (macropterous) which will incur the metabolic investment of functional wings and flight muscles (Zera & Denno 1997).

In some Lepidoptera such as the winter moth (*O. brumata*), individual species have winged males and wingless females, the former being attracted along pheromone plumes released by the largely sedentary females (Roelofs *et al.* 1982). In the gypsy moth, *Lymantria dispar*, geographical races occur where the female can either fly or is flightless. This is seen in the European race, which is winged, but rarely flying compared with the males, whilst the Asian race is winged and a strong flier. These forms can be differentiated using molecular markers (Bogdanowicz *et al.* 1993, 1997). Presumably, there are trade-off benefits for the females that do not fly, such as increased fecundity. The existence of flightlessness appears to inhibit the range expansion or rate of expansion of the population in flightless forms compared with flighted forms (Bogdanowicz *et al.* 1993; cf. Brookes & Butlin 1994). The various phenotypes in an aphid life cycle (winged and wingless morphs of the same species) are also thought to have trade-offs in terms of host use versus reproductive success (Moran 1992). The wingless forms have higher fecundity but are largely restricted to the immediate locality of their hosts (Harrington & Taylor 1990), whereas the winged forms, whilst they may 'have slipped the surly bonds of earth' (Magee 1986), nevertheless have reduced fecundity (Dixon 1998).

With regard to morph interactions with dispersal, molecular markers have provided useful insights into their population dynamics. This is exemplified by the work of Liebherr (1986, 1988) in North America. Interestingly, he has failed to show a simple correlation between vagility in macropterous (flighted) versus brachypterous (flightless) beetles species (carabids) and gene flow. It was expected that the winged forms would show greater levels of gene flow compared with the non-fliers. Rather, both population types displayed equal levels of genetic heterogeneity measured using allozyme markers, suggesting comparable gene flow. A positive relationship was shown between genetic heterogeneity and elevation of collecting sites between 1100 and 1900 m. Liebherr concluded that lower levels of gene flow occurred in fragmented upland habitats because these were more stable. Therefore, flightless forms showed heterogeneity due to local niche adaptation. Similarly, winged forms did not travel across unsuitable terrain greater than 1 km and also adapted locally. Their overall population structure appeared to be linked to historical patterns of settlement and gene flow. The discrimination of the genotypes of the macropterous and brachypterous forms of the brown plant hopper, *N. lugens* (Kisomoto & Sogawa 1995) may yet be distinguished using molecular markers (cf. Lushai *et al.* (1997*b*) for intermorph, intraclonal variation in related homopterans).

## 5. THE ADVANTAGE OF USING CERTAIN MARKERS TO DISTINGUISH TRENDS IN MOVEMENT

In some instances, the amount of ecological information gleaned from a system can be limited by the molecular marker used. For example, in aphids, the lack of allozyme variation in *S. avenae* compared with that shown by DNA fingerprinting (Jefferys' probe; Carvalho *et al.* 1991) previously limited the examination of fine-scale population genetic substructuring (Loxdale *et al.* 1985; Loxdale & Brookes 1989). The DNA marker approach was extended to differentiate *S. avenae* populations across agricultural ecosystems using fingerprinting (synthetic oligonucleotide probe) and RAPDs. This allowed the discrimination of micro- and macrogeographical heterogeneity (De Barro *et al.* 1994) and some estimate of movement along with plant host-based substructuring of insect genotype (De Barro *et al.* 1995*b*). On analysis with microsatellite and mtDNA markers this genetic differentiation was found to be due to introgression events between sister species (*S. avenae* and *S. fragariae)* (Sunnucks *et al.* 1997), highlighting the apparent adaptation to the host range. The levels of differentiation and appropriate markers for certain applications are detailed elsewhere (Carvalho 1998; Loxdale & Lushai 1998).

Mitochondrial DNA is especially useful in population studies, for the reasons mentioned previously, especially including examining bottleneck effects (§ 3). Additionally, this marker could be used to indicate displacement events that can be classed (as in § 1 (b)) as migratory categories (ii) (dynamic one-way single), and (iii) (homeostatic two-way double migration). As *migratory demes* move together, then maternal genotypes will remain grouped and invariable due to a lack of gene flow in and out of these populations. This is because migratory populations will tend to move at around the same time to the same breeding sites each year, becoming genetically grouped over time. This is well exemplified in the monarch butterfly whose populations (summer non-migratory and autumn migratory) show low $F_{ST}$ values derived from allozyme data (Eanes & Koehn 1978) as well as low mtDNA variation (Brower & Boyce 1991). Whilst there are other explanations for the low mitochondrial variation observed, not enough data are available to form a consensus. It is also possible that the western and eastern populations of this butterfly are genetically isolated (Brower & Boyce 1991).

With individuals in a population, such concepts of movement can be developed further by studying the genetic variability between sexes that have a difference in vagility. There are several species of Lepidoptera in which females tend not to be displaced far from their site of emergence in comparison with the males, which fly some distance following a pheromone trail to the females. In such instances, as found in the gypsy moth, females have been found with very low mtDNA haplotypic diversity and mean allozyme heterozygosity (Harrison & O'Dell 1989; Harrison *et al.* 1983). In other insects with low vagility like periodic cicadas, *Magicicada* spp., and without sexual differences of displacement behaviour, very low mtDNA population variation is thought to be primarily due to the conventional bottleneck effect (Martin & Simon 1990), whilst in whirligig beetles, *Dineutus assimilis*, spatial scale has been found to be crucial in understanding the true patterns of population structure and gene flow (Nürnberger & Harrison 1995). Founder events have also been successfully determined using mtDNA markers, e.g. medfly, *Ceratitis capitata* (Sheppard *et al.* 1992) and strains of *L. dispar* (Bogdanowicz *et al.* 1993). Therefore from these examples it is evident that great care has to be taken in alluding to population dynamic events in a particular species. Also, greater reliance must be made on geographical and temporal histories as well as good experimental design and choice of molecular marker (see also Roderick 1996; Bossart & Pashley Prowell 1998).

Besides the work using nDNA markers on termites (Husseneder *et al.* 1998), Aphididae (De Barro *et al.* 1995*a–c*; Shufran *et al.* 1991; Sunnucks *et al.* 1997), Hymenoptera (honeybees, Hall 1992), Diptera (fruit flies, Haymer *et al.* 1992; He & Haymer 1997) and some Lepidoptera (Palo *et al.* 1995; Saccheri *et al.* 1998), few such markers have been employed to date in studies of population structure and dispersal in other herbivorous insects. Hence, there is much to be learnt regarding the mechanisms of gene flow and dispersal events (Strassmann *et al.* 1998; Villablanca *et al.* 1998). Many insect species showing variable flight behavioural forms have alternate genotypes which in turn give rise to different patterns of genetic variation and gene flow. If this is so, then the whole concept whereby individual species are assumed to be homogeneous genetic–functional entities needs reappraisal. In the end, whilst most inferences on population structure and movement are corroborated by direct observations on ecology and life history, molecular markers will enhance the understanding of insect displacements, especially including estimates of movement of particular genotypes and/or biotypes, reproductive strategy and success.

## 6. OVERVIEW

In order to understand insect spatial displacement, it is revealing to compare moving insects with animals that are either sessile or show minimal dispersal for most of their lives. Such animals obtain their energy sources passively, e.g. mature filter feeding molluscs and coelenterates (there are no insect homologues to this). Alternatively, they obtain all their resources within a limited area, e.g. the larvae of the cave-dwelling glow-worm fly, *Arachnocampa luminosa*, which catch their prey as it flies by using illuminated sticky lures (Pugsley 1983). Most other adult insects, including the adult glow-worm fly, have to undergo spatial displacements either to obtain resources and/or exchange genes.

As the arguments presented here show, insect displacement is a very multifaceted behavioural activity and in most instances has to be viewed case specifically. This is not surprising since evolution tends to drive animal populations towards adaptive specializations which minimize both intra- and interspecific competition (cf. Thompson 1994). Even within apparently morphologically and genetically uniform species populations, favourable mutations which allow successful adaptations split such populations into reproductively isolated communities. Very occasionally, as with the apple-maggot fly, these adaptations occur sympatrically. More usually, they have an allopatric dimension.

Because of these genetic trends, which can involve behaviours reinforcing population isolation, it is not surprising that in insects different dispersal behaviours and abilities have arisen so that animals can exploit the resources to which they have become adapted and inexorably linked. It is also not surprising that dispersal and life-history trends coevolve and have genes in common (Dingle 1991). Whilst there must be strong selection for insects moving and discovering suitable resources, nevertheless a great deal of wastage probably exists in such systems, for example due to high mortality and low reproductive success, etc. Possibly for insects such as the monarch butterfly, which tracks its host over a large geographical scale, such wastage is to some extent minimized because of the great synchrony of the movement to fresh resources, i.e. innate directed migration.

Where insects move from a 'refugia' outwards to discover fragmented geographically distant habitats, which involves some degree of navigation, such as locusts following weather fronts, wastage could be immense if suitable habitats are not located within a particular timeframe of the displacement. With insects undergoing random stochastic movements in search of a resource, like the autumn-winged aphids moving to an overwintering host or on a smaller scale, fruit flies (*Drosophila* spp.) searching for decomposing fruit (Hodge & Arthur 1996), only a tiny proportion of the original starting population eventually reaches its goal (perhaps less than 0.001% with dispersing aphids: Johnson (1969)).

In certain species undergoing long-distance movements to discover new resources, whether these movements are directed or generally random (as with some butterflies and moths, locusts, plant hoppers and aphids), they can involve large swarms which tend to move *en masse*. This can entail considerable losses, which are ameliorated by *r*-type reproduction rates. Such migration events occur within the lifetime of the individual. In contrast, with insects undergoing smaller-scale displacements, the normal mode of the majority of insect species, these movements usually involve singletons or relatively much lower numbers of individuals. Here, range expansion may involve many generations and occur over many years, perhaps hundreds (as found in the case of the Knopper gall wasp) or even thousands and ultimately cover a large geographical area (Hewitt 1999). Whatever, for all those insects blown off course over inhospitable habitats, death is the outcome when body resources are drained. Because of this, movement is potentially always risky, only undertaken when present resources reach a threshold where the risk of leaving is less than that of staying on.

The surprising thing is that as a result of the high mortality inflicted on dispersing insect populations, selection has not either limited dispersal genes or behaviour, or driven such populations towards a greater number of species or populations showing the innate, directed-type of behaviour pattern. Perhaps the reason that this has not occurred for many insects undergoing population displacement, is that there is a balanced polymorphism maintained by weak selection of the gene(s) concerned, or, that the bidirectionality noted in some species (Benvenuti *et al.* 1996; Spieth & Kaschuba-Holtgrave 1996) is more commonplace than has been found. Hence, the so-called 'Pied Piper' effect (Drake & Gatehouse 1995) never occurs for the 'migratory genome'. Second, if insect populations were to move in a very directed fashion from one habitat to another, and this occurred over a long enough period, it might eventually lead to specialization and/or inbreeding. This may reduce the genetic plasticity in the population suitable for adaptation to new environmental changes. Insects of the kind displaying innate, directional migration that get locked into a specialized ecology and behaviour with reduced genetic plasticity, therefore would tend to constitute a rigid life pattern with limited flexibility unable to respond and adapt to alterations in their habitat.

In contrast to this scenario, insects undergoing a more risky displacement behaviour in terms of locating suitable resources, have the advantage of greater genetic mixing and recombination coupled with enhanced resource opportunities. It is for this reason that it is important to delineate between dispersal on the one hand and true innate, directional migration on the other. We speculate that the relative abundance of dispersal strategists is testament to this. Even so, the common driving force behind all displacement strategies is that ultimately, the insects concerned are 'slaves of the environment'.

The relative extent and success of displacement can only be estimated approximately. However, much greater resolution is now available using appropriate molecular markers where dispersal and migratory modes in populations can be studied more accurately, leading to more refined and lucid definitions. In conclusion, it is clear that this topic needs much more genetic correlation with ecological trends and a parallel understanding that a population is not a genetically uniform entity.

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