THE RELATIVE IMPORTANCE OF SHORT- AND LONG-RANGE MOVEMENT OF FLYING APHIDS

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CONTENTS

I. INTRODUCTION

The flight of winged aphids in the field is often termed *migration*; however, agreement as to the precise meaning of the term has yet to be reached. There is a dichotomy between population movement (ecological) *versus* individual (behavioural) aspects of migration as emphasized by Kennedy (1985). In the present review, migration refers to both the ecological view as 'a population re-distribution by movement, whether or not the movement is controlled through some specialized migratory behaviour' (Kennedy, 1985, after Taylor & Taylor, 1983) and the more specific behavioural understanding of it as 'a persistent and straightened-out movement affected by the animal's own locomotory exertions or by its active embarkation on a vehicle. It depends on some temporary inhibition of station-keeping responses, but promotes their eventual disinhibition and recurrence' (Kennedy, 1985). Ecological migration may well involve behavioural migration (Johnson, 1969; Pener, 1985; Dingle, 1989) but can occur in its absence – for example when host-seeking flight is overtaken

by climatic conditions. The direction of flight is controlled by the insect within the boundary layer (Taylor, 1965), but determined by the wind at higher altitudes. To make the distinction between population redistribution effected by local movement, as might occur by walking apterae (Ribbands, 1963; Harrington & Taylor, 1990; Hodgson, 1991) or alatae during foraging flight at low wind speeds (0.5 m s^{-1} or less), we refer here to a long-distance migration as flights of more than 20 km.

Despite many studies concerning the dynamics of aphid population dispersal, especially over the last forty years, much remains to be learned of the behaviour and movement of individual insects under natural conditions.

Assessment of aphid flight behaviour in the field is difficult because aphids are small and there is an enormous dilution effect, even when huge field populations take to the air. Aphids cannot be readily marked individually to obtain information regarding flight direction and duration – unlike birds, mammals or large insects such as Danaid butterflies (Baker, 1978; Urquhart, 1960) – whilst studies using radiolabelling of populations of aphids (e.g. Taimr & Kříž, 1978; Harrewijn et al., 1981) have proved problematic, again due largely to the small size of aphids and their low rate of recapture.

Most studies of aphid population movements have involved three basic approaches. (1) 'Observational studies' such as placing traps in distant regions lacking suitable host plants and thus inhospitable to feeding and reproducing aphids (for example, traps at sea or in deserts) and monitoring the species and numbers caught, the *inference* being that, to be caught, aphids must first have flown into and across these regions (e.g. Dickson, 1959; Wiktelius, 1984); (2) by examining the spatial dynamics of given aphid species by using a network of suction traps. Aerial densities can then be monitored, and dynamics and distances flown are then *inferred* from contour maps of aphid density changes in space and time (Taylor et al., 1979; Cammell et al., 1989); (3) by examining spatial and temporal changes within and between natural aphid populations using genetic markers, especially allozymes (Loxdale & Brookes, 1989; Steiner et al., 1985), radioactive tracers (Taimr & Kříž, 1978) or physiological markers (Smith & MacKay, 1989).

Even though all three approaches provide some information on aphid population movement (usually distance, much less so direction and/or duration), clearly (1) is the most direct. The other categories, while they can involve 'marked individuals', generally relate to population changes assumed to be brought about by the movement and mixing of alatae between regions.

Although approach (1) is perhaps the least unequivocal, some studies include assumptions about aphid behaviour which may be inaccurate. In addition, such studies often involve backtracking of winds and other meteorological data to define migrant origin. These techniques demonstrate the possibility that aphids could have come from the proposed location, but often do not preclude a more local source. It seems that while a lot of data exist concerning aphid distribution, much information relating to the distance these insects actually travel is often guesswork (Smith & MacKay, 1989).

Aphids as a group should not be lumped together in terms of their migratory abilities – either their readiness to migrate or the ability to do so (Dixon, 1971 a). Indeed, there is great variability even within one aphid morph (Shaw, 1970), while more extreme migratory behaviours may be seen with different morphs and even individuals of the same clone (David & Hardie, 1988; Nottingham & Hardie, 1989). It may be disadvantageous for an aphid to fly too far from the region in which it and its immediate

forebears have found suitable host(s) and habitat. That is not to say that at the population level, such *r*-selective behaviour may be disadvantageous (Dixon, 1985*b*); however, selection acts directly on the individual genotype and only indirectly on populations. If an individual aphid has a particular selectively advantageous trait, for example, resistance to insecticides, long distance flight could clearly be beneficial, i.e. to a pesticide sprayed area, whereas selectively neutral individuals moving to new habitats may become competitors of aphids already present. Hence, long distance movement is beneficial only if aphids derive some special advantage. Indeed, one can envisage situations where long distance migration could be a disadvantage and actively selected against, especially if this means moving away from host plants and habitat.

Aphids must and do migrate or, at any rate, populations disperse. This is determined by their life-cycles which in many species involve host alternation, short lived hosts and changes in food quality, i.e. host phenology. For many aphid species, their primary and/or secondary hosts may be restricted in distribution. As a result, where hosts occur in the same area, short distance movement may be selectively advantageous.

It is apparent to us that in the 1950s and 1960s, the interpretation of aphid 'migration' was sometimes overstated. This is especially so in the case of the *normal* readiness and ability of given species to travel long distances, i.e. of the order of tens or even hundreds of kilometres.

To make realistic models of aphid movement patterns and for forecasting outbreaks, accurate knowledge of aphid biology is required (Woiwod *et al.*, 1984). Even one aphid carrying a plant virus a long distance could start an infection. Similarly, a single insecticide resistant aphid could produce, firstly, a clonal population of resistant descendants and, if conditions are favourable, could further spread its genes after sexual reproduction, thereby increasing the frequency of the resistant gene(s) in the new locality. Hence, knowledge of aphid population dispersal is essential if such economically undesirable events are to be understood in terms of the frequency of their occurrence, let alone be predicted or prevented.

This review examines the published literature concerning aphid movement in an attempt to re-assess the 'migratory' abilities of these insects in relation to the information available and in the light of modern concepts of aphid physiology, phenology and behaviour. We have not attempted to review every aspect of aphid migration (for detailed reviews see Kring, 1972; Johnson, 1969; Taylor, 1965, 1986*a*; Taylor & Taylor, 1983), but have concentrated our efforts on re-assessing the biological impact of short- and long-distance migration by aphids. Our aim is not to show that aphids cannot or do not fly long distances, but rather to emphasize that this long-distance movement may be the exception rather than the rule. If it is an uncommon form of behaviour its biological significance may have been over stated. Also, we wish to focus attention on the importance of local migrations, say < 20 km, in the biology of these insects, in the maintenance of local sources of resistance to insecticides (Devonshire, 1989) and in the conveyance and transmission of plant virus infections from local viral 'hot spots' to nearby crops (Garrett & McLean, 1983).

II. THE EVIDENCE

(1) *Factors influencing take off, flight duration and landing*

Aphids are weak fliers and cannot make progress against a headwind of more than about 0.5 m s^{-1} (≈ 2 km h^{-1}) (Johnson, 1954; Heathcote, 1970; Kennedy & Thomas,

1974); at greater speeds, they are borne on the wind. The density of airborne aphids shows a mono- or biphasic daily periodicity in summer (Johnson, 1952; Taylor, 1958; Lewis & Taylor, 1965) related to general development and critical activity threshold values of light and temperature (Johnson, 1954; Berry & Taylor, 1968; Dry & Taylor, 1970; Berry, 1969; Davis, 1966; Halgren, 1970a, b). In southern England after dusk, these values fall below the threshold and few aphids are able to fly (Johnson *et al.*, 1957). However, in North America (Kansas) where the night-time summer temperature is warm and often exceeds the flight threshold ($\approx$ 17 °C), a relatively much larger proportion of insects remain airborne (Berry & Taylor, 1968; Halgren, 1970b). Clearly then, aphids not only have the power to get aloft, but also to remain there and to descend, except perhaps under certain climatic conditions (Johnson 1954, 1969; Taylor, 1965; Berry & Taylor, 1968; Thomas *et al.*, 1977).

Aphids leave unsuitable hosts. Some species host alternate, especially in temperate climates, and need flight to transport them from primary to secondary host and vice versa as the seasons and environmental conditions dictate (Hille Ris Lambers, 1966). Hence, as well as evolving wings, they must have evolved a change(s) in host-plant preference at certain points in the life cycle (cf. Dixon, 1971b).

There are fundamental differences related to the actual readiness of winged aphids to fly. Shaw (1970, 1973) has shown that amongst alate virginoparae of the black bean aphid, *Aphis fabae* Scopoli, there are several behavioural/physiological types. He termed these 'migrants' (aphids which fly before larviposition), 'flyers' (which fly after deposition of some larvae), and 'non-flyers' (aphids which never fly but reproduce on their natal plant), the readiness to fly being correlated with the degree of crowding. More recently, Kidd & Cleaver (1984, 1986) reported that 'migrants' were more willing to take off than 'flyers', although once airborne, flight duration was associated with size rather than prior reproductive history; larger aphids (*A. fabae*) were less inclined to fly for long periods of untethered flight against a glass ceiling and more readily settle on bean plants than small aphids.

The elegant laboratory experiments of Kennedy & Ludlow (1974) on free-flying aphids divided flight into a 'migratory' phase which was oriented towards an overhead light source and a 'targeted' phase, which consisted of horizontal flight towards plant-like (visual) targets. The 'migratory' flight was not, however, strictly synonymous with the definition of Kennedy (1985) because migratory behaviour can only be demonstrated by the lack of response to plant-like visual targets during presentation. In contrast, the 'migratory' flight of Kennedy & Ludlow (1974) was defined as oriented towards an overhead light source, whether plant-like targets were present or not.

Evidence, recently reviewed by Niemeyer (1990), suggests that flying aphids use visual and olfactory cues for host location, but only during the host-seeking phase of flight.

It has only recently been unequivocally demonstrated that laboratory aphids can undertake a strictly 'Kennedian' migratory flight phase (David & Hardie, 1988; Hardie *et al.*, 1989; Hardie, 1989; Nottingham & Hardie, 1989; Nottingham *et al.*, 1991). In two host-alternating species, *A. fabae* and the bird cherry-oat aphid, *Rhopalosiphum padi* (L.), the short-day induced gynoparae have an obligatory migratory phase during the initial period of maiden flight. This is typified by their persistent flight towards an overhead white-light source and the lack of response to a laterally-presented green target. After a prolonged flight period of up to 6·5 h (Nottingham & Hardie, 1989), the

plant-mimicking target becomes attractive and, on presentation, the insect flies towards it. Spring- and summer-winged forms differ from the gynoparae in that some individuals show no migratory component during the maiden flight and are immediately attracted to the plant-like target, whilst others have a short migratory component (measured in minutes rather than hours). The rates of climb are also less in virginoparae than gynoparae (David & Hardie, 1988; Nottingham & Hardie, 1989; Nottingham *et al.*, 1991). These flight components cannot be measured in the field but the finding that gynoparae of *R. padi* tend to fly higher than the spring and summer virginoparae is an indication that these behavioural distinctions do exist in the field (Tatchell *et al.*, 1988).

Therefore, it is clear that aphid flight is more complex than simple take off, flight and landing and involves behavioural responses, including readiness to fly, to maintain flight and to land in the presence of suitable visual and olfactory stimuli (Robert, 1987). Flight is, as Taylor (1986 *b*, *c*) describes, active and orientated. But unlike, for example, the two-way migration of monarch butterflies [*Danaus plexippus* (L.)] (Urquhart, 1960), it is a one way move. On arrival at a suitable host plant, the aphid produces asexual forms or produces oviparae which mate with separately migrating males prior to oviposition. There is no return journey for any individual (Taylor, 1986 *c*).

Flying aphids at first use glycogen as fuel and, later, lipid reserves stored in fat bodies (Cockbain, 1961 *a*; Liquido & Irwin, 1986). In tethered flight, *A. fabae* has been induced to fly for up to 12 h (average 6·8 h) (Cockbain, 1961 *a*–*c*). In that time, the lipid content may decline by 50 % (Cockbain, 1961 *a*; Liquido & Irwin, 1986). However, a flight of 1–3 h may be normal under more natural conditions (Johnson, 1954, 1969; Taylor, 1965, 1986 *a*).

To fly for 3 h in a prevailing wind of around 50 km h^{-1} might carry an aphid about 150 km, possibly beyond the range of available hosts in many instances. To fly for longer may take it even further from suitable host plants and seriously deplete its lipid reserves although, in *A. fabae* at least, this does not affect subsequent fecundity following tethered flight to exhaustion so long as a suitable host is available thereafter (Cockbain, 1961 *a*). Laboratory experiments have, however, shown that *A. fabae* will land well before they become fatigued by long flight (Kennedy & Booth, 1963); the readiness to probe and settle increases with the flight duration. *A. fabae* flown to exhaustion will even settle permanently on a poor host (Cockbain *et al.*, 1963; Taylor, 1965). Furthermore, certain species, once settled, show wing muscle autolysis (Johnson, 1953, 1957; Cockbain, 1961 *c*; Hardie *et al.*, 1990).

Blackman (1990) comments 'that aphids are not, as a group, naturally polyphagous insects. Their methods of host selection, feeding and reproduction seem to favour the development of intimate, finely-tuned relationships with their host plants'. If this is so, it would be counter-productive for aphids to move from a region where host plants (primary and secondary) necessary for completion of the life-cycle are present to an area where one or both may be rare or absent.

(2) *The wind as transport medium*

Aphids have been captured using suction traps attached to balloons at altitudes up to 1220 m; 99 % of aphids caught between 300 and 1220 m were alive and those tested were able to reproduce (Taylor, 1960, 1965). Therefore, in theory, single aphids blown long distances by the wind are able to establish new colonies. Taylor (1965, 1986 *a*) discusses several modes of atmospheric transport of aphids, including stratiform drift,

boundary layer movements, dispersive transport by convection currents and 'low level' jet streams which are persistent horizontal airstreams at altitudes between 300 and 1000 m. He considers that the latter may be responsible for long distance movements such as apparently occur in central USA. According to Taylor, these winds, usually warm and averaging about 58 km h^{-1}, could maintain aphid flight 'until [this is] inhibited by reversion of migratory behaviour, by neural or physiological "exhaustion" or by inadequate light' (Taylor, 1965).

(3) *Evidence for local movement*

The evidence for short range aphid movement comes from direct observation and experiments using sticky traps, suction trapping and enzyme electrophoresis. In addition, evidence is also derived from studies of virus dissemination, the movement of radioactively-labelled aphids and the distribution of insecticide-resistant strains of pest species.

During a study of the population genetics of the damson-hop aphid, *Phorodon humuli* Schrank in Britain using enzyme markers (Loxdale & Brookes, 1993), it was found that the aphid is rare in spring on its primary hosts, *Prunus spinosa* and *P. domestica* outside the immediate vicinity of the hop growing regions sampled in Hereford and Kent, England. This observation suggested that the movement during the previous autumn from hop (*Humulus lupulus*) to *Prunus* had been very local, probably no more than 5–10 km.

Eppler (1988) in Germany, has performed detailed studies of the migration of *P. humuli* from hops to *Prunus*. His work showed that *P. humuli* does not need a long distance flight phase prior to settling on *Prunus*. He classified flight distances from hops and showed that 86 % of *P. domestica* plants were colonized up to 20 m away, 43 % between 20 and 100 m, 25 % from 100 to 1000 m and only 17 % at more than 1 km distant. With *P. spinosa*, only plants at 0–20 and 20–100 m were found to be colonized and then at low levels of 7 and 8 % respectively. These results are supported by similar data from suction traps in eastern Washington State, USA (Pike *et al.*, 1987–90). In each of four consecutive years, more than 90 % of the hop aphid alatae were caught in the autumn within 10 km of Washington's hop production area. However, these results may have resulted from population dilution effects.

Electrophoretic (Eggers-Schumacher & Sander, 1988), radioactive tracer (Taimr & Kříž, 1978) and large scale suction trap (Taylor *et al.*, 1979) studies of *P. humuli* migration have also emphasized a generally local migratory range in this species. In the work by Taimr & Kříž (1978), aphids labelled with radiophosphorus (^{32}P) via systemically-treated *P. domestica* were found to have flown to nearby cultivated hops from 165 to 788 m away, and in only one direction. Analysis of meteorological data suggested that the aphids had flown by stratiform drift (cf. Taylor, 1965, 1986a) at a low height in stable air in one 3 h period in the afternoon. Due to dilution, aphids at a greater distance were not detected and may have been carried further on higher currents of air (Taimr & Kříž, 1978).

Suction trap data have shown that in England autumn migrants of *P. humuli* originated from 'dense, isolated and persistent population patches' – that is hop gardens monitored in the main hop regions of Hereford and Kent (Taylor *et al.*, 1979). Using gamma regression models (Taylor, 1979), mean density multiplied by distance

profiles revealed that the mean distance moved by autumn alatae was 15–20 km, with a 95 % confidence limit of 100–150 km.

In Britain and mainland Europe, *P. humuli* is resistant to some insecticides (Lewis & Madge, 1984; Wachendorff & Zoebelein, 1988). In Czechoslovakia the spread of insecticide resistance in this species, especially to Thiometon, has been closely monitored since the late 1960s (cf. Hrdý, 1984, and references therein) following the discovery of resistance in a hop growing region near Žatec in Bohemia in 1967 (Hrdý & Zelený, 1968). Within a few years, resistance was recorded hundreds of kilometres away from the site of the original report and by 1977, was nationwide (Hrdý, 1984). Since *P. humuli* remains on the primary host *P. domestica* late into the spring, sometimes even into late June (H. D. Loxdale, pers. observ.), it is possible that the rapid, long-distance spread reflects transport on infested *Prunus* trees or leaves by human agency rather than direct aerial migration. [One of us (S. H.) has seen *P. humuli* colonies on ornamental plum trees for sale in Idaho discount stores!]

The distribution of insecticide-resistant forms of the peach-potato aphid, *Myzus persicae* (Sulzer) also suggests that short range rather than long-range migration occurs under most circumstances. There have been persistent records of the highly cross-resistant variant R_2 (Devonshire, 1989) occurring at higher frequency in northern England and southern Scotland than in the rest of the UK (Sykes, 1977; Furk, 1986). More recently, R_2 variants have been found at Rothamsted and in Humberside (ffrench-Constant & Devonshire, 1986, 1988), which may reflect either a new mutation or a southward migration of aphids of this genotype from areas of high frequency. Even so, other resistant variants [S, R_1, French-R, etc. (Devonshire, 1989)] show stable regional distributions in frequency (ffrench-Constant & Devonshire, 1988), which indicates a restricted interpopulation/regional gene flow, there being a high proportion of S (Susceptible) aphids in the west (Sawicki *et al.*, 1978; Furk, 1986) and south (ffrench-Constant & Devonshire, 1988) of Britain. These observations could reflect regional (selective) differences in pesticide use (Furk, 1986), but this is disputed (ffrench-Constant & Devonshire, 1988).

As well as regional genetic differences related to insecticide resistance levels, more localized differences have been found in *M. persicae* which apparently reflect genetically-based differences of host plant adaptation. Thus Weber (1985) has collected clones of this species in the Lower Rhine Valley, western Germany, which displayed larger than average indices of performance on the host plant from which they were collected. Populations on potatoes or sugar beet could be differentiated even when the sampled fields were in mixed farmland. However, the differences broke down at field boundaries, possibly due to short-range migration by alatae and some apterae.

Suction trapping has also provided evidence of short-distance rather than long-distance movements of pest aphids. For example, the appearance of spring generations of the grain aphid, *Sitobion avenae* (F.), in three sites in southern England correlated well with local mean temperatures in the previous January and February (Walters & Dewar, 1986). Although the first catches occurred later in northern England, a similar relationship held. Such a correlation supports the view that, at least these first catches are local insects (K. Walters, pers. comm.); if the spring migrants came from a distance the temperature/arrival association would not be so well correlated. On the other hand, there was no correlation between these variables in Scottish populations nor in any

populations of the closely-related blackberry-grain aphid, *Sitobion fragariae* (Walker). *S. avenae* is largely anholocyclic in England (Loxdale *et al.*, 1985; Hand, 1989) while in Scotland, it is predominantly holocyclic (Newton & Dixon, 1988; Hand, 1989). In contrast, *S. fragariae* is normally holocyclic throughout England and Scotland (Dicker, 1940; Hand, 1989; Loxdale & Brookes, 1990). The correlation between spring generations and temperature is thus associated with anholocyclic aphids, over-wintering parthenogenetically, but not holocyclic aphids, over-wintering as eggs. Eggs are more likely to be influenced by host phenology and temperatures in spring than by previous winter temperatures.

Walters (1987) has also found that the spring migration of *M. persicae* in south-east Scotland is significantly correlated with mean temperatures in the previous January and February. Since the primary host, peach (*Prunus persica*), is rare in Britain, especially in Scotland, the Scottish populations are probably predominantly anholocyclic (Blackman, 1971, 1974). This would account for the good correlations found and supports the notion of a local origin for these populations.

The displacement in time of the single peak of the green spruce aphid *Elatobium abietinum* Walker flight in early summer from northern to southern Britain is positively correlated with accumulated spring temperature; this is an anholocyclic species in Britain, and so again this suggests that the numbers trapped are derived predominantly from regional sources (Carter & Cole, 1977).

There is enzyme electrophoretic evidence that migration may be localized in some aphid species. Loxdale & Brookes (1990) have shown that local populations of *S. fragariae* infesting primary and secondary hosts (*Rubus fruticosus* and *Dactylis glomerata* respectively) within a 50 km radius of Rothamsted, south-east England, are heterogeneous for allele frequencies at the GOT (glutamate-oxaloacetate transaminase) locus, especially on the secondary host. In addition, even on *D. glomerata* on which parthenogenetic reproduction occurs, many populations have GOT genotype frequencies in accordance with, or near to, Hardy–Weinberg expectations, whilst both GOT allele and genotype frequencies are often stable over a number of consecutive years. These findings indicate some degree of genetic stability within local sub-populations and a restriction of gene flow between sub-populations in this predominantly holocyclic species. There is also evidence that some genotypes bearing a slow (S) GOT allele may represent parthenogenetic strains of the species (Loxdale & Brookes, 1990; Loxdale, 1990).

In western Europe, Tomiuk & Wöhrmann (1984) found significant allele frequency differences at two enzyme loci (phosphoglucomutase, PGM and malate dehydrogenase, MDH) in populations of the rose aphid, *Macrosiphum rosae* (L.). Their samples include British, Norwegian, Danish, German and Swiss populations; the authors suggest that a longitudinal cline of PGM frequencies apparently exists from Norway to Switzerland. The clear heterogeneity between geographical populations strongly suggests that this species is not very migratory and that there is interpopulation restriction of gene flow over the area sampled.

Singh & Rhomberg (1984), studying the population genetics of the apple aphid *Aphis pomi* de Geer in eastern Canada using enzyme electrophoresis, also found regional allelic differences between sub-populations of the aphid maximally about 210 km apart. They found variation at three loci (GOT, EST-1 and EST-2) and the genotypes were

categorized into A and B types (cf. Singh & Rhomberg, 1984 for details). The B genotype aphids varied from absence to predominance in different orchards when monitored between 1978–82. Furthermore, it was found that in many orchards, the proportion of B types increased rapidly in successive seasons. However, in one sub-population at least (Niagara), the frequency of the B genotypes declined after being common. It appears that two differentiated, non-interbreeding populations exist and that orchards seem to have been invaded by B types; aphids moved up the Niagara Peninsula with the B genotype rapidly displacing the A types. Even so, in 1978, some western sites had a low overall frequency of B types, or a high proportion of these on individual trees. Only later in 1982 did the B types become generally common at these western sites. Presumably, the B genotype moved slowly and took 2–3 years to cover an area of 200 × 60 km. It is possible that these forms represent different species (*A. pomi* and *Aphis spiraecola* Patch) (Blackman *et al.*, 1989).

Hebert *et al.* (1991) examined genetic variation in the sumac gall aphid, *Melaphis rhois* (Fitch), at a range of enzyme loci in southern and eastern Ontario, Canada. The aphid alternates between sumac (*Rhus typhina*) and moss. Fifty-two populations were studied for two polymorphic loci. Marked allele frequency differences were often noted between gall populations only a few kilometres apart and, while some gall populations had genotype frequencies in accordance with Hardy–Weinberg expectations, most showed strong deviations (usually with heterozygote deficiency). These findings suggested extensive inbreeding, probably as a result of clonal matings, and the authors concluded that most *Rhus* stands were colonised from local sources.

Other evidence that aphid migration is highly localized comes from ecological work by Gilbert (1980) on the comparative population dynamics of the thimbleberry aphid *Masonaphis maxima* (Mason) in California. This aphid is a non-economic species, with a maximum of five summer generations which infests a single host, thimbleberry (*Rubus parviflorus*). New patches of host plant are normally colonised in two stages. Initially, second generation gynoparae fly to the new patch and produce sexual females. Thereafter, third generation males fly in and fertilize these females. As Gilbert states 'Since winged forms normally fly less than 100 m, this two-stage colonization is unlikely to jump gaps of 1 km or more between suitable patches of host plants; for it requires that first a gynopara and then a male, shall cross the gap and find the same patch.' Alate virginoparae, produced in the second generation, also fly up to 0·5 km, but since these morphs produce only apterous virginoparae, another three generations are required to produce sexual females (namely virginopara–gynopara–sexual female), and the clone may die out unless suitable plants are available in the new patch to support aphids through to the fifth generation. The apparent short-distance movement of this aphid species clearly influences its rate and range of spread, even assuming wide dispersal of the host which ranges along the Pacific coast from British Columbia to California (Gilbert, 1980).

The epidemiology of aphid-borne plant viruses also provides evidence for local aphid movement. Garrett & McLean (1983) have reviewed evidence showing that aphid infestation of a range of crops in Australia (cauliflower, tulip, sweetcorn, lettuce, French beans, cereals and grasses, lupin and watermelon) and the spread of virus diseases associated with these crops appears to come from local sources. They argue that 'the virus sources *could* have been far from the crops, but in no case is it necessary to

postulate that this occurred to account for the observed patterns of distribution. In no instance is long-distance spread of virus likely to have contributed substantially to the active growth of epidemics. In each instance there was sufficient local activity to account for the virus spread'. In the case of viruses of cauliflower and maize (cauliflower mosaic virus, ClMV and maize dwarf mosaic virus, MDMV respectively), 'the marked patches of diseased plants and the spread of virus [observed] from the margins of the patches would have been less obvious if there had been large influxes of viruliferous aphids throughout the year'. They question the epidemiological importance of viruliferous aphids caught far from a susceptible crop, more especially relevant (one assumes) when non-persistent viruses (Harris & Maramarosch, 1977) are being transmitted (cf. also Hodgson, 1991).

In North America, studies have shown that local movements of the peach potato aphid, *M. persicae*, were responsible for the transmission of potato viruses (in particular, potato leaf roll virus). Infestation levels of aphid and virus within potato crops were found to be related to the proximity of townships with gardens (Bishop & Guthrie, 1964; Bishop, 1965, 1967). It appeared that gardeners brought in aphids from outside the area, populations built up on garden plants and weeds and overwintered on peach and apricot seedlings. Local movements resulted in the infestation of nearby potato crops. The success of control programmes aimed primarily at garden aphid populations strongly indicated these were focal points for crop infestation.

(4) *Evidence for longer distance movements*

The most famous and oft-quoted example of long-distance migration concerns the finding of aphids on the floating ice floes of the north polar sea (82 °N) by Captain William Edward Parry in 1827 (Parry, 1828) and on the snowfields of Spitzbergen in the Arctic Ocean by Elton in 1924 (Elton, 1925). These aphids are now known to be *Cinara* spp., which are relatively large insects (body length 5–8 mm) which usually feed on conifers [esp. *Abies* spp. (firs)] (Eastop, 1972). There are no conifers on Spitzbergen (G. Halliday, pers. comm.), so the nearest source of hosts is in northern Scandinavia and Russia, some 800–1000 km away. During the apparent migration of aphids to Spitzbergen, winds were from northern Europe (see Fig. 1 in Johnson, 1969, p. 508). However, the aphids could possibly have come from living fir trees floating in the sea near the islands, rather than by long distance movements (Elton, 1925). Parry (1828) came to a similar conclusion regarding the aphids he found a century earlier.

Aphids trapped using mist nets attached to ships in the North Sea by Hardy and colleagues in the 1930s and by Gressitt, Yoshimoto and others in the Pacific, Atlantic, Indian and Antarctic oceans in the 1960s (Bowden & Johnson, 1976) are more likely to be true migrants. Of a total of 6968 insects captured in this work, 2982 or 43 % were Homoptera and of these, 56 % were aphids. In the North Sea, 60 % of the total insects caught 160 km from the nearest land were aphids (Hardy & Cheng, 1986). The most abundant aphid species were *S. avenae*, *R. padi* and *M. persicae*, which apparently originated from the direction of the British Isles (Hardy & Cheng, 1986). The first two species are also abundant in the Rothamsted Insect Survey 12·2 m suction trap samples in the summer and autumn (Woiwod *et al.*, 1987).

Wiktelius (1984) used a 40 cm diameter suction trap placed on a lighthouse 50 m from the coast of Smygehuk, southern Sweden, to investigate aphid movements across

the Baltic sea from Denmark, Germany and Poland. He correlated trap catches for 4 years with meteorological data, especially temperature and wind direction and speed. Sometimes there appeared to be a good correlation between wind direction and/or passage of a cold front across the Baltic and an increase in aphid numbers, especially of *R. padi*. The inference was that the aphids had travelled at least 50 km across open water. The conclusion is supported by the fact that, when large numbers of aphids were caught, the wind was coming from the sea and the windspeed exceeded the maximum flight speeds of aphids.

Another apparent example of long distance aphid migration across the sea is given by Close & Tomlinson (1975). They provide evidence for the arrival of the grain aphid, *Sitobion miscanthi* (Takahashi) in New Zealand from Australia in 1967, a distance of ≈ 1600 km and a flight time of 2–3 days. During the time of the hypothesized migration, the weather fronts and air movements necessary for such transport were suitable and evidently, aphids must have travelled for part of the time in the dark. However, reports that aphids have crossed the Atlantic from Africa to South America and vice versa are probably related to passive transport of insects on ships or by aircraft (Johnson & Bowden, 1973; Halbert & Pike, 1991).

There have also been convincing reports of long distance migration events over deserts. Dickson (1959), in a classic study using yellow sticky traps in the Colorado and Mojave deserts of the western USA, caught aphids, a large proportion of which were species which most probably originated from arable land at a considerable distance from the traps. In one experiment in the Mojave desert, of 2354 aphids caught representing 23 species, 1051 (16 species) were presumed to have come from cultivated land between ≈ 90–110 km distant; 74% of the aphids caught (5 species) were associated with grain crops.

More recently, Halbert *et al.* (1990) have used a network of 8 m high suction traps in Idaho, western USA, to examine aphid population structure and dynamics within the state. They have collected cereal aphids at traps in desert regions at least 30 km from the nearest agricultural host plants while large numbers of such aphids were caught at the same time in traps in arable areas. Similarly, the proportion of aphid species with desert host plants was higher in desert regions (2·6 % of the total over 2 years) compared with arable regions in which no such aphids were captured. Halbert *et al.* (1990) conclude that trap collections probably reflect flight activity within a 30–80 km radius of a trap, but that for 'the most part [aphids] represent emigrants from local crowded colonies rather than long distance migration'.

Electrophoretic studies have also indicated the apparent potential of some aphid species to migrate long distances. Loxdale *et al.* (1985) studied the population genetics of the grain aphid *S. avenae* at a number of enzyme loci. They examined genetic variation within and between field populations of this species collected from wheat in Britain and Spain, including calculation of inter-population genetic distance coefficients (Nei, 1972). Whilst allele frequency differences were found between populations, especially between those in Britain and Spain, the average genetic distance values were small ($\approx 0·025$), within the range associated with geographic species populations. There was no indication of race formation or higher levels of differentiation between populations in the two countries. It was therefore concluded that despite being separated by over 800 km of sea and mountain barriers, British and Spanish *S. avenae*

populations were similar genetically, suggesting that enough gene flow occurred between national populations to prevent significant divergence.

Another study of the bird cherry oat aphid *R. padi* (Loxdale & Brookes, 1988) also indicated significant interpopulation gene flow. In contrast with *S. avenae*, *R. padi* collected from the primary host *P. padus* showed less enzyme variation, but did nevertheless have two variable loci (SORDH, sorbitol dehydrogenase and GOT, glutamate oxaloacetate transaminase) each with allele frequencies which were generally similar throughout Britain.

Other data, whilst substantial, are open to more ambiguous interpretation. The rose grain aphid *Metopolophium dirhodum* (Walker), whose outbreak in 1979 was monitored using a network of 12·2 m high suction traps widely distributed throughout Britain and France (Dewar *et al.*, 1980), first appeared at high density in the south of France (Montpellier) in early April. Later, the high density contours produced by monitoring aerial density and extrapolating between traps, shifted steadily north. By the end of June or the beginning of July, the largest populations of aphids were caught in N.W. France and southern England. By early September, the highest populations were found in northern Britain and southern Scotland. However, the winds were from the west rather than the south when the outbreak was observed at the Channel, which makes it probable that what was actually recorded was a northward shift of local population increase, rather than mass migration.

In North America there is a wealth of diverse evidence for the long distance migration of aphids, especially the corn-leaf aphid *Rhopalosiphum maidis* (Fitch) and the greenbug *Schizaphis graminum* (Rondani), from overwintering sites in the southern states to summer breeding grounds, the wheat and barley fields hundreds of kilometres away near the border of Canada (recently reviewed by Irwin & Thresh, 1988). Several methods have been used to monitor aphid movements including direct observation and suction trapping, sometimes using helicopters with attached traps, radar detection and backtracking of infestations based on meteorological data, incidence and spread of plant viruses. However, enzyme electrophoretic studies of *R. maidis*, using a range of soluble enzyme markers, showed genetic differences between southern (Texas, Louisiana, Oklahoma) and northern (Illinois) populations studied in several different years (1983, 1984). The conclusion was that the northern populations were not, in these instances, derived from those in the south (cf. Steiner *et al.*, 1985, 1987, and Voegtlin *et al.*, 1987, for details).

Recent evidence for long distance migration of aphids in the USA has come from study of the Russian wheat aphid, *Diuraphis noxia* (Mordvilko). This aphid, which was first detected in Texas in late March, 1986 (Valiulis, 1986) had by 1987, infested tens of millions of hectares of cereals in Texas, New Mexico, Colorado and Kansas (Araya *et al.*, 1987), up to 200 km north from the original area of discovery. However, it is probable that the insect was in the USA prior to 1986 (Araya *et al.*, 1987) and that spread was not as rapid as it appeared.

Peak collections of several species of cereal aphids (*D. noxia*, *S. graminum* and *M. dirhodum*) in crops/traps occur progressively later in the year at higher elevations across southern Idaho. However, when the time of maximum number was plotted against the date of lilac bloom (an independent phenological indicator for which published data are available for Idaho (Everson & Caprio, 1974)), a straight line

relationship was obtained (Halbert *et al.*, 1990). Peak flight times of these aphid species in southern Idaho can thus be explained as easily by crop phenology as by migration up the Snake River Valley.

The spread of the north American lupin aphid, *Macrosiphum albifrons* Essig, a newly arrived non-endemic species to Britain and continental Europe, has been monitored by the damage it causes. Its dispersal over much of western Europe since its discovery at Kew, England in 1981 has nevertheless taken 6 years (Carter *et al.*, 1984; Carter & Nichols, 1989).

Other studies have used the observation that the photoperiodic response of the pea aphid, *Acyrthosiphon pisum* (Harris), is related to the photoperiod at particular latitudes. For example, it has been shown that aphids in the spring derived from over-wintering eggs of northern Canadian clones had a short-day response while southern clones had a relatively longer-day response (Smith & MacKay, 1990). However, clones derived from alatae collected later, which could have migrated into the northern sampled area, had significantly different photoperiodic responses, a finding which indicated that they may have originated from some 300 km further south (Smith & MacKay, 1989). These 'immigrants' contributed little to the total population as the photoperiodic responses of that year's summer clones were similar to those of spring clones. The contribution to gene flow was also negligible or the original correlation of photoperiodic response and latitude would not hold true. Even so, these 'immigrants' may contribute to the variability in photoperiodic response and may mate and reproduce sexually with local clones, where the appearance of the sexual morphs in different clones overlaps. The inheritance of photoperiodic responses in aphids has not been studied.

It is clear that some aphid species can fly long distances ($>$ 100 km) over the sea (Hardy & Cheng, 1986) or desert (Dickson, 1959). Such events may involve several hours active flying but successful colonization of fresh host plants cannot be assumed. The flight may be atypical (i.e. visual deprivation) and climate induced (i.e. wind). It is now well established that aphids can return earthwards and interrupt flight given suitable visual targets (Kring, 1972; Thomas *et al.*, 1977; Hardie, 1989).

Over 25 years ago it was shown in the USA that aluminium foil greatly decreased landing of aphids onto crop plants (Smith *et al.*, 1964; Kring, 1964). Reflective aluminium sheets placed between rows of gladiolus and *Veronia anthelmintica* decreased the number of aphids captured in yellow water traps by 96 and 98% respectively (Smith *et al.*, 1964). Infection of the gladiolus crop by cucumber mosaic virus (CMV) was reduced by 67%. Aluminium sheets repelled at least 12 aphid species including the apple grass aphid, *Rhopalosiphum insertum* (Walker), *S. avenae*, *M. persicae* and the potato aphid, *Macrosiphum euphorbiae* (Thomas). Aluminium foil reflects short- and long-wave light: indeed only surfaces that reflect short-wave light are effective in repelling aphids from settling (Kring, 1962, 1964, 1970, 1972). The shorter wavelengths of light ($<$ 500 nm) may be involved in the migratory (distant) flight of aphids characteristic of the early phase of maiden flight (Moericke, 1955; David & Hardie, 1988; Hardie, 1989) and inhibit landing, but this has not been demonstrated experimentally.

Hence, the normal landing behaviour of aphids aimed at green/yellow surfaces with a wavelength of reflectance in the range 500–600 nm may be disrupted when flying over

water or desert (Hardie, 1989; Hodgson & Elbakheit, 1985). Under other circumstances, aphids might have oriented much earlier in their flight to green objects (foliage), or yellow surfaces which represent a super-normal foliage-type stimulus (Hardie, 1989) and perhaps would have landed and settled.

As cited by Garrett & McLean (1983), the density of aphids at high altitudes (over 1000 m), i.e. those which are potentially capable of long-distance transport, is at most 1 per 3000 m^3 (Berry & Taylor, 1968). Similarly, some common aphids, such as *P. humuli*, are very scarce at large distances ($\approx$ 160 km) from their presumed original source (Taylor *et al.*, 1979). In addition, the aerial distribution of some aphids, e.g. *M. persicae*, is largely determined by the local distribution and abundance of its summer hosts (Taylor, 1977), a situation which may especially apply to those species with rare or geographically-restricted hosts (Cammell *et al.*, 1989).

In his comprehensive review Taylor (1986a) made the importance of local migrations of aphids clear, both biologically and economically. Even so, and despite such evidence as Taylor himself presents, others, for example Irwin & Thresh (1988) are still convinced of the biological and economic importance of long distance transport of aphids in the USA. They dismiss anholocyclic overwintering of cereal aphid virginoparae in the northern states as a possible source of infection in the following spring and summer. This seems contrary to the evidence that cereal aphids, and other species, regularly overwinter as virginoparae, a high percentage of insects even surviving temperatures as low as -8 °C for prolonged periods (cf. Dean, 1974; Hand, 1989; Williams, 1987; Williams & Wratten, 1987; Araya *et al.*, 1987, for cereal aphids, and Parry, 1978; Carter, 1972; Carter & Nichols, 1989; Harrington & Cheng, 1984; Bale *et al.*, 1988; Knight & Bale, 1986, for other species). While the evidence (Bale *et al.*, 1988) suggests that temperatures in the range -10 to -18 °C severely decrease numbers of overwintering aphids, if the initial autumn population is large, sufficient aphids may survive to found substantial populations in the next year (Blackman, 1981). For example, if a local summer population of aphids comprises around 10^{11} individuals, as calculated for the spotted alfalfa aphid *Therioaphis maculata* Buckton in one area of the USA alone (approx. 69000 ha) (Dockson, 1960; Sammeta & Levins, 1970), only one in a million aphids need survive the winter to provide 10^5 individuals to found the new spring populations. For *S. graminum*, at least, there is evidence for holocyclic populations existing in North America (Puterka & Peters, 1990).

Cereal aphids surviving deep within thick tussocks of grass, especially under a blanket of snow, do not experience the severe conditions on exposed sites where direct frosts and the wind chill factor of wind and wetting and surface freezing of aphids is liable to cause a high mortality (Bale *et al.*, 1988). In species such as the lupin aphid *M. albifrons*, surface wax is also present giving added protection against freezing (Carter & Nichols, 1989).

If cereal aphids can indeed overwinter as virginoparae in the northern states of North America, long distance migration from warmer climes is not a pre-requisite to explain the re-appearance of aphids in the spring in cereal growing regions.

III. CONCLUSIONS

Although aphids, under certain circumstances, travel long distances, this appears to be exceptional. Most probably, local movement is more significant, as aphids find suitable plants on which to land/settle at the earliest opportunity. Aphids are able to fly

for long periods of tethered flight or in wind tunnels in semi-sensory deprived laboratory conditions and 'atypically' over unsuitable habitat (water or desert). Such abilities should not be confused with their normal flight behaviour which maximizes their chances of finding a suitable host(s) in the shortest possible time. The apparent long distance movement of some individuals between subpopulations may assume a disproportionate importance in our assessment of the biological, ecological and genetic relevance of such migrations compared with shorter flights. It is a seemingly impossible task to estimate the probability of the successful conclusion (i.e. colonization of a fresh host plant) to long distance flight of the individual but an intelligent guess might put it at zero or extremely close to zero, $\leqslant$ 0·001 % (C. G. Johnson, 1969). We do know that host-alternating aphids comprise < 10 % of total aphid species (Dixon, 1985a), that this life style has arisen separately in 4 of the 10 sub-families of the Aphididae (Dixon, 1985b) and that these species, of necessity, complete successful movements between separate host-plant species. For all movements, success will depend to a large extent on host-plant abundance. The long distance migrations of aphids over water or desert as shown in the studies of Elton (1925), Dickson (1959) and Hardy & Cheng (1986) have been less than successful for the individual insects concerned, i.e. they most probably die without feeding and reproducing.

Aphids are highly polyphenic insects (i.e. they occur in many adult forms) and each winged parthenogenetic female is part of a genetic clone which originated from a single egg (Blackman, 1981). This genetic identity is preserved through many generations and morphs until sexual reproduction or mutation occurs. The development of winged aphids is an environmentally-induced expression of the genotype and we now know that not all clonal winged aphids fly and not all fliers show a behavioural migration. Indeed, this inherent variation in behaviour is undoubtedly advantageous for survival of the clone; spreading the risk as part of an overall strategy. The polyphenic clonal population can be considered as a clonal individual (Blackman, 1981), and the evolutionary pressures which may select against a seemingly suicidal migratory behaviour are possibly less restrictive than those operating on non-clonal insect species with less phenotypic plasticity. However, there are indications that there has been selection against the obligatory migration of host-alternating species since most extant autoecious species utilizing herbaceous hosts have evolved from heteroecious ancestors (Blackman & Eastop, 1985).

Aphids are not passive objects. They are dynamic creatures with complex host seeking, host recognition, landing and probing/feeding behaviour. They are bound in close biological association with one or more host plant species and therefore need to remain in the vicinity of these plants. This phenomenon of local movement would appear to have considerable relevance for forecasting outbreaks, the persistence and movement of insecticide resistant strains of aphids, the spread of virus disease and for control programmes (Bishop, 1967). It is important that these local movements should now be re-assessed and receive the same attention as has, in the past, been given to the 'marvel' of long-distance movement.

IV. SUMMARY

1. Aphids are notorious pests of world agriculture. Even so, uncertainty persists as to their capacity for successful aerial dispersal. Evidence exists that, under some conditions, aphids can be wind-borne over long distances, i.e. hundreds of kilometres

over desert or sea. It has been argued, in the recent past, that this phenomenon may be part of a strategy to locate fresh host plants in new distant areas. However, the proportion of these insects successfully colonizing new hosts is unknown.

2. Other work using meteorological backtracking has also indicated long-distance movement, but the accuracy of such predictions is dubious unless the altitude of transport is known. Mark–release–capture experiments with such small insects have limited potential due to large dilution effects. Static 'snap-shots' of demographic population densities, using suction traps, cannot accurately distinguish local aerial density fluxes and population movements from a distance. However, genetic and physiological markers may provide more direct information on population mixing; for example, some allozyme studies have shown a limited level of inter-population gene flow.

3. Under suitable conditions, aphids take off, maintain flight and alight in response to the appropriate visual and olfactory cues. Undoubtedly successful long-distance movement occurs from time to time, but its ecological relevance may have been overstated in the past. It may be selectively disadvantageous for aphids to move from areas containing their host plants. In contrast, it is advantageous for aphids to maximise their chances of survival and reproductive success by landing on suitable plant hosts at the earliest opportunity.

4. The clonal nature of aphids (a single genotype may comprise vast numbers of individuals) means that there may be advantages to phenotypic variation between individuals in the readiness to move. Recent evidence indicates that such a variation exists in the duration of the behavioural migratory phase, the initial period of maiden flight when host-plant cues are ignored and when landing is inhibited.

5. The relative biological importance of short- vs. long-distance movements is reassessed with reference to plant virus epidemiology and the spread of new genotypes, e.g. insecticide resistance. It is concluded that the biological relevance of short-distance movements have a much greater impact on population and genotype distribution than long-distance movements, which may be comparatively infrequent.

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