

## Review Article

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# Non-volant modes of migration in terrestrial arthropods

**Abstract:** Animal migration is often defined in terms appropriate only to the ‘to-and-fro’ movements of large, charismatic (and often vertebrate) species. However, like other important biological processes, the definition should apply over as broad a taxonomic range as possible in order to be intellectually satisfying. Here we illustrate the process of migration in insects and other terrestrial arthropods (e.g. arachnids, myriapods, and non-insect hexapods) but provide a different perspective by excluding the ‘typical’ mode of migration in insects, i.e. flapping flight. Instead, we review non-volant migratory movements, including: aerial migration by wingless species, pedestrian and waterborne migration, and phoresy. This reveals some fascinating and sometimes bizarre morphological and behavioural adaptations to facilitate movement. We also outline some innovative modelling approaches exploring the interactions between atmospheric transport processes and biological factors affecting the ‘dispersal kernels’ of wingless arthropods.

**Keywords:** Migration syndrome, embarkation behaviours, anemohoria, anemohydrochoria, aquatic insects, surface skimming, pedestrian migration, phoresy, wingless arthropods

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## 1 Introduction

The ability to fly is undoubtedly one of the major factors in the extraordinary success of the class Insecta, and the characteristic mode of insect migration is by flapping-wing flight. The long-range movements by locusts, dragonflies, butterflies and moths, for example, are well-known and often spectacular [1-5]. However, other important but

rather overlooked means of migration occur in insects, and in non-insect terrestrial arthropods. These include: aerial transport without powered flight (with or without the use of silk), pedestrian and waterborne migration, wind-propelled migration on the surface of water, and phoresy. (‘Parasitic dispersal,’ the movement of true parasites in or between their hosts, is outside the scope of this paper.) There is a large body of literature on some of these topics (e.g. phoresy in mites), so the current paper will be illustrative rather than comprehensive.

The movements by which animals are able to change their physical location can be categorized behaviourally into ‘station-keeping’ movements (e.g. foraging), ‘ranging,’ and migration [2]. The present review is concerned with *migratory* movements, and we adopt the widely-accepted behavioural definition of this process formulated by J.S. Kennedy [6]:

*“Migratory behaviour is persistent and straightened-out movement effected by the animal’s own locomotory exertions or by its active embarkation on a vehicle. It depends upon some temporary inhibition of station-keeping responses but promotes their eventual disinhibition and recurrence.”*

The temporary suppression of station-keeping responses – responses which would otherwise retain the animal within its current habitat patch or ‘home range’ – is a key behavioural component in this definition (and arguably the ‘acid test’ of whether a movement should be categorised as migratory or not). For example, many cases of directed gliding and manoeuvring behaviours have been recently discovered in wingless hexapods (e.g., worker ants of several families, bristletails (Insecta: Archaeognatha)) falling from trees [7,8]. These are fascinating as they may shed light on early stages in the evolution of winged flight [7]; nonetheless, the purpose of the glides is to get back onto a tree trunk, and the behaviour is clearly a station-keeping rather than a migration or ‘dispersal’ behaviour. In winged volant insects, emigration (i.e. escape from their present habitat) usually involves active ascent high into the air followed by a more or less sustained period of wing-beating which enables the migrant to maintain altitude, e.g. [9,10]. The various specialized behaviours by

which a range of animal taxa migrating in air or water use to launch into, and orient within, an airstream or current have been recently reviewed [11]. In terrestrial arthropods without functional flapping wings, we would expect migration to begin with analogous special embarkation or launch behaviours, and this is often the case (see examples below). In other situations, however, the context of a documented arthropod presence in, say, air or water currents is still unclear, and further investigation is required to determine whether these movements form part of an adaptive ‘*migration syndrome*’ of behavioural, physiological and other correlated traits [12,13].

If a required resource is not available, or is not found within a given time, a foraging individual may switch to a different mode of behaviour which allows it to explore a wider area than its current home range. These movements, which Dingle [2] terms ‘*ranging*’, resemble migration in that station-keeping behaviour does not predominate and the animal is therefore able to leave its home range. But ‘*ranging*’ differs from migration in that there is no significant suppression of the ‘*appetitive*’ responses – movement will cease when a new habitat patch containing the sought-after resource is found. ‘*Natal dispersal*’ – young birds and mammals leaving the birth site and exploring new territory in order to find their own place of residence, is a form of ranging. The movement of parasites in order to locate new hosts is also best classed as ranging [2], because there is usually an immediate response to the newly-encountered host’s body.

## 2 Aerial migration by non-volant terrestrial arthropods

The movement on air currents (anemohoria) of wingless terrestrial arthropods occurs by two basic mechanisms: the first uses silken lines, and is often termed ‘*ballooning*,’ while in the second, the wind drag on the diminutive migrant’s body alone is enough to carry it away. In both categories, migrants show various types of highly distinctive and specialized behaviour preparatory to ‘*lift-off*,’ indicating that the airborne movements are ‘*intentional*’ and not the result of inadvertent dislodgement.

### 2.1 ‘*Ballooning*’

According to Bell et al. [14], who review the subject in detail, ‘*ballooning*’ species are only known in three orders: spiders (Araneae; particularly small species like the Linyphiidae, and immature stages of other

families), spider mites (Acari: Tetranychidae), and the larvae of various moths (Lepidoptera). Spiders about to migrate will scale vertical objects, and typically assume a characteristic ‘*tip-toe*’ posture, facing into the wind, with the end of the opisthosoma (abdomen) raised up at an angle to the cephalothorax [15]. A thread of silk is then released from the spinnerets on the opisthosoma until the wind drag on the silken line is strong enough to pull or lift the spider from the substrate. Sometimes multiple silk drag-lines are released, and these can lift relatively large spiders. Schneider et al. [16] observed adult *Stegodyphus* (body length 7–14 mm) being carried up in thermals after each spider had released a large number of threads which fanned out to form a triangular ‘*sheet*’ of length and width of ~1 m. Some more primitive taxa of spiders, e.g. some mygalomorphs, use ‘*suspended ballooning*’ in which the spiderling descends on silken thread from an exposed position, and remains there occasionally lengthening the drag-line while gusts of wind blow the line more towards the horizontal. Eventually, wind breaks the extended drag-line and a length of it and the attached migrant are carried away [14,15,17].

The young first instar larvae (neonates) of various lepidopteran families (Cossidae, Geometridae, Lymantriidae, Noctuidae, Pyralidae, Psychidae and Tortricidae) also use ‘*suspended ballooning*’ for aerial movement [14]. In lepidopteran larvae, the silk glands represent highly modified salivary glands opening by way of a spinneret on the labium just below the mouth. The pre-ballooning behaviour in which the caterpillars lower themselves on a silk line from a plant surface is termed ‘*silking*’. In some tree-dwelling lepidopteran species the adult females are flightless, and ballooning by the young larvae is the means of colonizing new hosts. Examples include *Lymantria dispar* (gypsy moth), *Operophtera brumata* (winter moth), *O. bruceata* (bruce spanworm), *Orgyia* spp. (tussock moths) [18], and many species of bagworms (family Psychidae) [19]. In the evergreen bagworm, *Thyridopteryx ephemeraeformis*, neonate larvae readily silked during their first 24 hours, but this behaviour declined after that, and older larvae were likely to remain on a non-preferred and unsuitable host [20].

Many species of spider mites (Tetranychidae) e.g., the citrus red mite (*Panonychus citri*) and the six-spotted spider mite (*Eotetranychus sexmaculatus*), ‘*balloon*’ in a similar way to the moth larvae mentioned above. An individual drops down from the host plant on a silk strand, and when this breaks, the mite is carried off by the wind [21]. The spider mites produce the silk line from large unicellular glands opening through a hollow seta at the apex of each pedipalp.

The aerial migrations of the two-spotted spider mite, *Tetranychus urticae*, appear to differ from that of the other Tetranychidae [22,23], and are more akin to the lift-off behaviour used by phytoseiid mites and scale insects, which do not involve the use of silk (see below). The situation is complicated, however, because *T. urticae* utilizes silk in various other circumstances. For example, clusters of mites may produce a dense silk mass at the apices of the host plant, which provides some protection against predatory mites. Thick silken ‘ropes’ can develop from these aggregations, formed from threads of many individuals (nymphs and adult females) which are moving from heavily infested plants onto the ground [24] from where the mites presumably go in search of more suitable hosts. Although these ropes are used mainly in still air, it is easy to envisage that the dense mass of webbing and the enclosed mites may occasionally be carried away by a gust of wind [22].

Spider mites and moth larvae often travel relatively short distances (from a few metres up to a few hundreds of metres). The relatively slow spread of the gypsy moth (*Lymantria dispar*) in north-eastern North America over the last century [25,26] indicates that airborne movements by the first instar larvae are rather limited compared to what most winged migrants might achieve. We also note Pugh’s view [27] that movement of mites on air currents has not enabled them to colonize Antarctica; the few records from sub-Antarctic islands of mites capable of ‘ballooning’ on air currents were attributable to anthropogenic introductions.

Some spider movements, on the other hand, can cover hundreds of kilometres [14,15]. Modern Lagrangian stochastic models of the atmospheric processes help to account for movements over these distances [28]. When the atmosphere is ‘fully convective,’ spider movement is less effective than might be imagined: the hot days will certainly produce plenty of updrafts, but there may not be sufficient horizontal wind to carry the spiders far. Conversely, if the wind becomes too strong, ballooning will be impossible because thermals are suppressed. Therefore, the best spider ballooning conditions occur when the atmospheric stability is ‘non-ideally convective,’ i.e., in moderately warm weather with light breezes that typically occur in spring and autumn in temperate latitudes, and there is in fact evidence that ballooners preferentially select these meteorological conditions [28]. In another modelling initiative [29], earlier theoretical studies were improved upon by allowing the spiders’ draglines to stretch, twist and become highly contorted under turbulent atmospheric conditions, rather than being rigid and straight. The ability of the silk to follow

the turbulent eddies of the airflow reduced the terminal velocity of the spiders and thereby promoted long-range movement.

Before leaving the topic of silk as a dispersal aid, we might mention another type of dispersive movement shown by spiders – in this case covering very short distances – namely ‘drop and swing’. Here the spiderlings do not ascend to elevated sites on a plant or assume tiptoe postures, but drop on a dragline, which is gradually lengthened until the spider swinging on the end manages to contact another structure (such as a nearby leaf) after which it detaches from the line [30]. Again, specialized behaviour is involved; for example, the behaviour tends to be elicited under certain conditions of wind speed and air turbulence [30].

## 2.2 Windborne migration without the use of silk

Some minute wingless arthropods (e.g., first instar nymphs of scale insects (Homoptera: Coccoidea), and some mites (Acari), particularly the plant-infesting Eriophyidae and the predatory Phytoseiidae) do not use silk threads but simply launch themselves into the air, or allow themselves to be lifted off by the turbulent airflow over the plant canopy. Small body size, dorso-ventral flattening of the body, long hairs or setae, and in some cases the production of wax filaments [31-33], all serve to increase drag forces on the arthropod and to reduce the terminal velocity at which it falls. Many of the migrants carried away in updrafts will move distances of only a few metres, but some will travel much longer distances, e.g., [34]. Once again, we note that the take-off or launch phase involves specialized behaviours in response to specific environmental stimuli and is largely under the control of the individual (see below), so that even these diminutive arthropods usually enter the air-stream as part of an active migration syndrome, rather than being carried away accidentally. Once airborne they are largely at the mercy of the wind, but even here the migrant may be able to alter its fall speed (and thus the distance travelled) by, say, extending or drawing in its appendages [35,36].

Aerial migration in the predatory phytoseiid mite, *Neoseiulus (Amblyseius) fallacis*, occurs particularly in the adult females—these have usually mated, and thus would be capable of forming a new colony by themselves. In response to a wind current of  $> 0.45 \text{ ms}^{-1}$ , the mites changed from random searching movements and moved to the periphery of a leaf. They then faced in the *downwind* direction, elevated the anterior of the body so that only the two hind pairs of legs were in contact with substrate, and held this stance until they were carried away (or until

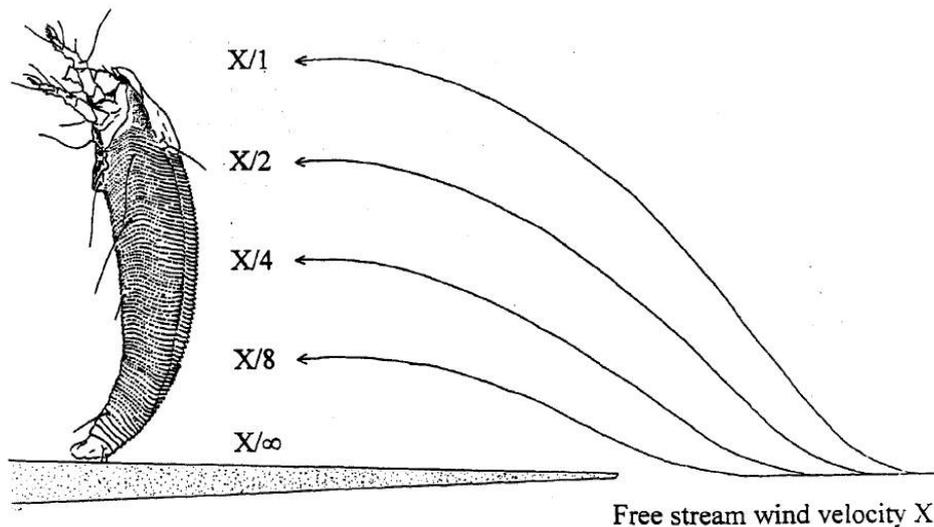
the air speed had decreased below the threshold) [37]. *N. fallacis* lifting-off from apple trees could be transported ~ 70 m away. Starvation in the ovipositing females greatly increased their tendency to adopt the rearing-up stance in the presence of air currents [37]. It is not clear why *N. fallacis* and some other small wingless arthropods such as the coccid *Pulvinariella* [35] do not raise themselves up facing into the wind because this would seem to provide more lift. Possibly unhooking the tarsae from the substrate may be easier when facing downwind.

Sabelis & Afman [38] demonstrated that phytoseiid mites are not just passively dislodged, but really do exert control over the initiation of aerial movement. The authors first established the conditions which would produce a good take-off in *Phytoseiulus persimilis*, and then showed that after 24 hours of starvation, about 80% of the females became airborne if given a 10 minute exposure to wind velocities of  $2 \text{ ms}^{-1}$  or higher. There was a significant reduction in lift-off if females were exposed to volatile chemicals emanating from leaves that had been previously infested by their prey species, *T. urticae*. In other words, the presence of the odours caused the predator to postpone airborne movement and continue searching the original leaf for spider mites. Interestingly, *P. persimilis* did not show the characteristic rearing-up posture considered to be important for lift-off in other species of phytoseiid mites (e.g. *N. fallacis*), and Sabelis and Afman [38] suggested that control of lift-off is exerted mainly via the grasp of the claws and the adhesive

empodia. *P. persimilis* also exhibited a ‘crouching’ behaviour (bending the legs so that the body was brought nearer the substrate) which would reduce dislodgement in increasing wind speeds, and occasionally the mites were observed to have anchored themselves very firmly to the leaf surface by their mouth appendages [38].

Eriophyid mites initiate migration by moving to the edge of a leaf, particularly on the upper, more exposed parts of the host plant. In response to air movements, these minute (~100-200  $\mu\text{m}$ ) mites hold their rather elongated bodies perpendicular to the substrate, thus exploiting the air velocity gradient near the leaf surface, and increasing their chances of being carried away by the wind [32,39,40]. Instead of using their hind legs (like phytoseiid mites or scale insect first instars) eriophyids use their anal suckers (caudal lobes) to support their bodies before releasing their hold on the substrate (Fig. 1a). Some species, such as the citrus rust mite *Phyllocoptruta oleivora*, as well as exhibiting the perpendicular standing behaviour, arch their backs and project themselves into the air by muscular action [41]. Apparently, the blackcurrant gall mite, *Cecidophyopsis (Phytoptus) ribis*, can leap 5 cm into the air by this means (B.D. Smith 1960 cited in [39]) – a distance 200 times the mite’s body length! The number of mites launching themselves from blackcurrant buds showed a positive correlation with wind speed, up to a speed of  $10.8 \text{ ms}^{-1}$ , after which fewer mites left the buds [39].

Descriptions of the initiation of aerial movement in some grass-infesting eriophyids are rather extraordinary.



**Fig. 1a:** Schematic representation of the wind velocity gradient at a leaf margin, and the effect on an aeriolly-migrating eriophyid mite, *Abacarus hystrix*. Velocity increases with: (i) height, and (ii) proximity to the leading edge. The take-off behaviour of *A. hystrix*—attaching itself to the leaf surface by its anal sucker and projecting its body perpendicularly through the wind velocity gradient—increases the intensity of surface drag forces on the mite, facilitating the crossing of the laminar boundary layer around the leaf. [From W.E. Frost, *Physiol. Entomol.*, 1997, 22, 37-46, reproduced with permission from John Wiley and Sons]

For example, the wheat curl mite, *Eriophyes (Aceria) tulipae*, moves to the uppermost tips of the leaves in such numbers that it forms “fuzzy-appearing, seething masses” of the tiny mites, which “crawl upon one another forming chains of several individuals attached to one another by their anal suckers. These chains break apart from the mite mass and disperse as a cluster of several individuals” [42]. Virtually all the windborne mites trapped were adults, which provides further evidence that the movements are actively initiated [42]: if they had been accidental, one would expect to have caught some immatures as well.

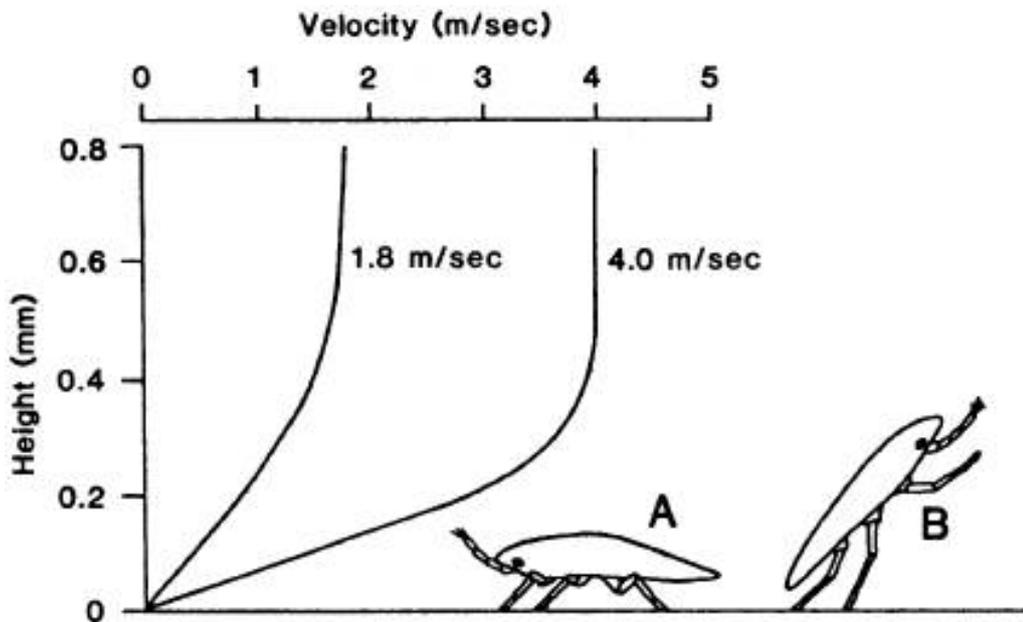
Frost [32] studied the behavioural and physiological adaptations that promote aerial migration in the mid- to late-summer generations of another eriophyid, the cereal rust mite *Abaracus hystrix*. The summer generations of *A. hystrix* adults (but not the winter ones) developed lateral and dorsal bands of wax plates or filaments along the body, which probably enhance airborne buoyancy of the mites by increasing the total drag relative to cuticular surface area; they may also have a role in reducing water loss during migration. Wax production appeared to be under phenotypic, rather than genetic, control and was stimulated by high temperatures [32].

As mentioned above, many tetranychid spider mites initiate aerial migration by descending on silk threads, but the primary mode of airborne movement is completely different in the two-spotted spider mite, *T. urticae* [22,23]. In response to certain conditions, of which the deterioration of host plant foliage and desiccation play an important role, various stages of *T. urticae*, particularly the adult females (but not the adult males), show a distinctive migration behaviour. The mites first show a positive phototaxis, which causes them to move upwards and concentrate around the periphery of the plant. Then, if exposed to a wind of  $1.5 \text{ ms}^{-1}$ , they face *away* from a light source, and lift up their forelegs and the anterior part of the body [23]. Under natural conditions this means the mite would be oriented downwards on a vertical part of the plant, or have its fore-body extended out over the edge of a leaf. Under the test conditions, about half of the mites assuming the ‘dispersal posture’ became airborne, while none of those crawling, or standing in a normal posture, did so.

Finally, we might mention the inert form of the deutonymph produced in some astigmatic mites (e.g. *Glycyphagus* spp. – see below, under Phoresy), which are thought to be moved around on air currents [43]. As this type of deutonymph remains enclosed in the exuvium of the previous (protonymphal) stage, this might be one of the few cases of completely ‘passive’ windborne movement.

In the Homopteran superfamily Coccoidea (scale insects and mealy bugs) the females are neotenous, wingless, often have atrophied legs and are consequently immobile. Even in taxa where the females possess legs, the second instar to adult stages are sedentary, and colonisation of new host plants relies on the mobile first instar nymphs, known as ‘crawlers’ [33,44]. Newly-emerged crawlers wander for a few hours or a day or two on the natal host plant and, if they have not settled during this period, they may become airborne. According to Hanks & Denno [33], coccoid species can be divided into two groups: those in which the crawlers show ‘active aerial dispersal’ and those where the process is ‘inactive.’ The active dispersers move to exposed positions on the tips of leaves or spines where they are easily dragged from the substrate by air currents; they may assist this process by assuming distinctive ‘rearing up’ body postures – lifting the front legs and anterior of their body into the air while supporting themselves on their rear legs [35] (see Fig. 1b). In contrast, the behaviour of the ‘inactive dispersers’ in response to the wind is to cling to the plant, flatten themselves against it, or to seek shelter in crevices; any aerial movement in these cases would seem to be ‘accidental’. It should be noted that even the active dispersers seldom moved more than a few metres from their natal host, although a small percentage of crawlers (~ 0.7– 7%) were caught above the plant canopy and these may move longer distances (~ several kilometres or even tens of kilometres) [33]. Successful displacement will, however, be constrained by the limited period that crawlers can survive without feeding, or before they are killed by desiccation.

The crawlers of the cochineal insect, *Dactylopius austrinus* (Coccoidea: Dactylopiidae), are larger than those of other scale insects, and the crawler stage is more prolonged. This would presumably increase the chances of successful colonisation movements in this species, and the crawlers show other adaptations for aerial migration [31]. Both sexes, but particularly the females, develop long wax filaments on the dorsal surface of the body which reduce the fall speed of the crawlers and thereby enhance aerial movement. Under the influence of a positive phototaxis, female crawlers climbed to the uppermost parts of the cactus host during the morning, ready to take advantage of stronger wind speeds which typically occurred in the early afternoon. This climbing behaviour was most evident in individuals which were 3 - 4 days old (i.e. rather older than in crawlers of most other coccid species), but the timing corresponded with the completion of wax filament development. After aerial movement, the female crawlers became photonegative,



**Fig. 1b:** Vertical velocity profiles for two freestream air velocities in the laminar boundary layer formed 2 mm (five body lengths) away from the leading edge of a flat plate (mimicking the edge of a leaf), along with scaled illustrations of a *Pulvinariella mesembryanthemi* (Homoptera: Coccoidea) first instar 'crawler' in (A) walking and (B) 'rearing' postures. By positioning itself near the leading edge of the plant substrate and then adopting the rearing posture, the minute crawler subjects itself to maximum drag force in order to take to the air. [From Washburn and Washburn 1984, *Science* 223, 1088-1089, reproduced with permission from AAAS.]

the upward climbing behaviour ceased, and individuals undertook exploratory walks before finally settling. Male crawlers did not show the positive phototactic response and did not ascend to the tops of the host, but males can move to new hosts (in order to mate with mature females) by flight in the adult stage.

Springtails (class Collembola) are wingless non-insect hexapods, which are occasionally found high in the air [45, 46] – Glick, for example, caught specimens of *Bourletiella* at several altitudes up to 11000 feet (3350 m). Generally, captures tended to be from the surface-active families (e.g. Entomobryidae and Sminthuridae) rather than soil-dwelling taxa, but there seems to be little evidence for any specialized behaviour promoting aerial movement, so perhaps individuals are carried into the air accidentally, for example, while springing to avoid predators, or while clinging to wind-blown leaves. However, an intriguing report by Farrow & Greenslade [47] from Australia documented large numbers of the isotomid collembolan *Cryptopygus* sp. crawling up the trunks of trees (at a rate indicating that about 0.5 million individuals ascended just one tree during a 5-hour period), and it was suggested that the collembolans may have been launching themselves from the canopy in order to migrate on the wind. Support for this hypothesis was provided by the aerial movement of juvenile entomobryid Collembola between rain-forest trees in Indonesia [48]; in this case it

was suggested that the partially attached exuviae of the moulting animals aided wind dispersal. Tree climbing and aerial movement were invoked to explain the apparently low genetic differentiation in Netherlands populations of the collembolan *Orchesella cincta* [49], but note [50].

Collembola are rather susceptible to desiccation, and this may hamper aerial movement over long distances [51]; long-range waterborne movement may be more likely, as discussed below. Successful airborne relocation over short distances does occur, however, as shown by the trapping of live specimens in Antarctica [51].

### 2.3 The physics of the aerial migration of minute wingless arthropods within and just above plant canopy

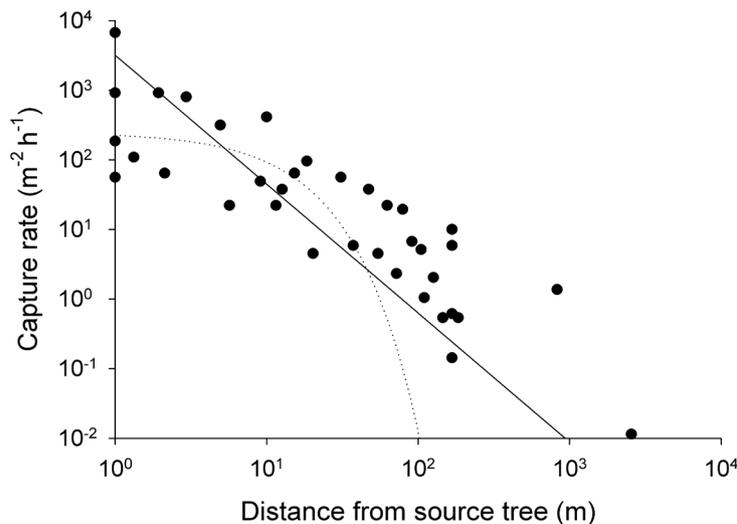
The 'rearing up' behaviours (mentioned above) are a key part of the embarkation process of minute wingless arthropods because these tiny creatures need to penetrate the laminar boundary-layer at the leaf surface, as pointed out by Washburn & Washburn [35] and Frost [32] (Fig. 1a,b). A recent perspective on aerial transport within and just above plant canopies emphasises that, after launch, turbulent processes will dominate airborne movement, particularly the presence of high-velocity downdrafts and updrafts that punctuate the otherwise quiescent flow [52]. In other words, the airflow is much more akin to an atmospheric

‘mixing layer’ than to the boundary layer flow over flat ground, and the wingless arthropod will be circulated around by downward ‘sweeps’ and upward ‘ejections’ which contribute to turbulent transport. Reynolds [52] developed a non-Gaussian Lagrangian stochastic model of these turbulent processes, and he specifically assumed that the organisms would launch into updrafts. This model performed better than the earlier Gaussian Lagrangian stochastic models, e.g. [53], in accounting for the distance moved by minute aerially-transported organisms within and just above plant canopies.

Although the direction and distance of travel are determined by air movement after take-off, the launch phase is, as we have seen, largely controlled, and many arthropods only become airborne under particular weather conditions. Recently it has been proposed that conditions chosen for take-off (light daytime breezes rather than stably-stratified conditions or more strongly convective conditions) may maximize the likelihood of dispersing to the nearest unoccupied site, thereby making the most of expected fitness on landing [54]. The proposal draws inspiration from a variety of theoretical and empirical evidence that the ability to become airborne during days with warm temperatures and light breezes results in the distances moved approximating to a  $-3/2$  power-law distribution [55]. This in turn changes the apparent aerial lottery of landing in suitable places into an evolutionarily-stable winning strategy [54] which is analogous to an

near-optimal gaming strategy in online ‘lowest unique bid’ auctions [56]. The power-law distribution is a hallmark of ‘Lévy flights’ where the distances travelled between consecutive touch-down points are in isotropic random directions and are drawn from a distribution with a heavy ‘power-law’ tail [57]. Thus, the rather limited movements of, say, scale insect crawlers may be more adaptive than they might appear at first sight. Rather than being rather feeble attempts to maximize dispersal over the longest distances, they may represent an optimal trade-off between staying close to where resources are abundant and predictable but are becoming depleted, and moving to a unique landing location, thereby minimizing competition for resources from fellow dispersers.

These optimal Lévy fliers may comprise a range of ‘ballooning’ taxa such as mites, caterpillars and spiders, and possibly some coccoids such as the felted beech scale (*Cryptococcus fagisuga*) whose movements are characterized by fat-tailed travel-distance distributions [58]. In an attempt to marshal empirical evidence for a shortest unique flight strategy in wingless arthropods that do *not* use silk draglines, data presented in Figure 11.1 of Hanks & Denno [33] on the relationship between crawler capture rate and the distance from their source trees were re-analysed using maximum likelihood techniques. We found (see Fig. 2) that a fat power-law distribution does indeed fit the data, with an exponent of about 1.8 (which is not too far removed from the optimal value of  $3/2$ ).



**Fig. 2:** Relationship between rate at which scale insect first instar crawlers were captured on sticky traps and the distance that traps were positioned from source trees. Observational data (solid-circles) are derived from ten field studies cited in fig.11.1 of Hanks and Denno (1998). As reported in the original comparison, these studies were not standardized for a variety of factors which could influence crawler dispersal (e.g., trap height, number of source plants, density of scale insects on source plants, and wind conditions). Shown on the figure are the best fit power-law (solid-line) and best fit exponential (dotted-line) distributions. The Akaike information criterion convincingly favours the power-law over the exponential as being the better model of the observations. The maximum likelihood estimate for the power-law exponent is 1.85. (Re-analysed from data presented in Hanks and Denno [33].)

We should note, however, that among wingless arthropods which do not use silk to become airborne (and which are dispersing in conditions near neutral stability), the ‘best possible dispersal pattern’ scenario is only available for organisms whose fall speed is less than about  $0.1 \text{ ms}^{-1}$ . This would seemingly exclude largish mites – phytoseiid mites weighing from 8.5 to  $21.7 \mu\text{g}$  had fall speeds of  $\sim 0.5 \text{ ms}^{-1}$  [36] – but would certainly include the tiny eriophyid mites which we estimate (from a comparison with phytoseiids) had fall speeds  $\sim 0.03\text{--}0.08 \text{ ms}^{-1}$  (A.M. Reynolds, unpublished). Where the fall speeds of scale insect crawlers have been determined, they were  $\sim 0.27 \text{ ms}^{-1}$  [35,53,58]), which is probably near enough to the  $0.1 \text{ ms}^{-1}$  threshold for these organisms to be included in the theory. More generally, we note that there is a need for empirical studies which focus on the evolution of ‘movement distance kernels’ (i.e., the probability density function of dispersal distance from a source) in windborne non-volant arthropods, rather than just on their behavioural propensity to disperse.

### 3 Pedestrian migration

Arthropod migration by walking and other types of limbed locomotion on land, i.e. running (cursorial movement), walking (ambulation) and hopping or jumping (saltation), and the various types of limbless crawling is likely to be very limited compared to what can be achieved using wind or water currents. Nevertheless, some large insects can displace surprising distances by pedestrianism during their lifetimes. For example, nymphs (known as ‘hoppers’) of the gregarious phase of various locust species form large cohesive groups that ‘march’ persistently in a relatively consistent direction. Estimates of the distances moved by bands of *Schistocerca gregaria* or *Locusta migratoria* during the life-span of the hoppers can total up to 30 km (see Tables 36 and 37 in [59]). Somewhat similar marching bands are found in the gregarious form of the Mormon cricket, *Anabrus simplex*, a large katydid (Orthoptera: Tettigoniidae), but here the flightless adults also contribute to the bands. One individual was observed to have moved about 2 km in 24 h, and this appears to be the longest recorded daily movement for any walking insect [60]. Distances covered by bands of older instar nymphs and adults of *A. simplex* during a season may be as much as 40 to 80 kilometres.

Kennedy [61,62] noted that the gregarious bands of desert locust nymphs are plainly much closer to the ‘migratory’ end of the movement spectrum than are solitary hoppers of the same species. Solitary

hoppers are visually attracted to clumps of desert plants – a ‘station-keeping’ response which prevents them moving far over bare ground. They also prefer to come to rest near inanimate objects and tend to avoid other hoppers (Ellis 1953 cited in [61]). The gregarious hoppers, in contrast, avoid obstacles and prefer open ground; a sun compass response keeps them on a straight course and their movement is also aligned and stimulated by the marching of their fellows. Feeding is, of course, necessary to replace the energy used up on the march, but this tends to occur during roosting periods in the morning and evening. Feeding on the march itself is brief unless the hoppers are particularly hungry (e.g., after a long movement over bare ground).

These early findings have generally been confirmed, and much extended, by more recent studies, e.g., [63]. Indeed, the sensory, neural and chemical mechanisms which trigger the switch from the mutual aversion found in solitary hoppers to coherent group formation in crowded conditions have been the focus of considerable scientific interest (e.g. [64] and the references therein). Another area of active research is the modelling of the abrupt density-related transitions from disordered ‘milling’ movement of individual *S. gregaria* hoppers to highly-ordered collective marching seen in large bands; this transition was documented in a ring-shaped arena in the laboratory and replicated using variants of Vicsek’s self-propelled particle (SPP) models with individuals following simple ‘nearest neighbor’ rules, e.g. [65]. Features of the predicted transition were later captured during a field study of migratory bands of Australian plague locust, *Chortoicetes terminifera* [66]. These locust examples form part of the huge field of research on ‘swarm intelligence’ (SI) which is well outside the scope of the current review.

Among other spectacular examples of insect pedestrianism are the mass movements of the New World army ants, *Eciton burchelli* and *E. hamatum* [67,68]. The movement pattern differs depending on which of the two alternating phases the *Eciton* colony is in, i.e., the ‘nomadic’ or the ‘statory.’ During the statory phase, the workers undertake relatively small-scale ‘raids’ during most days from a central bivouac which stays in the same place for about 12 to 20 days (dependent on the species) – this is evidently an example of central-place foraging. During the nomadic phase, however, there are major foraging raids virtually every day, and towards late afternoon the whole colony (including the queen and brood) migrates from the old bivouac site, along one of the main scent trails made during the day, to a new bivouac location several hundred metres away, the exodus being

completed by about midnight. Major raiding *and* bivouac change then continue daily until the colony subsides into its stary phase. The whole activity cycle takes about 35 days and is closely related to the condition of the brood. The onset of the nomadic phase coincides with the hatching of the eggs and pupae, and the increased raiding activity is due to the adult ants having to feed the voracious larvae. The movements that relocate the whole colony to a new nest site are plainly different from the foraging raids – the workers do not form repeatedly branching trails and their predatory response is inhibited [62]. This suppression of ‘appetitive’ responses, and the intense rectilinear nature of the bivouac-change movements, is strong evidence that this activity is migratory.

At the other extreme from the pedestrian migrations of locust hoppers or army ants, there may be many small-scale pedestrian migrations of small insects which typically do not, or cannot, fly [69]. In many of these instances there will not be sufficient information to distinguish true migration from ranging movements. Frequently (e.g., when young larvae disperse from their natal location) one suspects ranging because individuals exploring new territory will often respond immediately to stimuli signifying a new habitat patch. On the other hand, some pedestrian movements in terrestrial arthropods that are referred to as ‘migrations’ are probably straightforward appetitive movements in search of food, mates, or more favourable physical environments. For example, the spectacular seasonal movements of the male brown tarantula, *Aphonopelma hentzi*, seem more attributable to extended mate-finding searches than to migrations in the Kennedian sense used here [70]. In the case of millipedes (Class Diplopoda) and Collembola, pedestrian movements can entail astonishing numbers of individuals aggregated together [71,72]. Mass movements of Collembola mostly refer to species in the families Hypogastruridae or Isotomidae, and ‘swarms’ are frequently reported from snow and glaciers [72,73]. They occur following synchronized reproduction in conditions of ideal humidity and temperature and abundant food supply, and numbers can be huge (up to several thousand per m<sup>2</sup>) so that a ‘swarm’ may easily comprise several millions of individuals. The reasons for this behaviour are not entirely clear, although in most cases the Collembola are probably searching for food or a more favourable habitat after water-logging or freezing of a particular soil or litter horizon [73,74]. Experiments are required to see if movements terminate when the desired resource is encountered, i.e., there is no inhibition of appetitive responses – in that case the collembolan ‘swarms’ would be examples of ranging (see above) rather than truly migratory.

Be that as it may, collembolan species taking part in mass movements (e.g. *Hypogastrura socialis*) can exhibit interesting ‘track-straightening’ orientation behaviours utilising a ‘sun/polarised light compass’ or, in overcast weather, patterns of light and dark elements in the surroundings [75,76]. Each individual collembolan jumped in a rather straight line, although different individuals moved in different directions relative to the sun’s position [75,76]. In the case of *H. socialis*, the animal lands from a jump with anal sacs extended, allowing it to stick to the snow surface, often in an vertical stance; from this position it bends forward into the normal horizontal position, withdraws the anal sacs, and then rotates itself horizontally on the spot in order to select the direction of next jump [76]. Progress during the mass movement could be remarkably rapid for such tiny (1.2 mm) animals – perhaps covering up to several hundred metres per day.

Mass movement of millipedes seem to occur when favourable conditions, resulting in a population ‘explosion,’ are followed by excessive rain, drought, or shortage of food. This can result in huge aggregations, sometimes comprising millions of individuals (in one case, the numbers were estimated at more than 65 million), which sometimes move in a consistent direction [71,77]. These millipede ‘migrations’ have stopped trains due to the squashed bodies making the wheels loose traction, wells have been filled by 20 cm of drowned corpses, cattle have refused to graze, and workmen cultivating the fields have become nauseated by the odour of millipedes crushed by their hoes! Due to its unpredictable nature, the phenomenon is poorly understood, but most of the mass movements may be ‘appetitive’ (caused, for example, by responses to unfavourable humidity regimes) rather than true migratory movements in the sense used in this review.

## 4 Waterborne migration

Insects whose larval stages dwell in rivers and streams use the water current to move from natal sites to colonize suitable micro-environments in which they can spend their sometimes long larval stage. Because there is a distinct unidirectional current, individuals are exposed to ‘drift,’ as is shown by their capture in plankton nets [78], and there has been much debate whether this downstream larval drift is accidental or non-accidental, and the extent to which it is counter-balanced by other movements. Compensatory movements could include positive rheotaxis (orientation against the current) of the aquatic larval stages, or upstream flight by the adults before oviposition. Although it is not universal [78], there does appear to be

evidence for compensatory upstream flight by the adult stages (e.g. in some caddisflies (Tricoptera) and mayflies (Ephemeroptera) [78,79]). Moreover, some models have indicated that *random* dispersal by adults should be sufficient to return enough individuals upstream and thereby maintain the population, particularly if the larvae can reduce the amount of downstream advection [80].

In contrast to the ‘typical’ scenario of downstream drift by larval stages and upstream dispersal by adults, Olsson & Söderström found that nymphs of some mayflies actively migrate *upstream* from a main river into small temporary tributaries. Before the small streams dry up completely the nymphs have emerged, and their movement was at least partially counterbalanced by a subsequent ‘downstream’ return flight of adults to the main river [81]. Because assessing the varying contributions of larvae and adults to dispersal patterns of aquatic insects is challenging, many recent studies have employed indirect ‘population genetic’ approaches using molecular markers. A review of these studies [82] concluded that adult flight, rather than larval dispersal, was the major dispersal mechanism in most stream insects. The colonisation of unconnected aquatic systems would require adult movement away from the stream or river channel, i.e., so-called ‘lateral dispersal.’ In stoneflies (Plecoptera), which are poor fliers, or effectively non-fliers, there was less genetic differentiation between populations from different watersheds in a species which normally dispersed by flight (albeit weakly) compared with a species which generally just skimmed on the water surface (see below), crawled, or glided down from trees and vegetation [83].

In many species of chironomids (Diptera: Chironomidae), the first instar larvae show behavioural adaptations (e.g. a positive response to light) which cause them to be temporarily planktonic in the surface waters of lakes. Here the larvae can be moved around by wind-induced water currents, perhaps being displaced several kilometres per day (see review by Davies [84]). The positive phototaxis declines in the later instars and these are more sedentary, living in the sediment, although they may re-enter the water column in response to deteriorating conditions. In rivers and streams, larval drift was responsible for re-colonisation of habitats by chironomids after they had been eliminated by, for example, drought or heavy pollution, although some movements may be non-adaptive as when larvae are carried away by floods (‘catastrophic drift’). Davies [84] stated that the general downstream movement was counter-balanced by positive rheotaxis in the young larvae.

The daily round-trip vertical and transverse movements of the aquatic larvae and pupae of phantom

midges, *Chaoborus* spp. (Diptera: Chaoboridae) between the bottom sediments and surface waters of lakes [85], although often called ‘migrations’ (as are similar diel vertical movements of marine plankton), are best categorized as ‘commuting’ – they are a type of extended foraging movement which ceases when the appropriate resource is encountered [2].

## 5 Rafting and floating of terrestrial arthropods on the water surface

Vast numbers of insects and other arthropods are first carried by the wind, then fall into sea or fresh water and are drifted along on the surface and may be cast up in enormous masses on beaches [86]. Although some individuals can remain afloat and alive in the sea for several days and thus survive their stranding, this mixture of wind and water dispersal (anemohydrochoria) is largely accidental and results in huge mortalities. The means by which the arthropods get on to the water surface include the following:

a. Winged insects landing, either for behavioural reasons or due to exhaustion.

Of the two explanations, landing due to exhaustion seems more likely because there is good evidence that flight is extended beyond the normal migration period if migrants find themselves over the sea [10], and there may well be cues from the surface of the water, e.g. the reflectance of short wavelength light [87,88], which reduce the tendency to alight.

b. The deposition of aerially-migrating arthropods (winged or wingless) by atmospheric downdrafts, or impaction by raindrops, particularly during thunderstorms.

Again, we assume that in most cases winged migrants will resist settling even if brought close to the water surface by downdrafts.

c. Flightless terrestrial arthropods being carried away by water, particularly due to surface run-off, the erosion of the edges of streams, and melt-water from snow and ice.

In this case, we note that dense aggregations of some species of Collembola are regularly found on snow (see above); these may be trapped in meltwater and carried along on the resulting streams [89].

d. Finally, the natural habitat of some species makes it likely that individuals will be taken up on the water surface.

For example, halobiotic species of flightless arthropods (e.g. mites and Collembola) which live in the

higher littoral zones may be carried away by inundation during storms or extreme high tides [90].

Although processes (a) and (b) above are generally maladaptive, it is possible that some cases of processes (c) and (d) may contain elements of adaptive behaviour, or at least adaptations to cope with (and thereby profit from) waterborne dispersal if it occurs. Among the means by which terrestrial arthropods can survive for considerable times on the surface of the sea or on fresh water are:

- ‘rafting’ on flotsam (e.g. see references in [91];
- floating on the surface film of the water, aided to a greater or lesser extent by the hydrophobic nature of the cuticle and, in some cases, by hydrofuge hairs and cuticular sculpturing [89,90, 92]; and
- surviving periods of immersion just below the water surface as manifested by certain terrestrial mites and Collembola [92].

Some terrestrial arthropods can survive for surprisingly long periods on the surface of the sea. Coulson et al. [92], for example, found that five species of Arctic soil Collembola with hydrophobic cuticles could survive on agitated seawater for periods of more than 14 days. More unexpectedly, two wettable (and therefore sinkable) species (a collembolan, *Tetracanthella arctica* and a cryptostigmatic mite, *Camisia anomia*) survived extended periods of *submersion* in seawater, apparently being able to obtain enough oxygen from the cold water by diffusion through the cuticle [92]. Hawes et al. [89] found that the maritime Antarctic collembolan *Cryptopygus antarcticus* not only survived for long periods on fresh and seawater, it also moulted and produced viable offspring. Moulting individuals survived better than non-moulting ones, and it was suggested that the exuviae provided a flotation aid and a source of food – a sort of ‘edible raft’ [89].

It is clear, therefore, that some small terrestrial arthropods can potentially travel considerable distances (several hundred kilometres) by sea-surface transport, and this may be one of the main mechanisms for the colonisation of islands, for example, the Galápagos [91], Surtsey (Iceland) [93], or deglaciated lands in the high Arctic [92] or Antarctic [89]. The ability of some Collembola to survive very low temperatures for extended periods (e.g.,  $-22^{\circ}\text{C}$  for over 4 years), which might even allow them to become incorporated into surface ice and then released again, would also facilitate the colonization of polar regions [92]. Long-distance transport on the sea surface would also be facilitated by the ability of some arthropods to survive for long periods without feeding, particularly in low temperature conditions. Finally, we note that some mites and Collembola are parthenogenetic, so a single

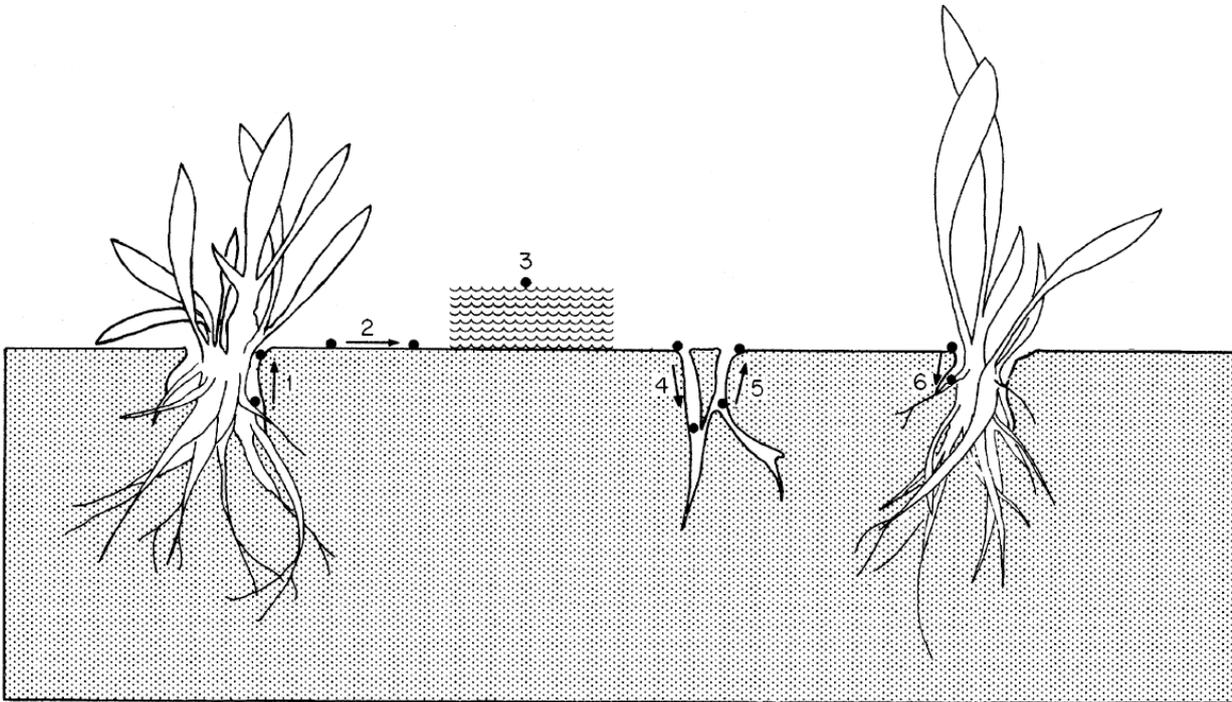
surviving female would suffice to colonize new habitats.

In most of the above cases, the travellers are more likely to be ‘vagrants’ rather than true migrants (but note the migration behaviour in the first instar of the aster root aphid, discussed below). Specialized migration behaviour might be involved in some of the Collembola adapted for life on the water surface, although we know of no convincing evidence of this at present.

## 6 Wind-propelled migration on the water surface (‘sailing’ and ‘skimming’)

Arthropods on the water surface film may be drifted by water currents, as discussed in the previous section, but they may also be blown along the surface by the wind, and evidently these two types of movement may occur simultaneously. In fact, the large numbers of Collembola found on the sea surface after flooding (see above) can often be blown into dense aggregations by the wind [90]. The extent to which these movements are adaptive, as opposed to an occasional consequence of the species’ life-style, is unclear – in some instances they no doubt lead to the colonisation of new habitat, but often large populations swept far out to sea may be doomed to drowning or starvation.

One case where there is definite evidence of specialized migration behaviour in a flightless littoral arthropod is the tidal ‘dispersal’ of the aster root aphid, *Pemphigus trehernei*, investigated by Foster and colleagues [94,95]; see Fig. 3. The secondary (summer) host of *P. trehernei* is the sea aster (*Aster tripolium*) which grows on tidal saltmarshes. Alate (winged) morphs are scarce in *P. trehernei*, and movement occurs mainly in the first instar, which colonizes new host plants by walking and also by floating on the water surface [94]–these modes of migration may be less risky than flight in a species which needs to remain within a restricted intertidal zone. The young 1st instar larvae of *P. trehernei* are photopositive; they crawl up to the soil surface, and are taken up and moved around by the incoming tide. They are also propelled rapidly across the sea surface by the wind and thus reach new hosts along the marsh edge [95]. Floating on seawater for about 30 min reverses the response to light of the young first instars, which then become photonegative (like the older first instars, and all subsequent stages including the adult), resulting in movement into cracks containing aster roots. However, they can be induced to become photopositive again if kept on a dry surface for a further 30 min after the initial 30 min



**Fig 3:** Diagrammatic representation of the scheme proposed for the dispersal of 1st instars of the aster root aphid, *Pemphigus trehernei*, with notes on some behavioural responses associated with the movements. (1) Movement out of soil of young 1st instars, possibly encouraged by crowding, shortage of food and dryness of soil. (Positive response to light overruling positive response to gravity.) (2) Movement on soil surface. (3) Floating on the tide. (4) Movement down into a soil crack by (a) older 1st instars (> 60-h old) that have not necessarily dispersed on the tides, and (b) younger firsts after dispersal on the tides. (Negative response to light reinforcing positive response to gravity.) (5) Movement up to soil surface by young 1st instars that have found no suitable aster roots. (Positive response to light overruling positive response to gravity.) (6) Movement of older 1st instars, or younger firsts after dispersal on tide, into cracks containing suitable aster roots, where the aphids may then found a colony. (Negative response to light reinforcing positive response to gravity.) [From W.A. Foster, J. Anim. Ecol., 1978, 47, 653-659, reproduced with permission from John Wiley & Sons Ltd.]

period on seawater [94]. Reversal from photopositive to photonegative behaviour also occurs if the larvae merely walk on the soil surface and are not taken up by the tide, but in this case the process occurs much more slowly.

Apart from the unusual primary method of migration, the migration of the first instar *P. trehernei* is remarkable because of the parallels [62] with the competing interactions between migratory and 'appetitive' responses found in flying aphids (e.g. Kennedy's classic work on winged *Aphis fabae*; summarized in Dingle [2] pp. 26-30). Here, a period of migratory flight leads to a change in phototaxis—initially there is a high responsiveness to short-wavelength light from the sky, but the ongoing flight primes the settling responses, including a stronger attraction to the long-wavelength light reflected from plants.

Being blown along the surface of water will obviously be easier if the organism has some sort of sail. Adult *Allocapnia* spp. stoneflies (Plecoptera) emerge on mid-stream rocks and walk on the water; they raise their rudimentary wings (but do not flap them) in response to

puffs of wind and are thus propelled from one location to another [96]. Other stonefly species show an array of wing-propelled surface-skimming behaviours in which contact with the water surface obviates the necessity for complete support of the body weight (as occurs in true flight). These behaviours range from: (a) weak wing-flapping while the body is in contact with the water, combined with lateral movement of the abdomen in a swimming-like motion; (b) skimming with body elevated above the water but with all six legs maintaining contact with the surface; (c) 4-leg skimming (also seen in some mayflies (Ephemeroptera)); (d) skimming with only the two hind legs on the surface (here the stonefly practically flies, but uses the water surface to steady itself); and (e) stoneflies that use their hind legs to jump from the water to initiate rather clumsy flapping flight [97]. This sequence is of particular interest because it has been proposed that similar progression might explain how the functional wings of insects originally evolved from the leg-derived gills of a crustacean-like ancestor [97,98]; this view is controversial, however [99].

## 7 Phoresy

A phoretic relationship between animals entails one organism ‘hitchhiking’ on the body of another (usually larger and more mobile) organism. A more precise (and widely-quoted) definition was given by Farish & Axtell [100], namely:

“Phoresy is a phenomenon in which one animal actively seeks out and attaches to the outer surface of another animal for a limited time during which the attached animal (termed the phoretic) ceases both feeding and ontogenesis, such attachment presumably resulting in dispersal from areas unsuited for further development, either of the individual or its progeny.”

It is worth noting the term phoresy is not applied to relationships where the individual being transported is directly parasitizing the carrier individual. However, the requirement in Farish and Axtell’s definition that the phoretic individuals always abstain from feeding is problematic, as some mites feed on host secretions apparently without harming the host (a phenomenon known as ‘paraphagy’) [101]. It is, incidentally, often difficult to decide where host-phoretic relationships lie on a spectrum ranging from mutualism (a few examples where the phoretic and host both benefit), commensalism (where the phoretic or host benefits, with a neutral effect on the other member of the partnership) to a situation where there are minor detrimental effects on the host (for example, in causing the host to expend more energy carrying the phoretic) and, finally, to explicit parasitism or parasitoidism. One can easily envisage how an increasingly close phoretic relationship could evolve into an explicitly parasitic one (through paraphagy, for example) and this has indeed occurred in various mite lineages [101]. In fact, there are examples in the Acari where some members of a genus are purely phoretic, while others in the same genus are parasitic [102]. There will no doubt be some marginal cases where one has to decide whether transport is the main purpose for the embarkation, as opposed to feeding, say, where behaviour would be classed as ‘appetitive’ – Krantz [103] (pp. 74-75) gives some interesting examples. We also note that Kennedy’s definition specifies *some* inhibition of appetitive activities – in other words, inhibition is not necessarily total throughout the migration period. Animals undertaking long-duration migrations like the monarch butterfly have bouts of feeding during journeys lasting weeks. Similarly, some breaks in the quiescent state found in most phoretics after embarkation may, perhaps, be tolerated within the definition.

Some other qualifications to the definition of Farish and Axtell are mentioned by Houck and OConnor [104], including:

- the ‘active seeking’ may be somewhat misleading

because some phoretics ‘lie in wait’ for their hosts [105];

- the term ‘superficially attached’ is better than ‘external’ because phoretic mites, for example, may be carried within host orifices or under host structures;
- the emigrant habitat is better characterized as merely ‘natal’ to avoid the generalisation that phoresy is necessarily directly correlated with habitat quality (it may be correlated with the host’s life cycle).

Houck & OConnor [104] then offer the following definition of phoresy:

“ a phenomenon in which one organism (the phoretic) receives an ecological or evolutionary advantage by migrating from the natal habitat while superficially attached to a selected interspecific host for some portion of the individual phoretic’s lifetime. Benefit is not conferred as a nutritional or developmental influence on the phoretic stage.”

[NB: We believe that the restriction to *natal* dispersal in the above definition may apply to mites, but seems less applicable to other taxa; for example, some pseudoscorpion (see below) species can live for 2 or 3 years, and at least some individuals will disperse via phoresy on more than one occasion. (D.W. Zeh, personal communication).]

In Farish and Axtell’s definition, and explicitly in Houck & OConnor’s, the phoretic transport is clearly a form of migration (see also [105,106]), and an amazing array of ‘migration syndrome’ traits has evolved to facilitate it. For example, there may be facultative induction of a highly-specialized phoretic stage in the life-cycle, e.g. the ‘hypopus’ of certain mites (see below). Many phoretic organisms (particularly mites) have evolved specialized structures to facilitate attachment, such as clamping or clasping devices, hooks, suckers, or glands producing adhesives [107]. There are also complex behaviours to ensure recognition of, and embarkation on, an appropriate host; this is often followed by a period of quiescence until cues are present which stimulate disembarkation into a suitable new habitat. This inactivity constitutes a contrast to the *persistent* locomotory exertions of a typical animal migrant, although there may be a frenzied bout of movement to board or disembark from the host. Phoresy in terrestrial arthropods is particularly characteristic of small, wingless forms, living in patches of specialized and ephemeral micro-habitat (dung, carcasses, rotten fruit or mushrooms, tidal debris, nests, beetle galleries, and phytotelmata (small bodies of water held by plants, e.g., treeholes and pitcher plants)) separated by distances which would otherwise be untraversable to the phoretic

species. As is well-known, migration is particularly associated with species exploiting such transient and spatially discontinuous habitats [108].

### 7.1 *Pseudoscorpions*

Pseudoscorpions (members of the arachnid Order Pseudoscorpiones) often rely on phoresy to colonize new habitats, particularly females of species which inhabit impermanent habitats [108]. They use one of their pedipalps (which end in a pincer) to grab hold of a leg or other appendage of a larger and more mobile insect, most often a fly or beetle species but also other insects or arachnids such as harvestmen (Opiliones). Altogether, at least 44 families of insects, and three families of Arachnida, have been recorded as carriers (reviewed by Poinar et al. [109]). Phoretic associations are found preserved in amber which is 40 million years old, but the relationships are thought to be much older than this. It is interesting to note that the fossil and modern pseudoscorpions have associations with very similar carriers, and even show similar methods of attachment [109]. Pseudoscorpions can be carried long distances by phoretic migration as demonstrated by the capture of specimens on airborne insects over the Pacific (Guilmette et al. 1970, cited in [109]).

Because pseudoscorpions frequently attach to arthropod hosts which are not greatly larger than themselves, there has been some controversy as to whether attachments were the consequence of unsuccessful predation rather than true phoresy [109]. Zeh & Zeh [110] studied a case where a pseudoscorpion, *Dinocheirus arizonensis*, preys on a neriid fly, *Odontoloxozus longicornis*, but also uses it for transport. There was a clear difference, however, between the predatory behaviour (where *D. arizonensis* grasps the *body* of the fly and injects venom) and the phoretic behaviour (where a grasp is maintained on the trochanter of a hind leg of the fly). Experiments confirmed [110] that the phoretic attachment behaviour facilitated pseudoscorpion migration between rotting saguaro cacti which form its (highly discontinuous) habitat, and the hypotheses that transport was accidental, motivated by hunger, or occurred because pseudoscorpions were incapable of consuming their hosts were rejected. Nonetheless, it still seems probable that phoretic behaviour in pseudoscorpions originally evolved from predatory activity [111].

Another telling piece of evidence indicating that phoretic behaviour facilitates transport to new patches of habitat is the interaction between the pseudoscorpion *Semeiochernes armiger* and the giant tropical fly *Pantophthalmus tabaninus* [112]: attachment was only

maintained to the *Pantophthalmus* females—the male flies were quickly released. This is adaptive because only female flies visit the newly-dead trees which constitute the pseudoscorpion's habitat.

After most phoretic pseudoscorpions have grasped an appendage of their host, they enter a quiescent state which is not conducive to other activities. In the case of the pseudoscorpion, *Cordylochernes scorpioides*, carried by the giant harlequin beetle *Acrocinus longimanus* (Cerambycidae), however, the pseudoscorpion engages in stereotypical behaviour (involving pinching the beetle's abdomen, and causing it to partially open its elytra) which allows *C. scorpioides* to get into the sub-elytral space [113]. Here the pseudoscorpion can prey on phoretic mites which are also being carried by the beetle, and males compete to establish territories on the abdomens of beetles where they can mate with females. *C. scorpioides* evidently has a complex relationship with the host, and occurrence of feeding and mating conflicts with the strict definitions of phoresy given above. Nonetheless, Zeh & Zeh [113] concluded that transport rather than predation was the primary reason for the pseudoscorpion/beetle association because *C. scorpioides* collected from trees were in a better nutritional condition than beetle-riding individuals, and large numbers of pseudoscorpions boarded beetles on old, depleted trees and disembarked on newly-fallen trees.

### 7.2 *Mites*

Many lineages of mites live in microhabitats which are extremely scattered and ephemeral, and an efficient way to locate these is by phoretic transport. Indeed, phoresy can be said to be the characteristic mode of migration in mites [105], and there has been a huge radiation of phoretic associations involving vertebrates, insects (particularly Coleoptera, Diptera and Hymenoptera), and virtually all other terrestrial arthropods (e.g., millipedes, centipedes, harvestmen, amphipod sandhoppers) [43,101,102,103,104, 105,114,115,116]. There are even hyperphoretic associations where the phoretic mite is itself carrying another species of mite. Hundreds of individual mites can be found on one host [105,114], which can be so burdened that it cannot fly or walk [15,116,117]), or feeding, copulation and oviposition can be seriously hindered [102]. Even vertebrate hosts can be affected—a lizard was so coated with phoretic uropodid mites that it eventually died (Domrow 1981 cited in [102]).

Some phoretic relations are non-specific, such as those of *Histiogaster arborsignis*, which has over 40 host species representing three insect orders [104], but others have become increasingly stenoxenic (restricted to a group of closely related hosts). For example, in mites of the genus

*Hemisarcoptes*, the phoretic deutonymph is carried only by ladybird beetles of the genus *Chilocorus* [118]. Highly-evolved morphological adaptations are widespread in the phoretic stage of mites, which enables them to ride in or on very specific parts of the host's anatomy [114,119]. One rather bizarre example is *Macrocheles rettenmeyer*, which only attaches to the pulvillus between the tarsal claws of the hind legs of certain types of worker of the New World army ant, *Eciton dulcium*. The mite's hind legs are greatly enlarged and held in a curved position, and are used in place of the ant's tarsal claws when it walks or hooks its legs on to those of another ant.

In some bee or wasp hosts, a special pocket or platform (the 'acarinarium') is provided to assist the secure transport of the mites [120]; this implies a mutualistic relationship between the phoretic and host. In an example studied by Okabe & Makino [121] the mites were mildly parasitic on the host wasp juveniles, but they also helped to protect these juveniles from attack by a mutual enemy – a parasitoid wasp.

Mites are generally phoretic during only one of their developmental stages (usually the deutonymph or the adult female), and in some cases this dispersal morph may show extreme adaptations for phoresy. Houck & OConnor [104] recognise three stages of increasing specialization in the phoretic stage (see fig. 1 in reference [104]). They are:

a. the unspecialized homeomorph – these have few morphological adaptations for phoresy – females may just clasp the host using normal-looking chelicerae or ambulacral claws. There may be some minor (though no doubt important) morphological adaptations. For example, phoretic *Macrocheles* mites have a bidentate subapical tooth on the moveable digit of the chelicerae, while this feature is absent in non-phoretic species of the genus.

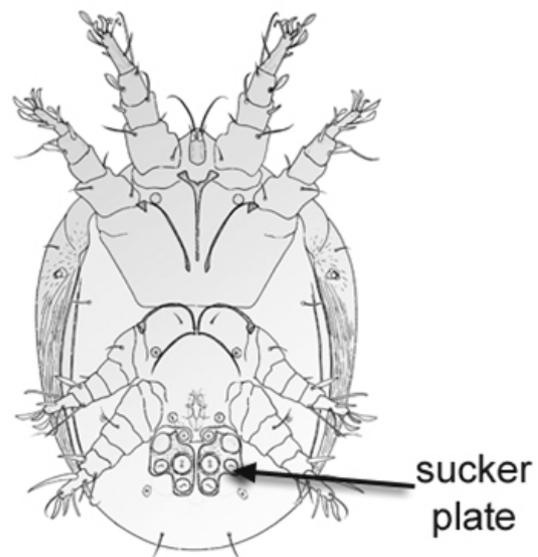
b. the specialized homeomorph – here the morphology of the phoretic stage deviates relatively little from the usual form. For example, in some groups of the Heterostigmata, two distinct female morphs are formed: 'normal' females which do not migrate and 'phoretomorphs' which are specifically adapted (e.g. with modified forelegs and enlarged claws) for attachment to a phoretic host [102, 104]. Another specialized attachment structure is the 'anal pedicel' of uropodid mites. Here the phoretic deutonymph fixes itself to the host by a stalk formed by a secretion from the anus of the mite, which solidifies on contact with the air.

c. the facultative heteromorph – in this case, there is an optionally-induced developmental stage which differs *radically* from the normal body plan for the instar. For example, many astigmatan mites which are phoretic

on insects, other arthropods or vertebrates do so by producing a *heteromorphic deutonymph* or 'hypopus' (plural: hypopi or hypopodes) (see Fig. 4).

The hypopus is a modified juvenile stage of the mite, and is thought to correspond to the deutonymph (the second of up to three nymphal stages) [104]. Hypopi typically have a dorso-ventrally flattened body, with a large ventral sucker plate (or a pair of claspers) for attaching to their phoretic host. They are often able to resist desiccation and other unfavourable factors (such as chemical pesticides) due to a thickened cuticle. Hypopi can often survive without feeding for long periods, and lack functional mouthparts and the foregut is closed off. [To complicate matters, however, the midgut and hindgut may still function in some species (e.g., *Hemisarcoptes cooremani* hypopi travelling on the beetle *Chilocorus*) with the hypopus extracting haemolymph from its host by means of the caudal ventral sucker plate [122]). As the host beetle is apparently contributing to the nutrition and the ontogenetic development of the mite, this relationship has evolved beyond the 'phoretic' (as defined by Houck & OConnor – see above), and may be parasitic.]

The presence of the dispersal (hypopus) stage is usually facultative, and whether or not it is present in the life-cycle depends on various environmental and genetic factors. When conditions are very favourable, the



**Fig. 4:** A hypopus, the heteromorphic deutonymph produced by many astigmatan mites, a stage highly adapted for phoretic transport on other animals [Reproduced with permission, from David E. Walter, Glossary of Acarine Terms, [http://itp.lucidcentral.org/id/mites/invasive\\_mite/Invasive\\_Mite\\_Identification/key/0\\_Glossary/Glossary\\_Images/Hypopus\\_line.jpg](http://itp.lucidcentral.org/id/mites/invasive_mite/Invasive_Mite_Identification/key/0_Glossary/Glossary_Images/Hypopus_line.jpg)]

protonymph develops straight into the tritonymph and then the adult mite [105,123]. Adverse conditions in the (often transient) habitat, such as drying out, overcrowding, lack of food, and accumulation of waste products, favour the interposition of a hypopus stage. In some *Glycyphagus* spp., there are three possible developmental pathways: directly-developing mites, phoretic hypopi, and inert hypopi. The actual developmental route taken is determined in the late larval to early protonymphal stage, and the complex genotype × environmental interactions involved in hypopus induction have been investigated by Knülle [123]. He found that the traits influencing the proportion of each hypopus type were highly polymorphic in local populations, but there was also a substantial environmental effect (e.g. through food quality) on genetic expression of the morphs.

The actual processes of host-finding and embarkation may involve periods of vigorous activity by the phoretic stage, and are analogous to the locomotor excitability occurring at the commencement of migration in, say, a winged insect [105]. Temporary inhibition of ‘appetitive’ functions, such as feeding and reproduction, is obvious when specialized heteromorphs (such as the hypopus) are involved, but even in less specialized phoretic adults host searching could not be interrupted by food items [105]. Further evidence of central inhibition is provided by the reattachment of mites to a host, sometimes of a different species, after they have been artificially removed from the original host [105].

The embarkation behaviour of some phoretic stages seems rather indiscriminating; for example, the hypopi of *Histiostoma laboratorium*, phoretic on cultures of *Drosophila* fruit flies, congregate in large numbers on the rim of the culture container from which they can leap as high as 2.5 – 5 cm toward objects passing overhead—even if the object is a small metal needle rather than a fly [124]! The mites assume a typical ‘questing’ stance, where the posterior of the body is attached to the substrate by the caudoventral suckers, the anterior of the body raised and buttressed by legs III and IV, and the first two pairs of legs are extended upwards [104]. The leap appears to be powered by the third pair of legs, and is apparently triggered by vibrations or air currents from passing objects [124].

In other cases, the degree of host specificity may be very high, with not only a preferred species, but a preferred sex and age range within the host species (e.g., *Poecilochirus* spp. mites phoretic on *Nicrophorus* burying beetles—see below). The phytoseiid mite *Kampimodromus aberrans* could distinguish between aphid morphs; mature female mites boarded alate filbert aphids but not

the wingless forms [125]. If the phoresy is *obligate*, the phoretic may not be able to develop properly or reproduce unless it has spent time on its specific carrier [105,116]. Incidentally, the phoretic succession of numerous mite species (arriving on, for example, necrophilous and necrophagous flies, burying beetles and carcass/hide beetles) has utility in forensic science, for example, in estimating the time of death [116].

Burying beetles (*Silphidae*: *Nicrophorus* spp.) construct a brood chamber around a small carcass that they have buried. After the larval brood hatches both parents spend a few days caring for them, before departing to find a new carcass. Schwarz & Koulianos [126] reviewed the strategies of mites reproducing in the brood chambers. The phoretic deutonymphs of the mesostigmatan mite, *Poecilochirus* spp., were vectored to the new brood chamber by the *Nicrophorus* parents, where the mites disembark, moult into adults and reproduce. The deutonymphs of the next generation then tended to disperse on the first parent beetle to leave the brood chamber (usually the male) which consequently may carry large numbers (~ 100 – 250) of the mites. Deutonymphs developing too late to migrate on the male congregate on the female beetle, and a small number which missed both parents had to wait and eventually attach to the beetles’ progeny. The phoretic deutonymphs further speeded-up their arrival at a new brood chamber by taking opportunities to transfer to more reproductively-active beetles if the original host came into contact with these at, for example, sites where male beetles are emitting pheromones or on large carcasses (on which the beetles feed, but which they do not attempt to bury). The phoretic stage mites were evidently able to discriminate between the (preferred) medium-aged sexually mature beetles, and either immature or very old individuals; they also favoured species of *Nicrophorus* which were likely to breed at that time of the year. The *Poecilochirus* spp. mites were, therefore, relatively independent of the generation cycle of a single phoretic host, and were able to pass through several generations in the time taken for one beetle generation [126].

The discrimination between potential host individuals by the deutonymphs of *Poecilochirus* demonstrates the precision with which some phoretics can recognise their hosts. Generally, it seems probable that the semiochemicals of the host cuticle play a kairomonal role in this recognition behaviour, which may include the sex, age, and condition of the host as well as specific sites for phoretic attachment. Semiochemicals were found to mediate host-finding behaviour in another mesostigmatan mite, *Macrocheles saceri*, which is phoretic on *Scarabaeus* spp. dung beetles (*Scarabaeidae*) [127]. Another example

concerns the broad mite, *Polyphagotarsonemus latus* (Tarsonemidae), which is phoretic on the legs of whiteflies (Homoptera: Aleyrodidae), but shows negligible attraction to other possible hosts such as aphids and thrips. Here, olfactory cues from the waxy particles on the whiteflies allow the mites to recognise their phoretic hosts [128].

Flower-dwelling mites are carried on hummingbirds and some other nectar-foraging birds, butterflies [129, 130] or even bats [131]. Mesostigmatan mites of the genera *Rhinoseius*, *Tropicoseius* and some *Proctolaelaps* (Ascidae) feed and reproduce in the inflorescences of plants pollinated by hummingbirds, and travel from flower to flower in the nostrils of these birds. In the few seconds that the hummingbird is feeding at a flower, the mites scramble on to its bill and race for its nostrils at the rate of 12 body-lengths per second (as fast, relatively, as the speed of a cheetah!) [129]. Each species of mite is particular about which species of flowers it can use so the chemical cues informing the mite to disembark at the correct host plant (which again must be done very rapidly) is highly specific [132]. A suite of physical and chemical cues must be responsible for mediating the detachment and dismounting behaviour of the phoretic from its host, but in most cases the specifics of this remains unknown. The occasional occurrence of large number of phoretic mites on dead insect hosts indicates that the phoretic stage cannot end until a specific disembarkation cue is received [102].

### 7.3 Insects

Finally, we might mention a few instances of insects as phoretic travelers as opposed to hosts. Clausen [133] gives numerous examples of phoresy in entomophagous insects where the phoretic relationship can be severely disadvantageous to the host species because it enables the immediate parasitization or predation of eggs laid by the host female. For example, the adult females of some scelionid wasps (Hymenoptera: Scelionidae), are phoretic on the adults of their host species, and when the host starts to lay the wasps immediately attacks and parasitizes the eggs. Thus the process could be regarded primarily as an aspect of host location and only secondarily as a dispersal strategy. Nonetheless, if the carrier species is a long-range migrant such as the Australian plague locust, *Chortoicestes terminifera*, the phoretic species (e.g., *Scelio fulgius*) may be transported into distant habitats which have only recently been invaded by swarms of the locusts. We note, however, that Farrow [134] found evidence that *S. fulgidus* has another option which is unambiguously migratory: the parasitoid and its host can migrate

independently, by day and by night respectively, via flight on the prevailing winds.

A remarkable example of ‘phoretic’ dispersal is the passive transport of *Chironomus salinarius* larvae (Diptera: Chironomidae) in the guts of migrating black-tailed godwits [135]. Currently, it is unclear whether this means of dispersal is important in the *Chironomus* species, because only a small proportion of the larvae managed to survive passage through the birds’ digestive tract, and adult chironomids can migrate by flight. However, as Green & Sánchez [135] point out, dispersal via the shorebirds may be over greater distances and be better directed towards suitable (saline, aquatic) habitats than the windborne movements of adult chironomids. Movement in the larval stage also enables the colonization of newly available habitats at times of the season when active dispersal by adult insects is not an option. Larvae of the weevil *Revena rubiginosa* (Coleoptera: Curculionidae) live within, and feed on, the seeds of *Syagrus romanzoffiana* palms, and when palm fruits are eaten by frugivorous birds such as guans and toucans, the larvae can survive passage through the birds’ digestive tracts [136]. It seems likely that the birds are instrumental in weevil dispersal, particularly as the adult beetles have not been observed to fly [136].

Crawlers of some species of scale insect are transported by air currents as previously mentioned. However, crawlers of some Diaspidid scales appear to use phoretic migration and have specialised attachment structures on the end of their legs [137]. It was suggested that phoresy may be more adaptive (because it was less risky than wind dispersal) in species which colonise patchily-distributed host plants and which have relatively low fecundities [137]. A remarkable form of phoretic dispersal occurs in the gall-forming genus *Cystococcus* (family Eriococcidae) whereby the minute female crawlers are transported out of the maternal gall, and on to nearby host plants, by clinging to the modified abdomens of their adult (winged) brothers [138].

## 8 Conclusion

The definition of migration proposed by Kennedy seems to have stood the test of time [2, 12, 13, 70, 139, 140]. His behavioural perspective on migration rests with the individual rather than the population; ecological and population dynamics aspects of migration are firmly viewed as *outcomes* of the individual movements, i.e., there is no mixing up of ‘integrative levels.’ Outcomes then feed back, through natural selection, on the *individual’s* genes for migration behaviour and other co-adapted traits

[12]. The behavioural perspective successfully includes the classic long-range two-way migrations of, say, birds or marine vertebrates, but it is also applicable to some much more obscure animal movements, as illustrated here by examples of migration in non-volant terrestrial arthropods. Under the influence of particular endogenous and environmental factors, these animals are observed to switch from their everyday foraging activities to behaviours clearly adapted to facilitate departure from their current habitat patch, either by persistent rectilinear locomotion, or (often) by deliberate embarkation on a transporting ‘vehicle’ (air, water, or another animal). The behavioural and physiological adaptations that initiate and maintain migratory movements indicate that they all form part of a distinctive biological process – in other words (and perhaps surprisingly) there *does* seem to be a ‘common migratory syndrome’ [139] manifest across a huge array of animal taxa. Even in cases where our knowledge of a particular movement does not permit immediate categorization (into station-keeping movements, ranging, or migration itself), the behavioural definition is ‘predictive’ [2] suggesting appropriate experiments which will lead to significant insights into the observed journeyings. Some borderline cases such as those mentioned in connection with phoresy may be difficult to pigeonhole (“a definition without exceptions is hard to find in biology” [6]), but considering them in light of the Kennedy–Dingle conceptual framework seems likely to result in a deeper understanding of animal movement, and to aid the integration of migration behaviour with what is known of processes and linkages occurring at other organizational levels of an animal ‘migration system’ [12,140].

**Conflict of Interest:** The authors declare that they have no conflicts of interest.

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## References

- [1] Johnson C.G., Migration and dispersal of insects by flight, Methuen, London, 1969
- [2] Dingle H., Migration: the biology of life on the move, Oxford University Press, Oxford, UK, 1996
- [3] Anderson R.C., Do dragonflies migrate across the western Indian Ocean? *J. Trop. Ecol.*, 2009, 25, 347-348
- [4] Stefanescu C., Páramo F., Åkesson S., Alarcón M., Ávila A., Brereton T., et al., Multi-generational long-distance migration of insects: studying the painted lady butterfly in the Western Palearctic, *Ecography*, 2013, 36, 474-486
- [5] Chapman J.W., Bell J.R., Burgin L.E., Reynolds D.R., Pettersson L.B., Hill J.K., et al., Seasonal migration to high latitudes results in major reproductive benefits in an insect, *Proc. Natl Acad. Sci. USA*, 2012, 109, 14924-14929
- [6] Kennedy, J.S., Migration, behavioural and ecological. Pages 5-26 in Rankin M.A. (Ed.), *Migration: Mechanisms and Adaptive Significance*, Contributions in Marine Science, 27 (Supplement), 1985
- [7] Yanoviak S.P., Kaspari M., Dudley R., Gliding hexapods and the origins of insect aerial behaviour, *Biol. Lett.*, 2009, 5, 510-512
- [8] Yanoviak S.P., Munk Y., Kaspari M., Dudley, R., Aerial maneuverability in wingless gliding ants (*Cephalotes atratus*), *Proc. R. Soc. Lond. B*, 2010, 277, 2199-2204
- [9] Chapman J.W., Drake V.A., Reynolds D.R., Recent insights from radar studies of insect flight, 2011, 56, 337-356
- [10] Drake V.A., Reynolds D.R., *Radar entomology: observing insect flight and migration*, CABI, Wallingford, UK, 2012
- [11] Chapman J.W., Klaassen R.H.G., Drake V.A., Fossette S., Hays G.C., Metcalfe J.D., et al., Animal orientation strategies for movement in flows, *Curr. Biol.*, 2011, 21, R861-R870
- [12] Dingle H., Drake V.A., What is migration? *BioScience*, 2007, 57, 113-121
- [13] Chapman J.W., Drake V.A., Insect migration, Pages 161-166 in Breed M.D., Moore J. (Eds), *Encyclopedia of Animal Behavior*, vol. 2, Academic Press, Oxford, UK, 2010
- [14] Bell J.R., Bohan D.A., Shaw E.M., Weyman G.S., Ballooning dispersal using silk: world fauna, phylogenies, genetics and models, *Bull. Entomol. Res.*, 2005, 95, 69-114
- [15] Szymkowiak P., Górski G., Bajerlein D., Passive dispersal in arachnids, *Biological Lett. (Poland)*, 2007, 44, 75-101
- [16] Schneider, J.M., Roos, J., Lubin, Y., Henschel, J.R., Dispersal in *Stegodyphus dumicola* (Araneae, Eresidae): they do balloon after all! *J. Arachnol.* 29, 2001, 114-116
- [17] Coyle F.A., Aerial dispersal by mygalomorph spiderlings (Araneae, Mygalomorphae), *J. Arachnol.*, 1983, 11, 283-286
- [18] McManus M.L., Weather, behaviour and insect dispersal, *Mem. Entomol. Soc. Can.* 1988, 146, 71-94
- [19] Rhoads M., Davis D.R., Price P.W., Bionomics of bagworms (Lepidoptera: Psychidae), *Annu. Rev. Entomol.*, 2009, 54, 209-226
- [20] Moore, R.G., Hanks, L.M., Aerial dispersal and host plant selection by neonate *Thyridopteryx ephemeraeformis* (Lepidoptera: Psychidae), *Ecol. Entomol.*, 2004, 29, 327-335
- [21] Fleschner C.A., Badgley M.E., Ricker D.W., Hall J.C., Air drift of spider mites, *J. Econ. Entomol.*, 1956, 49, 624-627
- [22] Kennedy G.G., Smitley D.R., Dispersal. Pages 233-242 in Helle W., Sabelis M.W. (Eds), *Spider mites: their biology, natural enemies and control*, vol. 1A, Elsevier, Amsterdam, 1985
- [23] Smitley D.R., Kennedy G.G., Photo-orientated aerial-dispersal behaviour of *Tetranychus urticae* (Acari: Tetranychidae) enhances escape from the leaf surface, *Ann. Entomol. Soc. Am.* 1985, 78, 609-614
- [24] Hussey N.W., Parr W.J., Dispersal of the glasshouse red spider mite *Tetranychus urticae* Koch (Acarina: Tetranychidae), *Entomol. Exp. Appl.* 1963, 6, 207-214
- [25] Liebhold A.M., Halverson J.A., Elmes G.A., Gypsy moth invasion in North America: a quantitative analysis, *J. Biogeogr.*, 1992, 19, 513-520.
- [26] Wainhouse D., *Ecological methods in forest pest management*, Oxford University Press, Oxford, UK, 2005
- [27] Pugh P.J.A., Have mites (Acarina: Arachnida) colonised Antarctica and the islands of the Southern Ocean via air currents? *Polar Rec.*, 2003, 39, 239-244

- [28] Reynolds A.M., Bohan D., Bell J.R., Ballooning dispersal in arthropod taxa: conditions at take-off, *Biol. Lett.*, 2007, 3, 237-240
- [29] Reynolds A.M., Bohan D.A., Bell J.R., Ballooning dispersal in arthropod taxa with convergent behaviours: dynamic properties of ballooning silk in turbulent flows, *Biol. Lett.* 2006, 2, 371-373
- [30] Barth F.G., Komarek S., Humphrey J.A.C., Treidler B., Drop and swing dispersal behavior of a tropical wandering spider: experiments and numerical model. *J. Comp. Physiol. A*, 1991, 169, 313-322
- [31] Moran V.C., Gunn B.H., Walter G.H., Wind dispersal and settling of first crawlers of the cochineal insect *Dactylopius austrinus* (Homoptera: Coccoidea: Dactylopiidae), *Ecol. Entomol.*, 1982, 7, 409-419
- [32] Frost W.E., Polyphenic wax production in *Abacarus hystrix* (Acari: Eriophyidae), and implications for migratory fitness, *Physiol. Entomol.*, 1997, 22, 37-46
- [33] Hanks L.M., Denno R.F., Dispersal and adaptive deme formation in sedentary coccoid insects. Pages 239-262 in S. Mopper, S.Y. Strauss (Eds), *Genetic structure and local adaptation in natural insect populations: effects of ecology, life history, and behaviour*, Chapman & Hall, New York, 1998
- [34] Lehmitz R., Russell D., Hohberg K., Christian A., Xylander W.E.R., Wind dispersal of oribatid mites as a mode of migration, *Pedobiologia*, 2011, 54, 201-207
- [35] Washburn J.O., Washburn L., Active aerial dispersal of minute wingless arthropods: exploitation of boundary-layer velocity gradients, *Science*, 1984, 223, 1088-1089
- [36] Jung C., Croft, B.A., Aerial dispersal of phytoseiid mites (Acari: Phytoseiidae): estimating falling speed and dispersal distance of adult females, *Oikos* 2001, 94, 182-190
- [37] Johnson D.T., Croft B.A., Laboratory study of the dispersal behaviour of *Amblyseius fallacis* (Acarina: Phytoseiidae), *Ann. Entomol. Soc. Am.*, 1976, 69, 1019-1023
- [38] Sabelis, M.W., Afman B.P., Synomone-induced suppression of take-off in the phytoseiid mite, *Phytoseiulus persimilis* Athias-Henriot, *Exp. Appl. Acarol.*, 1994, 18, 711-721
- [39] Linquist E.E., Oldfield G.N., Evolution of eriophyoid mites in relation to their host plant. Pages 277-300 in Lindquist E.E., Sabelis, M.W., J. Bruin, J. (Eds), *Eriophyoid mites: their biology, natural enemies and control*, Elsevier, Amsterdam, 1996
- [40] Sabelis M.W., Bruin J., Evolutionary ecology: life history patterns, food plant choice and dispersal. Pages 329-366 in Lindquist E.E., Sabelis M.W., Bruin J. (Eds), *Eriophyoid mites: their biology, natural enemies and control*. Elsevier, Amsterdam, 1996
- [41] Bergh J.C., Ecology and aerobiology of dispersing citrus rust mites (Acari: Eriophyidae) in Central Florida, *Environ. Entomol.*, 2001, 30, 318-326
- [42] Nault L.R., Styer W.E., The dispersal of *Aceria tulipae* and three other grass-infesting eriophyid mites in Ohio, *Ann. Entomol. Soc. Am.*, 1969, 62, 1446-1455
- [43] Evans G.O., *Principles of acarology*, CAB International, Wallingford, UK, 1992
- [44] Greathead D.J., Crawler behaviour and dispersal. Pages 339-342 in Ben-Dov Y., Hodgson C.J. (Eds), *Soft scale insects: their biology, natural enemies and control*, Elsevier Science, Amsterdam, 1997
- [45] Glick P.A., The distribution of insects, spiders and mites in the air, Technical Bulletin no. 673, United States Department of Agriculture, Washington D.C., 1939
- [46] Freeman J.A., Occurrence of Collembola in the air, *Proc. R. Entomol. Soc. Lond. A*, 1952, 27, 28
- [47] Farrow R.A., Greenslade P., A vertical migration of Collembola, *Entomologist*, 1992, 111, 38-45
- [48] Blackith R.E., Disney R.H.L., Passive dispersal during moulting in tropical Collembola, *Malayan Nat. J.*, 1988, 41, 529-531
- [49] Van der Wurff A.W.G., Isaaks J.A., Ernsting G., Van Straalen N.M., Population substructures in the soil invertebrate *Orchesella cincta*, as revealed by microsatellite and TE-AFLP markers, *Mol. Ecol.*, 2003, 12, 1349-1359
- [50] Timmermans M.J.T.N., Ellers J., Mariën J., Verhoef S.C., Ferwerda E.B., Van Straalen N.M., Genetic structure in *Orchesella cincta* (Collembola): strong subdivision of European populations inferred from mtDNA and AFLP markers, *Mol. Ecol.*, 2005, 14, 2017-2024
- [51] Hawes T.C., Worland M.R., Convey P., Bale J.S., Aerial dispersal of springtails on the Antarctic Peninsula: implications for local distribution and demography, *Antarct. Sci.*, 2007, 19, 3-10
- [52] Reynolds A.M., Incorporating sweeps and ejections into Lagrangian stochastic models of spore trajectories within plant canopy turbulence: modeled contact distributions are heavy-tailed, *Phytopathology*, 2012, 102, 1026-1033
- [53] Stephens G.R., Aylor, D.E., Aerial dispersal of red pine scale, *Matsucoccus resinosa* (Homoptera: Margarodidae), *Environ. Entomol.*, 1978, 7, 556-563
- [54] Reynolds A.M., Beating the odds in the aerial lottery: passive dispersers select conditions at take-off that maximise their expected fitness on landing, *Amer. Nat.* 2013, 181, 555-561
- [55] Reynolds A.M., Exponential and power-law contact distributions represent different atmospheric conditions, *Phytopathology*, 2011, 101, 1465-1470
- [56] Radicchi F., Baronchelli A., Amaral L.A.N., Rationality, irrationality and escalating behaviour in lowest unique bid auctions, *PLoS One*, 2012, 7, article e29910
- [57] Viswanathan G.M., Luz, M.G.E., Raposo, E.P., Stanley, H.E., The physics of foraging: an introduction to random searches and biological encounters, Cambridge University Press, Cambridge, UK, 2011
- [58] Wainhouse D., Dispersal of first instar larvae of the Felted Beech Scale, *Cryptococcus fagisuga*, *J. Appl. Ecol.*, 1980, 17, 523-532
- [59] Uvarov B.P., *Grasshoppers and locusts: a handbook of general acridology*, vol. 2, Centre for Overseas Pest Research, London, 1977
- [60] Lorch P.D., Sword G.A., Gwynne D.T., Anderson G.L., Radiotelemetry reveals differences in individual movement patterns between outbreak and non-outbreak Mormon cricket populations, *Ecol. Entomol.*, 2005, 30, 548-555
- [61] Kennedy, J.S., Phase transformation in locust biology, *Biol. Rev.*, 1956, 31, 349-370
- [62] Kennedy J.S., Insect dispersal. Pages 103-119 in D. Pimental (Ed.) *Insects, Science and Society*. Academic Press, New York, 1975
- [63] Simpson S.J., McCaffery A.R., Hägele, B.F., A behavioural analysis of phase change in the desert locust, *Biol. Rev.* 74, 1999, 461-480

- [64] Anstey M.L., Rogers S.M., Ott S.R., Burrows M., Simpson S.J., Serotonin mediates behavioral gregarization underlying swarm formation in desert locusts, *Science*, 2009, 323, 627-630
- [65] Buhl J., Sumpter D.J.T., Couzin D., Hale J.J., Despland E., Miller E.R., et al., From disorder to order in marching locusts, *Science*, 2006, 312, 1402-1406
- [66] Buhl J., Sword G.A., Clissold F., Simpson S.J., Group structure in locust migratory bands, *Behav. Ecol. Sociobiol.*, 2011, 65, 265-273
- [67] Schneirla T.C., The army-ant behavior pattern: nomad-statory relations in the swarmers and the problem of migration, *Biol. Bull.*, 1945, 88, 1945, 166-193
- [68] Franks N.R., Fletcher C.R., Spatial patterns in army ant foraging and migration: *Eciton burchelli* on Barro Colorado Island, Panama, *Behav. Ecol. Sociobiol.*, 1983, 12, 261-270
- [69] Harrington R., Taylor L.R., Migration for survival: fine-scale population redistribution in an aphid, *Myzus persicae*, *J. Anim. Ecol.*, 1990, 59, 1177-1193
- [70] Janowski-Bell M.E., Horner N.V., Movement of the male brown tarantula *Aphonopelma hentzi* (Araneae, Theraphosidae), using radio telemetry. *J. Arachnol.*, 1999, 27, 503-512
- [71] Hopkin S.P., Read H.J., The biology of millipedes, Oxford University Press Oxford, UK, 1992
- [72] Hopkin S.P., Biology of the springtails (Insecta: Collembola), Oxford University Press, Oxford, UK, 1997
- [73] Hågvar S., A review of Fennoscandian arthropods living on and in snow, *Eur. J. Entomol.*, 2010, 107, 281-298
- [74] Hågvar S., Fjellberg A., Autumn migration of a colony of *Hypogastrura socialis* (Uzel) (Collembola, Hypogastruridae), *Norw. J. Entomol.*, 2002, 49, 145-146
- [75] Hågvar S., Long distance, directional migration on snow in a forest collembolan, *Hypogastrura socialis* (Uzel), *Acta Zool. Fenn.*, 1995, 196, 200-205
- [76] Hågvar S., Navigation and behaviour of four Collembola species migrating on the snow surface, *Pedobiologia*, 2000, 44, 221-233
- [77] Cloudsley-Thompson J.L., The significance of migration in Myriapods, *Ann. Mag. Nat. Hist. Series 12*, 1949, 2, 947-962
- [78] Waters T.F., The drift of stream insects, *Annu. Rev. Entomol.*, 1972, 17, 253-272.
- [79] Brittain J.E., Biology of mayflies, *Annu. Rev. Entomol.*, 1982, 27, 119-147.
- [80] Speirs D.C., Gurney W.S.C., Population persistence in rivers and estuaries, *Ecology*, 2001, 82, 1219-1237
- [81] Olsson, T., Söderström O., Springtime migration and growth of *Parameletus chelifer* (Ephemeroptera) in a temporary stream in northern Sweden, *Oikos* 1978, 31, 284-289
- [82] Hughes J.M., Schmidt D.J., MacLean A., Wheatley A., Population genetic structure in stream insects: what have we learned? Pages 268-288 in Lancaster J., Briers R.A. (Eds), *Aquatic insects: challenges to populations*, CABI, Wallingford, UK, 2008
- [83] Yasick A.L., Krebs R.A., Wolin J.A., The effect of dispersal ability in winter and summer stoneflies on their genetic differentiation, *Ecol. Entomol.*, 2007, 32, 399-404.
- [84] Davies B.R., The dispersal of Chironomidae larvae: a review, *J. Entomol. Soc. S. Afr.*, 1976, 39, 39-62
- [85] Franke C., Detection of transversal migration of larvae of *Chaoborus flavicans* (Diptera, Chaoboridae) by the use of a sonar system, *Arch. Hydrobiol.*, 1987, 109, 355-366
- [86] Palmén E., Die anemohydrochore Austbreitung der Insekten als zoogeographischer Faktor, *Ann. Zool. Soc. Zool. Bot. Fenn. Vanamo*, 1944, 10, 1-262
- [87] Kennedy J.S., Fosbrooke I.H.M., The plant in the life of an aphid. Pages 129-140 in van Emden, H.F. (Ed.), *Insect/Plant Relationships* (Symposia of the Royal Entomological Society of London, no. 6.) Blackwell Scientific Publications, Oxford, UK, 1973
- [88] Shashar N., Sabbah S., Aharoni, N., Migrating locusts can detect polarized reflections to avoid flying over the sea, *Biol. Lett.*, 2005, 1, 472-475
- [89] Hawes T.C., Worland M.R., Bale J.S., Convey P., Rafting in Antarctic Collembola, *J. Zool.*, 2008, 274, 44-50
- [90] Witteveen, J., Joosse E.N.G., The effects of inundation on marine littoral Collembola, *Holarctic Ecol.* 1988, 11, 1-7
- [91] Peck S.B., Sea-surface (pluveston) transport of insects between islands in the Galápagos Archipelago, Ecuador, *Ann. Entomol. Soc. Am.*, 1994, 87, 576-582
- [92] Coulson S.J., Hodkinson I.D., Webb N.R., Harrison J.A., Survival of terrestrial soil-dwelling arthropods on and in seawater: implications for trans-oceanic dispersal, *Funct. Ecol.*, 2002, 16, 353-356
- [93] Ólafsson E., The development of the land-arthropod fauna on Surtsey, Iceland, during 1971-1976, with notes on terrestrial Oligochaeta, *Surtsey Research Progress Report 1978*, 8, 41-46
- [94] Foster W.A., Dispersal behaviour of an intertidal aphid, *J. Anim. Ecol.*, 1978, 47, 653-659
- [95] Foster W.A., Treherne J.E., Dispersal mechanisms in an intertidal aphid, *J. Anim. Ecol.*, 1978, 47, 205-217
- [96] Marden J.H., Kramer M.G., Locomotor performance of insects with rudimentary wings, *Nature*, 1995, 377, 332-334
- [97] Marden J.H., O'Donnell B.C., Thomas M.A., Bye J.Y., Surface-skimming stoneflies and mayflies: the taxonomic and mechanical diversity of two-dimensional aerodynamic locomotion, *Physiol. Biochem. Zool.*, 2000, 73, 751-764
- [98] Marden J.H., Evolution and physiology of flight in aquatic insects. Pages 230-249 in Lancaster J., Briers R.A. (Eds), *Aquatic insects: challenges to populations*, CABI, Wallingford, UK, 2008
- [99] Dudley R., Byrnes G., Yanoviak S.P., Borrell B., Brown R.M., McGuire J., Gliding and the functional origins of flight: biomechanical novelty or necessity? *Annu. Rev. Ecol. Evol. Syst.*, 2007, 38, 179-201
- [100] Farish D.J., Axtell R.C., Phoresy redefined and examined in *Macrocheles muscaedomesticae* (Acarina: Macrochelidae), *Acarologia*, 1971, 13, 16-25
- [101] Athias-Binche F., Ecology and evolutionary ecology of phoresy in mites. Pages 27-41 in Dusbábek F., Bukva V. (Eds), *Modern acarology*, vol. 1, Academia, Prague, and SPB Academic Publishing, The Hague, 1991
- [102] Walter D., Proctor H., Mites: ecology, evolution and behaviour, CABI Publishing, Wallingford, UK, 1999
- [103] Krantz G.W., Habits and habitats. Pages 64-82 in Krantz G.W., Walter D.E. (Eds), *A manual of acarology*, 3rd edn, Texas Tech University Press, Lubbock, Texas, 2009
- [104] Houck M.A., O'Connor B.M., Ecological and evolutionary significance of phoresy in the Astigmata (Acari), *Annu. Rev. Entomol.*, 1991, 36, 611-636
- [105] Binns E.S., Phoresy as migration – some functional aspects of phoresy in mites, *Biol. Rev.*, 1982, 57, 571-620

- [106] Camerik A.M., Phoresy revisited. Pages 333-336 in Sabelis M.W., Bruin, J. (Eds), Trends in acarology – Proceedings of the 12th International Congress, Springer, Dordrecht, The Netherlands, 2009
- [107] Gorb S.N., Attachment devices of insect cuticle, Kluwer Academic Publishers, Dordrecht, The Netherlands, 2001
- [108] Southwood T.R.E., Migration of terrestrial arthropods in relation to habitat, *Biol. Rev.*, 1962, 37, 171-214
- [109] Poinar G.O., Čurčić B.P.M., Cokendolpher J.C., Arthropod phoresy involving pseudoscorpions in the past and present, *Acta Arachnol.*, 1998, 47, 79-96
- [110] Zeh D.W., Zeh J.A., Failed predation or transportation? Causes and consequences of phoretic behavior in the pseudoscorpion *Dinocheirus arizonensis* (Pseudoscorpionida: Chernetidae), *J. Insect Behav.* 1992, 5, 37-49
- [111] Weygoldt P., The biology of pseudoscorpions, Harvard University Press, Cambridge, Massachusetts, 1969
- [112] Zeh D.W., Zeh J.A., Emergence of a giant fly triggers phoretic dispersal in the neotropical pseudoscorpion, *Semeiochernes armiger* (Balzan) (Pseudoscorpionida: Chernetidae), *Bull. Brit. Arachnol. Soc.*, 1992, 9, 43-46
- [113] Zeh D.W., Zeh J.A., On the function of harlequin beetle-riding in the pseudoscorpion, *Cordylochernes scorpioides* (Pseudoscorpionida: Chernetidae), *J. Arachnol.*, 1992, 20, 47-51
- [114] Hunter P.E., Rosario R.M.T., Associations of Mesostigmata with other arthropods, *Annu. Rev. Entomol.*, 1988, 33, 393-417
- [115] Athias-Binche F., La phorésie chez les acariens: aspects adaptatifs et évolutifs. Editions du Castillet, Perpignan, France, 1994
- [116] Perotti M.A., Braig H.R., Phoretic mites associated with animal and human decomposition, *Exp. Appl. Acarol.*, 2009, 49, 85-124
- [117] Elzinga R.J., Broce A.B., Hypopi (Acari: Histiostomatidae) on house flies (Diptera: Muscidae): a case of detrimental phoresy, *J. Kansas Entomol. Soc.* 61, 1988, 208-213
- [118] Houck M.A., Phoresy by *Hemisarcoptes* (Acari: Hemisarcoptidae) on *Chilocorus* (Coleoptera: Coccinellidae): influence of subelytral ultrastructure, *Exp. Appl. Acarol.*, 1999, 23, 97-118
- [119] Elzinga R.J., Rettenmeyer C.W., Berghoff S.M., Army ant mites: the most specialized mites found on any social insect. Poster presented at Congress XV of the International Union for the Study of Social Insects, July 30 - August 5, 2006, Washington DC., [http://www.armyantbiology.com/IUSSI\\_Mite\\_Poster.pdf](http://www.armyantbiology.com/IUSSI_Mite_Poster.pdf)
- [120] O'Connor B.M., Klompen, J.S.H., Phylogenetic perspectives on mite-insect associations: the evolution of acarinarina. Pages 63-71 in Needham G.R., Mitchell R., Horn D.J., Welbourn, W.C. (Eds), *Acarology IX*, vol. 2, Symposia. Ohio Biological Survey, Columbus, Ohio, 1999
- [121] Okabe, K., Makino, S., Behavioural observations of the bodyguard mite *Ensliniella parasitica*. Pages 193-199 in Moraes G.J. de, Proctor H. (Eds), *Acarology XIII: Proceedings of the International Congress*, Zoosymposia 6, 2011
- [122] Houck M.A., Cohen A.C., The potential role of phoresy in the evolution of parasitism: radiolabelling (tritium) evidence from an astigmatid mite, *Exp. Appl. Acarol.*, 1995, 19, 677-694
- [123] Knülle W., Interaction between genetic and inductive factors controlling the expression of dispersal and dormancy morphs in dimorphic astigmatic mites, *Evolution*, 2003, 57, 828-838
- [124] Hall C.C., A dispersal mechanism in mites (Acarina: Anoiidae), *J. Kansas Entomol. Soc.*, 1959, 32, 45-46
- [125] Krantz G.W., Dissemination of *Kampimodromus aberrans* by the filbert aphid, *J. Econ. Entomol.*, 1973, 66, 575-576.
- [126] Schwarz H.H., Koulianos S., When to leave the brood chamber? Routes of dispersal in mites associated with burying beetles, *Exp. Appl. Acarol.*, 1998, 22, 621-631
- [127] Niogret J., Lumaret J.P., Bertrand M., Semiochemicals mediating host-finding behaviour in the phoretic association between *Macrocheles saceri* (Acari: Mesostigmata) and *Scarabaeus* species (Coleoptera: Scarabaeidae), *Chemoecology*, 2006, 16, 129-134
- [128] Soroker V., Nelson D.R., Bahar O., Reneh S., Yablonski S., Palevsky E., Whitefly wax as a cue for phoresy in the broad mite, *Polyphagotarsonemus latus* (Acari: Tarsonemidae), *Chemoecology*, 2003, 13, 163-168
- [129] Colwell R.K., Stowaways on the hummingbird express, *Nat. Hist.* 1985, 94(7), 56-63
- [130] Boggs C.L., Gilbert L.E., Spatial and temporal distribution of *Lantana* mites phoretic on Lepidoptera, *Biotropica*, 1987, 19, 301-305
- [131] Tschapka M., Cunningham S.A., Flower mites of *Calyptrogynne ghiesbreghtiana* (Araceae): evidence for dispersal using pollinating bats. *Biotropica* 2004, 36, 377-381
- [132] Heyneman A.J., Colwell R.K., Naeem S., Dobkin D.S., Hallet B., Host plant discrimination: experiments with hummingbird flower mites. Pages 455-485 in Price P.W., Lewinsohn T.M., Fernandes G.W., Benson W.W. (Eds), *Plant-animal interactions: Evolutionary ecology in tropical and temperate regions*, John Wiley and Sons, New York, 1991
- [133] Clausen, C.P., Phoresy among entomophagous insects, *Annu. Rev. Entomol.*, 1976, 21, 343-368
- [134] Farrow R.A., Aerial dispersal of *Scelio fulgidus* [Hym.: Scelionidae], parasite of eggs of locusts and grasshoppers [Ort.: Acrididae], *Entomophaga*, 1981, 26, 349-355
- [135] Green A.J., Sánchez M.I., Passive internal dispersal of insect larvae by migratory birds, *Biol. Lett.* 2006, 2, 55-57
- [136] Guix J.C., Ruiz X., Weevil larvae dispersal by guans in southeastern Brazil, *Biotropica*, 1997, 29, 522-525
- [137] Magsig-Castillo J., Morse J.G., Walker G.P., Bi J.L., Rugman-Jones P.F., Stouthamer, R., Phoretic dispersal of armored scale crawlers (Hemiptera: Diaspididae), *J. Econ. Entomol.*, 2010, 103, 1172-1179
- [138] Gullan, P.J., Cockburn A., Sexual dichromism and intersexual phoresy in gall-forming coccoids, *Oecologia*, 1986, 68, 632-634
- [139] Dingle H., Animal migration: Is there a common migratory syndrome? *J. Ornithol.*, 2006, 147, 212-220
- [140] Drake V.A., Gatehouse A.G., Farrow, R.A., Insect migration: a holistic conceptual model. Pages 427-457 in Drake V.A., Gatehouse A.G. (Eds), *Insect migration: tracking resources through space and time*, Cambridge University Press, Cambridge, UK, 1995